

1 **Reconstruction of Atlantic herring (*Clupea harengus*) recruitment in the North**
2 **Sea for the past 455 years based on the $\delta^{13}\text{C}$ from annual shell increments of the**
3 **ocean quahog (*Arctica islandica*)**

4 Running title: Herring recruitment reconstruction

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17 **Abstract**

18 Understanding the recruitment variability of the Atlantic herring North Sea stock remains
19 a key objective of stock assessment and management. Although many efforts have been
20 undertaken linking climatic and stock dynamic factors to herring recruitment, no major attempt
21 has been made to estimate recruitment levels before the 20th century. Here we present a novel
22 annually-resolved, absolutely dated herring recruitment reconstruction, derived from stable
23 carbon isotope geochemistry ($\delta^{13}\text{C}$), from ocean quahog shells from the Fladen Ground (northern
24 North Sea). Our age model is based on a growth increment chronology obtained from fourteen
25 shells. Ten of these were micromilled at annual resolution for $\delta^{13}\text{C}$ analysis. Our results indicate
26 that the anthropogenically-driven relative depletion of ^{13}C , the oceanic Suess effect (oSE),
27 became evident in the northern North Sea in the 1850s. We calculated a regression line between
28 the oSE-detrended $\delta^{13}\text{C}$ results ($\delta^{13}\text{C}\dot{\text{S}}$) and diatom abundance in the North Sea, the regression
29 being mediated by the effect of phytoplankton on the $\delta^{13}\text{C}$ of the ambient dissolved inorganic
30 carbon. We used this regression to build an equation mediated by a nutritional link to reconstruct
31 herring recruitment using $\delta^{13}\text{C}\dot{\text{S}}$. The reconstruction suggests that there were five extended
32 episodes of low recruitment levels before the 20th century. These results are supported by
33 measured recruitment estimates and historical fish catch and export documentation. This work
34 demonstrates that molluscan sclerochronological records can contribute to the investigation of
35 ecological baselines and ecosystem functioning impacted by anthropogenic activity with
36 implications for conservation and stock management.

37 **Keywords**

- 38 • Catch per unit effort

- 39 • Ecosystem functioning
- 40 • Herring recruitment
- 41 • Historical documentation
- 42 • Sclerochronology
- 43 Stable carbon isotope geochemistry

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62 **Acknowledgments**

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64

65 **1 Introduction**

66 The North Sea herring has been a source of wealth and nutritional stability for the countries
67 bordering the North Sea going at least as far back as the Middle Ages (Pitcher & Lam, 2014).
68 Recruitment variability, i.e. the number of juvenile fish that survive from egg production to join

69 the stock, is known to be a crucial contributor to stock productivity (Pinnegar et al., 2016). The
70 socioeconomic impacts of extended low recruitment intervals were evidenced twice in the past
71 50 years. In the 1970s, herring recruitment failure led to a collapse of the fish stock and
72 temporary closure of the fishery. Later, in the 2000s, reduced recruitment levels caused the
73 fisheries management agencies to reduce the total allowable catch of the North Sea stock by half
74 (Corten, 2013). While annual estimates of herring recruitment in the North Sea are available for
75 the 20th and 21st centuries (Burd, 1978; ICES, 2018), understanding the long-term variability,
76 magnitude and drivers of recruitment can inform management efforts to keep the stock at
77 sustainable levels (Dickey-Collas et al., 2010; Simmonds, 2007).

78 In the classical view of the marine food-web in temperate seas, fisheries recruitment and
79 production is linked to diatom blooms (in spring and autumn); particularly, the energy of the
80 diatom bloom flows to fish, either directly (e.g. with large colonial diatoms; Chavez, Messié, &
81 Pennington, 2011; Ryther, 1969) or mediated through copepods (Cushing, 1989; Irigoien et al.,
82 2002). In fact, the phytoplankton community biomass of the North Sea is dominated by diatoms
83 during the spring bloom (e.g. (Halsband & Hirche, 2001; Nielsen & Richardson, 1989).

84 Other factors are also likely to contribute to fish recruitment and significant efforts have
85 been undertaken to understand the drivers of recruitment variability in the North Sea. These
86 include regression analyses between recruitment, stock densities and water temperature
87 (Akimova, Núñez-Riboni, Kempf, & Taylor, 2016; Bogstad, Dingsør, Ingvaldsen, & Gjørseter,
88 2013), and models based on the interaction of major climatic variability modes such as the North
89 Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) and stock densities
90 (Axenrot & Hansson, 2003; Gröger, Kruse, & Rohlf, 2010). Of these, Akimova et al., (2016) and

91 Bogstad et al. (2013) agree that water temperature is a poor herring recruitment predictor. On
92 the other hand, Axenrot and Hansson (2003) and Gröger et al. (2010) successfully modelled
93 herring recruitment in their studies but these were limited to the second half of the 20th century
94 and neither was able to provide an adequate mechanism to explain the interaction between
95 modes of climatic variability and recruitment.

96 The difficulty of defining a mechanism that associates climatic variability with fish
97 recruitment was evidenced in a study by Capuzzo et al. (2018). Although these authors found a
98 significant positive correlation between primary production and recruitment levels in different
99 fish stocks in the North Sea, they did not find a link between the NAO and primary production,
100 instead relating the latter to riverine nutrient inputs and sea surface temperature. Riverine runoff
101 is in turn influenced by the combined effects of the NAO and AMO (Hurrell, 1995; O'Reilly,
102 Woollings, & Zanna, 2017).

103 For periods before the 20th century, research has concentrated on fish landing
104 reconstructions from historical records. High quality records exist for Dutch, Scottish and Swedish
105 herring fisheries (Alheit & Hagen, 1996; Corten, 1999; Coull, 1986, 1990; Höglund, 1978; Jones,
106 Cathcart, & Speirs, 2016; B. Poulsen, 2008, 2010). While these records have been used to assess
107 the climatic impacts on herring migratory patterns (Alheit & Hagen, 1996; Corten, 1999), they
108 may not always be useful as a guide to estimate recruitment levels as this also requires
109 information about levels of natural and fishing mortality (Tester, 1955). To effectively address
110 this information gap, we require a set of reliably dated proxy data that are tightly coupled to
111 ecosystem variability, which extend at least as far back in time as the historical catch
112 reconstructions, and that also cover the 20th and 21st centuries.

113 In this study we present an annual reconstruction of North Sea herring recruitment for the
114 time interval 1551 to 2005 CE (hereafter all references to dates assume years CE) based on the
115 stable carbon isotopes of shells of the ocean quahog from the Fladen Ground in the northern
116 North Sea. The stable carbon isotope values (deviations of the $^{13}\text{C}:^{12}\text{C}$ ratio of a substance when
117 compared to the $^{13}\text{C}:^{12}\text{C}$ ratio of a standard, $\delta^{13}\text{C}$) from the ocean quahog's shell have been shown
118 to be proportional to the $\delta^{13}\text{C}$ of the dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) in the water column
119 (Beirne, Wanamaker Jr., & Feindel, 2012) and to not be affected by ontogeny or growth-rates
120 (Schöne, Pfeiffer, Pohlmann, & Siegismund, 2005; Schöne, Wanamaker Jr., Fiebig, Thébault, &
121 Kreutz, 2011). $\delta^{13}\text{C}_{\text{DIC}}$ and DIC concentration in the North Sea are largely controlled by primary
122 production and respiration (Bozec et al., 2006; Burt et al., 2016). Robust growth increment
123 chronologies can be built from the annual increments in the ocean quahog's shell (Butler et al.,
124 2010; Butler, Wanamaker Jr., Scourse, Richardson, & Reynolds, 2013; Butler, Richardson, et al.,
125 2009; Schöne et al., 2003; Scourse et al., 2006; Thompson, Jones, & Dreibelbis, 1980; Witbaard,
126 1996) which provide an accurate age model for stable isotopic results. The work presented here
127 reconstructs herring fish recruitment through the interpretation of temporally aligned $\delta^{13}\text{C}$
128 values of the ocean quahog's shell, through the relation between $\delta^{13}\text{C}_{\text{DIC}}$ and the wider ecosystem
129 in the North Sea.

