



## Research paper

# Too old to be new? A recent discovery of a pteropod *Limacina lesueurii* (d'Orbigny 1836) at the Swedish west coast (Skagerrak, North Sea)

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## ABSTRACT

The pteropod *Limacina lesueurii* (d'Orbigny 1836) is a subtropical species, which in the Atlantic Ocean shows maximum abundance between 30°N and 25°S. In the North Sea, this species has so far only been occasionally reported from the coastal waters off the northern Scotland and in the English Channel. In this short note, we for the first time report presence of *L. lesueurii* in two sediment cores taken in the Kosterfjord (Skagerrak, North Sea). The pteropod, generally absent or occurring in low numbers throughout both cores, showed distinctly higher abundances between 100 and 130 cm core depth, which based on dating by <sup>137</sup>Cs, <sup>210</sup>Pb and lead pollution records corresponds to ~1920–1950s. During this period positive sea surface temperature anomalies were reported in the North Atlantic and number of oceanic water inflows have been documented for the North Sea. Some of these inflows were accompanied by "enormous shoals" of *L. lesueurii* observed in the English Channel and NE of Scotland. We hypothesize that *L. lesueurii* was transported into the Skagerrak in connection with these and propose this pteropod species as a new valuable stratigraphic marker for oceanic water inflows in the study area.

## 1. Introduction

Pteropods are pelagic organisms characterized by living in the open water column and swimming by using a pair of wing-like parapodia. The order Pteropoda comprises the three suborders Euthecosomata, Pseudothecosomata and Gymnosomata, two of which are represented in Swedish waters, the phytophagous Euthecosomata, also referred to as "sea butterflies", and the predatory Gymnosomata or "sea angels" (Lalli and Gilmer, 1989; Pierrot-Bults and Peijnenburg, 2015). The euthecosomatans and pseudothecosomatans have hard shells, but gymnosomatans have those only at the larvae stage and shed shells as they grow into adults. In contrast, the Euthecosomatans and Pseudothecosomatans maintain their shells as adults, but in the latter group the adult shell is highly modified. The pteropods contribute through shell precipitation to the ocean carbon cycle by transporting carbon from the surface to the deep ocean and by contributing to the total carbonate flux worldwide by at least 12% (Bernier and Honjo, 1981; Buitenhuis et al., 2019). The euthecosomatans shells are thin, transparent, usually smaller than 100 µm and are made of aragonite, a metastable polymorph of CaCO<sub>3</sub>, which is &50% more soluble in seawater than calcite (Mucci, 1983). Hence, euthecosomatans pteropods are sensitive to ocean acidification and are

used as indicators in monitoring of such environmental changes (Manno et al., 2017 and refs therein). Shell-bearing pteropods, including both orders of Euthecosomata and Pseudothecosomata, feed on phytoplankton caught by thin threads of mucus (Gilmer and Harbison, 1986). They occur in all the world's oceans but have higher species diversity in tropical waters than in polar regions, although the latter have much larger biomass (Bednaršek et al., 2012). Many euthecosomatans pteropod species have extensive fossil record and are used as important stratigraphic markers for identifying and dating specific strata in marine sediments (e.g., Janssen and King, 1988; Gürs and Janssen, 2004; Janssen, 2012). The euthecosomatans pteropods have a robust fossil record, which goes back as far as the Eocene (56 Ma), whilst the oldest fossil find together with molecular clock data have recently demonstrated much earlier origins during the Cretaceous at 72–133 Ma when euthecosomatans and pseudothecosomatans pteropods diverged from gymnosomatans lineages (Janssen et al., 2016; Janssen and Peijnenburg, 2017; Peijnenburg et al., 2020).

Euthecosomatans species of the family Limacininidae are characterized by a well-developed adult shell (teleoconch) and a larval shell (protoconch), both of which are sinistrally coiled. The only extant genus within the Limacinidae is the genus *Limacina* Bosc, 1817 encompassing

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six extant species, of which only three species occasionally have been reported from the North Sea, i.e. the holarctic species *Limacina helicina* (Phipps, 1774), the subtropical *Limacina lesueurii* (d'Orbigny, 1835) and the subpolar *Limacina retroversa* (Fleming, 1823). Of these three, only *L. retroversa* hitherto has been reported from the Swedish west coast (Hansson, 2011; Lundin et al., 2020). In this short note, we report the first finding of *L. lesueurii* in two sediment cores taken in the Kosterfjord (Skagerrak, North Sea). In the North Sea, this species has only been so far occasionally reported from off northern Scotland (Hardy, 1923) and in the English Channel (Fraser, 1961). To our knowledge, there are no records of *L. lesueurii* present at the Swedish west coast and possibly neither from the Skagerrak.

## 2. *Limacina lesueurii* (d'Orbigny, 1836): taxonomy and ecology

### 2.1. Taxonomic description

The shell of *L. lesueurii* is thin, transparent, flatly coiled and distinguished by small size (height up to 0.8 mm, diameter up to 1.3 mm) (van der Spoel et al., 2021). The shell normally consists of 4.5 transparent whorls. It has a depressed spire, straight columellar side of the aperture and a smooth surface with very faint transverse growth lines. Weak spiral striation is sometimes found around the umbilicus. The umbilicus is large in young specimens, but becomes narrower in fully grown individuals. Also, the aperture is rounded in young, but it gets more straight on the columellar side in fully grown specimens, with an angle on the lip at the apical edge. *L. lesueurii* can readily be distinguished from the locally occurring *L. retroversa* forma *retroversa* (J. Fleming, 1823), which is larger (to 2.5 mm high and 3 mm in diameter) and has a shell with a moderately high spire, up to seven transparent whorls, with fine and densely placed spiral striations and weak transverse growth lines (van der Spoel et al., 2021; Lundin, own observations from museum specimens). The other species potentially occurring in the area is *L. helicina* forma *helicina* (Phipps, 1774), which has a depressed spire in similarity with *L. lesueurii*, but the shell is much larger (up to 6 mm high, up to 8 mm in diameter) and have distinct transverse striations on the whorls. Also, *L. helicina* has generally much more northern distribution with its closest known occurrence to the Swedish west coast is reported 57°N off Stonehaven, north-eastern Scotland (León et al., 2020).

