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# The climate-induced changes in the life history of the common cuttlefish in the English Channel.

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# The climate-induced changes in the life history of the common cuttlefish in the English Channel

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KEYWORDS: Cuttlefish, *Sepia officinalis*, spawning, English Channel, climate change, stock structure

# Abstract

The population of common cuttlefish *Sepia officinalis* in the English Channel recently developed two life cycles: annual (spawning 1 y.o.) and biennial (spawning 2 y.o.) instead of the biennial strategy known before, associated with increasing environmental temperatures in recent decades because of climate changes. Both groups differ in size of mature animals (110–196 mm mantle length vs. 140 to 262 mm) and the numbers of chambers in the cuttlebone (60–97 in annual vs 93–152 in biennial). The annual group was observed in some 15–20% of the population, and the proportion of early spawners increased during the reproductive period, from 3–5% in February/March to 50–70% in June/July. Among spawning cuttlefish males predominated as ~2:1. Such environmentally driven changes in historical ecology as exemplified by the cuttlefish might be a critical link in adaptation of the cephalopod life cycles to changing ecosystems.

**Key words**: cuttlefish, *Sepia officinalis*, evolution of life histories, population structure, climate change, historical ecology

# 1 | INTRODUCTION

The common cuttlefish *Sepia officinalis* L. (hereafter cuttlefish) is distributed in the northeast Atlantic from the African coast to the North Sea. The northernmost large population of this species inhabits waters around the United Kingdom (UK), including the English Channel and North Sea (48–52°N), but occasionally, when forming foraging migrations, the population moves as far north as the Faroe Bank and south of the Shetland Islands (60°N; Jereb et al. 2015). Cuttlefish in the English Channel are genetically distinct from the population inhabiting the adjacent waters of the Bay of Biscay (Wolfram et al. 2016), thus constituting a discrete stock unit (Bloor et al. 2013, Gras et al. 2016).

Cuttlefish in the English Channel forms the most commercially-important cuttlefish stock in the Atlantic and possibly the World. Landings from 1992 to 2021 fluctuated between 4 and 18 thousand metric tonnes (t) representing 41–78% (mean 58%) of the total catch of all cuttlefish and sepiolid species across the NE Atlantic, with most of catches taken by the UK and France (ICES, 2023). Trawlers catch cuttlefish mostly from autumn to mid-spring, harvesting both mature and immature animals, whereas potters target spawners that move inshore between March and July to reproduce. Cuttlefish is a valuable commercial species, with discards of this non-quota species in the English Channel equating to only 0.16% by weight in 2022 (data of ICES WGCEPH) so total catches by commercial vessels are not very different from reported landings.

Cuttlefish lay eggs in an average of 10 m water depth (Guerra et al., 2015, 2016). In southern Brittany and the western English Channel, breeding occurs annually between mid-March and June, with the hatching period from June to September. Further east, the spawning period gradually shifts to later dates with reproduction in the southern North Sea and off the Netherlands occurring between late April / May and mid-September (Laptikhovsky et al., 2023). In the western part of this range, where cuttlefish are born relatively earlier, some of the juveniles begin their sexual development as early as November (males) and the end of December (females) and require only one year to complete their life cycle. Such cohorts reproducing at the age of around 1 y.o. and are called the Group I Breeders (GIB). The rest of the population, comprising Group II Breeders (GIIB) attain maturity and reproduce in the end of the second year of their life (Gauvrit et al., 1998).

In the relatively cold English Channel, catches of GIB had been scarce (4% of males and no females – Dunn, 1999) in 1994-1995 though some 3–17% of females and 13–30% of males caught were assigned to GIB during 2010–2011 (Gras et al., 2016). The annual spawners are much smaller and also have a lower fecundity and smaller eggs (Laptikhovsky et al., 2019), and presumably a lower fitness of hatchlings.

In comparison, GIB represented 40–50% of males and 12–27% of females in the 1980s and 1990s in the Bay of Biscay (Le Goff & Daguzan, 1991; Gauvrit et al., 1997; Gauvrit et al., 1998). The emergence of a GIB cohort in the English Channel poses the question about possible ongoing shifts in population structure in the English Channel due to warming waters, likely affecting cuttlefish ecology and distribution (Oesterwind et al., 2022).

Despite annual spawners (GIB) being smaller than the GIIB component, differences may be observed by an overlap in body sizes (Le Goff et al., 1998), due to the high flexibility of cephalopod growth rates. However, there is a precise tool to distinguish between two generations within the same spawning stock – cuttlebones. The cuttlebones contain numerous chambers of phragmocone separated by septae that help maintain neutral buoyancy, and those are deposited at rather regular rates depending on the environmental temperatures. These intervals vary widely, from 1.6 days per chamber at 25°C to 8 days per chamber at 13°C (Le Goff et al., 1998). Therefore, the number of chambers in 1 y.o. cuttlefish would be much lower than in 2 y.o. animal among spawners from a population living in the same seasonal environment. An additional indicator might be the band of narrow chambers seen as an inflexion point (Fig. 1) visible on the siphuncular surface (so called “Z1 streak”) that in cuttlefish of the Bay of Biscay is situated approximately between the 45th and the 60th chamber and is indicative of GIIB (Le Goff et al., 1998).