130 In presenting this reconstruction we will (a) determine the timing of the anthropogenic-
131 driven relative ^{13}C depletion in the North Sea (oceanic Suess effect) and determine a time-
132 dependent mathematical formulation for it, (b) explore the relationship between the $\delta^{13}\text{C}$ from
133 the shell of the ocean quahog and diatom abundance, and (c) associate this relationship with
134 patterns of herring recruitment in the North Sea. As the first attempt to link molluscan

135 sclerochronological data to wider ecosystem functioning, this work constitutes a novel
136 application of ocean quahog sclerochronology.

137 2 Materials and methods

138 To reconstruct and test herring recruitment for the North Sea we adopted techniques used
139 in different fields. First, we established our age model by applying crossdating techniques first
140 developed by the tree-ring community and later adapted in the study of long-lived bivalves. We
141 did this by extending an existing northern North Sea ocean quahog increment chronology (Butler,
142 Richardson, et al., 2009) to be used solely as an age model.

143 We then obtained geochemistry of stable carbon isotopes from the shells comprising this
144 chronology and used it to build a continuous $\delta^{13}\text{C}$ time series covering the 1551-2005 interval. As
145 modern marine $\delta^{13}\text{C}$ records show a characteristic negative trend related to the burning of fossil
146 fuels (oceanic Suess effect, see below), we applied a modified technique routinely used in the
147 tree-ring and bivalve-increment communities, i.e. detrending.

148 We calibrated the detrended $\delta^{13}\text{C}$ time series against 20th century measurements of diatom
149 abundance and age-0 herring recruitment and used this calibration to reconstruct herring
150 recruitment during the 1551-2005 interval. Finally, we tested our reconstruction with various
151 independent historical records of catch per unit of effort.

152 2.1 Shell collection and processing

153 The ocean quahog shells used in this research were collected from the Fladen Ground in
154 the northern North Sea at coordinates 58.994° N, 0.291° E. The collection was acquired by the

155 RV *Prince Madog* in 2004. Figure 1 shows the approximate location of the collection site, together
156 with average annual herring landings from 2012 to 2016 by the UK-registered fishing fleet. Given
157 that the majority of herring spawning in the North Sea occurs in the vicinity of Orkney and
158 Shetland in northern Scotland, near the Fladen Ground (Heath & Richardson, 1989; Lusseau,
159 Gallego, Rasmussen, Hatfield, & Heath, 2014), and the tendency of juvenile herring to stay in
160 shallow waters before recruitment, it is not unreasonable to assume that an important part of
161 recruitment would also occur in or nearby the Fladen Ground.

162 We used a total of 16 shells, being a combination of live-collected specimens (five adults
163 originally described in Butler, Richardson, et al., 2009, and two juveniles), articulated valves and
164 single valves. Once cleaned, the shells were embedded in resin and sectioned using a standard
165 procedure (Butler, Richardson, et al., 2009; Scourse et al., 2006) to produce acetate peel replicas
166 (Ropes, 1984). Annual growth increments were identified and their widths measured in both the
167 shell hinge and ventral margin.

168 2.2 Accelerator mass spectrometry radiocarbon dating and chronology construction

169 Radiocarbon dating was carried out on the umbonal shell portion (deposited in early
170 ontogeny) of nine of the previously mentioned sixteen specimens (Scourse et al., 2006). Typically,
171 the juvenile section in the ocean quahog's shell contains the broadest increments and, therefore,
172 umbonal shell samples incorporate less than five years of growth (Helama, Schöne, Black, &
173 Dunca, 2006; Scourse et al., 2006). The material was submitted to the Natural Environment
174 Research Council Radiocarbon Laboratory (East Kilbride, United Kingdom) or the Accelerator
175 Mass Spectrometry ^{14}C Dating Centre (University of Aarhus, Denmark).

176 Our results are based on an extension of the Fladen Ground, Site B increment-width
177 chronology (FGB) described by Butler, Richardson, et al. (2009). FGB was selected as its extended
178 version (1755-2003) is the longest of the five Fladen Ground chronologies described by Butler,
179 Richardson, et al. (2009), and because a substantial number of shells from that site have been
180 radiocarbon-dated. The nine radiocarbon-dated specimens described above were put in relative
181 stratigraphic order and then crossdated with the five specimens in FGB and among each other
182 following the crossdating methods described by Butler, Richardson, et al. (2009) and Scourse et
183 al. (2006). The final increment-width chronology was built using the standard dendrochronology
184 software package ARSTAN (Cook & Krusic, 2014) by applying the methods described by Butler,
185 Richardson, et al. (2009) and Cook & Peters (1997). Two juvenile (age <30 yr) live collected
186 specimens were not crossmatched to FGB, but were independently dated by counting
187 increments.

188 The strength of the chronology was analysed with the standard dendrochronology and
189 sclerochronology statistics \bar{r} (the average correlation between pairs of shells with overlapping
190 lifespans) and the expressed population signal (EPS; variance explained by a finite subsample of
191 a population chronology, see Wigley et al., 1984). Their interpretation and estimation of
192 increment counting error are presented in the Supplementary Materials.

193 2.3 Micromilling and stable isotope analysis

194 Eight of the shells contained in the newly extended FGB were selected for isotopic analysis
195 at annual resolution on the time interval from 1551 to 1980. The selection was based on temporal
196 coverage of the individual shells and their taphonomic state, with preference given to the shells

197 that showed the least erosion, the broadest increments and those that provided at least 10 years
198 of temporal overlap between shell pairs. Two live-collected juvenile specimens were selected for
199 micromilling at annual resolution for the time interval 1976-2005. These specimens came from
200 the same site as the FGB shells but they were not incorporated into the chronology.

201 Milling was carried out on polished shell sections at the School of Ocean Sciences, Bangor
202 University, using a computerised New Wave/Elemental Scientific micromill system fitted with a
203 spherical tungsten carbide dental burr with a diameter of 300 μm at the tip. To minimise
204 aragonite to calcite transformation due to heating and stress (Foster et al., 2008), the rotation
205 speed was limited to 10-12 %, equivalent to 3,710-4,450 rpm. The milling for every resin-
206 embedded shell was performed on the ventral margin section on the outer shell layer after the
207 increments had been internally crossmatched (i.e. the increments found on the ventral margin
208 of a given shell were crossmatched with those found in the hinge of the same shell) and after the
209 outermost surface of the shells was physically removed to avoid contamination with remnants of
210 the periostracum and resin (Schöne, Schmitt, & Maus, 2017). Figure 2 shows a schematic of the
211 micromilling process. To avoid chipping, the milling direction was from the surface of the outer
212 shell towards the inner part of the shell, taking care not to incorporate material from the inner
213 shell layer in the samples. The entirety of the outer layer in each annual increment was milled
214 between the growth lines to an average depth of 100 μm .

