Climate change and polar range expansions: Could cuttlefish cross the Arctic?

José C. Xavier[1,2], Lloyd S. Peck[1], Peter Fretwell[1] & John Turner[1]

1- British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, CB3 0ET Cambridge, UK

2- Marine and Environmental Science Centre (MARE), Faculdade de Ciências e Tecnologia, Universidade de Coimbra, Departamento das Ciências da Vida, Coimbra, PT

Abstract

Climate change can have major effects on the distribution of species. In marine ecosystems, the cold waters of the Arctic have restricted warmer water species from crossing between Eurasia and North America. However, with Arctic waters becoming warmer, various marine species have expanded their distribution. Cuttlefish are fast growing, voracious predators and are absent in American waters. The European cuttlefish *Sepia officinalis* is the most northerly-distributed cuttlefish, with potential to expand its range and cross to the American continent, potentially causing changes in shelf food webs. Climate model predictions suggest that the *S. officinalis* could potentially reach American shores, by 2300 via the north Atlantic with medium mitigation of greenhouse gas concentrations; we predict that adult dispersal of cuttlefish across the Atlantic sector would require a migration distance of over 1400 km at depths below 200 m and temperatures above 7°C (temperature below which cuttlefish can not maintain routine metabolic processes physiologically). For temperatures above 9.5°C (temperature above which cuttlefish can grow), 2500 km would be required, and such conditions will possibly exist by the year 2300. If they reach American shores they could have large impacts on coastal marine ecosystems, due to their wide diet (e.g. diet covers many shallow water crustacean and fish species) and its potential as prey, and due to their short life history strategy of "live fast, die young".

KEYWORDS: Invasion, Polar, predator, cephalopod, distribution - Climate change - *Sepia officinalis*

INTRODUCTION

Global warming is producing significant changes in marine ecosystems. Emerging evidence suggests that marine organism distributions may respond more rapidly to climate change than those on land, despite slower oceanic warming (Richardson and Poloczanska 2008; Kortsch et al. 2015). Range shifts of hundreds of kilometres in a few decades have been observed in various organisms, such as phytoplankton, zooplankton and fish (Beaugrand et al. 2002). However, studies have rarely investigated fast growing, carnivorous species with the potential for also marked impacts on new habitats. The short generation times of coastal cuttlefish, squid and octopods might enable them to adjust faster to changing environmental conditions than those with slow growth and late maturity (Boyle and Rodhouse 2005; Xavier et al. 2015). Indeed, the short life span and generation time of shallow water cephalopods has been suggested to enable a proportion of each new generation to actively avoid or exploit localised warming events (Rodhouse 2013). Some studies already investigated range shifting in Octopods, such as *Octopus tetricus* (Ramos et al. 2014) at the southerly extension of the warm East Australian Current, showing that this octopod maintains a fast growth rate (under warming conditions), high rate of population turnover, small body size and a short life span at the leading edge of their range extension. In squid, such as *Dosidicus gigas* (Zeidberg and Robison 2007; Ruiz-Cooley et al. 2013), *Sepietta oweniana*, *Todarodes sagittatus*, *Todaropsis eblanae* and *Teuthowenia megalops* (Golikov et al. 2013; Golikov et al. 2014), range expansion has been attributed to changes in climate-linked oceanographic conditions (e.g. warming waters), a reduction in competing top predators and/or of a decline in abundance of a commercial groundfish species. However, unlike octopods and squid, cuttlefish *Sepia* spp. do not occur in the Americas or Polar regions (Boletzky 1983 ; Xavier et al. 1999; Xavier and Cherel 2009; Rodhouse et al. 2014). Nearly 115 sepiid species are described inhabiting shallow tropical/temperate waters of Afro-Eurasia, along the coasts of the East Atlantic, Indian and West Pacific (Reid et al. 2005).The question arises: as the Arctic warms when will environmental conditions allow cuttlefish to cross the Arctic and reach American coastal waters?