### 2.2. Synonyms

- Atlanta lesueurii* (non Souleyet, 1852) n. sp. d'Orbigny, 1836: 177  
*Spirialis ventricosa* (non Adams, 1853):? Eydoux and Souleyet, 1840: 236  
*L. lesueurii* part Boas, 1886a: 46  
*L. lesueurii* (non Tesch, 1908) Munthe, 1888: 9  
*Limacina lesueuri* (non Tesch, 1908) part Pelseneer, 1888a: 24  
*Limacina crossei* (ms. Velain) Pelseneer, 1888a: 24  
*Limacina lesueuri* var. *minor* (nomen nudum) nov.var. Locard, 1897: 23  
*Limacina lesueuri* var. *alta* (nomen nudum) nov.var.? Locard, 1897: 23  
*Limacina lesueuri* var. *depressa* nom. Nud. Locard, 1897: 23  
*Limacina lesueuri* (non Tesch, 1908) Schiemenz, 1906: 22  
*Spiratella lesueuri* Hedley, 1917: 106  
*Limacina leseurii* Meek, 1923a: 95  
*Limacina (Thilea) lesueuri* Van der Spoel, 1967: 52.

### 2.3. Ecology

*Limacinaim lesueurii* is an epipelagic species commonly found dwelling within ~75–600 m water depth range and at water temperatures of 14–28 °C (Chen and Bé, 1964; van der Spoel, 1967). It shows some diel vertical migration of ~80–100 m (Wormelle, 1962; Vecchione and Grant, 1983; Ossenbrügger, 2010) and has been suggested to calcify

at 145 m water depth and 16.5 °C, based on shell geochemistry analysis (Sergent, 2020). The species feeds on phytoplankton caught by thin threads of mucus (Gilmer and Harbison, 1986) and reproduces as protandric hermaphrodite.

### 2.4. Distribution

Species *L. lesueurii* occurs in warm and temperate seas, with a typically bisubtropical distribution. In the Atlantic Ocean, *L. lesueurii* is recorded between 40°S and 50°N with some exceptional records in the North Sea (NE of Scotland and English Channel) reflecting influence of the Gulf Stream current (Hardy, 1923; Fraser, 1961). In the Mediterranean Sea, its presence has also been linked to the Atlantic water inflows (Rampal, 1965, 1970). Other known records worldwide include east of Sri Lanka, southern Indian Ocean, central Pacific, east and west off Australia and north off Papua Nya Guinea (van der Spoel et al., 2021).