215 All the powder extracted from a given increment was thoroughly homogenized before an
216 aliquot of the sample was isotopically characterised with a Thermo Fisher MAT 253 continuous-
217 flow isotope ratio mass spectrometer equipped with a GasBench II at the Institute of

218 Geosciences, University of Mainz (Germany). Samples were reacted with water-free H_3PO_4 at 72
219 °C for 2 hours. Isotope data were calibrated against an NBS-19-calibrated Carrara marble
220 standard ($\delta^{18}\text{O} = -1.91 \text{ ‰}$, $\delta^{13}\text{C} = +2.01 \text{ ‰}$) with 1σ external reproducibility (accuracy based on
221 421 blindly measured NBS-19 samples) better than 0.04 ‰ for $\delta^{18}\text{O}$ and 0.03 ‰ for $\delta^{13}\text{C}$ and
222 internal precision better than 0.06 ‰ for $\delta^{18}\text{O}$ and 0.04 ‰ for $\delta^{13}\text{C}$. Both isotope values were
223 reported relative to the Vienna Pee Dee Belemnite standard. Note that we did not apply a
224 correction for different acid fractionation factors of the shell samples (aragonite) and the
225 reference material (calcite). For more detailed description and reasoning see Füllenbach, Schöne,
226 & Mertz-Kraus (2015).

227 We inspected the results against the average peak intensity given by the mass
228 spectrometer and rejected those that showed abnormally high/low isotope values and those
229 with intensities falling significantly outside the range of the reference materials. Lower-than-
230 average peak intensities are related to insufficient mass in the carbonate powder sample.

231 [2.4 Adjustment for the oceanic Suess effect](#)

232 We approximated the oceanic Suess effect (oSE), i.e., the relative depletion of ^{13}C in
233 carbonate material due to fossil fuel burning since the second half of the 19th century, using a
234 weighted Fourier regression consisting of the two largest coefficients (Supplementary Material).
235 The weights were given by $1/\sigma^2$ where σ represents the internal $\delta^{13}\text{C}$ precision for each sample.
236 The purpose of this approximation is not to capture the entire variability of the oSE but, rather,
237 determine its onset in the northern North Sea.

238 To emphasise the high frequency variability, we subtracted the oSE as given by our
239 regression from the raw $\delta^{13}\text{C}$ data ($\delta^{13}\text{C}\dot{\text{S}}$, " $\delta^{13}\text{C}$ Sdot"). The $\delta^{13}\text{C}\dot{\text{S}}$ was weight-averaged into a
240 single series before comparison with diatom assemblages or herring recruitment data.

241 2.5 Modern diatom and recruitment data

242 We used diatom abundance data as a proxy of diatom biomass at our site (Leblanc et al.,
243 2012). Diatom abundance data was obtained from the Continuous Plankton Recorder (CPR)
244 Survey, operated by the Sir Alister Hardy Foundation for Ocean Science. The CPR is a near-surface
245 (10 m) plankton sampler voluntarily towed each month behind merchant ships on their normal
246 routes of passage. We used the annual maximum diatom count from the CPR standard area B2
247 (Figure 1) for the years 1958 to 2005 (Johns, 2016).

248 Annual age-0 herring recruitment data for the years 1947 to 2005 was obtained from the
249 International Council for the Exploration of the Sea (ICES) 2017 fish stock assessment for the
250 North Sea, Skagerrak, Kattegat, and east English Channel, the so called "North Sea autumn
251 spawners" (ICES, 2018). Annual age-2 recruitment for the years 1919 to 1973 was obtained from
252 Burd (1978) for central and northern North Sea. The recruitment for the two areas was averaged
253 into a single annual series. The Burd (1978) and ICES (2018) data overlap between the years 1953
254 and 1973 and, in general, show that the age-2 recruitment reported by Burd (1978) is ten times
255 smaller than the age-0 recruitment (ICES, 2018). However, herring catch statistics from ICES
256 (2017) show an approximate age-2:age-0 catch ratio of 5 to 1 in the overlapping time interval
257 which suggests that the recruitment reported by Burd (1978) may be an underestimation. We
258 thus scaled the Burd (1978) recruitment data by a factor of 10 before comparing to our analysis.

259 2.6 $\delta^{13}\text{C}\dot{\text{S}}$ calibration

260 The $\delta^{13}\text{C}\dot{\text{S}}$ data were compared to the *log-transformed* maximum diatom count (Johns,
261 2016) and *log-transformed* age-0 herring recruitment (ICES, 2018) (see Supplementary Material
262 for detailed description and reasoning). The latter two were also compared against each other.

263 A cross calibration/verification (CCV) using reduced major axis (RMA) regressions was
264 performed after removal of outliers in the $\delta^{13}\text{C}\dot{\text{S}}$ and herring recruitment and diatom count for
265 the interval 1947-2015. The outliers were identified graphically in a modified box and whisker
266 plot where the extent of the first and fourth quartiles (represented by the whiskers) is
267 constrained to be less than 1.5 times the combined height of the second and third quartiles
268 (represented by the box). Data outside this constraint is considered an outlier. Three outliers
269 were identified in MD and HR (1969, 1970, 1972, and 1975-1977, respectively) and one was
270 identified in $\delta^{13}\text{C}\dot{\text{S}}$ (1979).

271 Six equations were generated from the CCV procedure: two equations relate $\delta^{13}\text{C}\dot{\text{S}}$ to
272 maximum diatom count (MD), two relate MD to herring recruitment (HR) and two relate $\delta^{13}\text{C}\dot{\text{S}}$
273 to HR. The $\delta^{13}\text{C}\dot{\text{S}}$ /MD and MD/HR equations that produced the residuals with the lowest
274 heteroscedasticity were combined to generate an additional $\delta^{13}\text{C}\dot{\text{S}}$ /HR equation which was
275 compared with those generated from the regression procedure. We applied the $\delta^{13}\text{C}\dot{\text{S}}$ /HR
276 equation with the most significant statistics to the rest of the $\delta^{13}\text{C}\dot{\text{S}}$ series and further verified the
277 results against the scaled version of the Burd (1978) record.

278 2.7 Comparison to historical data

279 As a mean to verify our reconstruction prior to the 20th century, the recruitment was also
280 compared to historical catch per unit effort (CPUE, Garstang, 1900). CPUE is defined as

$$\frac{C}{E} = qN$$

281 where C represents the catch, E represents the effort, N is the fish density and q is the catchability
282 coefficient (Arreguín-Sánchez, 1996; R. T. Poulsen & Holm, 2007). The effort can be defined in
283 different ways, ranging from the number of ships in a given year's fishing fleet, the total area of
284 fishing net, or the ships' dimensions and power. For the purpose of this study, we worked with
285 the left-hand side of the CPUE equation only.

286 The CPUE calculations come from Dutch, Scottish, and English fisheries (Figure 1). The
287 Dutch record (1604-1856) was compiled and calculated by B. Poulsen (2008) from the archives
288 of the College van de Grote Visserij (CGV) which held a monopoly on the salted herring landings
289 in the Netherlands from the late 1500s until the 1850s. The catch data compiled by B. Poulsen
290 (2008) was registered in the southern towns of Schiedam and Vlaardingén. B. Poulsen (2008)
291 used the fishing ships' dimensions and power as his unit of effort which remain consistent
292 throughout the entire time series. The fishing vessels associated with the CGV carried hemp
293 driftnets until 1859 (B. Poulsen, 2008) so the adoption of lighter cotton nets does not factor into
294 the Dutch CPUE record.