FACTORS AFFECTING CUTTLEFISH DISTRIBUTION

Here, we focus our discussion on the European cuttlefish, *S.officinalis*, and the potential range expansion of the species to America via Europe. The route via the Bering Sea (i.e. Asia - America route) is not discussed further in this study because there are no published studies on the temperature tolerance of *Sepia kobiensis* (the most northern cuttlefish species distributed in the north Pacific) (Reid et al. 2005) nor any other North Pacific, cold-adapted cuttlefish species to support such hypotheses. However, due to the shallow waters between Asia and the Americas, via the Bering Sea, the dominating W-E currents could aid such range expansion of cuttlefish.

The most northerly distributed cuttlefish worldwide is *Sepia officinalis* (Family Sepiidae, Order Sepiida, Class Cephalopoda) at around 62°N in European waters, a well known opportunistic and voracious marine predator that can reach large size (up to 4-kg), and feeds on a wide range of prey (Reid et al. 2005). Physiologically, S. *officinalis* cannot maintain routine metabolic processes at temperatures ≤7°C, grows positively from water temperatures above 9.5°C and spawning peaks at 13 - 15°C (Boletzky 1983 ; Pimentel et al. 2012). Temperature has large effects on development is this species. When eggs are exposed to warming conditions (13 to 19°C), oxygen consumption increases throughout embryogenesis. At 15°C, 41% of the egg yolk is used for growth, and only 10% is used for catabolic processes, whereas at higher temperatures (24°C) yolk utilisation for growth is only 15%, but 52% is for catabolism, resulting in small hatchling size (Bouchaud 1991). *S. officinalis* is thus well adapted to cool temperate conditions and it has been suggested that, with warming, *S. officinalis* may lay their eggs in warmer and deeper environments (Pimentel et al. 2012). *S. officinalis* is, however, limited to a depth of 150-200 m as the chambers in the cuttlebone, the calcified internal shell, can implode beyond these depths (Ward and Boletzky 1984). Other cuttlefish species at lower latitude and warmer sites, on the other hand, can be found up to 1000 m deep, and may be better adapted to pressure. *Sepia elegans*, for example is found up to 60°N in depths of 500 m, and *Sepia orbignyana* up to 54°N in depths of 570 m (Reid et al. 2005).

Cuttlefish today are absent from the Americas, but this is probably not due to lack of habitat (Young et al. 1998), as potential prey are abundant. In fact, *Sepia officinalis* has been cultured during multiple generations in American laboratories where they have been fed with live local crustaceans and fish (Forsythe et al. 2002). One reason for their absence, appears to be low temperature in the Arctic and the depth/distance barriers of the other ocean basins, combined with the time of formation of these barriers (Young et al. 1998). The shallow-water tropical bridge between Africa and South America was severed in the late Cretaceous, leaving the northern rim of the Atlantic Basin as the only possible migration route for shallow demersal organisms between Europe and the Americas after this time. During the early Cenozoic (Palaeocene and Eocene), a series of radiations began in the warm Tethys Sea that resulted in the broad colonization of the Belosaepiidae (a cephalopod family known from the Eocene, closely similar to cuttlefish) (Khromov 1998). Migration across the Atlantic was possible around the top of the basin, where temperatures were tolerable. After the Belosaepiidae became extinct in the Oligocene, cuttlefish species emerged in Europe (North East Atlantic), the only location of fossils currently known (Young et al. 1998). Their distribution was, however, restricted by the colder conditions during this period, preventing colonisation across the North Atlantic as utilised by the Belosaepiidae.

Cuttlefish are also absent from the Antarctic, which is likely due to cold conditions and the deep water barriers between Antarctica and the other land masses, that were completed with the formation of the Drake Passage around 30-50 million years (Ma) ago (Livermore et al. 2005). There are cephalopod fossils in the Antarctic, from belemnites and Mesozoic teuthids (Doyle 1991), but none from the family Sepiidae probably due to the absence of marine Tertiary sediments (Dirk Fuchs, Freie Universität Berlin, pers. comm.). The sepiids closest to the Antarctic are in Australian waters, at 42°S, but a lack suitable habitat further south (Reid et al. 2005).