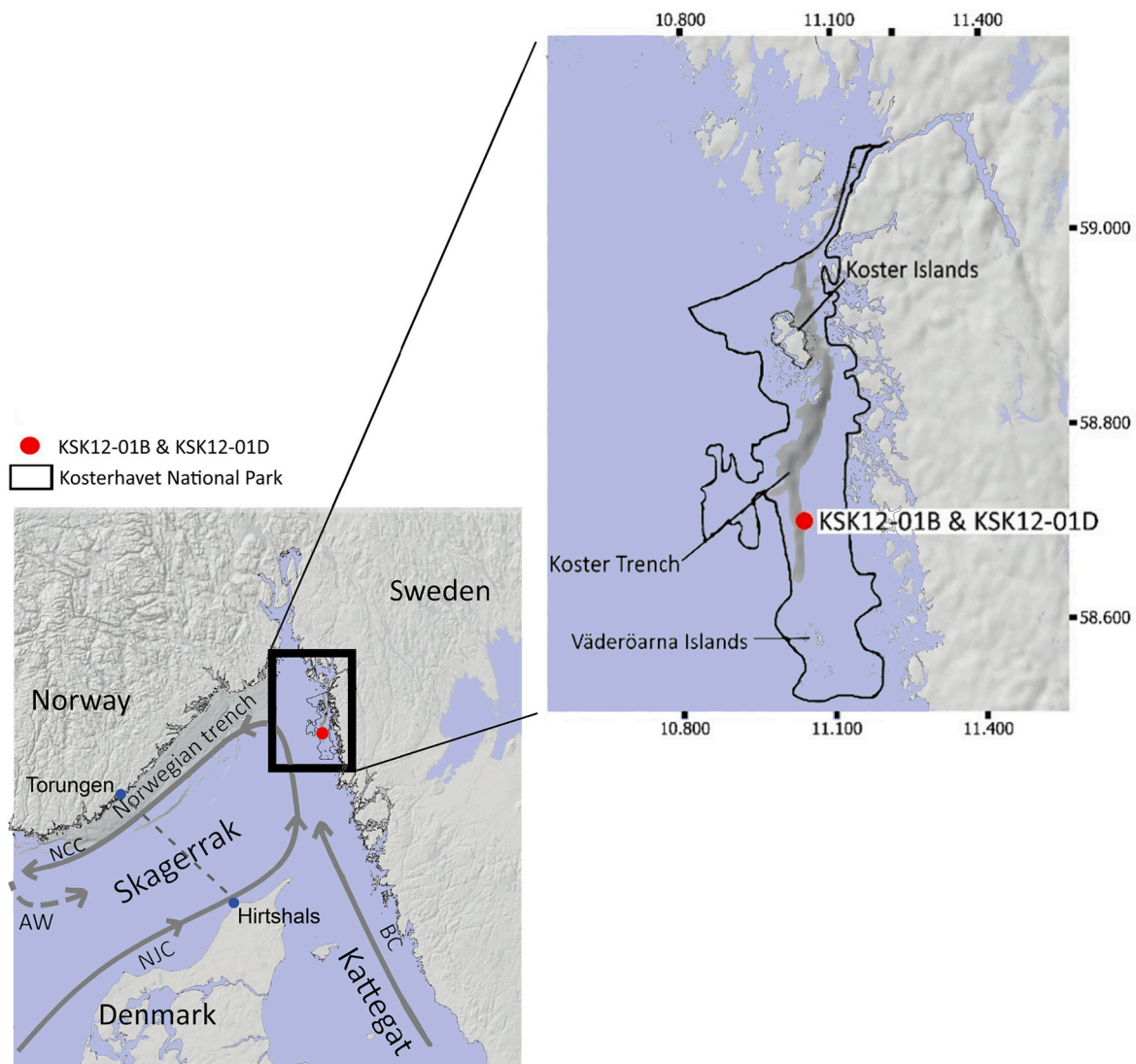
## 3. Study area

The Kosterfjord (Skagerrak, North Sea) stretches southward along the west coast of Sweden. It is not a true fjord but a tectonically formed structure, open at both ends and separated from the adjacent Skagerrak by the Koster Islands in the west, by a sill off the Tisler Islands in the north and by the Väderöarna Islands in the south (Fig. 1). The area is influenced by the major currents and general hydrography of the Skagerrak. A dense oxygenated saline ( $S > 35$ ) Atlantic water mass fills depressions at 150–200 m water depth beneath the Skagerrak intermediate water ( $S = 32$ – $35$ ), which occupies the middle part of the water column at 30–150 m (Andersson, 1996; Rodhe, 1996). The more brackish water mass defined as the Skagerrak coastal water ( $S = 25$ – $32$ ) lies on top at 0–30 m and is influenced by the land runoff and the out-flowing brackish water originating from the Baltic Sea (Svansson, 1975; Andersson, 1996; Rodhe, 1996). The intermediate and coastal water masses are separated in the study area by a pycnocline present most of the year at 10–30 m water depth (Polovodova Asteman et al., 2021). In the Kosterfjord area, the Baltic water mixes with the Skagerrak water, local river runoff, and the waters of the northern Jutland Current ( $S = 31$ – $34$ ), carrying North Sea and Atlantic water masses at surface. This mixed water mass flows to the west along the southern coast of Norway and exits the Skagerrak as the Norwegian Coastal Current (Rydberg et al., 1996). The dense and nutrient-rich Atlantic deep water ( $S = \sim 35$ ) enters the area as the subsurface Atlantic Current (Talpsepp et al., 1999) and is reflected in the Kosterfjord basin water, which has a salinity  $>34.2$  and temperature  $< 8$  °C with low annual variability (Linders et al., 2018).

The Kosterfjord hosts cold-water coral reefs dominated by *Desmophyllum pertusum* earlier known as *Lophelia pertusa* (Linnaeus, 1758). Due to the presence of coral reefs and a general high biodiversity, the Kosterfjord has since 2009 been included in the Marine Protected Area “Kosterhavet National Park”.

## 4. Material and method

Data on pteropods presented herein originate from two sediment cores, which both were recovered aboard R/V Skagerak in September 2012 in the deepest part of the Kosterfjord, Koster Trench (58°42,904' N; 11°02,407' E; 157 m water depth) (Fig. 1). First core, KSK12-01D, was taken with a Gemini corer ( $\varnothing = 80$  mm) and was 53 cm long. The Gemini corer allows obtaining an intact water-sediment interface and thus allows retrieving the most recently deposited sediments. Second core KSK12-01B (199-cm long) was taken with a gravity corer and due to a more destructive coring method the intact core top was not obtained (Fig. 2). Both cores were subsampled in 1-cm resolution down to 10 cm (KSK12-01D) and 30 cm (KSK12-01B), followed by 2-cm sampling resolution thereafter. All subsamples were wet-weighed, frozen, freeze-dried, dry-weighed and their water content was estimated prior to



**Fig. 1.** Map of the study area within the North Sea-Baltic Sea region and the Skagerrak. The red dot indicates the sampling site of the sediment cores KSK12-01D and KSK12-01B (58°42,904' N, 11° 02,407' E and 157 m water depth) and the Kosterhavet National Park is marked as a polygon outlined by black line. The main currents are shown as follows: The northern Jutland current (NJC), the Baltic current (BC), the Atlantic water (AW) and the Norwegian coastal current (NCC). The hydrographic transect Hirtshals-Torungen (Fig. 4) is marked by a gray dashed line, while the deepest part of the Kosterfjord (Koster Trench) is indicated by a dark gray area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

further analyses. In both cores, about 10 g of dry sediment was washed through a 63- $\mu$ m sieve, dried at 50 °C and was dry-picked for benthic foraminifera (Martinson, 2014; Polovodova Asteman et al., 2021; Kankainen, 2021) and along with foraminifera all available pteropod shells were picked and counted. For pteropods, every centimetre down to 10 cm core depth and every second centimetre thereafter were screened in KSK12-01D. In KSK12-01B, sample resolution for pteropod analysis was much lower and ranged between 4 and 22 cm between the analysed samples. Both cores were also subject for total organic carbon (TOC), total nitrogen (TN) and metal (Pb, Ni, Cu, Zr, As, Cd) analyses (Martinson, 2014; Polovodova Asteman et al., 2021).