295 The English record (1750-1789) was compiled by Cushing (1968) from "An historical
296 account of the ancient town of Lowestoft" by Edmund Gillingwater in 1790. In his book,
297 Gillingwater provides the "total average of each owner's boat" which is the total catch by that

298 owner divided by the number of boats. Cushing (1968) calculated the CPUE representing all
299 fishermen and suggests that their nets were made of hemp.

300 Two Scottish CPUE records are presented. The first one is from southeast Scotland (1845-
301 1889), compiled and calculated by Jones et al. (2016) from the archives of the United Kingdom
302 Fishery Board (UKFB). Jones et al. (2016) used the total area of driftnet in a given year as their
303 unit of effort. Using the total area of driftnet considers the adoption of lighter cotton nets
304 introduced c.1860 (Coull, 1986).

305 The second Scottish CPUE record is from the Peterhead district in the north of Scotland
306 (1835-1914). Herring cure records and number of fishing vessels were compiled by Coull (1986),
307 presumably from the UKFB archives which covered all of Scotland for the interval of interest and
308 recorded the landings of fish intended for cure (Jones et al., 2016). We calculated the Peterhead
309 CPUE by assuming that the cured herring represented the great majority of the catch and divided
310 it by the number of fishing vessels in a given year. Of all four CPUE used, this one is the weakest
311 as it fails to consider technological developments.

312 The CPUE data used in this study were standardised into dimensionless indices to account
313 for differences in definition of effort. We did this by subtracting the series average from every
314 data point and dividing the result by the series standard deviation. This harmonisation only scales
315 the CPUE data, so it can be plotted in a common axis. Correlation analyses are not affected by
316 standardisation.

317 3 Results

318 3.1 Chronology

319 We extended FGB from its original start point of 1755 back to 1545 (Figure 3a). In general,
320 the interval from 1545-1755 is represented by fewer shells than the interval from 1755-2003
321 (Figure 3b), with the average number of shells being 2.66 for the former and 6.49 for the latter.
322 The interval from 1545 to 1588 is represented by only one shell.

323 We observed a decreased \bar{r} and EPS (Figure 3c) in the 1545-1751 interval (average for the
324 complete segment: $\bar{r} = 0.41$, EPS = 0.67) when compared to 1764-2003 (average for the complete
325 segment: $\bar{r} = 0.63$, EPS = 0.91). These intervals are separated by an interval (1752-1763) of near-
326 zero average values (average: $\bar{r} = 0.03$, EPS = 0.02) which is represented by six shells, four of which
327 settled during that time, showing biological ages between 3 and 15 years in 1763.

328 An F-test on the year-to-year differences of the new segment of the chronology and that
329 originally constructed by Butler, Richardson, et al. (2009) suggests that our newly extended
330 chronology has an increment counting error lower than 5% (Supplementary Material), which
331 allows us to confidently base our stable isotopic results on the age model provided by FGB.

332 3.2 Annual stable carbon isotope values

333 We obtained annual $\delta^{13}\text{C}$ results from 1551 to 1980 from eight shells in FGB, while results
334 for 1975 to 2005 were obtained from two additional juvenile shells not contained in FGB. We
335 were not able to achieve the target temporal overlap of ten years between shell pairs as single-
336 increment sampling becomes increasingly difficult in later ontogeny as the increments get

337 compressed into a smaller area. The average temporal overlap between specimens was nine
338 years with a minimum of one year and a maximum of 26 years.

339 Following our sample-rejection convention in combination with samples that were under
340 the detection limit of the machine and powder samples that were lost in the milling process,
341 resulted in data being available for 422 out of the 455 years of temporal coverage. The longest
342 hiatuses occur in the 20th century in the intervals between 1939-1944 and 1955-1959.

343 The composite $\delta^{13}\text{C}$ results fall within the range 3.38 ‰ to 0.13 ‰ (Figure 4), the former
344 occurring in 1655 and the latter in 1979. The results from the 19th to 21st century show a depletion
345 of ^{13}C relative to times before the 19th century, reflecting the introduction of isotopically light
346 carbon from the burning of fossil fuels into the oceanic dissolved inorganic carbon (DIC) pool and
347 biogenic carbonate material (Butler, Scourse, et al., 2009; Moore, Charles, Rubenstone, &
348 Fairbanks, 2000; Schloesser, Rooker, Louchuoarn, Neilson, & Secor, 2009; Schöne et al., 2011;
349 Swart et al., 2010), the so-called $\delta^{13}\text{C}$ oceanic Suess effect (oSE). Our Fourier approximation of
350 the oSE was highly significant, with a coefficient of determination of 0.71 ($p < 0.0001$). The first
351 derivative of our approximation shows that consistent ^{13}C depletion began in c.1820. The second
352 derivative shows that there was an increase in the rate of depletion in c.1850 from $-0.0025 \text{ ‰ yr}^{-1}$
353 ¹ (1817-1848) to $-0.0104 \text{ ‰ yr}^{-1}$ (1848-1914). We take this sudden change in depletion rate as
354 the onset of the oSE at our location. The maximum rate of ^{13}C depletion occurs in 1914 (-0.0131
355 ‰ yr^{-1}). After that, the depletion slows down until it stops in 1986 after which we observe an
356 average increase in $\delta^{13}\text{C}$ at a rate of 0.0028 ‰ yr^{-1} until 2005.

357 After subtraction of the Fourier regression from the individual shell $\delta^{13}\text{C}$, the residuals
358 ($\delta^{13}\text{C}\dot{\text{S}}$) were weight-averaged (Figure 5). The resulting $\delta^{13}\text{C}\dot{\text{S}}$ series shows an average value of -
359 0.04 ‰ with a standard deviation of 0.35 ‰.

360 3.3 $\delta^{13}\text{C}\dot{\text{S}}$ -based maximum diatom abundance and herring recruitment estimates

361 We undertook two RMA linear regressions on the $\delta^{13}\text{C}\dot{\text{S}}$ /MD data using the temporal
362 intervals of 1962-1988 and 1988-2005 as cross calibration/verification (CCV) intervals. The same
363 was done for the MD/HR and $\delta^{13}\text{C}\dot{\text{S}}$ /HR pairs for the CCV intervals of 1959-1990/1991-2015 and
364 1960-1985/1985-2005, respectively. To obtain the highest correlations, MD was lagged by one
365 year (i.e., $\delta^{13}\text{C}\dot{\text{S}}_{\tau=2000\text{ CE}}$ was compared with $\text{MD}_{\tau=1999\text{ CE}}$). We obtained the following equations:

$$MD_{\tau-1} = (0.4969 \pm 0.1021) \delta^{13}\text{C}\dot{\text{S}} + (5.540 \pm 0.0016) \quad (1)$$

$$MD_{\tau-1} = (0.5727 \pm 0.1024) \delta^{13}\text{C}\dot{\text{S}} + (5.546 \pm 0.0008) \quad (2)$$

$$HR = (1.253 \pm 0.2221) MD_{\tau-1} + (0.4119 \pm 1.565) \quad (3)$$

$$HR = (0.8934 \pm 0.1717) MD_{\tau-1} + (2.551 \pm 0.9031) \quad (4)$$

$$HR = (1.133 \pm 0.2228) \delta^{13}\text{C}\dot{\text{S}} + (7.386 \pm 0.0040) \quad (5)$$

$$HR = (0.6237 \pm 0.1193) \delta^{13}\text{C}\dot{\text{S}} + (7.493 \pm 0.0016) \quad (6)$$

366 HR and MD are log-transformed and all uncertainties in Equations 1-6 represent the standard
367 error in slope and intercept. Table 1 summarises the equations' statistics and calibration
368 intervals.