The northern expansion of *S.officinalis* appears to be mainly limited by physiology, but life cycle constraints and habitat availability may also play a part. Eggs of this species, as for all sepiids, are large and attached to hard substrata in depths usually less than 50 m, producing benthic hatchlings with limited dispersal capacity. Lifespan is 18-24 months and dispersal is predominantly via sub-adult and adult migration (Reid et al. 2005). As cuttlefish spawning appears restricted to shallow depths, iceberg scouring might also limit their ability to colonise low temperature areas by restricting areas of suitable habitat to attach eggs to algae and hard substrata. If waters warmed, *S. officinalis* could potentially expand its northern range edge via two routes: either along the 200 m shelf towards the Arctic, and/or via the Faroe Islands – Iceland - Greenland to north Canada over deeper waters (Fig. 2), both aided by surface currents (Straneo and Heimbach 2013) that could transport adult cuttlefish (as they expand north) and/or, for example, rafting with marine (floating) debris (e.g. broken kelp, floating old fishing gear or plastic material initially at the bottom) (as cuttlefish eggs) (Boletzky 1983; Arkley et al. 1996; Blanc and Daguzan 1998; Sykes et al. 2014). Although cuttlefish are benthopelagic organisms, they are known to also swim into the water column (Okutani 1990), which could be transport them further north by currents. Furthermore, if these adults can reach Faroe Islands, Iceland, Greenland and North Canada, they would be able to reproduce and attach their eggs to available algae (e.g. sea grass or kelp) (Kjellman 1883; Mann 1973; Arkley et al. 1996; Short et al. 2007). This would permit a sequence of generations to allow the establishment of cuttlefish in these regions.

Depth may not be a total barrier for cuttlefish expansion, as between South Africa and Mauritius (Mascarene Ridge), the same cuttlefish species (*Sepia vermiculata*) occurs in both places, although separated by deep waters (Reid et al. 2005). If cuttlefish cross the Arctic, their life history characteristics would potentially allow them to adapt quickly and spread rapidly. A further consideration is that the aquarium industry might provide another colonisation or invasion route, as cuttlefish are readily available in the USA as pets. If released in the sea, under the right conditions, they could flourish, as has occurred for other invaders (Gido and Brown 1999).

PREDICTING THE NORTHERN RANGE EXPANSION OF *S. OFFICINALIS*

How much do Arctic waters need to warm for cuttlefish to cross the Arctic? As *S. officinalis* is the most abundant, largest and the most known northerly distributed cuttlefish, we use this species as the candidate for exploring the likelihood of range expansion. The total reported annual landings of cuttlefish in Europe range from 35 000 to 41 000 tons, showing that a considerable population exists in European waters (Pierce et al. 2010). Recent Arctic Ocean warming is thought to be closely connected with increased heat content of the Atlantic water masses with a 1.3°C increase in annual water temperatures from 1990 to 2005 (Walczowski and Piechura 2006).

An expected migration route for *S. officinalis* across the Arctic would be from northern Europe via Iceland to North America (Fig. 1). Based on the HadGEM2-ES model (Hadley Centre Global Environmental Model version 2 Earth System configuration) with medium mitigation of greenhouse gas concentrations (following the "Representative Concentration Pathway" RCP4.5) (Caesar et al. 2013), we predict that adult dispersal of cuttlefish across the Atlantic sector would require a migration of over 1400 km at depths deeper than 200 m and temperatures above 7°C. For temperatures above 9.5°C, 2500 km would be required, and such conditions will possibly exist by the year 2300 (See supplementary material).

