Northerly range expansion and first confirmed records of the smalltooth sand tiger shark, *Odontaspis ferox*, in the United Kingdom and Ireland

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Abstract

Three *Odontaspis ferox* (confirmed by mtDNA barcoding) were found in the English Channel and Celtic Sea in 2023 at Lepe, UK (50.7846, -1.3508), Kilmore Quay, Ireland (52.1714, -6.5937) and Lyme Bay, UK (50.6448, -2.9302). These are the first records of *O. ferox* in either country, and extend the species' range by over three degrees of latitude, to >52°N. They were ~275 (female), 433 (female), and 293 cm (male) total length, respectively. These continue a series of new records, possibly indicative of a climate change induced shift in the species' range.

Keywords

English Channel; Celtic Sea; climate change; *Odontaspis ferox*; range expansion; stranding

Main text

Many marine species are expected to shift their distributions poleward and into deeper waters as a result of climate change (Harvey *et al.*, 2013; Perry *et al.*, 2005; Pinsky *et al.*, 2020; Rosa *et al.*, 2014). In the short term, many elasmobranch species – sharks, skates, and rays - move across habitats and depths to thermoregulate and/or reoxygenate in response to unfavourable environmental conditions (Andrzejaczek *et al.*, 2022; Bernal *et al.*, 2012; Braun *et al.*, 2021; Matern *et al.*, 2000; Nakamura *et al.*, 2020; Thums *et al.*, 2013; Vedor *et al.*, 2021). However, how elasmobranchs may respond to longer term impacts associated with climate change, is poorly understood. Given their high mobility, it is likely that they will shift their geographic and vertical distributions to meet their thermoregulatory needs (Niella *et al.*, 2020; Sunday *et al.*, 2015), and elasmobranchs might exhibit greater polewards shifts than teleosts given their increased physiological sensitivity to temperature (Watanabe & Payne, 2023). Understanding how large sharks may redistribute is of particular importance, given the increased risk of human-shark conflict and a need for proactive management (Abrahms, 2021; Bastien *et al.*, 2020).

The smalltooth sand tiger shark, or bumpytail raggedtooth shark, *Odontaspis ferox* (Risso 1810) is a large-bodied shark. Primarily a deep-water species, *O. ferox* inhabits broad temperature (6 °C to more than 20 °C, Fergusson *et al.,* 2008) and depth ranges (10–900 m) and is commonly associated with remote islands, seamounts or narrow continental shelves with access to deep water (Compagno, 1984; Graham *et al.*, 2016). Size segregation has been previously reported for this species, with subadults occurring at depths of less than 150 m, while adults and juveniles occupy a deeper depth range (Ebert & Stehmann, 2013). However, it is generally a poorly understood and cryptic species, with the relatively few known records suggesting low population densities and fragmented populations (Bonfil, 1995). As a result, its geographical range is unclear, although it likely occurs worldwide in warm-temperate and tropical deep water (Ebert *et al.*, 2021), extending as far north as the Bay of Biscay (Graham *et al.*, 2016). From the limited data available, females are estimated to reach a maximum size of 450 cm (total length), with males generally smaller and documented to reach 344 cm (Ebert *et al.*, 2021; Fergusson *et al.*, 2008). As with many elasmobranch species, it is believed that *O. ferox* males mature at a smaller size (200-250 cm) compared to females (300-350 cm) (Ebert *et al.*, 2021). It has also been postulated that female *O. ferox* migrate to shallower waters to give birth to minimise predation risk and show seasonal use and site fidelity to shallow areas, such as around El Hierro, Canary Islands between 1 and 20 m depth (Barría *et al.*, 2018).