369 When applied to their respective verification intervals, Equations 1, 3 and 6 perform
370 better than their counterparts, the linear-space standard deviation of residuals being 82.09×10^3
371 diatoms for Equation 1 and 183.62×10^3 diatoms for Equation 2, 16.85×10^9 recruits for Equation
372 3 and 17.65×10^9 recruits for Equation 4, and 19.34×10^9 recruits for Equation 5 and 16.50×10^9

373 recruits for Equation 6. The residuals from Equations 1, 3 and 6 also show the lowest levels of
374 heteroscedasticity, given by the Breusch-Pagan score, meaning that they maintain a stable
375 variability within their predictive range. However, by combining Equations 1 and 3 we derive an
376 equation with lower residual heteroscedasticity, higher coefficient of determination and higher
377 significance than those obtained from the equations derived from the RMA regressions:

$$HR = (0.6228 \pm 0.1690) \delta^{13}C\dot{S} + (7.356 \pm 1.991) \quad (7)$$

378 Equation 7 has a standard error of prediction of 11.60×10^9 recruits (equivalent to the
379 standard deviation of residuals), the lowest of all the HR equations, calculated for the same
380 calibration interval as for Equation 6 (Figure 6a, 6b). In the verification interval of 1960-1985,
381 predictions made by Equation 7 fall within 24×10^9 recruits of the real value 62% of the time,
382 compared to 57% for Equation 6.

383 As an independent verification of Equation 7, we used the scaled age-2 recruitment data
384 from Burd (1978) for the northern North Sea (1919-1973). This comparison shows that Equation
385 7 overestimates the scaled recruitment by an average of 7.16×10^9 recruits (Figure 6b). The
386 residuals, however, are normally distributed ($W = 0.9865$, $p = 0.9135$, $JB = 0.0592$, $p = 0.9709$)
387 with a standard deviation of 5.80×10^9 recruits, well within the standard error of prediction.

388 In addition to the low recruitment levels during the early 2000s and the late 1970s, our
389 reconstruction shows that there were five extended episodes (≥ 4 yr, interrupted by ≤ 2 yr) of low
390 herring recruitment levels prior to the 20th century (1589-1607, 1629-1638, 1759-1762, 1799-
391 1802, and 1885-1893). These were defined as values lower than the average 1551-2005 annual
392 reconstructed recruitment (24.79×10^9 recruits) minus one standard deviation (13.02×10^9
393 recruits). Similarly defined episodes of extended high recruitment levels occurred between 1552-

394 1564, 1653-1665, 1681-1700, 1840-1847, 1901-1904, and 1982-1988. The average duration of
395 the extended low recruitment episodes is 8.5 years and occur with an average periodicity of 69.2
396 years (this calculation includes the 1976-1980 episode). The average duration of extended high
397 recruitment episodes is 10.8 years and occur with an average periodicity of 75.4 years.

398 3.4 Relationship to historical catch per unit effort

399 Our HR reconstruction shows positive correlations with the Dutch, English and Scottish
400 CPUE standardised indices. When compared to the CPUE reconstruction of the Dutch herring
401 fishing fleet, we find the strongest HR:CPUE correlation when the fishing occurs between one
402 and three years after the herring recruitment (Figure 6d, Figure 7a). During the 17th century
403 (1604-1698) the Dutch CPUE reconstruction has an average temporal resolution of 2.35 years
404 and shows the weakest overall HR:CPUE correlation when analysed within ± 5 years of
405 recruitment (i.e., correlation analysis done by lagging the CPUE series five years before and five
406 years after recruitment). The strongest correlation after recruitment occurs at a one year lag but
407 does not show significance ($r = 0.23$, $p = 0.14$) while a significant HR:CPUE correlation is present
408 when the fishing precedes the recruitment by 3 years ($r = 0.35$, $p = 0.03$). The 18th century CPUE
409 data (1700-1781) has an average temporal resolution of 1.25 years and shows significant
410 correlations with HR at lags between one year preceding recruitment and four years after, the
411 most significant occurring two years after recruitment ($r = 0.47$, $p = 7.8 \times 10^{-5}$). The 19th century
412 Dutch CPUE data, representing the years 1820-1855 at a two-year resolution, shows the
413 strongest correlation to our HR reconstruction when fishing occurs one and three years after
414 recruitment ($r = 0.47$, $p = 0.04$ and $r = 0.48$, $p = 0.04$).

415 A similar pattern arises when comparing our reconstruction to the English CPUE from
416 Lowestoft (Figure 6d, Figure 7b). The Lowestoft CPUE has annual resolution from 1750-1789 and
417 does not show significant correlation with HR within ± 5 years of recruitment. If we expand the
418 window to include year 6 after recruitment, however, we find a significant HR:CPUE correlation
419 of 0.31 ($p = 0.049$).

420 The pattern of positive HR:CPUE correlations is also present in the Scottish fisheries (Figure
421 6c, Figure 7b). We found significant positive correlations with the southeast Scotland CPUE (Jones
422 et al., 2016) for the years 1845-1871 (annual resolution) and our reconstruction at lags between
423 one and four years after recruitment has taken place, the most significant occurring two years
424 after recruitment ($r = 0.50$, $p = 0.0008$). The relationship is weaker but still significant when
425 comparing against the CPUE derived from the Peterhead District for the years 1835-1914 (annual
426 resolution, Coull, 1986), where we find significant correlations to our HR reconstruction when
427 fishing occurs three and four years after recruitment ($r = 0.29$, $p = 0.009$ and $r = 0.24$, $p = 0.03$).
428 If the Peterhead data are divided into two segments (1835-1870 and 1871-1914) and the
429 correlation analysis is repeated, we find a significant correlation with our HR reconstruction when
430 fishing occurs three years after recruitment ($r = 0.36$, $p = 0.04$) for the first segment. Similarly, a
431 significant correlation when fishing occurs between two and five years after recruitment has
432 taken place in the second segment, the most significant occurring three years after recruitment
433 ($r = 0.57$, $p = 0.0001$).

434 4 Discussion

435 4.1 Nutritional link between stable isotopic signal and abundance estimates

436 In 2012 Beirne et al. showed that $\delta^{13}\text{C}$ variability in the shell of the ocean quahog is
437 controlled by $\delta^{13}\text{C}_{\text{DIC}}$ variability in the water column, itself being partly controlled by primary
438 production. Equation 1 is used to reconstruct the maximum diatom abundance because, as
439 primary production increases (during the spring diatom bloom, for example), ^{12}C is preferentially
440 incorporated into the blooming biomass, leaving the ambient water enriched in ^{13}C (Gruber et
441 al., 1999). The likely reason for the one-year lag in the maximum $\delta^{13}\text{C}_{\text{S}}:\text{MD}$ correlation is the
442 timing of the phytoplankton bloom and the onset of the water column stratification at the Fladen
443 Ground. CPR data from the northern North Sea (Johns, 2016) indicates that the MD occurs on
444 average (1958-2015) late in April and is closely followed by the onset of thermal stratification
445 (van Leeuwen, Tett, Mills, & van der Molen, 2015; Warrach, 1998). The ocean quahog community
446 at the Fladen Ground is, therefore, disconnected from the phytoplankton bloom for most of its
447 growing season (February to August, see Schöne, Pfeiffer, et al., 2005) and only has access to the
448 ^{12}C -depleted DIC from the previous year.