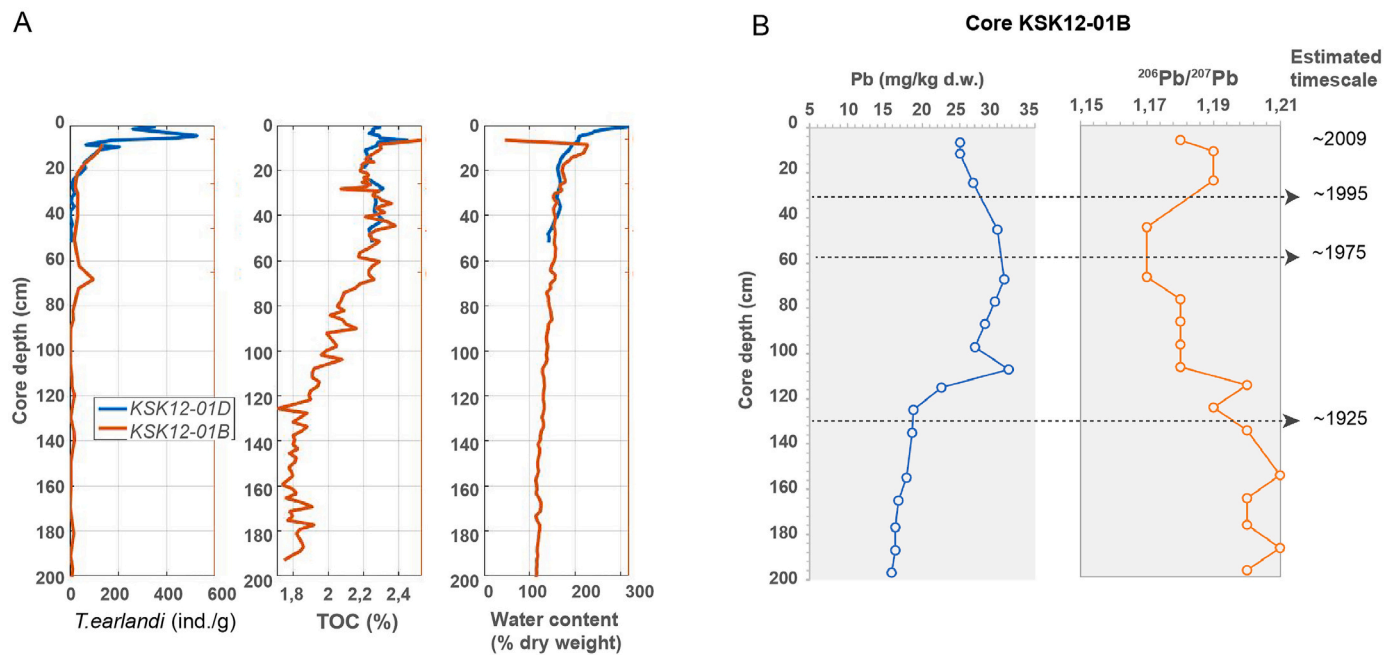
Gemini core KSK12-01D was dated by radioisotopes  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  (Polovodova Asteman et al., 2021), while the gravity core KSK12-01B has only relative dates provided by lead (Pb) pollution records and by temporal changes in the  $^{206}\text{Pb}/^{207}\text{Pb}$  ratio in the sediments (Martinson, 2014).

## 5. Results

### 5.1. Core dating and age model

To estimate the sediment loss of the core top in the gravity core KSK12-01B we used the  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$  dates from the Gemini core KSK12-01D taken at the same site (Polovodova Asteman et al., 2021). This, together with correlating TOC, water content and the absolute abundances of the most abundant benthic foraminiferal species *Textularia earlandi* in both cores, allowed to estimate the upper sediment loss in the gravity core KSK12-01B to about 6 cm (Fig. 2A). This implies that the surface (youngest) sediment in the gravity core corresponds to ~6 cm in the Gemini core KSK12-01D, which has been dated by  $^{137}\text{Cs}$  and  $^{210}\text{Pb}$  to ~2009 ( $\pm 6$ ) suggesting a similar age for the core top in KSK12-01B. Knowing ages of the Gemini core KSK12-01D (Polovodova Asteman et al., 2021), we could estimate age of the KSK12-01B part overlapping with the core KSK12-01D down to 49 cm, which was likely deposited during ~2009–1986 (Fig. 2A).

The part of the KSK12-01B core below 49 cm was dated based on changes in the  $^{206}\text{Pb}/^{207}\text{Pb}$  ratio and Pb pollution records (Fig. 2B)



**Fig. 2.** Age model for the studied sediment cores. A: Correlation of cores KSK12-01B and KSK12-01D based on their TOC (%), water content and the abundance of foraminifer *Textularia earlandi* (Kankainen, 2021). This procedure estimated the surficial sediment loss in gravity core KSK12-01B to ~6 cm as its topmost sediment layer appears to correspond to 6 cm core depth in KSK12-01D. B: The temporal changes of isotopic ratio  $^{206}\text{Pb}/^{207}\text{Pb}$  and the Pb concentration in the core KSK12-01B are shown together with an estimated timescale based on lead pollution records (Martinsson, 2014).

(Martinsson, 2014). Using this method, a decrease in  $^{206}\text{Pb}/^{207}\text{Pb}$  ratio at 130 cm core depth is interpreted as ~1925 ( $\pm 10$ ). This is based on an increase of lead emissions into the atmosphere, which in Europe started in 1925 and are linked to the decreasing  $^{206}\text{Pb}/^{207}\text{Pb}$  ratio measured in marine sediments (Renberg et al., 2001). Such a  $^{206}\text{Pb}/^{207}\text{Pb}$  decrease in KSK12-01B starts just below 130 cm and has a fairly stable decreasing trend until ~40–60 cm core depth (Fig. 2B). From 40 cm, the ratio starts to increase again, which is interpreted as post ~1975 ( $\pm 10$ ). The known ban of leaded petrol in Sweden in 1995 was associated with the decline in Pb and increased  $^{206}\text{Pb}/^{207}\text{Pb}$  ratio (Renberg et al., 2001), which both occur at ~30 cm core depth in KSK12-01B. This agrees rather well with our estimated age for the core top in KSK12-01B using radiometric dates of the Gemini corer KSK12-01D (Polovodova Asteman et al., 2021), where the year 1995 was associated with a core depth of 29 cm.