Globally, the species is listed as 'Vulnerable' on the IUCN Red List of Threatened species (Graham *et al.*, 2016), while the European and Mediterranean populations are considered 'Critically Endangered' due to declines and absences in catch records (Dulvy *et al.*, 2016). The population is likely decreasing, primarily due to the species' intrinsic vulnerability to fishing pressure, especially as incidental catch within bottom gill nets, longlines, and trawlers (Fergusson *et al.*, 2008). Indeed, although *O. ferox* had been reported widely across the Mediterranean during the 20th century, recent records have been limited and predominantly occur from the eastern Mediterranean (Akbora *et al.*, 2019; Corsini-Foka, 2009; Damalas & Megalofonou, 2012; Kabasakal & Bayrı, 2019)

On 17th March 2023, video footage emerged on social media of a large shark struggling to swim off of Lepe Beach, Hampshire, United Kingdom in the shallow coastal waters of the

Solent, with members of the public attempting to refloat the animal. On the 18th March 2023, a large shark believed to be the same individual was found stranded dead on Lepe beach (Figure 1) (50.7846, -1.3508). The stranding was reported to the Cetacean Strandings Investigation Programme (CSIP), which also has a remit for the investigation of stranded large-bodied sharks in England and Wales. However, before the body could be recovered for necropsy, the caudal fin, dorsal fin, and head were removed overnight by unknown individuals. The body was also partially eviscerated, with removed organs left nearby on the beach. A partial necropsy and associated sampling was undertaken, at the Zoological Society of London (ZSL), on 22nd March 2023 on the remaining body parts that could be recovered.

Given the loss of the head before further assessment, morphological identification was undertaken based on photographs taken of the stranded shark by members of the public (Figure 2A). From scaled photographs, it was estimated that the total length of the animal was approximately 275 cm. Key features used to aid identification included the conical, bulbous snout, a large first dorsal fin originating over the free rear tips of the pectoral fins, large second dorsal, pelvic, and anal fins, and prominent dentition with long and narrow teeth (Figure 2A and B). Other notable features included the skin colouring which was blotchy dark grey and brownish dorsally and lighter ventrally. However, there was significant autolysis of the carcass on recovery, which had impacted the colouration. These characteristics were consistent with the Odontaspididae family and, specifically, *O. ferox* (Ebert *et al.*, 2021). This visual identification was initially verified in consultation with several elasmobranch taxonomists and experts and later through genetic analyses (see Supplementary Materials for detailed methodology).

The shark was a female and, given the estimated length and histological appearance of the ovaries, it was identified as a subadult. The body was in fair condition, with limited evidence of decomposition. The animal visually appeared to be in good nutritional condition. However, no evidence of recent feeding was recorded, with it having an empty stomach, consistent with either a compromised individual or recent migration (Mucientes *et al.*, 2023) - although the stomach had been damaged during the evisceration and was open to the environment and therefore no firm conclusions could be drawn. Small, sparsely distributed tapeworms were found within the spiral valve - these may potentially represent *Lithobothrium gracile* infestation (Dailey, 1971), although formal identification is pending.

Approximately two weeks later, on the 31st March 2023, researchers at Trinity College Dublin were notified by a member of the public of a very large shark dead stranded on the rocks, at Kilmore Quay, County Wexford, Ireland. The team got to the specimen around 15:00 (GMT) the next day. The individual was located at 52.1714, -6.5937, close to the spring tide high water mark (consistent with the strong wave surge that occurred the previous day at the location). Upon initial examination it was visually identified as *O. ferox* (Figure 2C and D). This was also subsequently confirmed through genetic analysis. The specimen was in a moderate state of decomposition, with death estimated as occurring within just a few days of initial reporting. Most injuries on the body appeared to have occurred post-mortem caused by the shark stranding on a rocky shore. Unlike the individual in Lepe, researchers were able to examine the entire body. The individual was a considerably larger and mature female, with a total length of 433 cm (332 cm precaudal length and 374 cm fork length). The stomach was, again, empty, with one unidentified tapeworm noted at the entrance to the spiral valve. No parasites were observed externally or within the mouth of the individual. The specimen appeared in good nutritional condition with half girths of ~104 cm on the anterior side of the dorsal, and ~98 cm on the posterior side. A series of samples were taken for subsequent histological, pathological and genetic analyses.

