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Review Article

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Cuttlefish conservation: a global review of methods to ameliorate unwanted fishing mortality and other anthropogenic threats to sustainability

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Cuttlefish are an important global fisheries resource, and their demand is placing increasing pressure on populations in many areas, necessitating conservation measures. We reviewed evidence from case studies spanning Europe, Africa, Asia, and Australia encompassing diverse intervention methods (fisheries closures, protected areas, habitat restoration, fishing-gear modifications, promoting egg survival, and restocking), and we also discuss the effects of pollution on cuttlefish. We conclude: (1) spatio-temporal closures need to encompass substantial portions of a species'

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range and protect at least one major part of their life cycle; (2) fishing-gear modifications have the potential to reduce unwanted cuttlefish capture, but more comprehensive trials are needed; (3) egg survival can be improved by diverting and salvaging from traps; (4) existing lab rearing and restocking may not produce financially viable results; and (5) fisheries management policies should be regularly reviewed in light of rapid changes in cuttlefish stock status. Further, citizen science can provide data to reduce uncertainty in empirical assessments. The information synthesized in this review will guide managers and stakeholders to implement regulations and conservation initiatives that increase the productivity and sustainability of fisheries interacting with cuttlefish, and highlights gaps in knowledge that need to be addressed.

Keywords: cephalopod, conservation, cuttlefish, fisheries, methods, review, sustainability.

Introduction

General life histories and distributions

Cuttlefish are typically short-lived (1–2 years) and semelparous, with a single breeding season toward the end of their life cycle (Boletzky, 1983; Le Goff *et al.*, 1998; Hall *et al.*, 2007). Moreover, most cuttlefish have low fecundity (300–3000 eggs per female; Jereb *et al.*, 2015), producing large eggs and benthic hatchlings with limited dispersal potential (Villanueva *et al.*, 2016), making it imperative that each generation lay adequate numbers of eggs across appropriate habitats to ensure sufficient annual recruitment. Introducing conservation measures to ensure adequate annual recruitment requires not only that sufficient adults survive to reproduce, but the integrity of the mating system of each species remains intact, which includes the complex behavioural dynamics of how males and females interact for normal gene flow in the population (Hanlon, 1998).

Although the sex ratios in populations of cuttlefish are roughly 1:1, the "operational sex ratio" on spawning grounds is always skewed towards more males than females, thus many cuttlefish have evolved complex reproductive behaviours and mating systems through sexual selection (Emlen and Oring, 1977; Hall and Hanlon, 2002; Hanlon and Messenger, 2018). Various fishing techniques during seasonal reproduction can interfere with sexual selection processes that lead to other longer-lasting reductions in reproductive success through fisheries-induced evolution (Kuparinen and Merilä, 2007). Therefore, more holistic conservation measures, such as marine protected areas (MPAs), may be required to protect sexual selection processes along with population numbers (e.g. Sørdalen *et al.*, 2020). The overarching goal is to adjust fishing practices in line with the population dynamics and behavioural ecology of the target species to ensure sustainability of the population and the fishery.

Cuttlefish comprise 195 species among five families and are distributed across shallow reefs and channels of every continent, except for the Americas (Jereb and Roper, 2005). Many cuttlefish species undergo ontogenetic migrations, which affects their spatio-temporal distributions, densities, and stock structures (Boyle and Boletzky, 1996). Cuttlefish nursery areas have not been definitively identified in most cases, but likely occur within shallower coastal areas due to the low resistance of juveniles' cuttlebones to water pressure (Sherrard, 2000). As they grow, juveniles gradually move further offshore into deeper grounds where they feed on larger prey as subadults before migrating back into coastal areas as mature adults for spawning and subsequent death (Dunn, 1999). This pattern of ontogenetic migration is well-established, although the exact migration routes remain unknown for many species.

Fisheries and impacts

Owing to their inshore life stages, cuttlefish are highly accessible and support important commercial, recreational, and subsistence fisheries throughout their distributions. While various methods, including seines, gillnets, trammel nets, jigs, and set nets, are fished in some areas, most cuttlefish are caught using benthic trawls or traps (Belcari *et al.*, 2002). Global estimates of total catches are notoriously difficult to obtain because most trawl catches are taken as incidental 'by-product' to other priority species and are often collectively reported as 'cephalopods'. Nevertheless, cuttlefish are known to comprise the main cephalopod resource in many areas, especially in the northeast Atlantic, where annual landings are 13,000–28,000 tonnes (t) (ICES WGCEPH, 2020), and in some European countries, cuttlefish are a key target of small-scale fisheries (Batista *et al.*, 2009; Gil *et al.*, 2018). However, of the European landings declared as cephalopods, cuttlefish generally make up a small proportion of the total catch.

Globally, a total of 348,000 t of cuttlefish (including bobtail squids, nei, Sepiidae, and Sepiolidae categorized as cuttlefish) were landed in 2018 (FAO, 2020). A large proportion of this harvest is the common cuttlefish (*Sepia officinalis*) which dominates catches along the coasts of Europe and Africa in the Atlantic Ocean and Mediterranean Sea (Denis and Robin, 2001; Belcari *et al.*, 2002; Pierce *et al.*, 2010; Pereira *et al.*, 2019). For example, of nearly 50,000 t of cuttlefish, bobtail squids nei, Sepiidae and Sepiolidae landed from the NE Atlantic and Mediterranean during 2018, 37% of Sepioidea cephalopods were identified as *S. officinalis* while 63% were a mix of Sepiidae and Sepiolidae (FAO, 2020).

Compared to trawling, baited traps ("pots" or "basket traps") are often a preferred method for targeting cuttlefish, because they ensure a higher quality of catch and are more cost-effective (Uhlmann and Broadhurst, 2015). Typically, traps exploit the inshore migrations of adults to mate and lay eggs (Blanc and Daguzan, 1998; Watanuki and Kawamura, 1999; Barile *et al.*, 2013). Overall, this fishing method is more ecologically and environmentally benign than trawling because traps are usually highly selective for sexually mature cuttlefish at the end of their life cycle (Lazzarini *et al.*, 2014; Melli *et al.*, 2014; Bettoso *et al.*, 2016; Vasconcelos *et al.*, 2019; Ganias *et al.*, 2021a), providing individuals some opportunity to reproduce before harvest (Watanuki and Kawamura, 1999). Traps also cause fewer benthic impacts than trawls. Traps also cause fewer benthic impacts than trawls, although ghost fishing may occur if traps become lost at sea (Uhlmann and Broadhurst, 2015).

Irrespective of the type of mortality caused by fishing, and as for all aquatic stocks, amelioration is only possible through four general management approaches (Uhlmann and Broadhurst, 2015). Where cuttlefish are the primary target, the first approach is to simply introduce effective general fisheries management (e.g. catch quotas, limited entry, etc.) that promotes sustainable harvesting. For unaccounted fishing mortality, the amelioration options broaden to encompass spatio-temporally regulating the deployment of fishing gears to minimize or avoid key times and locations important to the life history of the species; modifying the gears used, or deploying alternatives that reduce the number of unwanted species and/or sizes caught (e.g. Kennelly and Broadhurst, 2014); and adjusting operational or post-capture handling procedures to minimize discard mortalities (e.g. Revill *et al.*, 2015).

All four management approaches have been used, or suggested, to directly or indirectly reduce the unwanted fishing mortality of cuttlefish. Further, in some cases, excessive, prolonged fishing mortalities have been addressed via restocking efforts. However, there has not yet been an overview of specific efforts utilizing the general approaches above, or their relative effectiveness. Additionally, citizen involvement, a growing source of information in conservation efforts, can provide data which may reduce uncertainty in cuttlefish responses to these approaches, which can then inform further measures to be taken. Such work is important because cephalopod stocks may become increasingly targeted/impacted by commercial and subsistence fisheries where local teleost populations decline (Boyle and Rodhouse, 2005; Doubleday *et al.*, 2016).

This review seeks to address a deficit of any comprehensive overview of the cuttlefish conservation and management efforts described above. The main objective was to collate selected case studies from both peer-reviewed and grey-literature or unpublished reports regarding efforts to reduce unwanted cuttlefish fishing mortalities in order to inform fishery managers, conservationists, and stakeholders. The review also identifies other key related anthropogenic impacts on cuttlefish to provide an holistic overview of threats to populations and to encourage future conservation.

Methods

A systematic approach with some consideration to the "preferred reporting items for systematic reviews and meta-analyses (PRISMA) method was used. Specifically, predetermined stem keywords (and variants), and combinations thereof ("AND") were used to search databases on ISI Web of Science, Proquest, and Google Scholar. Search terms were: "cuttlefish"; "bycatch"; "conservation initiatives"; "conservation interventions"; "protection"; "sustainable"; "management"; "*Sepia*"; and "unaccounted fishing mortality". Papers were filtered for content beyond the main points above, and any additional specific examples were reviewed and, if relevant, included to support the identified conservation methods. Evidence was submitted from Europe, Africa, Asia, and Australia and organized into six broad categories of conservation methods (Table 1). Summaries of salient details and the main points of learning from each case study were compiled.