By combining the lead pollution dating with the radiometric data of KSK12-01D (Polovodova Asteman et al., 2021) we interpolated the dates in the core KSK12-01B to the core depth 49–130 cm and from there linearly extrapolated dates for the rest of the core base by using R-Studio. This dated the bottom-most sediment sample at 197 cm to ~1880. Obviously, this procedure has introduced higher uncertainties for dating of KSK12-01B levels below 49 cm core depth and between the samples corresponding to tie points of 1995 ( $\pm 10$ ), 1975 ( $\pm 10$ ) and 1925 ( $\pm 10$ ), see above. On the other hand, the KSK12-01B part at 0–49 cm overlapping the Gemini core KSK12-01D have a slightly lower uncertainty ( $\pm 6$  years) as compared to the dates downcore that are based on Pb pollution dating, interpolation, and linear extrapolation.

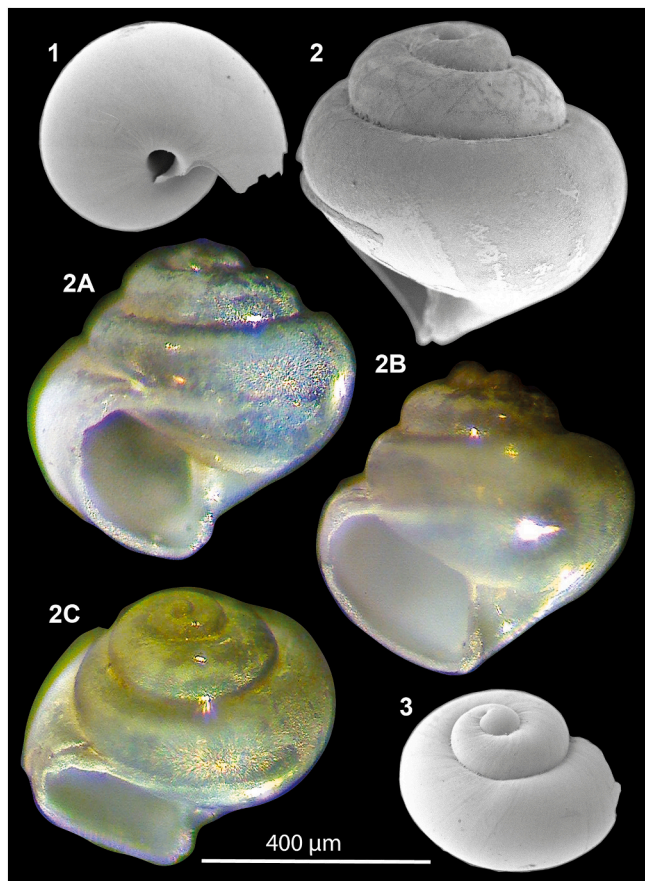
## 5.2. Occurrence of *Limacina lesueurii* in the sediment cores

During benthic foraminiferal analysis it was noted that some core horizons in KSK12-01B were unusually rich in pteropod shells, which were identified as *L. lesueurii* (Kankainen, 2021; Figs. 3 and 4 herein). This pteropod generally occurred in low numbers ( $> 5$  ind.  $10\text{ g}^{-1}$  dry sediment) but showed distinctly higher abundances between 100 and 130 cm core depth (~1920s to 1950s) where it increased to 40–160 ind.  $10\text{ g}^{-1}$  dry sediment (Fig. 4). We were curious to see if *L. lesueurii* was

present in more recent sediments in the Kosterfjord as well and for this purpose we re-checked the Gemini core KSK12-01D, which was previously analysed for foraminifera and covers the time period ~2012–1986 (Polovodova Asteman et al., 2021). The results showed that this pteropod has become rare in the study area as its abundances did not exceed 6 ind.  $10\text{ g}^{-1}$  dry sediment for the major Gemini core part with a slight increase to 11–14 ind.  $10\text{ g}^{-1}$  dry sediment in the KSK12-01D core base (Fig. 4).

## 6. Discussion

Marine zooplankton, such as pteropods, are sensitive indicators of oceanographic changes because both themselves and their prey organisms rely on physical oceanographic processes and changes in waters masses (McManus et al., 2016 and references therein). Thereby, appearance of *L. lesueurii* in the Kosterfjord sediment record can potentially indicate such changes. Based on the age model and estimated time scale, two peaks of *L. lesueurii* abundance appear to be associated with the 1920s and the late 1930s/ early 1940s in our sediment record (Fig. 4). But how does this timing agree with other regional findings of this pteropod species in the North Sea? To date there are no documented reports of *L. lesueurii* from the Swedish waters (Hansson, 2011; Lundin et al., 2020), and a search in the register of marine species showed that *L. lesueurii* has neither been reported in the Danish or Norwegian Skagerrak waters (Arter, 2021; Artsdatabanken, 2021; van der Spoel et al., 2021). Being known as a subtropical (but cold-water tolerant) species occurring between 50°N and 40°S in the Atlantic Ocean, with maximum abundances at 30°N–25°S (Chen and Bé, 1964; Burrige et al., 2017a), pteropod *L. lesueurii* was not recorded north of the Bay of Biscay before 1906 (Fraser, 1961). In the Atlantic Ocean, Burrige et al. (2017b) report *L. lesueurii* often observed together with another warm-water pteropod species *Heliconoides inflatus*, which is often more abundant than *L. lesueurii* but was not detected in this study. Presence of *L. lesueurii* in the western Mediterranean Sea has been attributed to influence of the Atlantic Current (Rampal, 1965, 1970), and its highest numbers were found in the subsurface waters just below the pycnocline (Florida