On the 1st May 2023, a fisher in Lyme Bay, Dorset encountered a large-bodied shark floating on the surface, reportedly with its head and tail hanging down, whilst fishing on West Tennants Reef (50.6448, -2.9302). The fisher recovered the body, brought it into harbour at Lyme Regis, and then kept it in a refrigerated van (3-4 °C) before being collected by the ZSL team on 3rd of May 2023 (Figure 2E). A subsequent necropsy was undertaken on the 4th of May 2023. Again, the shark was initially identified as *O. ferox* based on morphology and dentition and later confirmed by genetic analysis. Unlike the other two individuals, this shark was a mature male, with a total length of 293 cm (222 cm precaudal length and 248 cm fork length). A cluster of copepods were found on the right hand-side of the head and inside the mouth, possibly *Anthosoma crissum* (as reported by Mucientes et al., 2023). Externally, several cuts and lacerations to the fins were observed (Supplementary Figure 1B), notably at the base of the dorsal fin, which appeared to be recent in nature. These injuries were considered to be potentially consistent with recent interaction with fishing gear. Additionally, a 'J' fishing hook was found in the right third gill arch (Supplementary Figure 1C). Given that the fisher recovering the body was targeting Dover sole *Solea solea* with a fine net and gaffed the shark near the tail to recover the animal (as was observed on the body), this would likely be more indicative of a historical fishery interaction. No evidence of recent feeding was noted, although the stomach was partially prolapsed into the mouth (Supplementary Figure 1D). However, the shark appeared robust and was visually judged to be in reasonable nutritional condition.

To evaluate the possible role in these occurrences played by changes in water properties, specifically seawater temperatures at the seabed where *O. ferox* typically reside, we analysed the output from the E.U. Copernicus Marine Service Information Global Ocean Physics Analysis and Forecast product (2021 - present), and Reanalysis (2010 - 2020) products. Temperatures at the seabed were extracted from the Operational Mercator global ocean, eddy-resolving numerical model that generates output with a horizontal resolution of 1/12 degree and monthly temporal resolution (https://doi.org/10.48670/moi-00016). We then calculated a monthly mean seabed temperature (Figure 3A) between 2010 and 2020 over a region of Celtic Sea (bounding box 48° to 51°N, -5.25° to -9°E) corresponding to the NW European shelf sea to the west of the UK and south of Ireland (Figure 3B). In addition to monthly values, a 23-month running average was computed to highlight the warming trend over the 13 years of available model output. Interestingly, we found that the two most recent summers (2021 and 2022) exhibited the highest seabed temperatures since 2010, reaching 12.5°C compared to <11.5°C in 2011. The running average clearly indicates a warming trend over the past 13 years with a 4-5 cyclicity, suggesting a warming of approximately 1°C between 2010 and 2023 (Figure 3A).

To highlight whether the conditions during the shark strandings were anomalous, the mean seabed temperature over the period January 2010 - April 2023 were computed for each month. The temperatures for each month were then computed as anomalies relative to the time-mean for that month; for each month, at grid points for which the seabed temperature was exactly the same as average conditions, a ΔT_{seabed} of zero is obtained. For positions where the monthly temperature was warmer than usual for that month of the year, a positive value is obtained and vice versa for locations at which it was colder than usual for that time of year. We found anomalously hot conditions on the NW European shelf from August 2022 through to February 2023. Specifically, in the southern Celtic Sea, sea bottom temperatures exceeded the August average by >3°C (Figure 3D and E). The heat that would have been predominantly concentrated in the surface layers would have been subsequently mixed into the underlying water throughout the winter of 2022/2023. Given the dynamic constraints on exchange between the shelf seas and surrounding deep oceans, this resulted in a warmer than average winter seabed regime throughout the entire NW European shelf (Figure 3E).