449 Similarly, the reconstruction of herring recruitment using Equation 3 depends on how well
450 it can represent food availability for the fish. Capuzzo et al. (2018) showed that a decline in
451 primary production in the North Sea for the years 1988-2013 produced a knock-on effect on
452 higher trophic levels, indicating a bottom-up control of the local ecosystem. In their study,
453 Capuzzo et al. (2018) found that the 25-year decline in primary production caused a decline in
454 small copepod abundances which, in turn, caused a decline in fish recruitment in seven

455 commercially-important fish stocks in the North Sea. The correlation ($r = 0.45$) between primary
456 production and fish recruitment index observed by Capuzzo et al. (2018) is similar to that which
457 we found between MD and HR ($r = 0.50$, Equation 3). The slightly stronger covariance is not
458 surprising as small copepods show a preference for consuming diatoms (Frederiksen, Edwards,
459 Richardson, Halliday, & Wanless, 2006; Irigoien et al., 2002, 2000) while constituting a staple of
460 North Sea herring diet (Last, 1989; Segers, Dickey-Collas, & Rijnsdorp, 2007).

461 The HR: $\delta^{13}\text{C}_S$ relationship shown in Equation 6 is more subtle. According to Kürten et al.
462 (2013), North Sea copepods from the North Dogger Bank occupy higher relative trophic levels in
463 February than during the rest of the year. The higher trophic position of the copepods
464 corresponds to higher overall somatic $\delta^{13}\text{C}$ as they consume ^{12}C -depleted phospholipid-derived
465 fatty acids. The small copepods are then preyed upon by juvenile herring (Last, 1989), also in
466 February (Segers et al., 2007). As the food is being digested, high-magnesium carbonates with
467 relatively high $\delta^{13}\text{C}$ values are precipitated within the fish intestine, later to be excreted in mucus-
468 coated tubes and faecal pellets (Jennings & Wilson, 2009). These excretions fall through the water
469 column while being rapidly degraded by zooplankton and bacteria (Hansen & Bech, 1996;
470 Lampitt, Noji, & von Bodungen, 1990) and the high-Mg CaCO_3 precipitates contained within the
471 excretions dissolves as they reach the benthos (Viitasalo, Rosenberg, Heiskanen, & Koski, 1999;
472 Woosley, Millero, & Grosell, 2012). This dissolved carbonate would change the overall local
473 $\delta^{13}\text{C}_{\text{DIC}}$ which would, in turn, be reflected in the ocean quahog's shell (Beirne et al., 2012). Most
474 of this heavy high-Mg CaCO_3 will be precipitated in the intestines of age-0 to age-1 recruits when
475 the fishing mortality rates are $\sim 6\%$ or higher, assuming a constant natural mortality rate of $\sim 27\%$
476 (Jennings & Wilson, 2009; Ricker, 1975).

477 By combining Equations 1 and 3 into Equation 7 we are explicitly including the diatom-
478 mediated nutritional link between HR and $\delta^{13}\text{C}_s$. Equation 7 is therefore to be preferred over
479 Equation 6, which expresses a purely statistical relationship.

480 4.2 Dutch, English and Scottish herring industry in the context of recruitment variability

481 Our herring recruitment reconstruction (Figure 6a) is supported by a variety of historical
482 records derived from different sources that cover different geographical extensions. The decline
483 in recruitment observed from the second half of the 16th century until the beginning of the 17th
484 century coincides with a decline in salted herring exports from east Scotland that began in 1541
485 at an average rate of $-7.6 \times 10^3 \text{ kg yr}^{-1}$ (Rorke, 2001, 2005). An apparent recruitment failure in the
486 early 17th century is reflected in the Scottish herring exports to Sweden as the export per ship
487 declined from $19.0 \times 10^3 \text{ kg}$ in 1592 to $5.8 \times 10^3 \text{ kg}$ in 1604 (Dow, 1969). No Scottish fish exports
488 to Sweden were made in 1605-06 and the exports remained infrequent until 1616 (Dow, 1969),
489 the year which, according to our reconstruction, the recruitment is fully stabilised and on a
490 positive trend.

491 ICES (2018) data shows that, for the second part of the 20th century, there is a strong and
492 significant correlation between recruitment and catch, especially when the catch occurs four
493 years after recruitment has taken place ($r = 0.68$, $p \ll 0.01$). Thus, a general positive correlation
494 between historical CPUE and reconstructed HR was expected. However, using the CPUE model
495 defined in section 2.7 assumes a linear relation between catch and fish abundance which may
496 not always be correct (Erismann et al., 2011; Harley, Myers, & Dunn, 2001). This is due to
497 hyperstability, the tendency of CPUE remaining elevated as stock declines due to the schooling

498 behaviour of fish. Hyperstability can be observed in overexploited stocks. Nevertheless, the
499 historical data presented here comes from intervals when overexploitation of the complete
500 North Sea herring stock was unlikely, and it is the only assessment tool available.

501 The change in the strength and significance of the Dutch CPUE:HR correlation is revealing
502 when examining the historical catches within the biological context. For example, the Dutch
503 CPUE:HR correlation is at its lowest during the 17th century. During this time, the Dutch fishing
504 season started in June and lasted until January and the fishing fleet distributed its effort between
505 Shetland, Scotland and Northern England from June to September while the rest of the season
506 the fleet went south to the Dogger Bank, East Anglia and the English Channel (B. Poulsen, 2008).
507 The apparent early 17th century recruitment failure, combined with the Anglo-Dutch wars in the
508 second half of the 17th century, might have forced the Dutch fleet to spend more time fishing
509 further south which would have caused a decoupling between recruitment in the northern North
510 Sea and the fisheries records.

511 We observe a stronger CPUE:HR coupling in the 18th century when the fishing occurs two
512 years after recruitment. As the Dutch fleet regained access to the Fladen Ground, the fishing
513 season lasted from June to November and the Dutch spent the first two-thirds of the season in
514 the northern North Sea between Shetland, Scotland and northern England when they would land
515 the majority of the fish for the season (B. Poulsen, 2008).

516 In the 19th century we observe the highest CPUE:HR correlation for our record for the Dutch
517 fishing fleet (B. Poulsen, 2008). The strengthening of the correlation with the Dutch CPUE is likely
518 related to the fishing patterns adopted in the 1800s. As was the case in the 18th century, the

519 fishing season lasted from June to November and the fleet would spend its time between
520 Shetland, Scotland and northern England and would not head much further south than the
521 Dogger Bank. The fleet would dedicate the second half of the season to fishing in Scottish waters,
522 with the months of October and November being spent in the Fladen Ground (B. Poulsen, 2008).

523 The case of the Lowestoft herring fishery CPUE stands out as the only one without a
524 significant correlation with HR within ± 5 years of recruitment. As with the case of the Dutch
525 fishery, this can be explained by the fishing practices adopted in Lowestoft. Here the fishing
526 season was shorter than in the Dutch Republic, going from the 29th of September (Michelmas
527 Day) to the 22nd of November (Martinmas Day) and the fishermen would stay within 70 km of
528 the coast (Cushing, 1968). Cushing (1968) suggest that if the fish behaved in the 1700s as they
529 did in the first half of the 20th century then the average age of capture was between five and
530 eight years. The 6-year lag after recruitment required to obtain significance between our HR
531 reconstruction and CPUE is in good agreement with this assumption.