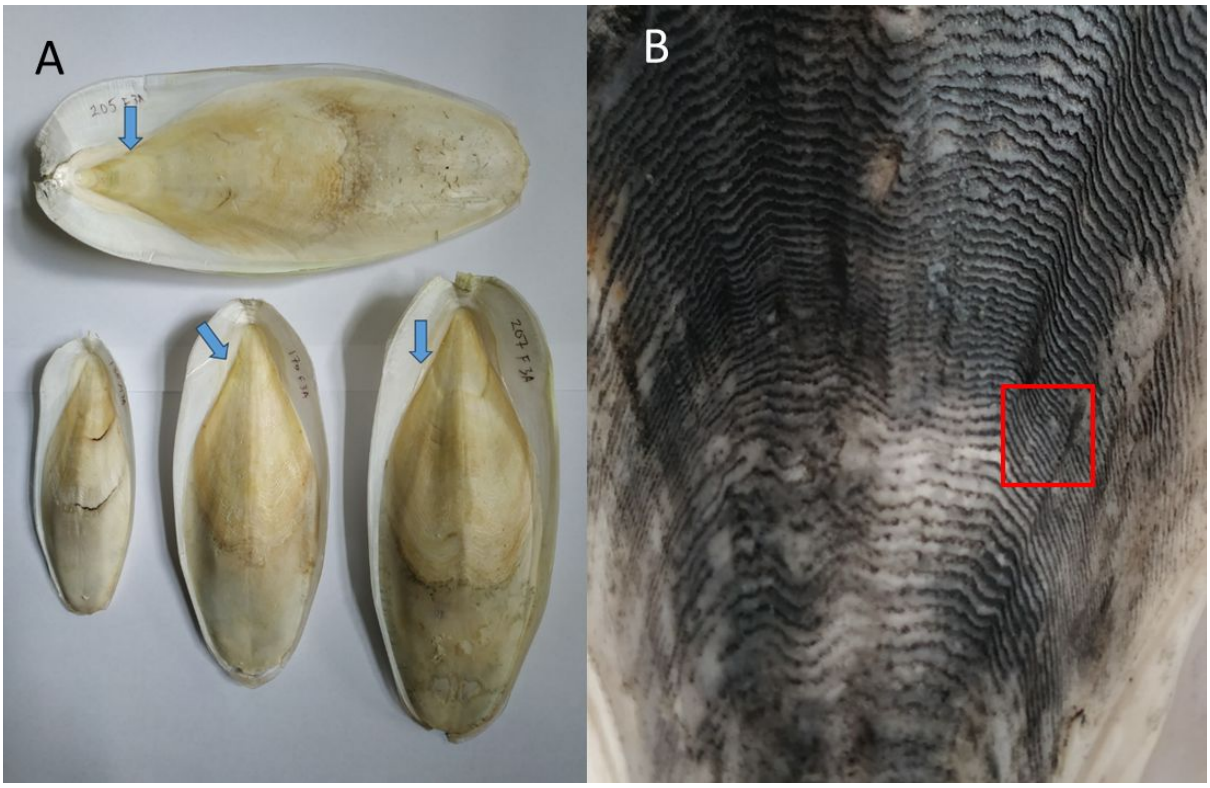



**Fig. 1 A-** Cuttlebones of the annual spawner (left, lower row) and biennial (three others). The Z1 band of very narrow growth increments formed during the second winter marked by blue arrow. B - Part of Z1 band in red rectangle. The cuttlebone is soot-stained for better visibility.

This study aimed to a) investigate possible separation between GIB and GIIB cuttlefish in the English Channel under the influence of ongoing water warming due to climate change (L’Hévéder et al., 2017) and b) to estimate relative input of early spawners into the entire breeding stock in recent years.

# 2 | MATERIALS AND METHODS

The material consisted of several different data sets that were collected in 2019–2022 (**Fig. 2**). They encompassed 2,846 cuttlefish specimens (of which 1,287 were mature) and included:

1. A total of 1,664 cuttlefish were sampled onboard RV “Cefas Endeavour” in February – September 2019–2021 during research surveys in the English Channel. Cuttlefish were measured (mantle length, ML) to the nearest 5 mm and maturity assessed against the ICES

maturity scale (ICES 2010). A total of 105 of them (54 females and 51 males) were found to be late maturing or mature (stages 2b and 3a) and were used for this study. Most of these adult cuttlefish (103 of 105) were caught by either otter trawl (100 mm codend) in the western English Channel (February; n = 39) or beam trawl (40 mm codend) in the eastern English Channel (July; n = 64).

2. A total of 613 mature animals (262 males and 351 females) out of the total sample of 849 collected from unsorted commercial catches from trawlers (N = 348) and potters (n = 265) that had been landed in Brixham (February and May 2019, January 2020, March and June 2020, April and May, 2021) or Portsmouth (June 2022). Cuttlefish were measured to within one mm and maturity was assessed using the ICES maturity scale.

3. A total of 569 cuttlefish sampled from unsorted landings of potters in Brixham (March–May 2019) and Plymouth (April–May 2019) were assumed to be mature because only mature cuttlefish were found in catches from potters during our study. Therefore, they were incorporated into length-frequencies of the spawning part of the population.

A total of 536 cuttlebones (290 trawl-caught and 246 pot-caught) were extracted from cuttlefish sampled in the laboratory and used for relative ageing (see below). The relative age was calculated by counting the number of chambers of phragmocone under 10x magnification either under binocular microscope or with headband magnifying glass with light emitting diode (LED) light. The GIIB spawners were identified by a narrow band of thin growth lines formed during the second winter, this band is supposed to be absent in GIB spawners, as in the Bay of Biscay (Le Goff et al., 1998).

Number of chambers in aach cuttlebone was counted at least twice. If the difference between two counts was >5%, it was counted by the 3rd reader, and occasionally by a 4th person until the agreement (difference within a 5% range) was achieved. The mean value of agreed reads was taken for analysis. If the embryonal shell was not clearly readable, it was assumed that it contained 8 chambers (Le Pabic et al., 2016).

Sea surface temperature (SST) information spanning the time-period were downloaded from the E.U. Copernicus Marine Service Information (https://doi.org/10.48670/moi-00169) into R (de Vries, 2023; R Core Team, 2023). These data were filtered to the summer months of interest, then the mean sea surface temperatures for each month during historical (1985–1991; period of sample collection in the Gulf of Biscay that were used in studies cited in this paper) and recent (2019–2022; current sample collection) time periods were computed. The difference in SST between the two time periods was calculated (Hijmans, 2023). This information was plotted to illustrate the changes in SST that have occurred over time (Campitelli, 2023; Massicotte, 2023; Wickham, 2016).

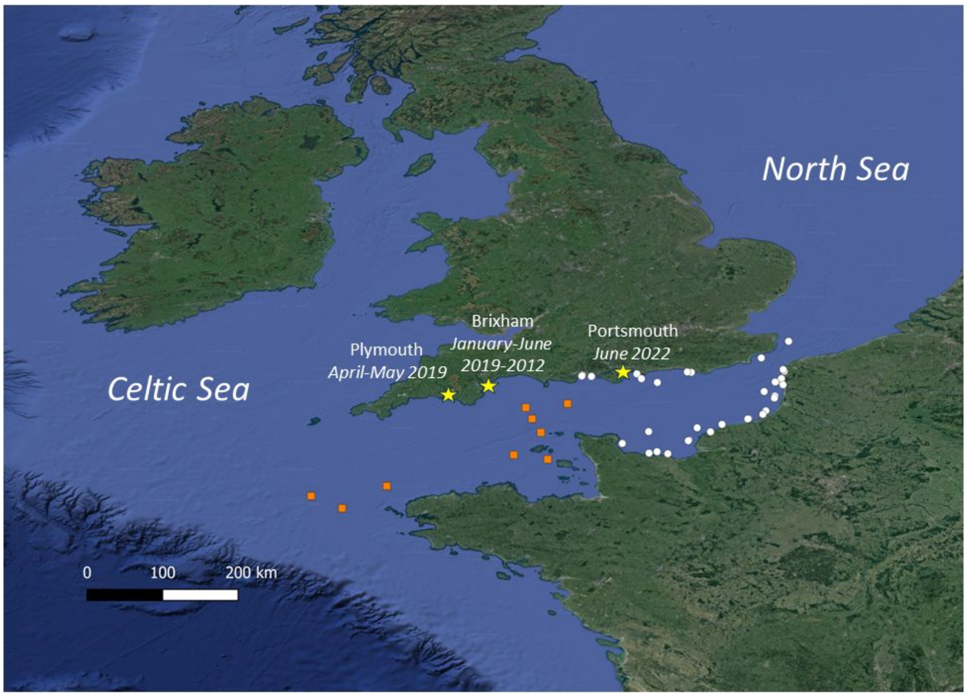



**Fig. 2** Position of sampling sites in the English Channel (squares: February samples by otter trawl; circles: July samples by beam trawl; stars: fishing ports).