Results and discussion

Following feedback from some 32 researchers, along with an additional 139 relevant papers and reports acquired through searches, we identified five general categories of conservation methods, supported by 15 general case studies. The categories are discussed sequentially below.

Conservation method 1: MPAs, fisheries closures, and habitat restoration

Marine protected areas (MPAs) typically provide ecosystem-level protection across various species, which may include cephalopods, while fisheries closures tend to be more targeted approaches to reduce population declines or protect species (Ovando *et al.*, 2021), life stages or habitats from fishing activities (e.g. nursery areas or spawning aggregations) (Roberts *et al.*, 2005). Habitat restoration can also serve as an alternative method to rebuild depleted populations when habitat availability or degradation may be limiting recruitment. Among cephalopods, MPAs have more commonly been applied to octopuses, because the ontogenetic migrations undertaken by more mobile cuttlefish and squid during their life-cycles complicate efforts to protect species via location-based protection (Abecasis *et al.*, 2013). Therefore, there are only a few case studies from which to draw insight on best practices specifically for cuttlefish conservation. The evidence concerning three such case studies involving cuttlefish fisheries in Vietnam, Australia, and Singapore is outlined below.

MPAs

Vietnam's South China Sea and Sunda Shelf are hotspots of cephalopod diversity (Rosa *et al.*, 2019). A total of 18 to 20 species of cuttlefish inhabit the area (Khromov, 1996; Norman *et al.*, 2016) of which 12 are regularly exploited by fisheries: paintpot cuttlefish (*Metasepia tullbergi*), needle cuttlefish (*S. aculeata*), golden cuttlefish (*S. esculenta*), kobi cuttlefish (*S. kobiensis*), broadclub cuttlefish (*S. latimanus*), kisslip cuttlefish (*S. lycidas*), Papuan cuttlefish (*S. papuensis*), pharaoh cuttlefish (*S. pharaonis*), *S. robsoni* (no common name), starry cuttlefish (*S. stellifera*), spineless cuttlefish (*Sepiella inermis*), and Japanese spineless cuttlefish (*S. japonica*). About half of these species are targeted by a large-scale fishing fleet (mostly purse seine, but also gillnets and trawlers), and the rest by artisanal fishers (using purse seines, gillnets, and traps; Bùi *et al.*, 1994).

The Vietnamese government has developed a network of eight MPAs to reduce fishing mortalities, with areas ranging from 0.07 to 209.78 km^2. However, observations (comparing historical and sampling data) do not support the conclusion that MPAs are completely effective for conserving cuttlefish in Vietnam because the diversity and abundance of cuttlefish within the MPAs versus outside the MPAs are not markedly greater (unpublished observations by Lishchenko and Yến). In general, this conclusion supports the findings of Abecasis *et al.* (2013) that small-sized (even numerous, as in this case) MPAs do not ensure conserving migratory species such as cuttlefish. Nevertheless, we postulate further expansion of MPA buffer areas and the MPA network in general across the waters of Khánh Hòa province and stricter control over the existing ones would decrease coastal development impacts, supporting the conservation of cuttlefish. Decreasing anthropogenic impacts on the iconic coastal ecosystems is the main purpose of MPAs in Vietnam, but they might also serve as a refuge for resident and migratory fish and cephalopods that have commercial value. A similar concept was postulated by Abecasis *et al.* (2013) who, assessing the impact of the MPAs on *S. officinalis*, showed that, owing to *S. officinalis*' tendencies to carry out large-scale migrations, small MPAs are not efficient in their conservation.

Spatial closures at a mass spawning aggregation site

Point Lowly in Whyalla, South Australia, is the only known site in the world where mass spawning aggregations of *S. apama* take place every winter. Underwater visual surveys conducted between 1998 and 2000 indicated *S. apama* was highly concentrated in key areas, and this aggregation was predictable both temporally and spatially across years, which made the cuttlefish particularly vulnerable to fishing

Table 1. Summary of the evidence gathered regarding cuttlefish conservation initiatives outlined in this manuscript.

Conservation methods	Study type	Region	Species
MPA, fisheries closures, and habitat restoration	MPA	Asia	*Sepia* spp.
	Spatial closures at a mass spawning aggregation site	Australia	*S. apama*
	Habitat restoration	Singapore	*S.* spp.
Gear modifications in trawl and trammel net fisheries	Reducing unwanted fishing mortality among penaeid trawls	Australia	*S. rosella* and *S. plangon*
	Reducing unwanted discards in trammelnet fisheries	Europe	*S. officinalis*
Increasing egg survival in trap fisheries	Reducing egg laying on traps		
	Diverting egg laying onto alternative substrates		
	Deploying alternative substrates		
	Salvaging eggs laid on traps		
	Hatching salvaged *S. officinalis* eggs		
	Cuttlefish code of practice to promote egg survival		
Restocking	Breeding *S. latimanus*	Asia	*S. pharaonis* and *S. latimanus*
Promoting sustainable harvesting	Prohibiting fish aggregating devices		*S. pharaonis*
	Minimum weight limit and indirect fisheries management	Africa	*Sepia* spp.
	Voluntary co-management of a small-scale fishery	Europe	*S. officinalis*

(Hall *et al.*, 2017). Spawning aggregations occur over a small, localized area of inshore rocky reef (8 km of coastline) during each austral winter (April to August), with a distinct peak in cuttlefish densities from late May to early June (Hall and Hanlon, 2002; Hall *et al.*, 2017).

Commercial jigging in the aggregation area rapidly increased during the 1990s (from <10 t to >250 t) and progressively larger fishing closures were introduced to protect the spawning cuttlefish as more scientific information became available (Hall, 2002). The regulations included: (1) an immediate closure at the start of the 1998 fishing season that encompassed ~43% of the aggregation area, but still permitted substantial catches (150 t) during 1998; and (2) a further extension of the closure in mid-1998 to reduce catches further in 1999 (<20 t) and all subsequent years (Hall, 2002; Steer *et al.*, 2013).

Despite the legislated fishing closures, *S. apama* abundance in the aggregation area declined by 90% from 1999 (183000 individuals) to 2013 (13492 individuals) (Steer *et al.*, 2013). The species was listed as "Near Threatened" by the IUCN (2011). Because there was a lack of data on population sizes before the heavy fishing in the 1990s, it is unknown what the normal population size was, and the cause of this population decline remains unknown. However, the data imply the extended closure may still have provided inadequate protection for the migrating cuttlefish or that other factors may have contributed. One potential contributing factor was increased rainfall, which might have altered water salinity and turbidity, increased pollution via run-offs and/or encouraged algal blooms that then affected cuttlefish spawning (Steer *et al.*, 2013). Although the cause was unclear, the sudden decline of this iconic species gained attention from local media as the community raised their concerns over the cause of the collapse, and a third, much larger closure encompassing the whole northern Spencer Gulf region was implemented in 2013.

Undermining the effectiveness of the original 43% closure was that it protected only 23–37% of total *S. apama* abundance because of the uneven spatial distribution of animals, highlighting the need for careful monitoring of cuttlefish population dynamics and spatio-temporal distributions before introducing fishing closures or protected areas (Hall *et al.*, 2017). Later, it was determined the northern Spencer Gulf *S. apama* population that forms the dense spawning aggregation is a distinct, isolated population, or even possibly a subspecies, with little mixing among other populations in southern Australia (Gillanders *et al.*, 2016). Thus, there was also a high risk of localized extinction of subpopulations.

In 2020, population estimates reached the highest on record at 247,146 individuals, whereas only 110,000 *S. apama* per year were consistently found in the preceding five years (Heldt, 2020). With the return to greater abundance in 2020, the wider northern Spencer Gulf was reopened to fishing, and only the second extended closure was reinstated permanently. It is uncertain whether this will provide adequate future protection, and the aggregation is being closely monitored to ensure numbers do not decline again.

Habitat restoration

As part of ongoing efforts in reef restoration, artificial reefs have been established and monitored since 1988 in Singapore (Chou *et al.*, 2018). Recently, cuttlefish (*Sepia* spp.) were observed for the first time at a coral nursery established in 2014 off Lazarus Island to culture scleractinian corals (Chou *et al.*, 2017). Adult cuttlefish were observed on site in early 2016 while eggs were seen among the corals between July and November 2016 at a density of 21.8 ± 13.8 (mean ± *SD*) eggs per coral colony (Sam *et al.*, 2018). Juveniles were then observed between November 2016 and March 2017 at the same site. No eggs were observed on exposed areas of the nursery tables nor on the granite seawall nearby. These observations suggest habitat restoration, while not directly targeted at cuttlefish conservation, can be beneficial for the recruitment of cuttlefish and other reef-associated animals and could help rebuild stocks depleted by fishing.