Before these occurrences, the most northerly record of the species was from the coast of Normandy, France, where a suspected *O. ferox* was found stranded in 2012 (Ouest-France, 2012). These three new records are therefore believed to be the most northerly occurrences of the species and are the first records for the United Kingdom and Ireland. This extends the northern range of the species from approximately 49°N to more than 52°N. In recent years, a series of new records and occurrences for the species have been published from around the world, including in the Caribbean (Tavares *et al.*, 2019), northwest Spain (Mucientes *et al.*, 2023), North Atlantic (Higgs *et al.*, 2022), South Atlantic (Richardson *et al.*, 2019) and the Mediterranean in Albania (Soldo *et al.*, 2022), Cyprus (Akbora *et al.*, 2019), and Turkey (Kabasakal & Bayrı, 2019). The drivers of this global series of occurrences are unclear but are most likely linked to climate induced changes in horizontal and vertical distributions, and/or population recovery.

The spatial and temporal co-occurrence of these three individuals in the North Atlantic within several weeks of each other raises the possibility of there being a common factor. *O. ferox* have been previously documented as occurring in small groups (Fergusson *et al.*, 2008) as has the closely related sand tiger shark (*Carcharias taurus*) (e.g. Bansemer & Bennett 2010). The driver of this aggregating behaviour in *O. ferox* is unresolved, but it is possible that the three individuals observed here were socially and/or spatially linked. Reproductive behaviour is a common driver of aggregations in other shark species (Sims *et al.*, 2022; Whitehead *et al.*, 2022), and it is believed *O. ferox* females migrate to shallow waters to give birth (Barría *et al.*, 2018). However, only two of the observed individuals were females and only one was sexually mature (Ebert *et al.*, 2021). Further, no evidence of pregnancy was present in the mature female. Thus, given the demographics of the individuals, we conclude that these occurrences are unlikely a breeding or social aggregation, but cannot rule out that the larger female had given birth in the relatively shallow seas of the Celtic Sea prior to stranding. Little is known regarding the reproductive capacity of this species, though it is considered likely low (two pups every two years) as with the morphologically similar *C. taurus* (Graham *et al.*, 2016).

A more likely explanation for these co-occurrences is that the elevated bottom temperatures created a suitable thermal environment for the species, allowing these individuals to move into Irish and UK waters. Indeed, we show that sea bottom temperatures across the Celtic Sea and The Channel were considerably elevated in summer 2022 and remained warmer than average throughout early 2023. We therefore suggest that unseasonably warm conditions brought the individuals up from lower latitudes and into water previously outside of their thermal niche. Given the projections that sea temperatures around the UK and Ireland will continue to warm over the coming decades (Gröger *et al.*, 2013; Holt *et al.*, 2018; Tinker *et al.*, 2016), we believe it is likely that there will be further records of *O. ferox* in UK and Irish waters, as well as other species traditionally associated with more tropical habitats. There is therefore, an urgent need to prioritise future research to explore the impacts of these sea temperatures anomalies on species distribution.

The cause of the near simultaneous strandings remains less clear. Given no evidence of recent feeding was noted in any of the three individuals, it is possible that the individuals came up onto the shelf during the high summer temperatures in 2022, encountered habitats encountered habitats they were not well adapted for and subsequently starved as foraging opportunities were limited in the shallow continental shelf. However, the necropsies found limited evidence of any significant deterioration in body condition. Alternatively, Mucientes et al (2023) cited the lack of stomach contents in *O. ferox* as an indicator of recent migration. An alternative hypothesis is that they were caught and released or discarded in the vicinity by a fishing vessel. Indeed, landings of *O. ferox* in commercial fisheries have been documented in several parts of the world (Barcelos *et al.*, 2018; Fergusson *et al.*, 2008; Vella *et al.*, 2017; White, 2007). However, we found no evidence of recent entanglement or other fishery interactions on either female and only limited evidence of a likely non-fatal fishing interaction in the male. We therefore conclude that fishery interactions were not a factor in the strandings. Finally, we cannot currently rule out that a common underlying pathological or toxicological factor may have contributed to these strandings, as have been previously associated in other strandings across the region (Barnett *et al.*, 2023; Dagleish *et al.*, 2010; Wosnick *et al.*, 2022).