# 3 | RESULTS

## 3.1 | Identity of annual and biennial spawners

Cuttlefish that had a second winter band of narrow chambers ("Z1 streak") were assumed to belong to GIIB. The mature female mantle length (ML) in this cohort varied from 140 to 262 mm (n = 195, mean = 196.5, CI = 3.82), mature male ML was 130–328 mm (n = 224, mean = 218, CI = 5.99). Mature cuttlefish that lacked this band, and therefore assumed to be GIB, were much smaller: the female ML was 110–163 mm (n = 12, mean = 133, CI = 8.48), the male ML was 90–196 mm (n = 31, mean = 137, CI = 6.84). Smaller mature males of 90–100 mm ML and females of 110 mm ML were recorded in research catches (Fig. 4), but their cuttlebones were not available for detailed analysis.

Nearly all cuttlefish larger than 170 mm ML belonged to GIIB, whereas all mature cuttlefish smaller than 130 mm ML belonged to GIB (Fig. 3). Length of animals among both spawning groups increased between January and May (Fig. 4) with a sudden drop in June.

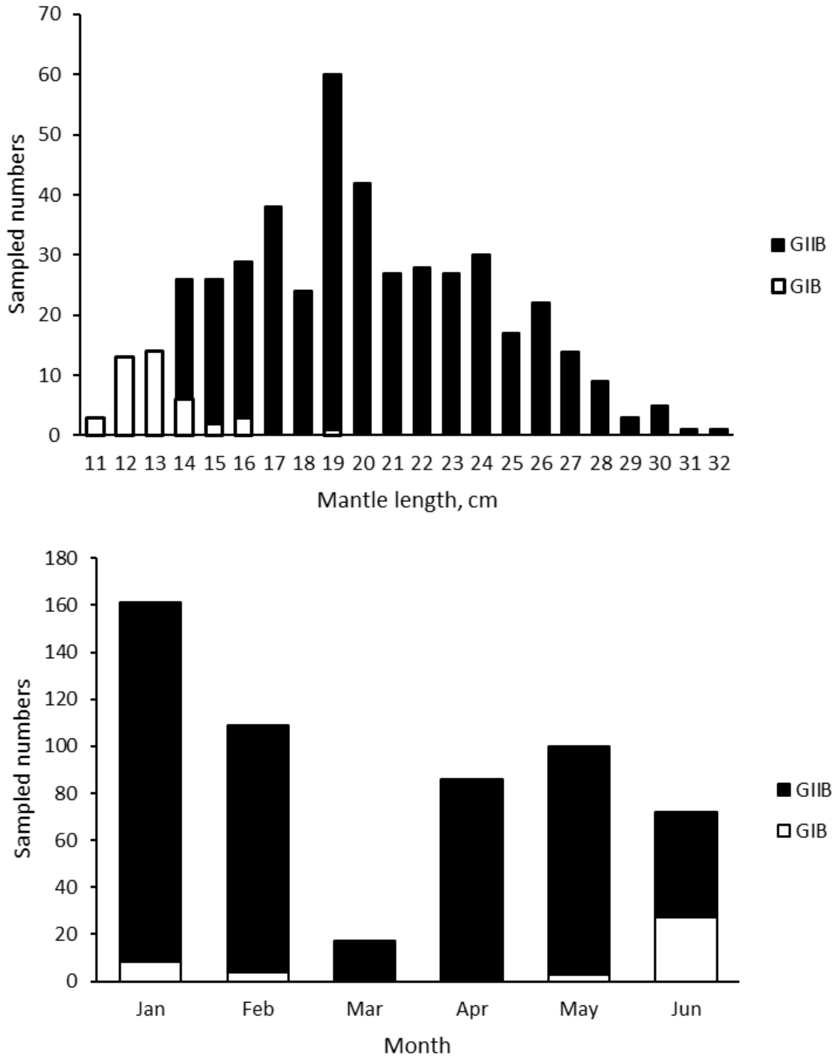



**Fig. 3** Proportion of GIB and GIIB among sampled cuttlefish of different sizes (**A**) and in the different months (**B**), all data sources combined.

Cuttlebones of GIIB had much larger counts of chambers (93–152 chambers, mean = 113.7, CI = 10.7) than those that did not possess this band that were considered to be GIB (60–97 chambers, mean = 75.0, CI = 8.4, the Wilcoxon rank sum test with continuity correction (W=19, p-value < 2.2e-16).