Conclusions regarding MPA, fisheries closures, and habitat restoration

While direct evidence is scant, some tentative conclusions about MPAs, fisheries closures, and marine habitat restoration efforts can be made. The Vietnam case study, which reported small MPAs as being inadequate for protecting cuttlefish due to the animals' large-scale migrations, suggests MPAs need to encompass a significant proportion of the geographic range that a species migrates through over its life cycle (Abecasis *et al.*, 2013). Thus, smaller MPAs may have limited success in protecting cuttlefish populations. Similarly, if fisheries closures are utilized, the Point Lowly case study from South Australia suggests implementing protections during critical parts of the cuttlefish lifecycle, such as the inshore spawning period can be effective, but requires a sound understanding of the underlying population dynamics (e.g. Hall and Hanlon, 2002; Hall *et al.*, 2017). Finally, the case study from Singapore shows that restoring habitats important to cuttlefish, particularly egg-laying substrate, may also benefit stocks. Certainly, the benefits of any such efforts are intuitive and likely to produce more holistic outcomes for other fauna and flora as well.

Conservation method 2: gear modifications in trawl and trammel net fisheries

A common method for conserving exploited marine resources, particularly for reducing bycatch (and therefore discard mortalities), involves modifying fishing gear. As with closures and protected areas, evidence from case studies using gear modifications to promote cuttlefish conservation is limited, but both "behavioural" and "mechanical-separating" gear modifications have been tested in penaeid-trawl fisheries off eastern and southern Australia to reduce cuttlefish bycatch (Broadhurst *et al.*, 2002). The results of these experiments serve as an informative starting point for similar efforts in other fisheries.

Reducing unwanted fishing mortality among penaeid trawls in eastern Australia

Off New South Wales (NSW) Australia, some 80 trawlers tow low-opening, tripled-rigged penaeid trawls (minimum mesh size of 40 mm stretched mesh opening; SMO). The main target is the eastern king prawn (*Penaeus plebejus* typically >23-mm carapace length; CL), though other species including cuttlefish are retained in variable quantities and sizes (~70 t per year and mostly >30-mm ML in recent years), depending on market prices (Macbeth *et al.*, 2012). The main cuttlefish species retained are the rosecone cuttlefish (*S. rozella*) and mourning cuttlefish (*S. plangon*), but also the magnificent cuttlefish (*S. opipara*), Hedley's cuttlefish (*S. hedleyi*) and *S. limata* (no common name), with species compositions varying from subtropical to temperate latitudes down the eastern Australian coastline (Nottage *et al.*, 2007; Beasley *et al.*, 2018). Frequently, small individuals of these species are discarded along with large quantities of non-target teleosts (Kennelly *et al.*, 1998).

Concerns over the mortality of discarded bycatch, especially of juvenile teleosts important to other interacting fisheries, have precipitated various efforts at improving NSW penaeid-trawl selectivity. Most of this work has involved exploiting the behavioural responses of unwanted teleosts and invertebrates to direct the former out of the codend via strategically located panels of square-shaped mesh, collectively termed behavioural-separating bycatch reduction devices (BRDs) (Broadhurst *et al.*, 1996, 2002, 2005, 2006, 2015; Broadhurst and Kennelly, 1997). Teleost escape was as much as 70% for some species and increased with greater proximity of the BRDs towards the codend. By contrast, during towing (speeds of ~1.2 m s^{-1}), there were virtually no reductions in cuttlefish catches across all sizes from various behavioural-separating BRDs at varying positions in codends (Broadhurst *et al.*, 2002).

The only evidence of any response to a trawl with a behavioural-separating BRD by cuttlefish was during an experiment to assess the effects of haul-back delay (i.e. the period between towing being stopped and the trawl being winched to the surface) on BRD performance. Significantly more larger cuttlefish escaped from a BRD located 1.2 m from the end of the codend when there was no delay in haul back (Broadhurst *et al.*, 1996). Unfortunately, the reasons for this pattern are unclear, and the interpretation of these results is limited due to small catch sizes (<1.5 kg 90 min^{-1} tow) and low replication (8 tows).

In addition to minimal responses to behavioural-separating BRDs, most cuttlefish encountered by NSW penaeid trawlers are physically wider than the targeted/other by-catch species, and their rigid body precludes compression. Thus, increasing lateral mesh openings (via larger diamond- or square-shaped mesh) throughout the codend to better match the desired sizes of *P. plebejus* (Broadhurst *et al.*, 2006; Macbeth *et al.*, 2012) or teleosts such as *Sillago* spp. (Broadhurst *et al.*, 2005) did not reduce cuttlefish catch. Maintenance of targeted catches and reductions in cuttlefish catches have only been achieved via mesh size changes in fish trawls (≥90-mm SMO) working to the south of the penaeid fishery (Broadhurst and Kennelly, 1995; Graham *et al.*, 2009). The only other variables shown to affect standardized catches of cuttlefish among penaeid trawlers were towing speed and depth, both of which were positive, implying that slower speeds and shallower depths might yield lower cuttlefish catches across all sizes (Macbeth *et al.*, 2012; Broadhurst *et al.*, 2015).

Reducing unwanted fishing mortality among penaeid trawls in South Australia

In the Spencer Gulf, South Australia, 39 double-rigged penaeid trawlers (using 2 × 14.6 m headline trawls) target the western king prawn (*Melicertus latisulcatus*), landing up to 2000 t per annum (Noel *et al.*, 2018). Whilst this fishery has Marine Stewardship Certification in recognition of its management through a suite of regulations, concerns were raised in 2012 over bycatches of *S. apama*.

With the aim to mitigate discard mortality for *S. apama*, four experiments were conducted, assessing variations of the generic mechanical-separating Nordmøre-grid. This BRD comprises a guiding panel/funnel in the posterior trawl that directs catches to the base of a grid with bar spaces sufficiently spaced to allow targeted penaeids (or other crustaceans) to pass through and into the codend, while all other animals are directed upwards and out of the trawl through an opening in the top (Figure 1).

Eight treatments were simultaneously compared against a control (conventional 41-mm SMO diamond-meshed codend) and randomly assigned to the double-rigged trawls. Replication varied from 7 to 15 deployments for each treatment over three to five nights across conventional fishing grounds and followed typical tow durations and a relatively rapid towing

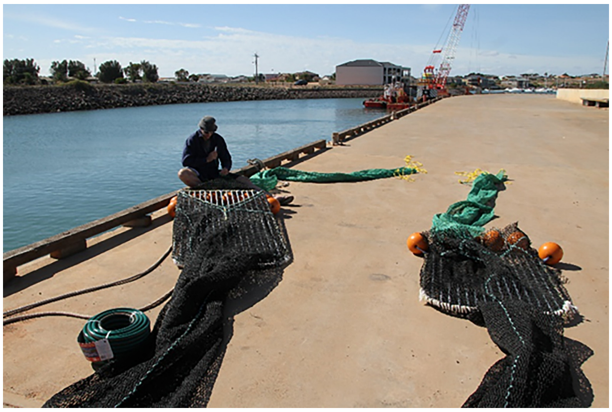

Figure 1. Nordmøre-grids designed to reduce bycatches of cuttlefish in penaeid trawls being assembled on a quayside (photograph by M. Broadhurst).

speed of ∼1.9 m s^{-1} (Kennelly and Broadhurst, 2014; Noell *et al.*, 2018).

Compared to control trawls, those containing Nordmøre-grids caught significantly fewer (34–90%) *S. apama* and another bycatch species. The maximum reductions in *S. apama* (mean weight of ∼450 g) catches were achieved using a Nordmøre-grid with 38-mm spaces between the bars and a very large surface area (∼2 × 1 m), steep incline (30°), large escape exit (>1 m^2), and short (2.7 m) guiding panel. This configuration did not negatively affect catches of the targeted *M. latisulcatus* but rather improved their quality, owing to fewer blue swimmer crabs (*Portunus armatus*) in the codend.

The effectiveness of the best-performing Nordmøre-grid configuration was attributed to its short, low-angled guiding panel, which directed the catch to the base of the similarly angled grid. This configuration provided minimal directional transition and clogging before sorting occurred across the entire surface of the grid (Silva *et al.*, 2011).

Other technical options for reducing unwanted trawl-fishing mortality

In addition to mechanical-separating BRDs in the codend, other gear-based options might have utility in reducing the collateral mortalities of some cuttlefish. There have been various attempts at altering headline and/or ground-gear heights to exploit species-specific vertical distributions in trawls, but a prerequisite for reducing interactions between focal species and fishing gears is information on their behavioural responses to visual and mechanical stimuli (Kennelly and Broadhurst, 2021). Future work would benefit from a greater understanding of these responses when redesigning trawl openings to exclude cuttlefish, ideally before they enter trawls. Two complementary approaches might involve sound (to startle; e.g. Mooney *et al.*, 2012), or more likely light, which is known to evoke variable responses among taxa and certainly has been used to attract some organisms into fishing gear, such as squids (Yamashita *et al.*, 2012), while excluding others (O'Neill and Summerbell, 2019). Nevertheless, cuttlefish morphology and their inability to maintain sustained swimming speeds suggest that such work should focus on understanding their movements and distributions as a means of excluding them.