Increasing temperatures may facilitate a range expansion of cuttlefish to the Arctic, but climate change may also bring environmental challenges such as ocean acidification. Polar marine calcifying organisms may be amongst the first affected by ocean acidification-driven changes in marine carbonate chemistry (Orr et al. 2005). In cuttlefish laboratory experiments with *S. officinalis* reported higher cuttlebone calcification associated with decreasing pH (Dorey et al. 2013). This hyper-calcification would likely change the cuttlebone buoyancy, and possibly change the implosion resistance of this structure. However, the behavioural or ecological significance of these changes are still unknown. When compared with other organisms, Perry et al. (2005) showed that the distributions of both exploited and non-exploited fish species have responded markedly to recent increases in sea temperature, with nearly two-thirds of species shifting in mean latitude or depth over 25 years. Furthermore, most of the fish species that shifted their distributions had faster life cycles (but still slower than cuttlefish) and smaller body sizes. Temperature rises are likely to have profound impacts on community interactions through continued shifts in distribution of marine organisms (Perry et al. 2005), particularly those that are fast growing, with short life cycles and a broad range of prey.

In summary, the cuttlefish *Sepia officinalis* is one of the marine organisms that, under a favourable climatic scenario and conditions (e.g. by currents, cross over deep regions), may be able to cross the Arctic region and occupy a niche in the marine ecosystems of the American continent. Due to its fast growth and metabolism, typical of cephalopods, cuttlefish may be able to occupy an ecological niche rapidly.

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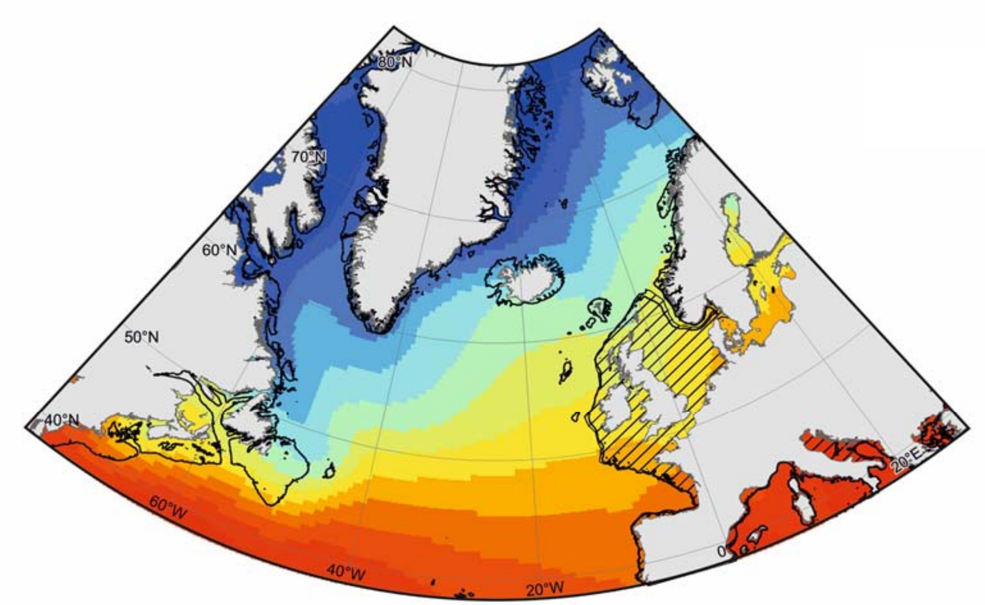
SUPPLEMENTARY MATERIAL. Distances across the Arctic from Europe to North America (upper) following the mean summer sea surface temperature contours of 7 °C (limit for *S. officinalis* adult survival) and 9.5°C (limit for *S. officinalis* reproduction) as predicted by runs of the HadGEM2-ES model using a medium mitigation run RCP4.5 (See methods in Caesar *et al*. 2013).