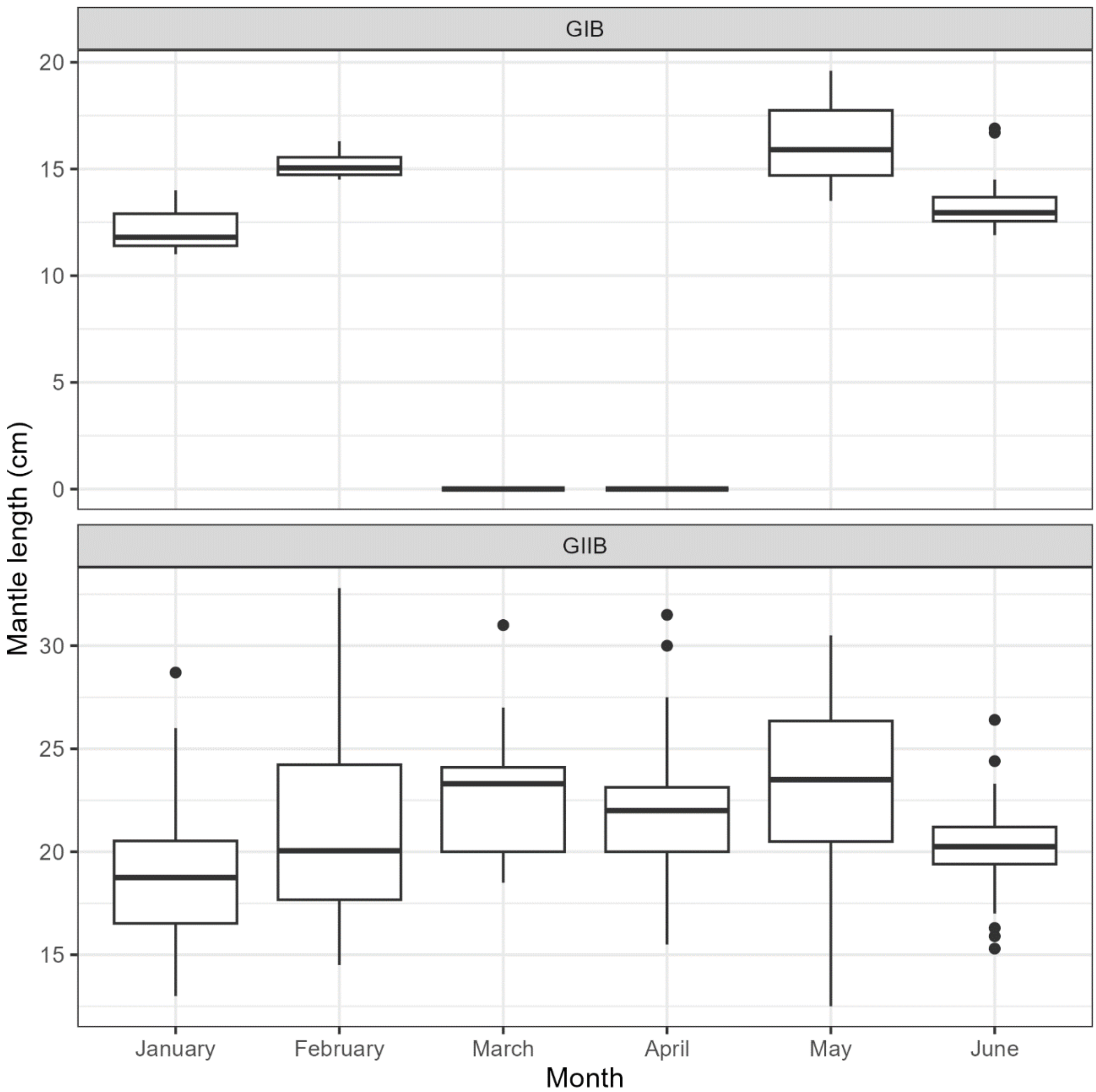



**Fig. 4** Monthly changes in length in two spawning groups. **A** with lower ML (<20 cm) is assumed to be GIB. **B** with higher ML (12–33 cm) is assumed to be GIIB.

## 3.2 | Seasonal changes in mantle length and proportion of the spawning cohorts

Mantle length data from the two survey datasets in which cuttlefish maturity was sampled and mature animals were found in high numbers did show very different distributions (Fig. 5). Judging by the mantle length, mature animals were represented mostly by GIIB in February in the Western English Channel, whereas the majority of adult cuttlefish (>60%) sampled in the Eastern Channel in July were GIB.

Length-frequencies of commercial trawl landings (January to April; Fig. 6) allows assuming that GIB represented only ~ 3% of mature cuttlefish, with only three mature GIB animals found in offshore catches; in June, two were GIB.

Judging from presence of some mature animals of 9–14 cm in landings from potting, the GIB cohort likely appeared first in March. The presence of two modal body sizes was obvious in April, though the proportion of GIB was difficult to estimate. In May, judging from length-frequencies (Fig. 5, 6), the proportion of GIB is estimated as 20%, in June ~45–50% and >50% in July. When only cuttlefish that were processed in the lab were taken into account, the proportion of GIB increased in females from 3.6% in January/February to 11.1% in May/June, and in males from 5.6% to 26.0%. When the percentage of each cohort per size class, as established from cuttlebone readings (Fig. 3), was applied to the entire sample of mature cuttlefish from combined onboard research surveys and landing data, GIB represented 8.1% of the spawning stock.