It might also be possible to assess the utility of changes to on-board handling/operational practices to reduce trawl mortalities, but cuttlefish have fragile skin and appendages and are easily damaged during capture (Revill *et al.*, 2015). Few studies have quantified discard or bycatch mortalities among cuttlefish, although like most cephalopods, there is a strong bias towards deaths (reviewed by Broadhurst *et al.*, 2006). While a few tagging studies using trawl-caught animals showed reasonable survival, these involved very short tows (<15 min) and water-filled containers in the codend to reduce dermal damage (e.g. Bloor *et al.*, 2013). Commercial tow durations (often two hours for penaeid trawls and longer for fish trawls), combined with deep water depths and other catches in the codends, likely exacerbate damage among cuttlefish and would probably minimize any utility of modified onboard-handling practices. In this regard, modifications that facilitate avoiding cuttlefish at the anterior end of the trawl might have the most benefit.

Reducing unwanted discards in trammelnet fisheries

In southern Europe, general discards from trammelnets are considered high (up to 80%; Gonçalves *et al.*, 2007). In Portugal, discards of *S. officinalis* were lowest using a 140-mm inner mesh compared to using 120- or 100-mm inner meshes (140 mm mesh = 25 specimens, 120 mm mesh = 58 specimens and 100 mm mesh = 43 specimens). However, these discards accounted for only 6% of the total *S. officinalis* landings and the reasons for discarding were unclear, although likely attributable to specimen size or poor condition/damage (Gonçalves *et al.*, 2007). Nevertheless, a larger inner mesh size may be the better option to reduce unwanted discards of cuttlefish.

Conclusions about fishing gear modifications

Of the BRDs tested in trawl fisheries, the mechanical-separating Nordmøre-grid has been the most effective for reducing cuttlefish bycatch. But the utility of this device will be very fishery and location-specific. Prior to testing in other fisheries, grid dimensions/design will likely need to be tailored to the morphological dimensions and behaviour of both the target species and any non-target cuttlefish. More research is also needed to determine if there are behavioural reactions that could be used to prevent cuttlefish from even entering trawls in the first place, considering all species are highly susceptible to subsequent mortality induced by dermal damage incurred inside the trawl and when handled onboard. The same issue might apply to cuttlefish interacting with and escaping from trammel net fisheries.

Conservation method 3: increasing egg survival in cuttlefish trap fisheries

Trap fisheries for *S. officinalis* in the eastern Atlantic Ocean, English Channel, and Mediterranean Sea take advantage of seasonal inshore migrations by adult cuttlefish to mate and lay eggs (Blanc and Daguzan, 1998; Watanuki and Kawamura, 1999; Barile *et al.*, 2013). Because females lay many of their eggs on the traps and these eggs are then destroyed when the traps are raised and cleaned, or left out in the sun to dry (Blanc and Daguzan, 1998; Melli *et al.*, 2014), trap fishing is associated with egg mortality in addition to the harvest of adults (Figure 2). Cuttlefish would otherwise lay eggs on natural objects like cnidarians, plants, algae, tube worms, and sponges (Boletzky, 1983; Blanc and Daguzan, 1998), but these substrates are not always readily available, and females

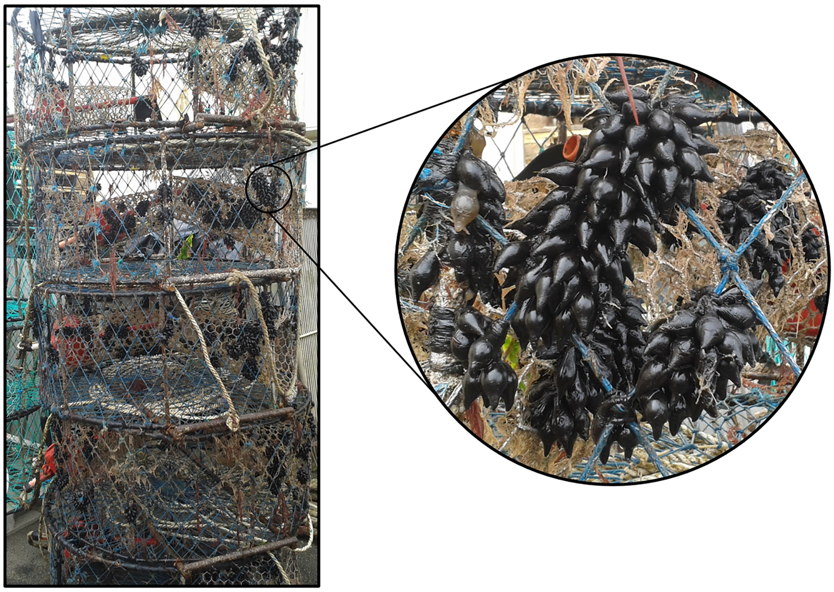

Figure 2. Stacked cuttlefish traps with *S. officinalis* eggs attached (Normandy, France) (photograph by O. Basuyaux).

may be trapped before having the chance to lay eggs elsewhere. In just two small fisheries where this phenomenon was studied, egg-laying on traps was estimated to result in the loss of millions of *S. officinalis* eggs every season: 18–40 million in Morbihan Bay, France (Blanc and Daguzan, 1998); and 3.5 million along 5 km of coast in the north-western Adriatic Sea (Melli *et al.*, 2014). The sustainability of *S. officinalis* trap fisheries can thus be improved by reducing egg loss, and several methods to divert egg-laying from traps and/or to salvage the eggs have been tested.

Reducing egg laying on traps

One method that has been shown to deter egg laying on traps involves applying antifouling compounds such as copper oxide and zinc pyrithione to trap frames (Ganias *et al.*, 2021b). Tests with these substances in the Thermaic Gulf, Greece, found almost no eggs were laid on coated surfaces, and this reduced maintenance time and the weight of the traps, making them easier to handle (Ganias *et al.*, 2021b). Both zinc-pyrithione and copper oxide are used successfully in the mariculture industry without any reported impacts on cultivated stocks (e.g. no greater mortalities, high disease rates, etc.). However, these antifouling compounds may also conceivably discourage cuttlefish from entering the traps, thus decreasing catch rates, as observed by Ganias *et al.* (2021b). Moreover, it is unclear if trapped cuttlefish ingest or absorb the toxic compounds, contaminating their tissues and rendering them unsafe to eat, although zinc pyrithione is considered a neutral material both for the environment and for human health (Amara *et al.*, 2018). More research is needed before this tactic is implemented broadly.

Diverting egg laying onto alternative substrates

Another strategy to reduce egg laying on traps is to provide objects on or near traps that are more enticing substrates for cuttlefish to lay their eggs (Zatylny-Gaudin, 2000). Ideally, these items would be naturally occurring, such as seagrass or tube worms, since these have been deemed more efficient than artificial solutions (CRESH, 2012). Thus, measures to conserve existing natural habitat (by banning nearshore trawling, for instance), and active habitat restoration (such as by replanting seagrass), are the best ways to ensure adequate amounts of natural egg-laying substrates (see conservation method 1 above).

However, where habitat degradation has already occurred, artificial alternative substrates (referred to hereafter as "alternative substrates") may be considered for egg laying. Several authors have assessed various materials as alternative substrates, including polyethylene, polypropylene, elastic and hemp rope, willow branches, and trap entrance fingers. Eggs were laid on all of these materials, particularly mesh (Ganias *et al.*, 2021b), trap entrance fingers (Davies and Nelson, 2018; Parkhouse, 2019) and rope comprising various materials (Blanc and Daguzan, 1998; Barile *et al.*, 2013; Melli *et al.*, 2014; Davies and Nelson, 2018; Grati *et al.*, 2018).

During tests with ropes, cuttlefish display a marked preference for fibres 8 mm in diameter, laying fewer eggs on 10- and 12-mm rope (Blanc and Daguzan, 1998; Barile *et al.*, 2013). If free-floating, it is also important that ropes are <50 cm so they do not sag onto the sediment under the load and smother the attached eggs (Blanc and Daguzan, 1998) or that floats are attached to the ropes free ends (see Barile *et al.*, 2013; Grati *et al.*, 2018; Ganias *et al.*, 2021b). The colour of rope may also be a salient factor in its attractiveness as an alternative substrate. While no difference was observed between light (yellow) and dark-coloured (blue) ropes (Melli *et al.*, 2014), those made from two contrasting colours (blue and white) attracted more eggs than solid-coloured ropes, although this effect weakened over time as epibiont growth obscured the original colours (Blanc and Daguzan, 1998). Plastic objects with oblong features, like pieces of plastic mesh netting or trap entrance fingers, can also operate as egg-laying substrate (Davies and Nelson, 2018; Parkhouse, 2019; Ganias *et al.*, 2021b), but they attract fewer eggs than rope during direct comparisons (Davies and Nelson, 2018), and no tests of optimal size or shape have been published.