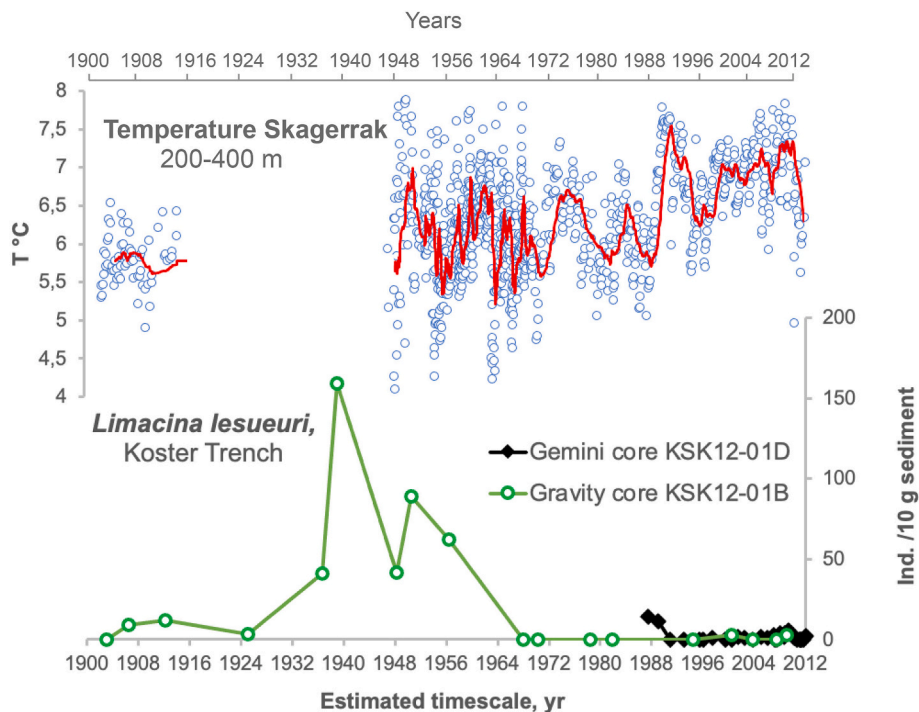
**Fig. 3.** Scanning Electron Microscope (1–3) and light microscope (2 A–C) images of *Limacina lesueurii*. 1. Young specimen seen from below with large umbilicus. 2. Side view of older specimen showing depressed spire and angle at columellar side of aperture. Some of the original smooth surface is visible, but most of the surface is worn. 2A–C: Detailed view of a straight columellar side of the aperture (2A, 2B) and depressed spire (2C) 3. Young specimen showing the depressed spire and faint transverse growth lines.

Current: Wormelle, 1962 and Cape Verde islands: Ossenbrügger, 2010). Kosterfjord receives oceanic water in its deepest part (Linders et al., 2018). Hence, presence of *L. lesueurii* in the Swedish coastal waters can likely be associated with a subsurface inflow of warm waters from the Atlantic Ocean.

Indeed, in the first half of the twentieth century, there have been three major Atlantic inflow events associated with faunal invasions and salinity anomalies in the North Sea during 1903–06, 1920–22 and 1931–35 (Reid et al., 2003 and references therein). Despite the higher uncertainty provided by the lead-isotope dating for the lower part of the gravity core KSK12-01B, the two peaks of *L. lesueurii* identified in the Koster Trench record, appear to be associated with the 1920s and 1930s inflows, with the latter being shown instead as the early 1940s (Fig. 4). This suggests that our estimated age model can be correct given the first documented record of *L. lesueurii* in the English Channel dates back to 1906 and a presence of pteropod shells in the lowermost KSK12-01B core samples corresponding to the 1890–1900s (Fig. 4). A major increase in *L. lesueurii* abundances in the mid-1920s in this study can either reflect the documented major oceanic inflow event of 1920–1923 (Fraser, 1949; Dickson, 1967) or the inflow of 1931–35 (Reid et al., 2003), given the core dating uncertainty. The inflow events over the time period 1900–1925 are reflected in high salinity anomalies in the North Sea during 1903–1906 and 1920–1923 (Lucas, 1946). Both of those periods had likely seen some major inflow events, based e.g., on a presence of deepwater fish of genus *Arnoglossus* in the northern North