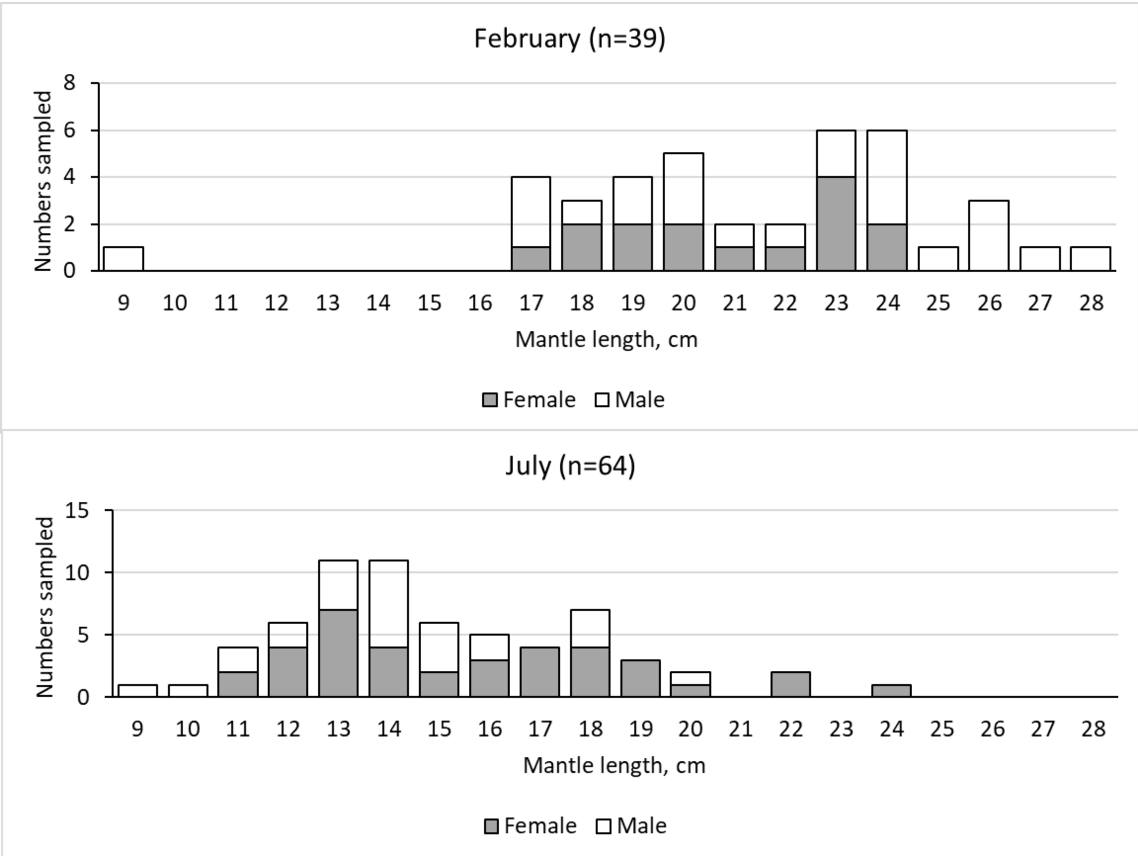



**Fig. 5** Length-frequency distribution of mature cuttlefish in catches of research surveys

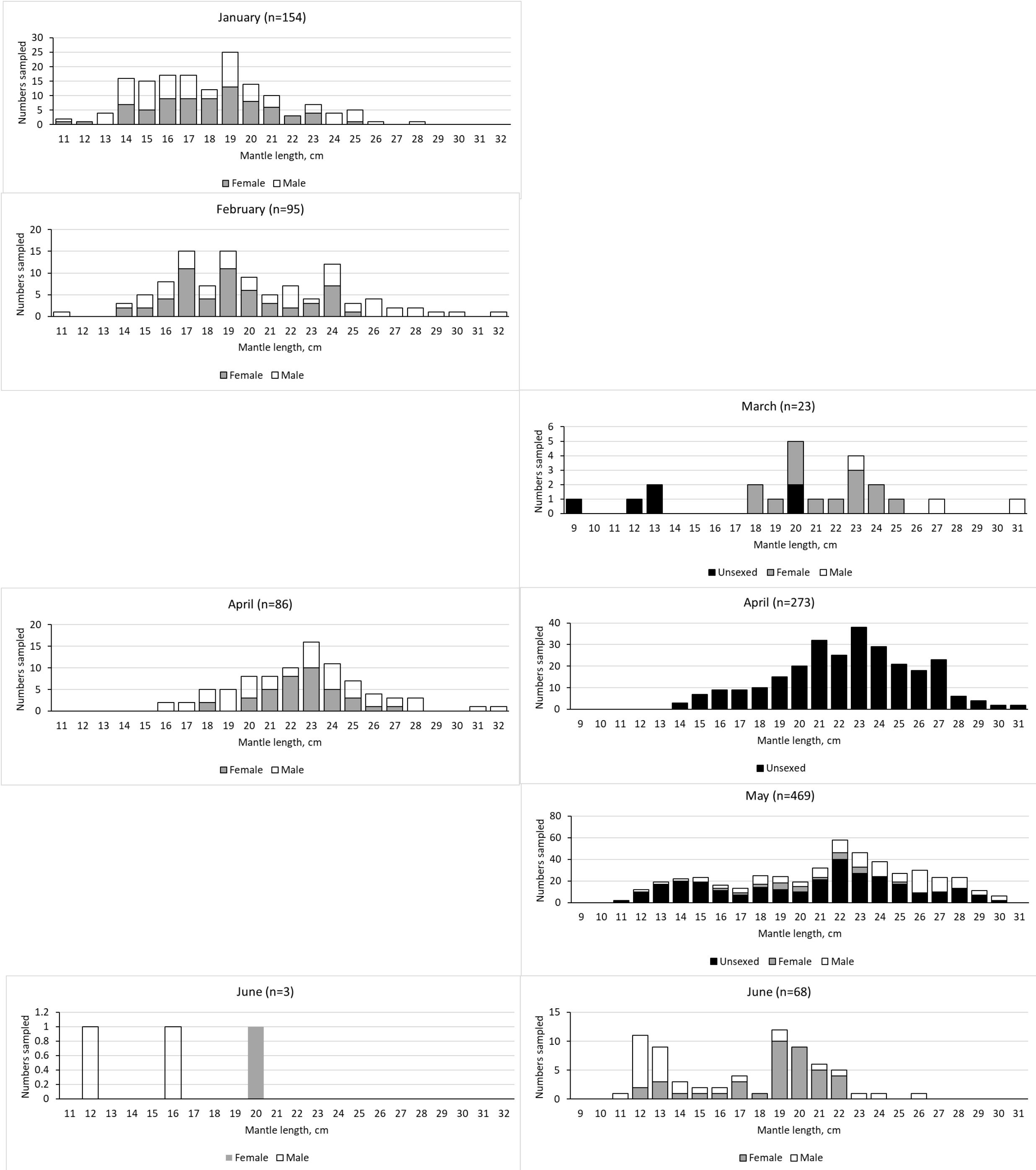
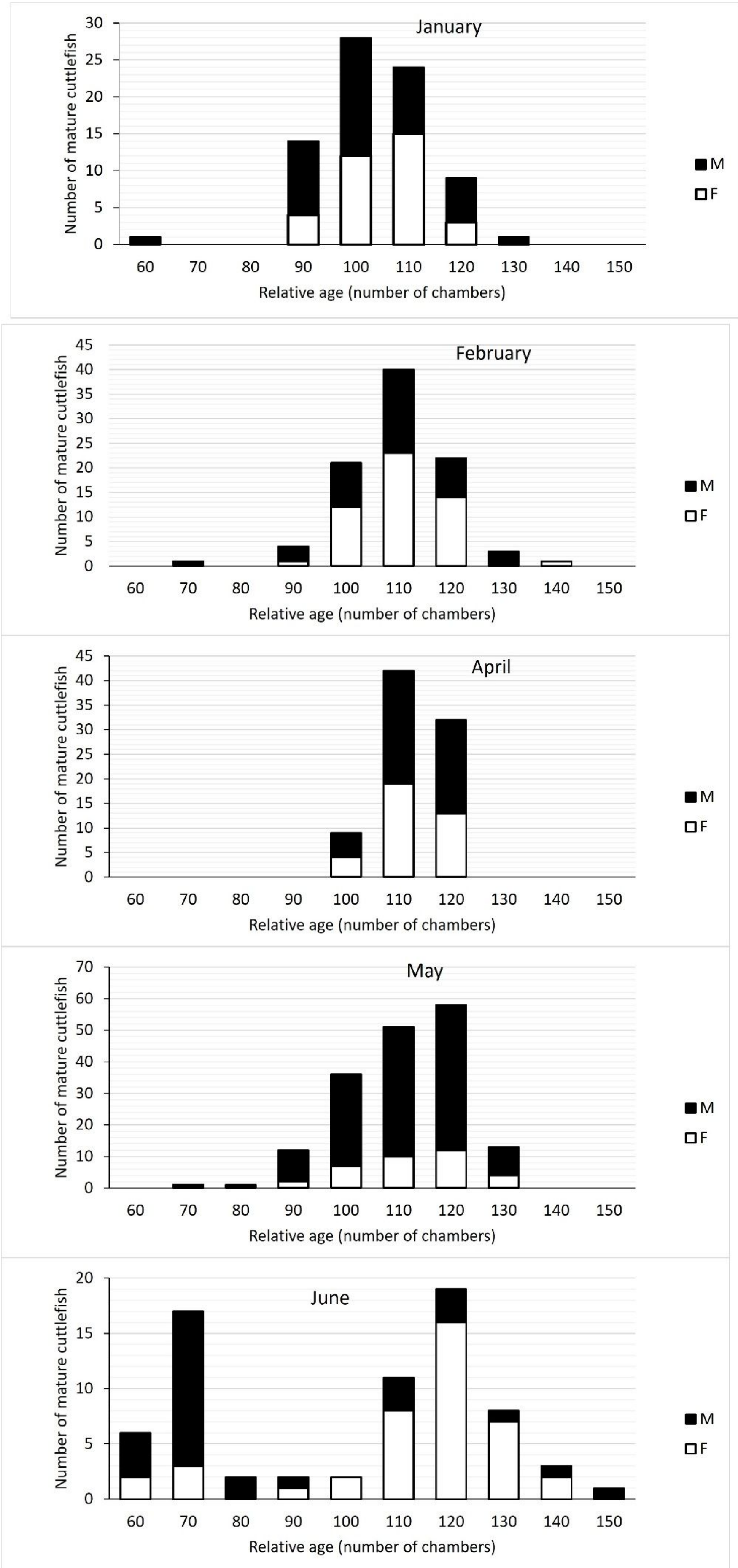