In some cases, it would be preferable if alternative substrates are constructed of biodegradable natural materials, such as natural fibre rope or rocks. Hemp rope was found to be an attractive alternative substrate to cuttlefish, and, being a natural fibre, has the advantage of being biodegradable. Unfortunately, this material was also associated with higher rates of egg detachment and epibiont growth on eggs during development, yielding lower hatching rates (Melli *et al.*, 2014). Thus, for the moment, the ideal alternative substrate material appears to be polypropylene, polyethylene, or elastic rope. The testing of other natural fibres or objects as alternative substrates to find a material that is both biodegradable and associated with better outcomes for eggs is strongly encouraged. Options include biodegradable plastic materials like aliphatic polyester (polybutylene succinate and polybutylene adipate-co-terephthalate), which is degraded by micro-organisms over time (Kim *et al.*, 2014).

Deploying alternative substrates

Alternative substrates can be deployed either as free-standing devices, attached to existing benthic infrastructure (e.g. a dock, pier, oyster racks, or mooring block), or affixed directly to operating cuttlefish traps. Various stand-alone configurations have been tested, all of which were successful in attracting eggs. Off northern France, Blanc and Daguzan (1998) observed that among six galvanized steel grids with 29 ropes attached to each, 7–100% of the ropes had eggs laid on them, and each unit collected between 100 and 4000 eggs, or between 3 and 138 eggs per rope. Basuyaux and Legrand (2013), working at various sites in northern France, found ropes tied to concrete slabs (radius and width of 40 and 3 cm) and oyster racks averaged 11–80 eggs per rope at one location, while a chain with 30 sections of rope tied along its length attracted some 10,000 eggs (320 eggs/rope) at a different location (Basuyaux and Legrand, 2013). A study in western France found 53% of 30 ropes deployed on a chain attracted 2300 eggs, or about 75 eggs per rope (Basuyaux and Legrand, 2013). This was compared to 84–457 eggs on natural supports and an average of 200 eggs per trap (Basuyaux and Legrand, 2013).

In the Mediterranean Sea, Barile *et al.* (2013) tested metal grids with attached ropes mounted onto three-dimensional frames as well as frames modified with criss-crossed diagonal ropes. Significantly more eggs were laid on the frames with criss-crossed ropes than on the grids (Barile *et al.*, 2013). Grids were also harder to handle, more expensive, and tended to be silted over despite being raised off the benthos (Barile *et al.*, 2013). Grati *et al.* (2018) tested flat electro-galvanized iron wire grids and lead longlines with short sections of polyethylene rope attached, as well as galvanized iron frames with crisscrossed diagonal polyethylene ropes in the Mediterranean Sea. A total of 20–39% of the ropes affixed to grids had eggs, with 78–144 eggs per rope, and 36–88% of the ropes affixed to the longline had —115–175 eggs per rope (Grati *et al.*, 2018). The frames with criss-crossed ropes had the most eggs of all, with 4–63% of the frames entirely covered with eggs, and 27 frames collectively attracting between 88,500 and 108,000 eggs (Grati *et al.*, 2018).

Based on the studies summarized above, it appears that, except for metal grids in certain locations, many diverse structures, including long chains, concrete slabs, three-dimensional frames, and two-dimensional grids, are suitable bases attaching ropes on which cuttlefish lay their eggs. The choice of structure to use can therefore be largely based on more practical considerations, such as the availability of materials already on hand, biodegradability, and/or ease of handling.

Ideally, a free-standing alternative substrate would be left in place after the cuttlefish traps are collected so any attached eggs could develop and hatch, and it could continue to serve as an alternative substrate in subsequent years. If, instead, a stand-alone alternative substrate is deployed with the intention of eventually retrieving it, removal must be timed late enough in the year to ensure the eggs have hatched—a timespan that usually depends on the date eggs were laid and water temperature (Bouchaud, 1991a). Eggs hatch between June and September in the European Atlantic Ocean (Bouchaud, 1991b), between May and November in the Mediterranean Sea, and between February and July in the Atlantic Ocean off North Africa (Roper *et al.*, 1984). Deploying stand-alone alternative substrates entails some effort and cost to fishers, mainly encompassing the labour required to construct alternative substrate objects and to deploy (and potentially retrieve) them. There is also the risk of alternative substrate loss to wave activity, trawling, or theft by beachcombers or divers (Basuyaux and Legrand, 2013), or that alternative substrates will become entangled with traps or other gear.

Alternative substrates can also be attached directly to cuttlefish traps and detached at the end of the season or when they become laden with eggs. Two experiments, one conducted in the Mediterranean Sea and one in the English Channel, involved modified traps with strands of 8-mm diameter elastic and polypropylene rope as alternative substrate and found that they diverted between 24 and 50% of the total number of eggs laid on the traps (an average of 947 and 140–230 eggs per trap, respectively) and facilitated the easy removal of those eggs (Melli *et al.*, 2014; Davies and Nelson, 2018). These authors placed the rope on the insides of traps, but alternative substrate could also be placed on the tops of traps (see Ganias *et al.*, 2021b) to increase the total amount of available surface area and potentially act as an additional attractant to adult females.

Like stand-alone alternative substrates, trap modifications entail a cost to fishers in terms of the labour of attaching and detaching alternative substrates, and potentially some added difficulty in handling traps. These costs may be offset, however, if alternative substrates may attract females to the traps. Indeed, in other cuttlefish fisheries, spawning substrates are already used as lures to entice cuttlefish into traps (Watanuki and Kawamura, 1999). Moreover, elastic and polypropylene ropes added to cuttlefish traps in the Mediterranean Sea and in the English Channel were found to either have no effect on catch rates (Melli *et al.*, 2014) or were associated with a more than doubling of catch (0.86 versus 1.8 cuttlefish per trap, Davies and Nelson, 2018).

Salvaging eggs laid on traps

Unfortunately, no matter what measures are taken to divert egg laying, some will almost certainly still be laid on the traps. One option would be to resubmerge traps until after the eggs hatch. However, this may have the unintended consequence of trapping and killing other organisms in the interim (ghost fishing; see Matsuoka *et al.*, 2005 for a review), and many fishers are unwilling to redeploy their gear in this way for fear of damage, wear, and loss (Basuyaux, 2011). Moreover, many traps often become so laden with eggs that they must be cleaned multiple times throughout the fishing season to remain functional (Melli *et al.*, 2014). One suggestion has been to provide fishers with multiple sets of traps, but this would be an expensive undertaking (Melli *et al.*, 2014) and does not circumvent the issue of ghost fishing. A better idea would be to remove eggs from traps as needed, and then deliver the eggs to an environment where they can develop and hatch.

The best way to remove eggs from a cuttlefish trap is to carefully cut the stalks of egg casing that are wrapped around the mesh or frame of the trap. If the bulbous parts of the eggs are undamaged, this frees them without affecting their viability (C.E. O'Brien, pers. obs.). Unfortunately, this practice is also very time-consuming, and many fishers instead opt to use a pressure washer, even in fisheries where that practice is illegal (Grati *et al.*, 2018). Pressure washing is very destructive to the eggs and should be avoided. Bouchaud (1991c) reported only 2% of pressure-washed eggs eventually hatched, whereas Melli *et al.* (2014) reported hatching rates as high as 88% when eggs were removed from traps by hand. If pressure washing is used, damage could be lessened by first salvaging any loosely hanging egg clumps that can be pulled off easily.

Hatching salvaged *Sepia officinalis* eggs

The eggs that are collected on detachable alternative substrates or removed from trap structures should be transferred to an environment where they can develop with the maximum likelihood of survival. Eggs that are simply released overboard rarely survive because they are likely to be buried in the sediment, physically damaged, or washed ashore (Melli *et al.*, 2014). For eggs on alternative substrate ropes that are detached from cuttlefish traps, the sections of egg-laden rope can be tied to rocks, a dock, a pier, a mooring block, or another anchor and resubmerged. Similarly, unattached eggs, such as those collected from the traps themselves, could be placed in mesh bags and affixed with short (<50 cm) sections of rope to anchors.

A key factor promoting egg survival is keeping the eggs suspended off the substrate during development. As mentioned, ropes that are too long (>50 cm) tend to become so heavy that they sag onto the bottom and the eggs are smothered (Blanc and Daguzan, 1998). Similarly, eggs on ropes attached to structures lying flat on the substrate had greater mortality than eggs attached to the tops of three-dimensional structures or those attached to ropes with small floats at the ends (Barile *et al.*, 2013; Grati *et al.*, 2018).

If possible, the eggs should be resubmerged at locations with moderate water movement to aerate and prevent sediment build-up but protected from extreme wave activity. Since *S. officinalis* generally spawn in 5–60 m of water and ~2–12 km from the shoreline (Nixon and Mangold, 1998; Basuyaux and Legrand, 2013), their eggs should be put at a location within these parameters. The bottom temperature should be 18–25°C, and the salinity within 30–35 PSU (Barile *et al.*, 2013). *Sepia officinalis* eggs can be transported for short periods (<8.5 h) in buckets of seawater (with or without aeration), gently wrapped in a damp material like paper towels or seaweed, or even transported dry if necessary (Jones *et al.*, 2009). Relocating eggs implies a cost to fishers in terms of labour, time, and possibly fuel. If, instead, eggs are thrown overboard, their chances of survival can be maximized (albeit not by much) by doing so while offshore so they are less likely to wash up on beaches and desiccate (Basuyaux, 2011).