532 The weaker Peterhead CPUE:HR correlation is most likely due to the definition of “effort”
533 as the number of fishing boats at a given time when we calculated the Peterhead CPUE. This
534 definition fails to consider the improvements in technology through time, such as the
535 introduction of the decked fife ships in the 1870s (Smylie, 1999) which were capable of going
536 into open waters (Jenkins, 1913) and the adoption of cotton nets in the 1860s (Coull, 1986).
537 Having to divide the record in segments before and after these technological improvements to
538 obtain stronger correlations highlights the importance of the “effort” definition when working
539 with CPUE data.

540 Jones et al. (2016) argues that the observed significant decline in standardised CPUE for
541 the SE Scottish fleet at a rate of -0.057 yr^{-1} ($p = 5.30 \times 10^{-7}$) in the years 1845-86 was due to over-
542 exploitation of the fishery. Overexploitation by the SE Scottish fleet is rather unlikely, as the
543 localised nature of fishing activities in Scotland (Harris, 2000; Jones et al., 2016) would have a
544 limited effect on the herring stock as a whole. The similar significant decline in standardised CPUE
545 observed in Peterhead (Coull, 1986) from 1835-70 (-0.051 yr^{-1} , $p = 1.52 \times 10^{-3}$) strongly indicates
546 a common cause rather than two local phenomena, especially because the North Sea herring are
547 considered a unit-stock (Mariani et al., 2005). Our reconstruction, which shows a decline in
548 recruitment that lasted most of the second half of the 19th century, provides a plausible
549 explanation for these two local negative trends. These results further suggest that declines in
550 recruitment are not caused by fishing mortality in an under-exploited fish stock.

551 5 Conclusions

552 In this study we developed an absolutely-dated 455-year long carbon stable isotope series
553 from the shells of the ocean quahog. This series is currently the longest in temporal extension for
554 the region and it suggests that the onset of the oSE occurred in the early 1850s. By subtracting
555 the oSE from the series we emphasised the high frequency variability in $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_\text{S}$) and
556 calculated a significant regression line between $\delta^{13}\text{C}_\text{S}$ and diatom abundance in the North Sea.
557 The two quantities in this regression line are linked by the effect of phytoplankton primary
558 production on $\delta^{13}\text{C}_\text{DIC}$. We used this regression to build an equation mediated by a nutritional link
559 (diatom abundance) that allowed us to reconstruct herring recruitment in the North Sea using

560 $\delta^{13}\text{C}\text{S}$. Our reconstruction is supported by independent recruitment estimates, by historical CPUE
561 documentation from the Netherlands, England and Scotland and by east Scotland fish exports.

562 Our work provides the longer time scale needed to understand the interaction between
563 climatic parameters and stock densities. It also demonstrates that molluscan sclerochronological
564 records can contribute to the study of the ecosystem functioning to which the socioeconomical
565 stability of the countries surrounding the North Sea is ultimately tied.

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844

845 Table 1. Summary statistics of Equations 1-7. Equation 7 is the result of substituting Equation 1 into Equation 3 and
 846 shows the highest coefficient of determination for herring recruitment, the smallest standard error of estimate and
 847 the residuals with the lowest heteroscedasticity.

Equation	Calibration interval	n	r ²	p _{Eq}	Standard error of estimate	Breusch-Pagan test on residuals	p _{BP}
1	1962-1988	18	0.3248	0.0135	163.0 x 10 ^{3†}	0.4703	0.4928
2	1988-2005	18	0.4888	0.0012	90.50 x 10 ^{3†}	1.044	0.3068
3	1959-1990	26	0.2461	0.0010	20.22 x 10 ^{9‡}	5.007	0.0252
4	1991-2015	26	0.0993	0.1168	15.02 x 10 ^{9‡}	12.86	0.0003
5	1960-1985	21	0.2650	0.0170	24.08 x 10 ^{9‡}	9.855	0.0017
6	1985-2005	21	0.3045	0.0095	12.62 x 10 ^{9‡}	0.6415	0.4232
7	-	41 [§]	0.6242 [§]	0.0013 [§]	11.60 x 10 ^{9‡}	0.3486 [§]	0.5550

848 † Units: diatoms

849 ‡ Units: recruits

850 § Calculated for 1960-2005

851

852 Figure 1. Approximate location of sites mentioned in the text along with annual average herring
853 landings by UK-registered ships between the years 2012-2016 (Richardson, 2017) per ICES
854 standard rectangle and the CPR standard area B2. Colour figure can be viewed at
855 wileyonlinelibrary.com.

856 Figure 2. Schematic of the micromilling process. All the powder extracted from an increment was
857 thoroughly homogenized before an aliquot of the sample was isotopically characterised. Colour
858 figure can be viewed at wileyonlinelibrary.com.

859 Figure 3. Newly extended chronology from Site B at the Fladen Ground (a). The extension of FGB
860 (1545-1754) is composed of fewer shells (b) than its original iteration (1755-2001) and shows
861 lower \bar{r} and EPS scores (c). The dotted line in c represents the commonly used threshold value for
862 EPS, 0.85. Colour figure can be viewed at wileyonlinelibrary.com.

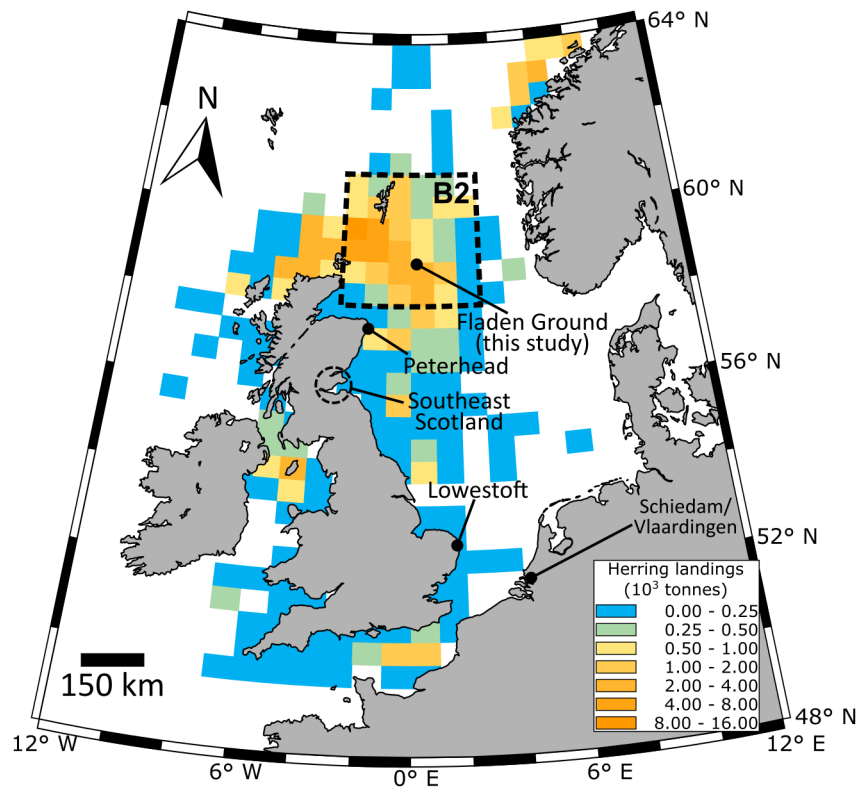
863 Figure 4. $\delta^{13}\text{C}$ results for every shell analysed. The results show the relative depletion of $\delta^{13}\text{C}$
864 starting in the second half of the 19th century, i.e., the oceanic $\delta^{13}\text{C}$ Suess effect. The
865 superimposed dashed line shows our weighted 2-term Fourier regression which suggests that the
866 onset of the oceanic Suess effect at the Fladen Ground occurs c.1850. Colour figure can be viewed
867 at wileyonlinelibrary.com.