Regardless of the driver behind the strandings, their occurrence in these temperate waters raises questions about our understanding of the species' distribution. However, more research is clearly needed in this area, but the rarity and cryptic nature of the species presents a considerable challenge. These recent observations highlight the value of systematic strandings programmes as effective monitoring systems for the occurrence of novel species, as climate change impacts drive shifts in distribution. In addition, compared to cetaceans, very few systematic necropsies are carried out on stranded sharks, yet this study highlights the importance of using them to better understand the causes of strandings and to collect a suite of valuable samples and data. An additional and promising option to better assess species distribution could be the application of environmental DNA techniques, through metabarcoding (e.g. Dunn et al., 2022) or species-specific primers using the recently published mitogenome (Vella *et al.*, 2017), such as those undertaken in the Mediterranean for another large but rare species, the white shark *Carcharodon carcharias* (Jenrette *et al.*, 2023). Additionally, understanding the population genetic structure of the *O. ferox* population across the Atlantic would be a pertinent next step.

We conclude that whilst the cause of these near simultaneous strandings remains unclear, we believe that the close temporal proximity of these three incidents is likely indicative of broader climate change drivers. Similar patterns have been observed elsewhere, such as the recent increase of white sharks in Atlantic Canada (Bastien *et al.*, 2020). Indeed, the emergence of *O. ferox* in multiple novel locations in recent years is indicative of broader population level changes that need to be researched further. As a precautionary approach, their potential future shifts into novel regions should be proactively managed in areas and with communities that are less familiar with the presence of large shark species.

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Ethical Statement

Work conducted in the United Kingdom by the Cetacean Stranding Investigation Programme, including the recovery, examination and sampling of dead stranded marine species is undertaken under a Class licence CL01 held by the Institute of Zoology. Work in Ireland did not require licensing and neither required ethical review.

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Figures

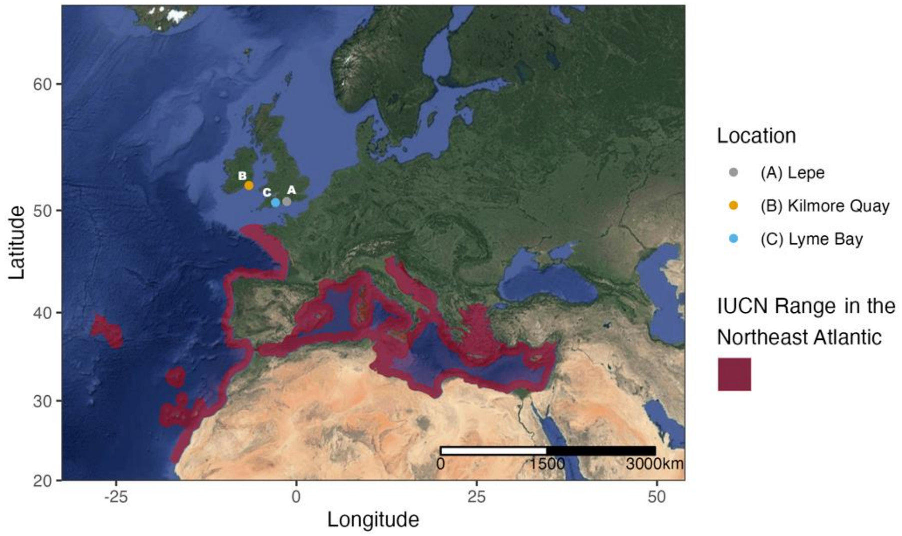

Figure 1. Locations of the *O. ferox* strandings in Lepe, United Kingdom (A), Wexford, Ireland (B) in March 2023 and the third stranding in Lyme Bay, United Kingdom (C) in May 2023. Sharks were ~275 (female), 433 (female), and 293 cm (male) total length, respectively. Red shading is the current described distribution range of the species in the Northeast Atlantic by the IUCN (Graham et al 2016).