Salvaged eggs can also be hatched in captivity if a running seawater system with high water quality and aeration is available and has been accomplished in both indoor laboratory-type settings (Boletzky and Hanlon, 1983). Melli *et al.*, 2014; O'Brien *et al.*, 2016) as well as in large outdoor salt-water pools, such as oyster cultivation ponds (e.g. Roussel and Basuyaux, 2016). In one study, captive rearing was found to almost double the hatching rate of eggs reared in a natural setting (88 versus 45%, Melli *et al.*, 2014). O'Brien *et al.* (2016) found that hatchlings from eggs that spent most of their development in the laboratory did not differ appreciably from hatchlings that developed largely at sea. Thus, laboratory rearing is not likely to lessen hatchlings' prospects of survival in the wild. Eggs maintained in their original clusters appear to fare better than those that float freely: clustered eggs developed more rapidly and had greater chances of hatching (Ciocan and McCabe, 2018).

Once eggs have hatched, juvenile cuttlefish require large amounts of crustacean prey, and their enclosures must be kept very clean (Boletzky and Hanlon, 1983). To avoid the associated labour costs, it is best to release hatchlings (if local legislation permits this) within a day or two of emergence. Because hatchlings' skin can be easily damaged, and they consume large amounts of food (Boletzky and Hanlon, 1983), the ideal release location would have low wave activity and be in an area with lots of small crustaceans to serve as prey.

Cuttlefish code of practice promoting egg survival

Since 2015, the Southern Inshore Fisheries and Conservation Authority (IFCA) of South England has promoted a "cuttlefish code of practice" (CoP) throughout their district (from the Devon/Dorset border in the west to the Hampshire/Sussex border in the east), developed in conjunction with local fishers to increase the survival of cuttlefish eggs laid on traps (https://secure.toolkitfiles.co.uk/clients/25364/sitedata/Redesign/Codes_of_Practice/Cuttlefish-Code-of-Practice.pdf). The CoP involves taking care to minimize egg damage: when hauling and deploying gears; avoiding cleaning or washing traps that contain cuttlefish eggs; leaving traps in the water after the cuttlefish fishing season until the eggs have hatched (usually late August–September); and regularly attending traps to remove ghost catches, or removing entrance panels to preclude ghost fishing.

Compliance with this CoP is good, with most fishers supporting it because of strong beliefs that promoting egg survival will lead to greater catches in successive years. However, some fishers who fish in more exposed coastal areas or busy waterways prioritize protecting their traps from damage or theft over egg survival, and they remove and jet wash traps at the end of the cuttlefish season. Elsewhere, other fishers are concerned about their gear and egg survival and believe it is best to remove egg clusters by hand and release them back to sea to prevent egg damage throughout the season during the hauling and setting process.

The success of such a CoP is therefore influenced by the location of the fishery, with compliance more likely in quiet, sheltered areas and with the support and input of local stakeholders. More importantly, a CoP should be accompanied with the information required to understand the background behind the suggested practice. This approach should ensure that assumptions regarding alternatives for both protecting gear and eggs are not made without understanding the impacts of different methods, such as simply releasing egg clusters back to the sea.

Conclusions about reducing egg loss in trap fisheries

The egg loss mitigation methods for *S. officinalis* outlined in the preceding sections are summarized in Figure 3. While

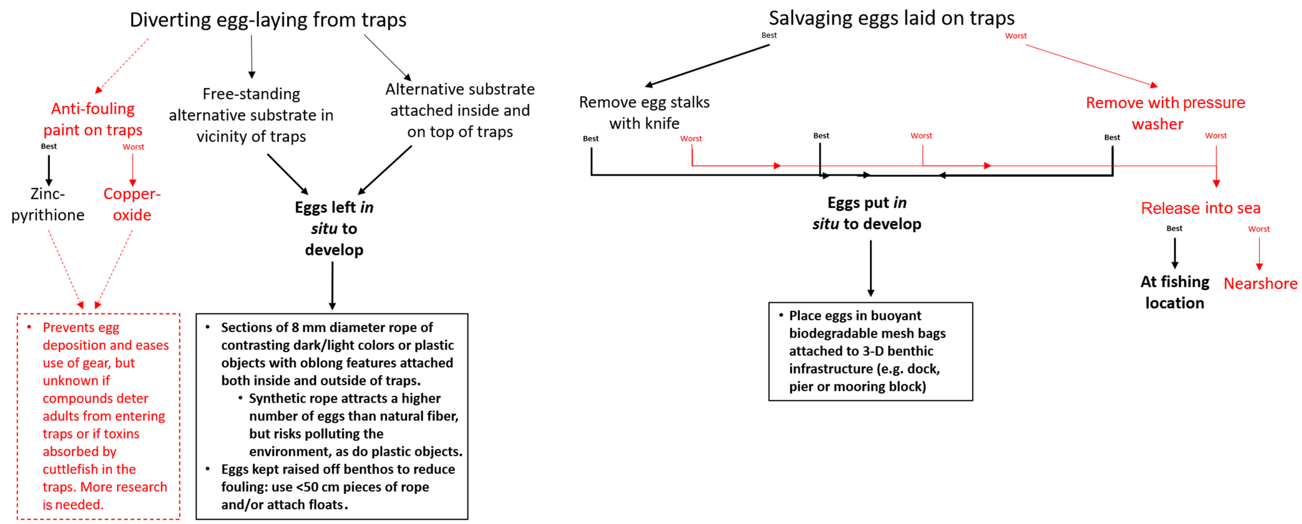

Figure 3. Flowchart of best practices for reducing egg mortality in *S. officinalis* trap fisheries. Where particular methods are clearly superior to others in terms of minimizing effort and/or lowest egg mortality, they are designated as "best" options and bolded. Those methods that are high effort, result in minimal egg survival and/or require further research are designated as the "worst" option and coloured red.

specific to *S. officinalis*, these techniques could likely be adapted to combat egg loss in other cuttlefish-trap fisheries.

Conservation method 4: restocking

Another potential means of increasing cuttlefish stocks is captive breeding to artificially restock a wild population. This approach has been attempted with *S. latimanus* in the East China Sea.

Breeding *Sepia latimanus*

In the Ryukyu Islands Archipelago, *S. latimanus* and the pharaoh cuttlefish (*S. pharaonis*) are commercially harvested by local fishers. Fishers use many methods to catch these cuttlefish, such as spearfishing, angling, and various netting, including small, fixed nets (less than 15 m depth). The total cuttlefish harvest was stable at around 200 t per year until the 1990s, but started to decline in 2000. By 2018, the total harvest was only 24 t (Ohta *et al.*, 2017). The cuttlefish fishery remains a culturally significant part of the Okinawan in-reef fishery, and the species are also popular sport fishing targets. Both species are harvested by non-commercial fishers without regulations, yet represent only 4% of the total annual cephalopod catch and are not considered a profitable target. Due to this lack of economic incentive, few conservation efforts exist for this fishery. This makes conserving cuttlefish challenging in Okinawa.

From 2001 to 2003, the National Research and Development Agency and the Japan Fisheries Research and Education Agency (FRA) designed and conducted a restocking programme at Ishigaki Island. In that programme, 128 adult *S. latimanus* (M18, F110) in 2001, 55 (M5, F50) in 2002, and 31 (M4, F27) were collected from a fixed net and placed in a 200 kl tank. During three years, 317389 eggs were laid, and 191388 juveniles were marked and released into Urasoko and Kabira bays located on the central west coast of Ishigaki Island. Between 0.02 and 0.08% of the released cuttlefish were then recaptured during each respective harvesting season, which consisted of 18 (2001), 16 (2002), and 4.5% (2003) of the total catch of *S. latimanus* by the number of animals in Kabira Bay. This study indicated hatch and release programmes could potentially increase the total number of animals in the wild due to the likely increase in survival of eggs in aquaria, though whether the released juveniles survive to make a significant difference to the overall wild population is uncertain. In this case, the yield per release rate remained low at 1.28 g (2001–2002) to 0.67 g (2002–2003), making the programme economically unviable (Dan et al., 2008).

Conclusions about restocking

While the breeding programme was successful in the Ishigaki Island case study, it remains unclear whether restocking efforts produce benefits in the long term. More mark-and -recapture studies with captive bred cuttlefish are needed to assess post-release fates. Other possible concerns that warrant assessing are any effects of ongoing limited genetic diversity among brood stock cuttlefish or habitat and prey availability at stocking locations and the implications for wild stocks.

Conservation method 5: promoting sustainable harvesting

Prohibiting particular gear types or implementing minimum harvestable sizes are other commonly used means of protecting fishing resources. Various combinations of these regulations have been utilized in three cuttlefish fisheries over the past two decades.