Sea in 1904–06 (Dickson, 1967). The 1920s event was associated with warming and large numbers of Atlantic plankton species such as salps (*Salpa fusiformis*), pteropods (*L. lesueurii*; as *Spiratella lesueri*) and radiolarians (*Phyllostaurus quadrifolius*) being transported to the North Sea (Hardy, 1923; Fraser, 1949), which was attributed to “the action of the Gulf Stream” (van der Spoel et al., 2021). The 1931–35 inflow event was also reported by the presence of Mediterranean water in the Faroe-Shetland Channel and unusually high salinities in the Southern Bight in 1933 (Dickson, 1967). This inflow was associated with horse mackerel (1932) and anchovy (1933) being transported into the Baltic from the North Sea, and an increase in the anchovy stock of the southern North Sea during 1930–34 (Dickson, 1967). Based on observations, the 1930s and 1940s were associated with high annual air and sea temperatures documented globally (Delworth and Knutson, 2000; McManus et al., 2016) as a part of an Early Twentieth Century Warming phenomenon (Brönnimann et al., 2009; Hegerl et al., 2018). During this time several remarkable weather extremes and climate anomalies were reported such as, a pronounced warming in the Arctic during 1912–1930s (e.g. Hanssen-Bauer, 2002; Drinkwater, 2006), a series of the North American droughts and unusual heat waves in the 1930s (Cook et al., 2009; Cowan et al., 2017; Donat et al., 2016; Schubert et al., 2004), a drought in Australia during 1937–1945 (Verdon-Kidd and Kiem, 2009) and the European summer droughts and heat waves of the mid-to-late 1940s (Sutton and Hodson, 2005). Also, higher sea surface temperatures (SST) were reported during the 1930s in the North Sea, the English Channel and the Baltic Sea (Beverton and Lee, 1965) and the Gulf Stream waters were 0.4 °C warmer as compared to the 1912–1918 (Scherhag, 1937). Between the 1930s and the 1960s, the distinct positive SST anomalies have also been documented for the entire North Atlantic, also known as the positive Atlantic Multidecadal Oscillation (AMO) mode (Kerr, 2000; Alexander et al., 2014; McManus et al., 2016) together with an increased Atlantic water inflow into the Norwegian and Barents seas (Bengtsson et al., 2004). In connection with these, Drinkwater (2006) reports on “a regime shift” in the North Atlantic in the 1930s associated with a northward expansion of “warm-water” fish species and a poleward retraction of cold-water species. Those changes were linked to significant shifts in zooplankton community composition caused by the wind and air/sea temperature changes driven by the large-scale climate changes, such as the AMO and the North Atlantic Oscillation (NAO) (Drinkwater, 2006; Drinkwater et al., 2003, 2014). The NAO is a measure of the sea level pressure gradient over North Atlantic between the Icelandic Low and the Azores High (Hurrell, 1995) and it affects water column mixing and stratification transporting oceanic waters to the coasts. The impact of the NAO and AMO on the marine ecosystem structure in the North Atlantic has been extensively documented for marine taxa at all trophic levels (McManus et al., 2016 and references therein) and the alternating “cyclic changes” of e.g. the quantity of fish larvae, the abundance of macroplankton and the appearance vs disappearance of fish species were noted between the 1920s and the 1970s in the English Channel (Cushing and Dickson, 1976; Cushing, 1982). In Scandinavia, bluefin tuna was highly abundant during the 1910s–1950s resulting in large landings and export of fish caught by Swedish fishermen (Tiews, 1978; MacKenzie and Myers, 2007; Bennema, 2018). Since the 1960s bluefin tuna was absent in the Skagerrak until it came back recently (MacKenzie et al., 2020) but it remains unclear if tuna migration patterns were climate-related or not (MacKenzie and Myers, 2007).

The presence of the warm-water pteropod encountered in this study in particularly high numbers between the 1920s and the 1950s (Fig. 4) is consistent with the abovementioned studies and suggests *L. lesueurii* as a new valuable indicator of oceanic water inflows to the Skagerrak. To check this further we present herein the time series of temperature data for the Skagerrak water mass below 200 m (associated here with the Atlantic Water) available at the International Council for the Exploration of the Sea (ICES) and compiled with data from Ljøen and Svansson (1972) for the period 1900–2010 (Fig. 4). Despite a large lack of the data



**Fig. 4.** Temperature observations for the water mass at 200–400 m based on ICES oceanographic data and Ljøen and Svansson (1972) for the Hirtshals (DK)-Torungen (NO) section taken across the Skagerrak, shown as a monthly mean (blue circles) and a 20-point running average (red line). Note absence of the data between 1916 and 1947. Stratigraphic occurrence of pteropod *Limacina lesueurii* in the sediment cores from the Kosterfjord is shown as green and black lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between 1915 and 1947 (Fig. 4), the figure clearly shows several temperature peaks during the early 1900s, the late 1940s to the early 1950s and the early 1960s. Period between the 1960s and the 1980s has been characterized by a generally cooler climate (Fig. 4), also based on the meteorological observations from Uppsala (Bergström and Moberg, 2002), which agrees with *L. lesueurii* being absent in the Kosterfjord sediments. At the same time data from the Continuous Plankton Recorder (CPR) in the North Sea demonstrate a considerable number of oceanic inflows occurring in the early 1950s, 1972, in the late 1980s, the early 1990s and in 1997/98 (Reid et al., 1992; Edwards et al., 1999), but again no records of *L. lesueurii* could have been found among published data for those periods.

It is interesting though that *L. lesueurii* has mostly been found as isolated individuals during the more recent warm period between the 1980s and the 2000s (Fig. 4) when a distinctly warmer climate prevailed in Sweden (e.g. Bergström and Moberg, 2002; Polovodova Asteman et al., 2018). Due to a low sampling resolution of the gravity core KSK12-01B it is difficult to see any changes in pteropod abundances in the area between 1980s and 2012 (Fig. 4), whilst higher-resolving data from the Gemini core KSK12-01D do show a subtle increase in *L. lesueurii* shells during the 1980s (Fig. 4), possibly reflecting the oceanic inflow and warming of the late 1980s (Reid et al., 1992; Edwards et al., 1999). In the English Channel, recently, there has been only occasional reports of *L. lesueurii* among marine zooplankton (Conway, 2012), suggesting that this species has become rare in the North Sea. Euthecosomatan pteropods are sensitive to ocean acidification (e.g. Manno et al., 2017), which is known as “the other CO<sub>2</sub> problem” threatening calcifying organisms in the oceans worldwide (Doney et al., 2009). León et al. (2020), report on shell dissolution in all pteropod taxa observed off NE Scotland between 2011 and 2013, despite “the seawater being supersaturated with respect to aragonite”, suggesting that aragonitic shell dissolution may occur at higher than previously thought saturation states. Communities of shelled pteropods in the North Sea generally show a declining trend from the late 1950s to 2010, which was attributed to combined impacts of climatic, chemical and biotic drivers rather than only to being caused by ocean acidification (Beare et al., 2013). In the Skagerrak part of the North Sea, based on observations, ocean acidification and dissolved pCO<sub>2</sub> over 2003–2015 do not show significant positive acidification