**Fig. 6** Length-frequencies of mature cuttlefish in landings of trawlers (left) and potters (right) over different months. Empty cells indicate absence of data.

## 3.3 | Seasonal changes in relative age

Chamber counts of GIB cuttlebones ranged from 60–90 chambers throughout the entire spawning season. Modal number of chambers in GIIB increased from 100 in January to 110 in February, 110–120 in April – May and 120 in June (Fig. 7).


January
February
April
May
June
Number of mature cuttlefish
Relative age (number of chambers)
M
F

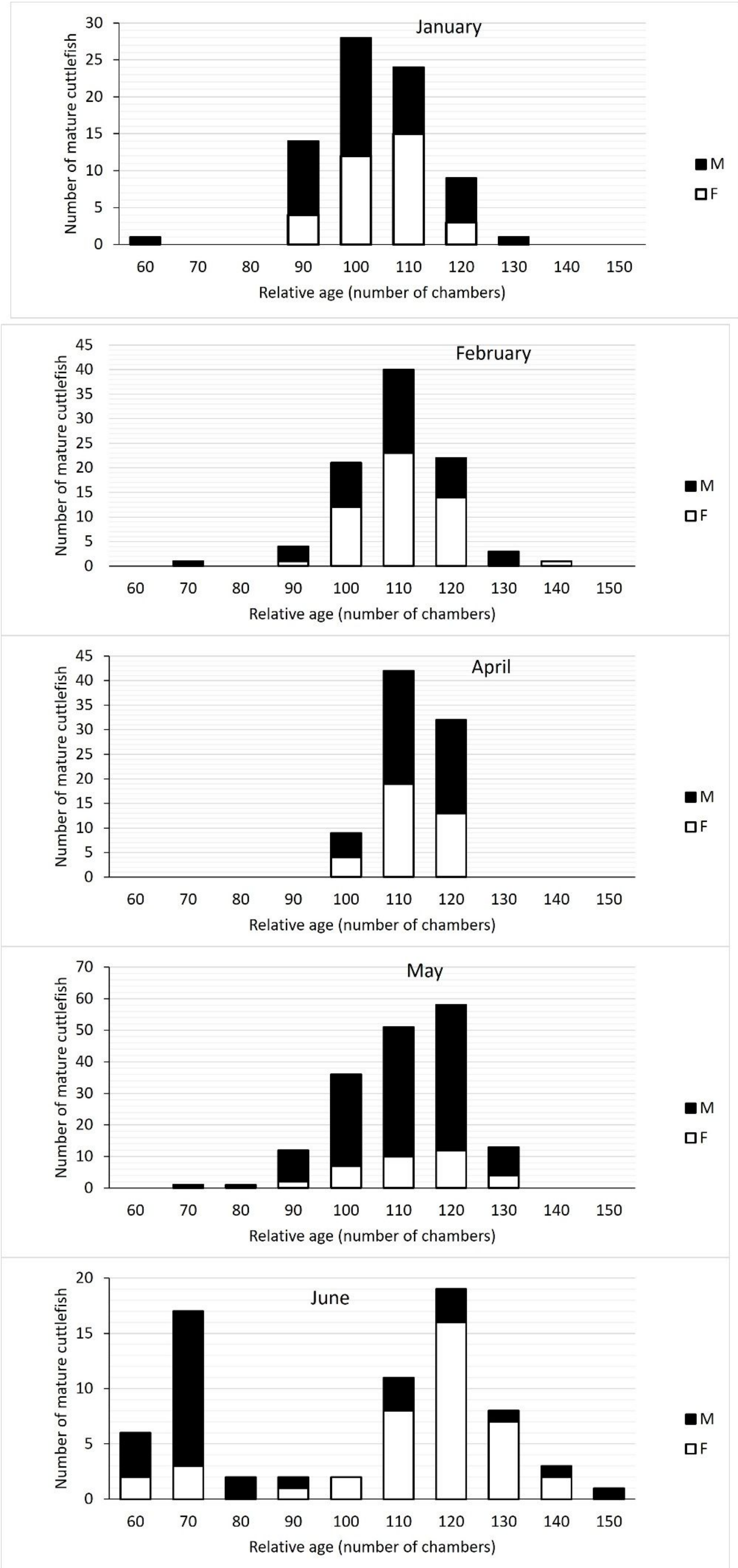

January
Number of mature cuttlefish
0
5
10
15
20
25
30
60 70 80 90 100 110 120 130 140 150
Relative age (number of chambers)
M
F
February
Number of mature cuttlefish
0
5
10
15
20
25
30
35
40
45
60 70 80 90 100 110 120 130 140 150
Relative age (number of chambers)
M
F
April
Number of mature cuttlefish
0
5
10
15
20
25
30
35
40
45
60 70 80 90 100 110 120 130 140 150
Relative age (number of chambers)
M
F
May
Number of mature cuttlefish
0
10
20
30
40
50
60
70
60 70 80 90 100 110 120 130 140 150
Relative age (number of chambers)
M
F
June
Number of mature cuttlefish
0
5
10
15
20
60 70 80 90 100 110 120 130 140 150
Relative age (number of chambers)
M
F

**Fig. 7** Seasonal changes in number of chambers in cuttlebones (all data sources combined)

### 3.4 | Sex ratio of spawners in potting trap catches

Males and females were captured in comparable numbers with overall male predominance over females (2:1) in the total sample. In May, when spawning is most intensive (Laptikhovsky et al., 2023), the sex ratio (male: female) was 4.28:1 (n = 190), whereas in June, by the end of the spawning season, females predominated, and the sex ratio fell to 0.41:1 (n = 69). Samples from April were not sexed, and only 17 pot-caught cuttlefish were examined in March (14 females and 3 males) that is not sufficient to contribute to sex ratio analysis.