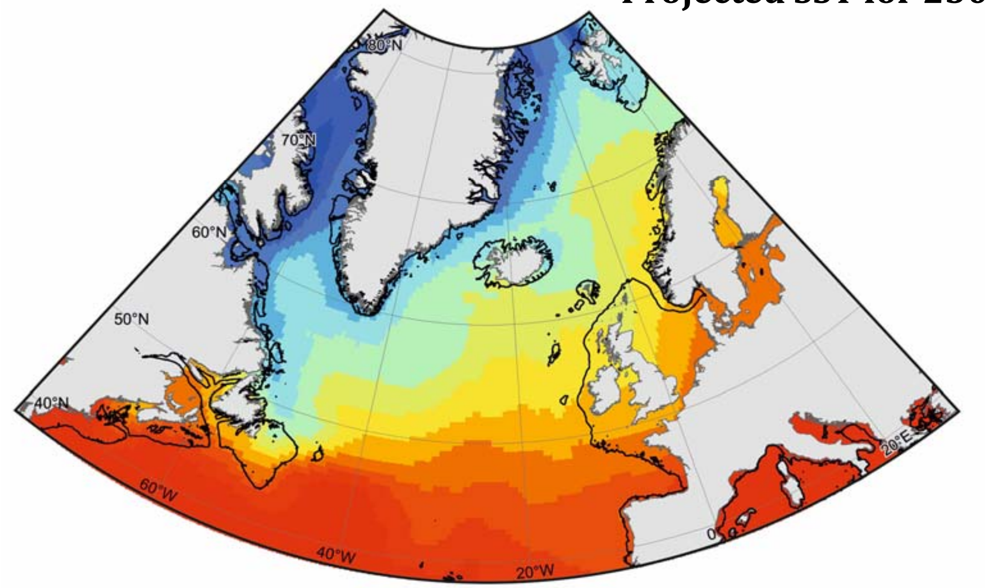
Europe to North America
(via Iceland)

	7 °C	7 °C	9.5 °C	9.5 °C
Year	Distance (km) coast to coast	Distance (km) to reach the 200 metre contour depth in North America East coast	Distance (km) coast to coast	Distance (km) to reach the 200 metre contour depth in North America East coast
2012	2960	2530	3042	2530
2020	2960	2530	3023	2530
2030	2953	2530	2953	2530
2040	2953	2530	2953	2530
2050	2953	2530	2953	2530
2060	2953	2530	2953	2530
2070	2953	2439	2953	2530
2080	2953	2439	2953	2530
2090	2930	2388	2953	2530
2100	2930	2064	2953	2530
2110	2930	2062	2953	2530
2120	2930	2008	2953	2530
2130	2930	2008	2953	2530
2140	2930	2008	2953	2530
2150	2930	2008	2953	2530
2160	2930	2008	2953	2530
2170	2930	2008	2953	2530
2180	2930	2008	2953	2530
2190	2930	2008	2953	2530
2200	2930	2008	2953	2530
2210	2930	1932	2953	2530
2220	2930	1781	2953	2530
2230	2930	1718	2953	2530
2240	2930	1487	2953	2530
2250	2930	1487	2953	2530
2260	2930	1469	2953	2530
2270	2930	1430	2953	2530
2280	2930	1430	2953	2530
2290	2930	1430	2953	2530
2300	2930	1430	2953	2530

Present day SST



Projected SST for 2300



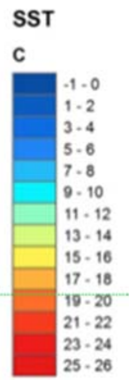


Figure 1. Mean summer sea surface temperatures (SST in °C) for the present day and projected for 2300, for the North Atlantic (The "present SST" also includes the present distribution of *Sepia officinalis*; Eastern Atlantic, from the Shetland Islands and southern Norway south through the Mediterranean Sea to northwestern Africa up to Senegal (Reid et al. 2005)). Projections are based from runs of the HadGEM2-ES medium mitigation run (see text) and are for mean summer temperature covering a 3 month period. The 200 m depth contours is also shown in all panels.