Prohibiting fish aggregating devices (FADs)

In the south-east Arabian Sea (along the south-west coast of India), FADs are used by artisanal fishers to attract and aggregate *S. pharaonis* closer to shore, where customary rights exist for fisher groups to use hooks and lines (Kurien, 1996). This practice is based on knowledge of the reproductive behaviour of cephalopods to aggregate near submerged objects for spawning (Fernandez, 1996; Samuel *et al.*, 2005). This aggregation-based hand-jigging cuttlefish fishery, which was historically popular in the southern part of the coast, spread to a much wider area beginning in 2004, catering to the export demand (Sasikumar *et al.*, 2006, 2015a, b). As a result, the exploitation of cuttlefish aggregations near FADs has increased considerably in the region since 2006.

Figure 4. A fish aggregating device (FAD) constructed of casuarina branches with cuttlefish eggs attached (photograph by J. Chembian, FSI).

The investment required for installing FADs is relatively low (Samuel *et al.*, 2005), because they are constructed of widely available and cheap biodegradable materials such as coconut spadices, casuarina branches, and similar materials (Figure 4). Given this low overhead cost and the resulting increases in catches, the number of FADs deployed has increased with expanding fishing grounds. The FADs have also been constructed using non-biodegradable materials, such as old fishnets and plastic bottles (PET bottles of 1–2 l), and are deployed in rocky, un-even grounds where cuttlefish naturally spawn. Since these are non-trawlable grounds, prior to the introduction of FADs, the cuttlefish spawners were protected in the sheltered areas from the negative impact of bottom trawling. With the deployment of the FADs in such sheltered areas, the catchability of egg-laying cuttlefish with jigs increased near the FADs, thereby increasing their fishing mortality. To document the impact, the catch rates, size composition, and reproductive status of *S. pharaonis* exploited near FADs were compared with those of free schools exploited by commercial trawling. The impact of the aggregation fishery on spawning stock biomass and recruitment was also assessed. Results suggested that the free schools were assemblages of immature, maturing, spawning, and spent individuals, whereas the FADs aggregated larger spawning cuttlefish. The occurrence of only gravid animals in the FAD-associated fishery suggests that the cuttlefish were attracted to the FADs for attaching their eggs (Sasikumar *et al.*, 2015a).

The analyses of cuttlefish samples from aggregation-based fisheries (FADs) and those from the free schools (trawl) strongly suggested: (1) the spawning cuttlefish population is vulnerable to FAD-associated fishing; (2) the aggregation-based fishery harvested cuttlefish before spawning, because fished individuals had a high gonado-somatic index; (3) the removal of spawners having high reproductive value led to recruitment overfishing; and (4) aggregations may be more valuable when unexploited, because fishing on pre-spawning individuals can have adverse effects beyond the removal of biomass. Aggregation-based fishing operations can rapidly remove a substantial portion of assemblages, with implications for reproductive and economic outputs. Consequently, the increase in targeted exploitation of cuttlefish aggregations has raised concerns about the sustainability of FAD-based fishing (Sasikumar *et al.*, 2015b).

Apart from the biological impacts caused by fishing practices, intersectoral conflicts also emerged in the area due to gear interactions. Incidents of trawls entangling with the detached FADs led to conflicts between trawlers and FAD fishers. To prevent further conflict, regulations were enacted by the State Department of Fisheries in July 2012 to ban the FAD-based cuttlefish fishery in coastal waters off the state of Karnataka. Subsequent to the ban, catch rates by trawlers increased by 2.5 times, and the catch rate nearly doubled from 1.2 to 2.3 kg h^{-1} in 2012–2013 for the inshore fishery. Thus, the ban on FADs in the region has also been associated with a partial recovery of stocks.

Minimum weight limit and indirect fisheries management

In Morocco, cuttlefish (*S.* spp.) are considered a joint catch alongside octopus, where they are exploited mainly along the southern Atlantic coast by cephalopod freezer trawlers and coastal trawlers. Occasionally, these species are caught by coastal vessels fishing with gillnets and trammel nets, and artisanal fishing boats fishing with trammel nets and jigs. The cephalopod freezer trawlers, coastal trawlers, and most artisanal boats are allowed to operate inside the octopus management unit located south of 26°24’00”N (MPM, 2021), where spatio-temporal closures and fishing gear regulatory measures exist. These regulations include fishing capacity regulations of 70 mm mesh size for the freezer cephalopod trawlers; 60 mm for coastal trawlers operating south of 26°24’00”N and 50 mm for coastal trawlers operating north of this latitude. The catches of cuttlefish along the south Atlantic coast of Morocco peaked at 31,300 t in 2000 and declined to ~7,200 t in 2003, though landings have been variable thereafter (e.g. reaching 27,600 t in 2016) (FAO, 2020).

The main management measure for cuttlefish fisheries off the South Atlantic coast of Morocco is a minimum weight limit of 100 g (all weight including visceral mass). Along with the aforementioned octopus-fishery regulations, these management measures seem to have worked well for cephalopods, though this may also be due to the overexploitation of demersal finfish species in the region (Balguerias *et al.*, 2000). The total catch of all cephalopods combined has been increasing in the last two decades (MPM, 2021). Post-release survival may be low for those <100 g cuttlefish, based on the Australian case studies, though region-specific mortality for Morocco is uncertain. Comparatively, in the English Channel, 31% of small (<15 cm dorsal mantle length) cuttlefish survived to reach the vessel’s sorting table, though the survival rate dropped to 16% after 72 h spent in an on-board aquarium system (Revill *et al.*, 2015). We therefore recommend conducting studies to estimate the ratio of Moroccan cuttlefish that die after being discarded, together with efforts to improve fishing gear selectivity.

The fishing effort of the three main fleet segments exploiting cuttlefish inside the octopus management unit (i.e. coastal and freezing trawlers, and artisanal boats) depends on fishing strategies, closures (Moroccan vessels tend to avoid fishing in cuttlefish nursery grounds during the recruitment periods), and the number of active units and quota consumption of octopus allocated to the three segments. The stock status was determined in 2018, based on a surplus stock assessment model, which concluded that the Moroccan South Atlantic stock is overexploited, with the fishing mortality above the level necessary to achieve maximum sustainable catch and target biomass (FAO, 2020). Therefore, it was recommended

Figure 5. A closed basket trip which, *in-situ*, would prevent unnecessary cuttlefish deaths or ghost fishing mortality (photograph by O. Escolar).

that existing indirect management measures (such as the octopus fisheries measures) may not be enough to curb the overexploitation status and that more direct management measures, such as a specific cuttlefish quota, and, as we suggest, further research into gear selectivity and an improved understanding of regional cuttlefish mortality, are essential for species recovery.

Voluntary co-management of a small-scale fishery

There are indications of increasing fishing mortality and biomass depletion for cuttlefish in the northwest Mediterranean Sea since 2000 (Maynou, 2015). Based on the success of the co-management of sand eels (*Gymanammodytes cicerelus* and *G. semisquamatus*) fisheries in the area (Lleonart *et al.*, 2014), the Catalan regional government promoted a co-management plan for the cuttlefish small-scale fishery in the gulfs of Pals and Roses in 2020. The co-management plan is supported by representatives of four stakeholders: fishers, non-governmental associations, regional governments, and scientists.

Based on the current local ecological knowledge, stakeholders in the co-management plan agreed to voluntarily enforce various measures to increase the ecological and economic value of the fishery. Specifically, fishers have voluntarily pledged to: (1) increase the inner, stretched mesh size of the trammel nets to 20 cm (to be implemented during the fishing seasons of 2022–2023) to reduce the capture of small individuals and thus discard mortalities; (2) limit trammel net lengths to 2000 m per boat with a single fisher and to 3000 m per boat with two fishers or more; (3) close the trap entrances (Figure 5) during the weekends, holidays, or expected periods of marine storms and thus avoid unnecessary death; and in the case of lost traps, ghost-fishing mortality; (4) delimit a protected area during the fishing season (usually across deeper and lower turbulence areas), in which basket traps are left in storm-protected sea areas to avoid the egg mortality associated with storage on land; (5) leave basket traps *in situ* for a month after the end of the cuttlefish fishing season to allow time for any attached eggs to hatch; and (6) limit each fishing boat to 160 basket traps.

Further, participatory monitoring has been implemented to record data on stock biology (e.g. sexs, sizes, and weights) and fishery characteristics (e.g. fishing effort and areas fished). Fishers record detailed information related to their fishing effort by trip (e.g. number of traps, length of settled mesh, and fishing time), as well as information on the basic biology of key species and bycatch.