### 3.5 | Temporal changes in water temperature in the English Channel

The study area and adjacent waters were gradually warmed between the periods of 1985–1991 and recent years, particularly during summer (Fig. 8) – a crucial period for cuttlefish growth. If the summer is hot enough, some animals would grow faster than usual and mature in August becoming annual spawners GIB (Dunn, 1999). Only a patch of shelf waters off westernmost Brittany became colder. Particularly intensive warming occurred in the English Channel and south of Brittany. The temperature background of inshore waters of the western English Channel in recent years was similar to that observed in the northern part of Bay of Biscay in 1985–1991 with temperatures mostly around 18-20°C.

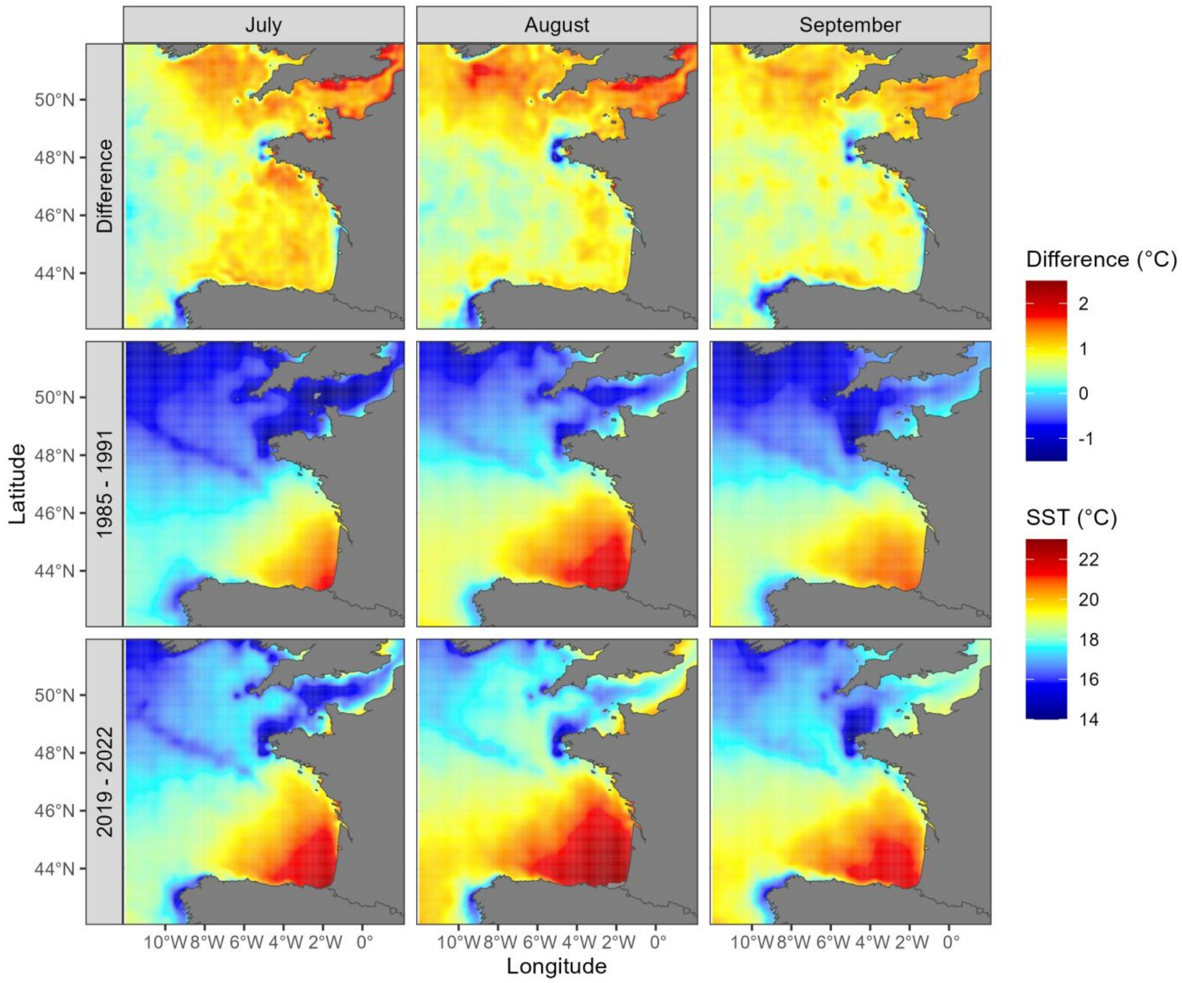



**Fig. 8 Comparison of mean summer water surface temperature between historical and recent time periods.**

# 4 | DISCUSSION

## 4.1 | Size of annual and biennial spawners

The size ranges of annual spawners (GIB) in the English Channel collected in this study (90–196 mm ML in males and 110–163 mm ML in females) were similar to that observed in the Bay of Biscay more than 30 years ago: 80–190 mm in males and 110–190 mm in females, with most of the cuttlefish caught in the April – June period (both sexes combined) being 110–130 mm ML (Le Goff, Daguzan, 1991). Meanwhile, our observations in 2019–2022 showed a larger size range of GIB than previous estimations for the English Channel (2010–2012) when the minimum size of mature annual spawners was found to vary from 70–80 to 100–110 mm depending on the sex and the year, the maximum size being 130 – 160 mm (Gras et al., 2016). A plausible explanation would be that annual spawners have begun to grow faster in the recent decade achieving similar growth rates as were recorded in the Bay of Biscay, where the environmental setting is different.

The size range of adult biennial cuttlefish (GIIB) was similar between our study (130–328 mm ML in males and 140–262 mm in females) and the southern Bay of Biscay population some 30–35 years ago, where the size range of these “normal” spawners was estimated as varying from 120–130 mm to 300–350 mm in males and from 150 to 270–290 mm in females (Le Goff, Daguzan, 1991).

The observed decrease in ML of both cohorts at the end of the spawning season might possibly be explained by engagement in reproduction of the smallest and slowest growing individuals that have just attained maturity by the end of the spawning season or earlier mortality of elder and larger spawners of the same cohort.

## 4.2 | Seasonal increase in numbers of chambers

Monthly changes in the number of chambers in cuttlebones included in this study coincided with those found in the Bay of Biscay in late 1980s: cuttlebones of GIB having around 60–90 chambers throughout the entire spawning season, and modal number of chambers in GIIB increasing from ~100 in January to ~115 in February, and to 115–120 in March–June (see Fig. 3 in Goff et al., 1998). Unfortunately, robust statistical analysis is not possible at present because primary data from earlier studies are not available to validate these assumptions. As the rates of chamber deposition are heavily dependent on environmental temperature, this coincidence is probably a consequence of a similar temperature regime controlling respective growth rates in both areas, during respective periods. This is consistent with changes in mean summer temperatures as shown in this study (Fig. 8) and is in line with known progressive warming of the waters of the western English Channel since the 1980 (L'Hévéder et al., 2017).