trends, suggesting that acidification is likely counteracted by a recent increase of total alkalinity in the Skagerrak waters and in the Baltic Outflow (Omar et al., 2019). The latter was suggested to increase in the area from 1993 to 2000 (Charrieau et al., 2019) and has been linked together with the increased precipitation and river runoff to the darkening of coastal waters in the Skagerrak (Frigstad et al., 2013). A decrease in surface water salinity has been also documented by hydrographic observations in the Kosterfjord (Polovodova Asteman et al., 2021). Manno et al. (2012) investigated the combined effect of freshening and ocean acidification on pteropods in the northern Norwegian Sea and reported increased mortality in *Limacina retroversa* when both salinity and pH were reduced. They suggested that pteropods could not cope with extra energy costs needed both to avoid sinking (at low salinity) and to counteract shell dissolution (at high pCO<sub>2</sub>), which decreased their survival. Whether the surface water freshening can be a cause behind the low recent numbers of *L. lesueurii* or it simply was absent along the Swedish west coast is unclear at this point as no regular observations of this species are available in the study area.

An interesting aspect of this study is related to preservation of pteropod shells, which are usually highly susceptible to taphonomic processes, such as carbonate dissolution, affecting sediment record. Hence, the high shell abundance of relatively well-preserved *L. lesueurii* in our record can be either explained by high sedimentation rates or by high pteropod abundances, or by both. The unusually high sedimentation rates of ~2 cm yr<sup>-1</sup> have indeed been previously reported for the KSK12-01 site (Polovodova Asteman et al., 2021). The same applies to the high pteropod abundances, which, according to the previous studies, may have resulted from the observed “enormous shoals” of *L. lesueurii* (Hardy, 1923; Fraser, 1961). In addition to this, a study performed in the English Channel reports on the “extraordinary high” abundance of *Clione limacina* (Lebour, 1931), a gymnosomatan pteropod, one of the major predators for *Limacina* species. *Clione limacina* is known to preferentially feed on soft tissues of *Limacina* pteropods leaving only empty shells behind (Lalli, 1970; Conover and Lalli, 1972). Hence, it is also reasonable to believe that if both *L. lesueurii* and *C. limacina* co-occurred together in the Kosterfjord, this coincidence could also have led to an increased sedimentation and preservation of *L. lesueurii* shells in our record.

Another rather intriguing explanation for a high pteropod shell abundance in sediment archives was proposed by Diester-Haass and Van der Spoel (1978), who compared the present-day occurrences of pteropods off Portugal and NW Africa with their abundances in a pteropod-rich layer from the Pleistocene-Holocene boundary. The authors suggested mass mortality of pteropods due to the harmful (toxic) algal blooms as another plausible cause for the formation of pteropod-rich layers. Based on historical data, there were indeed apparent cases of human poisoning by shellfish caused by the toxic algal blooms in the Skagerrak in the late 1930s (Karlsson et al., 2021 and references therein). Another toxic algal bloom in 1988 caused extensive fish mortalities and disrupted the entire ecosystem in the Kattegat-Skagerrak (e.g. Gjøsaeter et al., 2000). Both events fit in timing with deposition of sediments with high pteropod abundance between the 1920s and 1940s and increased abundances of *L. lesueurii* around the 1980s in the Kosterfjord. Also, over the past decade, toxic species of dinoflagellate *Alexandrium* have become increasingly common in the Skagerrak-Kattegat (Karlsson et al., 2021 and references therein), which is likely linked to the increased accumulation of *Alexandrium* spp. cysts in the sediments of the Kosterfjord since 2008 towards present (Polovodova Asteman et al., 2021). Whether this recent increase of harmful algal blooms in the area can be linked to the recent low occurrences of *L. lesueurii* in the Kosterfjord is unclear. This is because very little is known about how algal toxins affect fitness of pteropods. Some studies showed that pteropods can accumulate and retain dinoflagellate toxins and can cause extensive fish kills when being ingested (White, 1977, 1981). In the Indian Ocean, blooms of toxic algae and swarms of pteropods have been reported to co-occur together (Sakthivel and Haridas, 1974), but whether toxin production in microalgae is triggered by the presence of pteropods as grazers as it has been demonstrated for a dinoflagellate – copepod and a diatom – copepod relationships (e.g. Selander et al., 2015; Lundholm et al., 2018) is unknown as not much research has been done regarding this question.

## 7. Conclusions

Subtropical pteropod species *L. lesueurii* has been for the first time identified on the Swedish west coast in two sediment cores taken in the Kosterfjord. The pteropod, generally absent or occurring in low numbers throughout both cores, showed distinctly higher abundances between 100 and 130 cm core depth, which corresponds to ~1920–1950s. During this period positive sea surface temperature anomalies were reported in the North Atlantic and a number of oceanic water inflows have been documented for the North Sea. Some of these inflows were accompanied by “enormous shoals” of *L. lesueurii* observed off the coast of the UK. We hypothesize that *L. lesueurii* was transported into Skagerrak in connection with these inflows and due to the unusually high sedimentation rates in the Kosterfjord (and possibly also presence of toxic algal blooms) this event was preserved as a pteropod-rich layer in the sediment record of the Kosterfjord. We also propose the layer, rich in pteropod *L. lesueurii*, as a new valuable marker within event stratigraphy indicating oceanic water inflows and a general warming of the Skagerrak coastal waters.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2021.102083>.

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