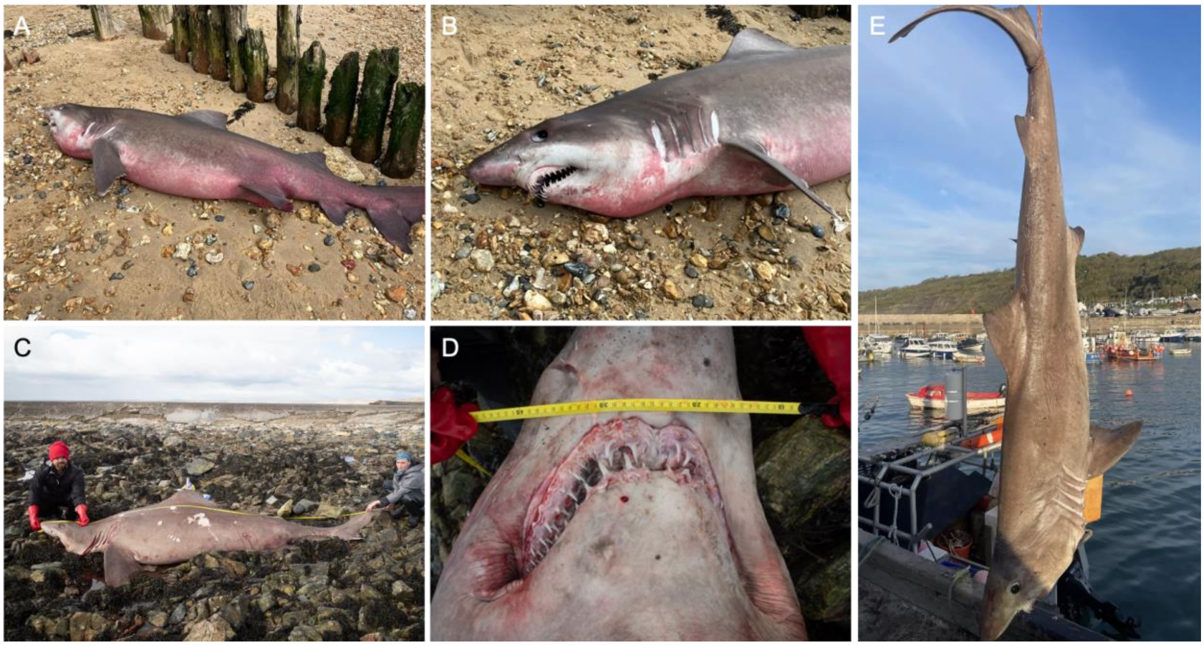

Figure 2. The bodies of the three smalltooth sand tiger sharks *O. ferox* found stranded between March and May in 2023. The first individual was a female and was found on a beach in Lepe, Hampshire, United Kingdom on 18th March 2023 (A and B). The second individual was also a female and was found stranded on the beach at Kilmore Quay, County Wexford, Ireland on 31st March 2023 (C and D). The third individual was a male that was found floating in Lyme Bay, Dorset on 1st May 2023 (E). All individuals were initially identified through the origin of the first dorsal fin and the long and narrow teeth (B and D) which are indicative of the species. Species identification was subsequently verified through mtDNA barcoding. Images provided by Peter Broomfield (A and B), Kevin J. Purves (C), Jenny R. Bortoluzzi (D), and fishers James and Barry (E).