## 4.3 | Importance of annual spawners in the spawning stock and their dynamics

Data presented in this study suggests that the observed early precocious maturation occurs more often in males than in females, which is consistent with earlier studies (Dunn, 1999, Gauvrit et al., 1997; Gras et al., 2016). Particularly in the Bay of Biscay, the occurrence of annual spawning has always been higher in males (26–40%) than in females (7–16%) (Goff, Daguzan, 1991). These values are much higher than the most recent estimations for the English Channel population - some 3–17% of females and 13–30% of males (Gras et al., 2016). Our estimates of the GIB percentage in the total random sample of spawning cuttlefish was ~8% in 2019–2022 but might not be representative for the entire population due to the uneven sampling rate throughout the year. Each female cuttlefish in this population lays her eggs during relatively short time, less than one month, and then dies (Laptikhovsky et al., 2019). Therefore, as the percentage of GIB strongly increases during the reproductive period, this increase should be accounted for together with seasonal changes in the numbers of spawners. Assuming that all landings of trap fishers are represented only by mature cuttlefish (Table 1) the relative abundance of annual spawners in the English Channel population probably might be roughly estimated as around 15–20%.

**Table 1.** The assumed percentage of GIB among spawners from the sampling data and the percentage of the total catch of cuttlefish by pot fishing in the UK in the period 2019–22

| Month | Seasonal percentage of the total UK catch (pots only) in 2019– | Assumed percentage of GIB among mature cuttlefish |
|---|---|---|

| | 2022 (Data ICES WGCEPH) | |
|---|---|---|
| Feb | 0.1 | ~3 |
| Mar | 0.1 | ~5 |
| Apr | 43.8 | ~10 |
| May | 48.8 | ~20 |
| Jun | 6.9 | ~50 |
| Jul | 0.1 | ~70 |

Higher percentage of GIB among males than among females is presumably because cephalopod males, in general, begin to mature earlier than females (reviewed by Jereb et al., 2015). Therefore, under higher environmental temperatures, driven by climate change, a short time window for precocious maturation among the English Channel population might be exploited more by males than by females. Maturation of males at the earlier age also stimulates the development of alternative reproductive strategies, well-known among squids and cuttlefish which includes behaviours such as harem guarding by large males and sneaking in by small males (Hanlon, Messenger, 1996). Involvement of GIB males, and to a lesser extent GIB females, into cross-breeding with the GIIB bulk of the population (Gauvrit et al., 1998) also supports an exchange of genes between generations and provides some additional resilience in the event that environmental conditions cause one annual reproductive event to fail.

The observed increase of relative abundance of GIB during the spawning season is in agreement with unpublished observations from studies in the Bay of Biscay, where large specimens of 2-years-old breeders arrive first, followed by smaller and less fecund 1-year-old breeders (Reveillac et al., 2022). This pattern might be explained if we consider that, by the end of the spawning season the cuttlefish born in the previous year would be older and of a larger size, so would have a higher chance to fit the "minimum maturity requirements" than at the beginning of the seasonal reproduction. For example, in the Bay of Biscay, GIB breeders live ~10–13 months post-hatching, whereas GIIB breeders live between 20–22 months. Taking into account the embryonic period that lasts around 2–3 months (Le Goff, Daguzan, 1991), the reproductive cycle of the biennial spawners is more or less 2 years supporting existing seasonality. Meanwhile, in annual spawners of GIB that all are born early in the spawning season, it takes 12–16 months from eggs to eggs, so they may catch up with biennial spawners from the previous generation only by the end of the next spawning season. Therefore, their offspring born late in the hatching season have no chance to mature precociously and they would grow and mature as GIIB.

The cuttlefish population of the English Channel has now acquired a life cycle nearly identical to that observed in the Bay of Biscay around 30–35 years ago. Cuttlefish are now also represented by two breeding cohorts with GIIB spawners being the majority, with their growth rate and longevity expressed both in adult ML size and number of phragmocone chambers deposited monthly being very similar to equivalent patterns observed in the Bay of Biscay several decades ago. The observed shortening of life cycle at higher temperatures is in line with observations on cuttlefish of this population grown in captivity. Animals (n=53) grown at 10°C and 15° were small (mean 50 and 68 mm ML respectively) and immature when aged 7 months, while in the group (n=21) grown at 20°C all males and females attained full maturity at the size of mean 141 mm ML and females began to lay eggs (Richard, 1971). Because of this in the Mediterranean and other warm water areas, individuals tend to reproduce mostly at the end of their first year being GIB, whereas in the English Channel until recently the life cycle was strictly biennial being GIIB (Bloor et al., 2013).

These environmentally driven changes in historical ecology lead not only to changes in the life expectancy, fecundity and mortality but also in adult size thus influencing position of the species in ecosystems. This shift of life-history parameters might be a critical link in evolution of the cephalopod life cycles.

**4.4 | Sex ratio of samples collected in pot fisheries**

Predominance of males in trap catches is consistent with fishers' practice to put a female inside the trap to attract males. A lower expressed male predominance (1: 0.85) was found in a trap fishery off the Algarve (Pereira et al., 2019), whereas males represented 60% of catches in the Adriatic Sea (Bettoso et al., 2016) and up to 90% of catches in the Aegean Sea (Ganias et al., 2021). The predominance of females in trap catches is also known for related species, such as *Sepia esculenta* (Watanuki et al., 1993; Watanuki, Kawamura, 1999) but this is not the case for the Common cuttlefish in spite of possible regional variations in trap construction and fishing tactics. Our data, combined with data from the literature, reject concerns that, as females come to the trap to lay eggs, this fishery might be highly selective for females by removing disproportionally high numbers of them and thus impairing reproductive capacity of the population.

# AUTHOR CONTRIBUTIONS

Vladimir Laptikhovsky, Christopher J. Barrett, Peter J. Barry, Chris Firmin, Samantha Stott and Rui Vieira participated in laboratory work to collect data for this paper. Eleanor MacLeod carried out analysis of oceanographic data. All authors contributed to analysis of results and wring the manuscript.

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# CONFLICT OF INTEREST STATEMENT

The authors declare that they do not have any interest or relationship, financial or otherwise that might be perceived as influencing an author's objectivity is considered a potential source of conflict of interest.

# DATA AVALABILITY STATEMENT

Data collected for this project may be provided upon request subject to approval of the funding source.

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