Conclusions about promoting sustainable harvesting

Methods for promoting sustainable harvesting can be beneficial, as demonstrated by banning FADs to help target large cuttlefish, thus presumably increasing the chance for spawners to lay eggs. But such methods can also be complex, and ultimately, there is often little benefit in protecting eggs if early juvenile stages are overexploited. In terms of fishing methods, a trade-off exists between the damage to eggs by trap fishing and the damage to juvenile cuttlefish by trawl fishing. Whilst cuttlefish may benefit from other fisheries management (such as indirect measures targeted at octopuses), benefits may be greater if management is species-specific. Buy-in from stakeholders such as fishers is crucial, because these cohorts are often the most experienced and knowledgeable about species' population dynamics, and so they should be involved in the management process from initiation to monitoring.

Re-enforcing evidence using citizen involvement

Citizen science has become a popular way of bringing public communities and scientific research closer (Dickinson *et al.*, 2010). Citizen science observations have been shown to be a valuable and cost-effective tool to gather quantitative and qualitative observations of wild animals, may fill knowledge gaps where data are lacking, and might be used in very diverse approaches (Bonney *et al.*, 2009).

Benefits of citizen science (and fisher participation) to regulate fishing mortality

One citizen-science project especially dedicated to cephalopods is the ongoing Cephalopod Citizen Science Project (CCSP), which helps divers understand how to best interact with cephalopods in the wild (see Drerup and Cooke, 2019a, b, c, and https://www.cephalopodcitizenscience.com/how-to-interact-with-cephalopods). The project has also provided valuable data on spatio-temporal population dynamics of cephalopod egg sightings (Figure 6), which could inform fisheries management (and ultimately conservation) in European waters as well as facilitate improved understanding of the life histories of various species (Drerup and Cooke, 2021; Drerup *et al.*, 2021).

The project identifies options to reduce various unaccounted fishing mortalities and then informs fishers about sustainable methods. For example, several fishers have altered their onboard handling methods to decrease the destruction of cuttlefish eggs after hearing about this issue from the CCSP's public engagement programme and other organizations that are concerned with this issue (e.g. Devon & Severn IFCA, and SeaSearch—a community of recreational scuba divers trained to record habitat information and species records from their dives, along with environmental parameters, with data submitted to the Marine Conservation Society: www.seasearch.org.uk). The CCSP has also brought together groups of people who have been saving, hatching, and returning cuttlefish eggs that washed up on shore. They have produced guides to aid local stakeholders in how best to hatch cuttlefish eggs with limited equipment and knowledge (e.g. https://www.cephalopodcitizenscience.com/stranded-cuttlefish-eggs). In addition,

Figure 6. (a) Citizen science has provided *in situ* recordings of cuttlefish breeding behaviour regarding egg laying on fishers' traps and (b) willing participants can provide year-round observations of egg development if traps are left in place, providing positive feedback to fishers who engage in sustainable practices. (c) Members of the Facebook groups (such as "UK cephalopod reports") are assisting in hatching cuttlefish eggs that wash up on the shore. (d) SCUBA dive groups are taking matters into their own hands by building artificial structures for cuttlefish egg laying that appear to be successful and benefit other cephalopod species, e.g. squid (eggs laid, below centre). (e) Citizen scientists may also provide evidence of where fishers engage in unsustainable practices, such as washing off eggs before landing. Photo credits: a–c Courtesy of Andrew Jackson and (d) source: Waarneming.nl, Stichting Observation International (permission granted by the author).

some SCUBA divers have assembled semi-permanent, artificial (using natural materials such as bamboo) egg-laying sites (Figure 6), which have proved successful at attracting eggs but may potentially infringe on local maritime laws.

Similar projects exist around other continents, such as the Cuttlefish Alliance (through the Scuba Divers Federation of South Australia Inc.; www.sdfsa.net), which monitors *S. apama* around Australia and has raised awareness of the species' decline in recent years among the public and highlighted the need for policymakers to have greater monitoring of the *S. apama* stocks. Other projects exist, such as www.projectsepia.com in Catalonia, Spain, although this initiative appears to be targeted to interact with local stakeholders with no English version of the site available.

Conclusions

Conservation measures have been applied to relatively few cuttlefish species to date, possibly because in many cases, stock assessment or biological information is inadequate to determine whether populations have declined and interventions are required. In many cases, cuttlefish are "data limited" fisheries, and stock assessments are not produced. In the absence of such assessments, the will to protect cuttlefish stocks derives from a blind approach, though there is now a greater need to understand stock-recruitment relationships or any idea of fishing mortality across the different life stages, particularly because climate change may alter stock structures and precautionary interventions are required to help prevent stocks from overexploitation (Boavida-Portugal *et al.*, 2022).

To address the dearth of a comprehensive review of existing information from various sources, we have sought to compile, for the first time, evidence from various global efforts to conserve cuttlefish populations. This information can act as a guide for policymakers and stakeholders to better understand what does or does not work in protecting these animals, particularly in instances where precautionary interventions may be required without adequate scientific information. Such efforts are especially crucial, considering the potential effects of accelerating climate change on spatio-temporal variations in distributions and abundances of different cuttlefish species (Doubleday *et al.*, 2016) and their renowned life-cycle plasticity in response to environmental variation (Pecl and Jackson, 2008).

Like all approaches to managing aquatic resources, the choice of conservation methods for cuttlefish will be fishery-specific and determined by a plethora of interacting factors, including but not limited to the fishing gear, targeted species, species of concern, each species' mating system, type of fishing mortality, extent of available management and compliance, and regional socio-economic status. For trawl fisheries, in some cases, simple BRDs can be retroactively fitted to existing configurations and realize considerable benefits in terms of reducing the bycatch of cuttlefish with an assumed (but unsubstantiated) reduction in unaccounted fishing mortality. Many BRD designs are available, although mechanical-separating designs would probably be the most appropriate, considering the established limited swimming capacity and response to active gears by some cuttlefish.

Substantial research efforts with gear modifications among traps have shown similarly positive outcomes as for trawling. Variations to materials used and alternative structures to divert eggs from traps can alleviate egg mortality caused by trapping. In terms of harvesting methods, traps are also the preferred option, because they can attract recently spawned specimens, and any selective discarding of smaller individuals might result in fewer deaths than for other methods. Nevertheless, it is recognized that cuttlefish incur high mortality after handing, and so preliminary underwater exclusion from any fishing gear would be more beneficial.

Notwithstanding the potential benefits of modifying fishing gears, in other cases where there are sufficient data, simply prohibiting fishing altogether at key locations and times is likely to have much greater benefits for cuttlefish, albeit with some economic costs to fisheries. Support for complete closures is compelling for some fisheries. For example, off northwest Spain, Guerra *et al.* (2016) considered ensuring two fully protected zones within the Parque Nacional de las Islas Atlánticas de Galicia would conserve and improve habitat for *S. officinalis,* though perhaps only for key components of their life (such as spawning), given the lack of success observed in small MPAs elsewhere in protecting cuttlefish (Abecasis *et al.*, 2013). These two zones have small surface areas (0.04 ha) and would be easily enforceable. Broader spatiotemporal closures (for entire gears or deleterious ancillary components such as FADs) could benefit cuttlefish stocks impacted by other fisheries, including hook and line and trapping.

As for depleted teleost stocks, there is potential for cuttlefish restocking efforts to augment wild populations negatively affected by excessive fishing mortalities. However, such work requires a better understanding of not only the survival of offspring but also the consequences of any limited genetic diversity. Potentially high post-release mortalities might limit the utility of this approach in the short term, and future research is required to assess the suitability of key species where populations have severely declined.

If such data are reliable enough to inform stock assessments, citizen science may help with broadening data sets (e.g. recreational fishers reporting catches voluntarily; Barrett et al. 2022), although mechanisms to ensure quality control must be in effect. A lack of data is also an issue for enhancing the survival of eggs because egg recovery tends to be small scale, and since larvae and juveniles disperse so widely and are difficult to tag, it is difficult to quantify how this intervention enhances stocks. Aquaculture may seem a more feasible solution to stock enhancement than enhancing egg recovery in terms of being able to quantify outputs, but may be economically unjustifiable. And, if the intention of aquaculture is to use the animals for food, this method may not suffice as a true conservation intervention unless reared animals are returned to the sea as part of restocking, which was found to be uneconomical in the East China Sea. We acknowledge that an increase in aquaculture may relieve pressures on wild stocks, although capture will still exist within trawl fisheries.

It is unlikely a single management approach will be suitable for conserving most stocks of cuttlefish. But regardless of the approaches taken, there needs to be strong collaboration with all stakeholders, including fishers, researchers, managers, and the general public, to ensure adoption and compliance. Ultimately, even partially effective strategies used all the time will have greater long-term benefits to cuttlefish conservation efforts than even very effective strategies implemented without consensus and compliance.

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Author contributions

All authors provided evidence of cuttlefish conservation efforts from their respective countries. Barrett, C. J. initiated the paper and compiled and edited the evidence. Broadhurst, M. K., O'Brien, C.E., Pierce, G. J., and Hanlon, R. T. also completed thorough edits and quality checks to improve earlier versions of the manuscript.

Conflict of interest

The authors have no conflict of interest to declare.

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Data availability statement

No new data were generated or analysed in support of this research.

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