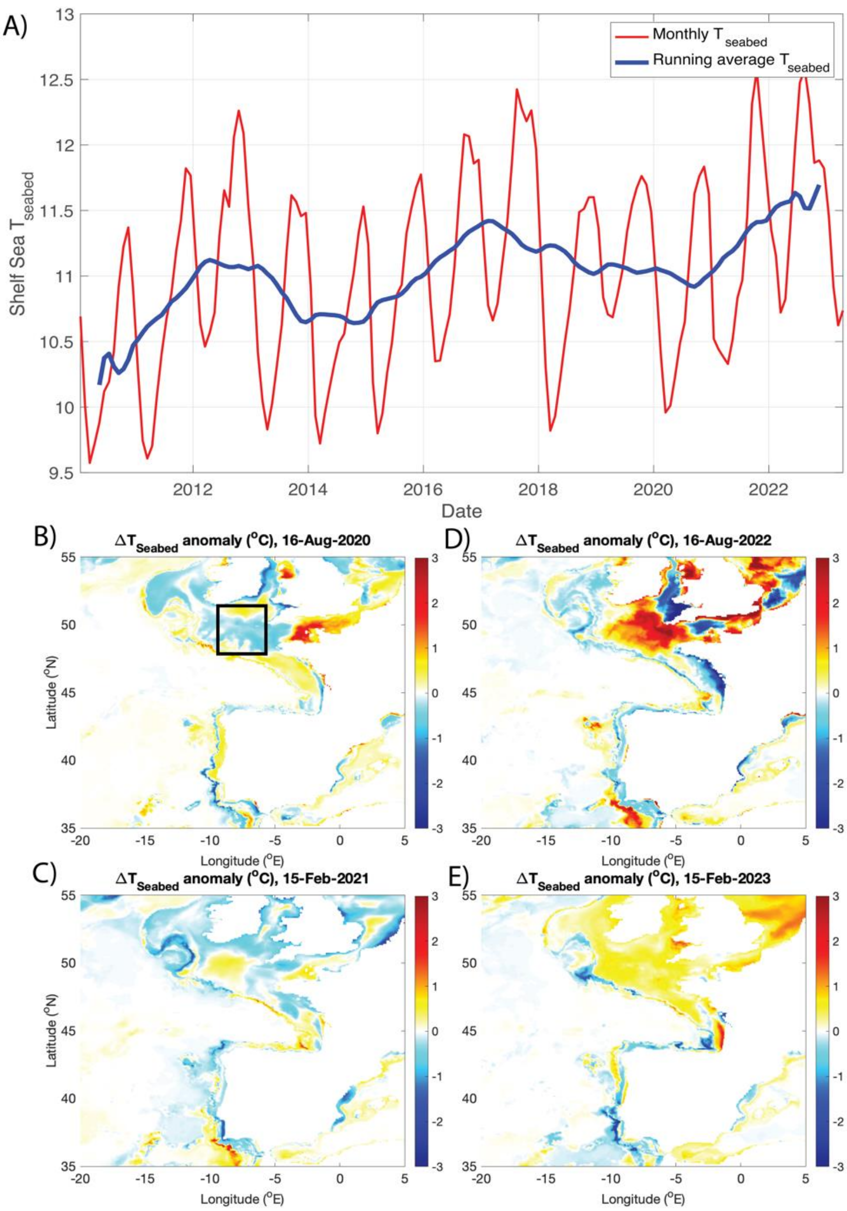

Figure 3. A) Monthly mean seabed temperature within bounding box indicated in B) during the period January 2010 - April 2023 (red line) and corresponding 23 month running average value (blue line); B) to E) seabed temperature anomalies for months indicated D) and E) highlight the impact of a hot preceding summer on the following winter shelf sea temperatures when the strandings occurred. Contrasting conditions are presented for August 2020 and February 2021 during which temperatures were lower than usual.