868 Figure 5. Weight-averaged $\delta^{13}\text{C}$ residuals from the oceanic Suess effect ($\delta^{13}\text{C}\dot{\text{S}}$). The great
869 majority of the uncertainties are smaller than the thickness of the line (not shown). $\delta^{13}\text{C}\dot{\text{S}}$ shows
870 an average value of -0.04 ‰ with a standard deviation of 0.35 ‰. Extended intervals (≥ 4 yrs)
871 with negative deviations greater than 1σ occur in the late 1500s to early 1600s, 1630s, and early
872 and late 1800s. Extended intervals with positive deviations greater than 1σ occur in the 1550s,

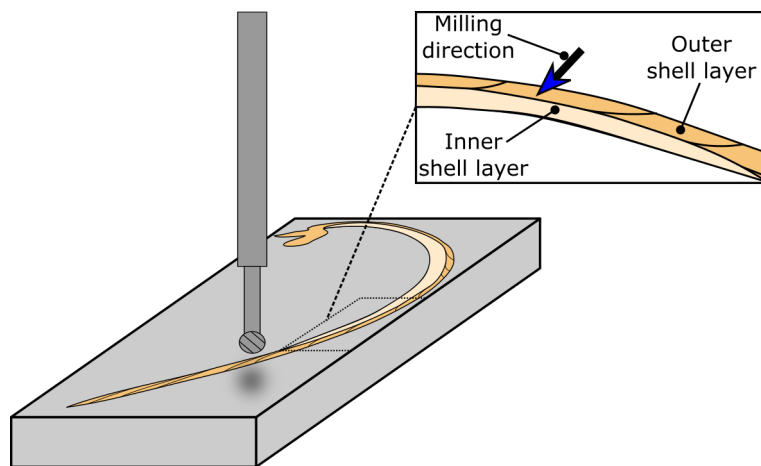
873 1650s, late 1600s, 1840s, early 1900s and in the 1980s. Colour figure can be viewed at
874 wileyonlinelibrary.com.

875 Figure 6. (a) Reconstructed herring recruitment based on Equation 7. Our reconstruction shows
876 extended intervals of low recruitment from 1600-1650, most of the 1700s, 1860-1900 and most
877 of the 1900s. (b) Reconstructed recruitment compared to instrumental recruitment for the 20th
878 century. Measured recruitment data for time intervals when predicted data are not available has
879 been omitted. The predictions made by Equation 7 lie within 24×10^9 recruits of the ICES, (2018)
880 value 62% of the time. (c and d) Reconstructed recruitment compared to historical CPUE from
881 the Scottish, English and Dutch fishing fleets. Colour figure can be viewed at
882 wileyonlinelibrary.com.

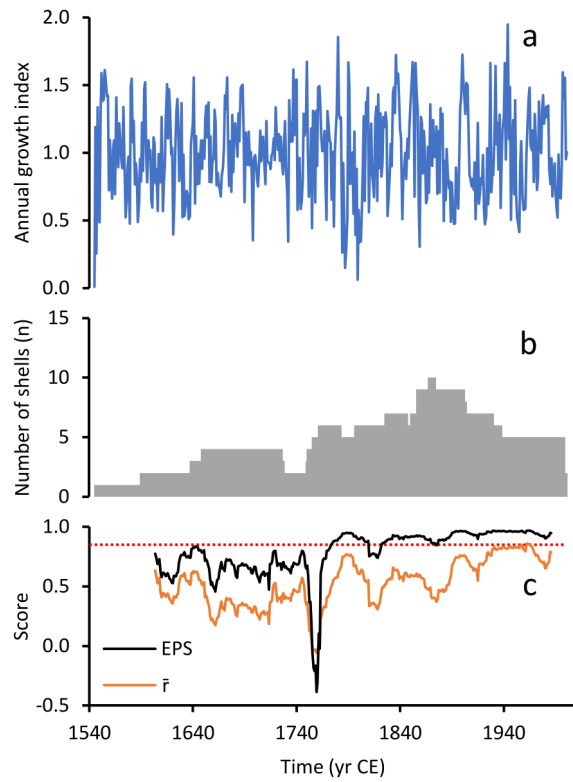
883 Figure 7. Relation between the reconstructed herring recruitment and CPUE from the Dutch (a),
884 east English and east Scottish fishing fleets (b) at different lags before and after the year of
885 recruitment. There is a general indication that the strongest HR:CPUE correlation occurs between
886 one and three years after recruitment. The strength of the HR and Dutch CPUE relationship varies
887 according to the century, the weakest being in the 17th century, coincident with the Anglo-Dutch
888 wars in the second part of the century (filled circles in c). HR is more strongly related to the SE
889 Scottish CPUE (1845-1871) two years after recruitment has occurred while the relationship is
890 stronger with the English CPUE six years after recruitment. The relationship is not as strong with
891 the Peterhead District CPUE. This may be due to the amalgamation of the data before and after
892 the introduction of cotton nets in the 1860s and decked fife ships in 1870 (see text for details).
893 The scatter plots in c and d show the CPUE data that has the strongest correlation after lagging.
894 Colour figure can be viewed at wileyonlinelibrary.com.



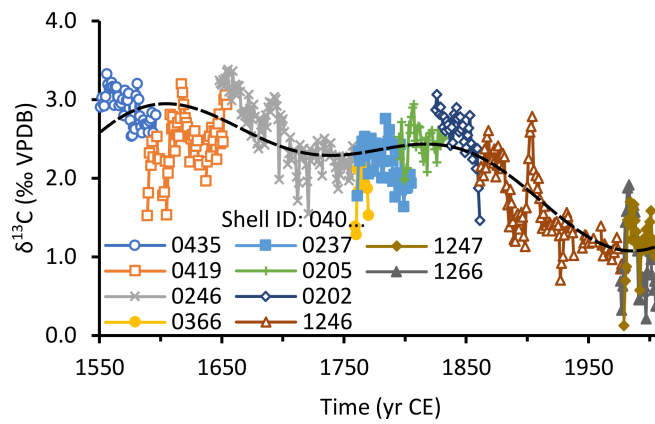
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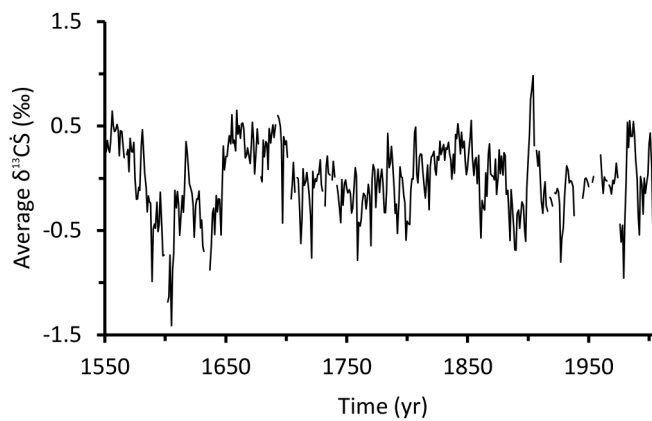
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