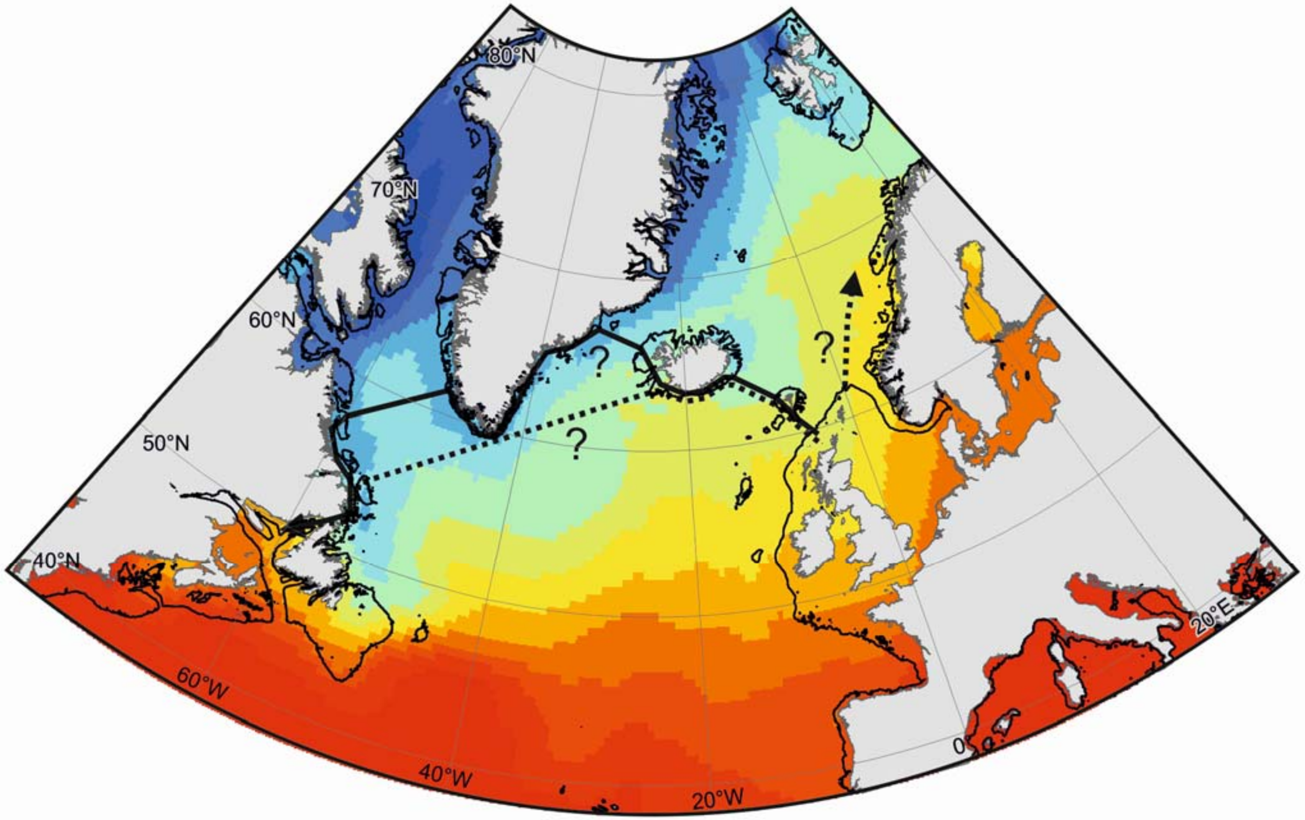


Figure 2. Predicted best migration routes of *Sepia officinalis* for the North Atlantic projected for 2300, under a mean summer sea surface temperatures (SST in °C) obtained from HadGEM2-ES medium mitigation run: solid arrows for optional route with water temperatures above 7°C and dash lines for the route above 9°C. The 200 m contour is also shown. See figure 1 for water temperatures for the corresponding colours.