1 **The nutritional quality of zooplankton in the Southern Ocean**

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19 **Abstract**

20 Knowledge of the trophic ecology of zooplankton is essential for evaluating their functional roles in

21 marine food webs and nutrient cycling since they represent the link between primary producers and

22 higher trophic levels. Here we investigated the fatty acid (FA) composition of different zooplankton

23 size classes and selected species collected at the vicinity of the Sub-Antarctic Kerguelen Islands in

24 late austral summer 2018 as part of the MOBYDICK research project. The analysis revealed that

25 zooplankton FA composition varied significantly across size classes and species but not among

26 stations. Larger zooplankton generally had higher total FA (TFA) amounts per dry weight (22.1 ± 3.0

27 vs. 61.9 ± 11.8 mg g^{-1}). Essential FAs (EFA) accounted for 40.5 ± 0.8 % of TFA, with 22:6n-3 (DHA)

28 and 20:5n-3 (EPA) being the most prominent. Diatom trophic markers (TM) were abundant in larger

29 zooplankton size classes, while non-diatom TM were more prevalent in smaller size classes. The FA-

30 based nutritional quality index (NQI) of zooplankton was positively correlated with EFA and DHA,

31 and it was higher than the NQI of phytoplankton concurrently collected, indicating its better

32 nutritional quality compared to primary producers. This study highlights the importance of size and

33 species-specific dietary preferences in determining zooplankton FA profiles and the high nutritional

34 quality of this group collected during late austral summer, which significantly contribute to our

35 understanding of zooplankton's ecological role in marine food webs in the Southern Ocean.

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37 **Keywords:** mesozooplankton, food web, fatty acid, biomarker, Kerguelen Islands, primary consumer

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1. INTRODUCTION

40   In the global ocean zooplankton have pivotal roles in the biological carbon pump and food web,

41   representing a key trophic link between the phytoplankton and higher trophic levels (e.g., fish,

42   seabirds, mammals), transferring organic matter through grazing (Steinberg and Landry, 2017). For

43   instance, mesozooplankton which range from 200 μm to 2 mm, has been estimated to consume ~12

44   % of global oceanic primary production annually (Calbet, 2001). Furthermore, zooplankton facilitate

45   organic carbon export to the deep ocean through vertical migrations and the downward flux of their

46   faecal pellets/carcasses (Halfter et al., 2022; Nowicki et al., 2022). The magnitude and quality of

47   particle flux are tightly linked to zooplankton community characteristics including abundance,

48   biovolume and size range (Buitenhuis et al., 2010; Kiørboe, 2013), while information on lipids and

49   fatty acid composition being generally overlooked.

50   Fatty acids (FA) and especially polyunsaturated FA (here after PUFA) are essential

51   components for any living organism, composed primarily of carbon, and mostly acquired through

52   dietary intake (Arts et al., 2001; Dalsgaard et al., 2003; Tocher, 2015). They represent an energy store

53   for consumers, while also playing key roles in several metabolic functions of organisms, including

54   regulating homeoviscous adaptation and cell membrane functioning (Copeman and Parrish, 2003).

55   Herbivorous zooplankton FA composition is tightly linked to FA of their main food source,

56   phytoplankton, which varies among taxa, with some groups (e.g., diatoms, dinoflagellates,

57   haptophytes) being characterized by a higher proportion of PUFA, and thus better food quality, in

58   comparison to others (e.g., cyanobacteria, chlorophyceae) (Cañavate, 2019; Jónasdóttir, 2019).

59   Certain phytoplankton groups produce specific FA which are subjected to limited or no

60   transformation across trophic levels and are therefore useful biomarkers and can represent good

61   proxies of food composition and quality. For example diatoms produce a relatively high percentage

62   of 16:PUFA and 20:5n-3 (EPA), haptophyte/dinophytes a high percentage of 18:PUFA and 22:6n-3,

63   and cyanobacteria produce mostly short-chain PUFA (i.e., ≤ C18 PUFA) (Cañavate, 2019;

64   Jónasdóttir, 2019; Parrish, 2013). Because consumers cannot synthetize PUFA in sufficient quantities

65 to satisfy their nutritional requirements and must acquire them through the diet (Bi and Sommer,

66 2020; Litzow et al., 2006), the variability in the FA composition of producers will be reflected in the

67 FA composition of the consumers and subsequent trophic levels (e.g., Müller-Navarra et al., 2000;

68 Vargas and González, 2004; Brett et al., 2006; Hanson et al., 2010).

69 The fatty acid-based nutritional quality index (NQI) has been recently developed to assess the

70 quality of a food source for higher trophic levels, based on the composition of essential FA (EFA;

71 i.e., 20:4n-6, 20:5n-3, 20:6n-3), given the key role that some FA have in regulating organism

72 functions (Arts *et al.*, 2001; Cañavate, 2019). While such index was initially developed for

73 phytoplankton as the main producers of EFA (Cañavate et al., 2021; Puccinelli et al., 2023; Remize

74 et al., 2022), there is potential to apply this index to primary consumers such a zooplankton as a

75 measure of their nutritional value to a wide range of commercially relevant fish species (Bi and

76 Sommer, 2020; Hicks et al., 2019).

77 The Kerguelen Islands are an archipelago located in the Indian sector of the Southern Ocean,

78 that lies within the Antarctic Circumpolar Current (ACC) (Tynan, 1998; Rintoul et al., 2001). The

79 archipelago is characterized by the presence of a relative shallow plateau (< 700 m) south-east of the

80 islands that favors topography-driven upwelling events (Park et al., 2008). These events supply

81 essential macro- (e.g., nitrate, silicate) and micronutrients (e.g., iron) to surface waters, supporting

82 high primary productivity over and downstream of the plateau (Bucciarelli et al., 2001; Quéroué et

83 al., 2015; Schallenberg et al., 2018). During the austral late spring-summer (November to February)

84 different phytoplankton regimes can be observed in the proximity of the Kerguelen Islands, including

85 High Nutrient Low Chlorophyll (HNLC) areas typical for the open ocean and upstream areas of the

86 plateaus, and Low Nutrient High Chlorophyll (LNHC) areas over the plateau and in the downstream

87 regions (Blain et al., 2007; Mongin et al., 2008). Micro phytoplankton, composed mainly of diatoms

88 that are known producers of high amounts of PUFA, may contribute 80–90% to the total primary

89 production in LNHC regions, whereas the HNLC areas are mainly dominated by small diatoms and

90 nano-flagellates (Uitz et al., 2009).

4

In this study we aim to investigate the FA composition and nutritional quality of different size classes and single species of zooplankton in LNHC and HNLC regions in the Southern Ocean, using the Kerguelen Plateau region as a case study. Specifically, we hypothesized that regardless of the size, zooplankton communities located in HNLC regions would be characterized by lower amount of FA and of lower quality (<PUFA) than communities at LNHC stations located on or downstream of the plateau.

2. MATERIAL & METHOD

2.1. Study area and sample collection

The sampling was performed abord the *R/V Marion Dufresne II* during late austral summer, as part of the "Marine Ecosystem Biodiversity and Dynamics of Carbon around Kerguelen" MOBYDICK program conducted in the proximity of the Kerguelen Islands (MOBYDICK PROJECT – Oceanographic cruise off Kerguelen Island (Southern Ocean) (osupytheas.fr)).

The sampling was conducted at four stations (Fig 1) located upstream (M3-M4), on (M2) and downstream (M1) of the Kerguelen Plateau. Stations M1 and M2 were classified as LNHC and M3 and M4 as HNLC based on published literature (de Baar et al., 1995). Station M2 was sampled three times (M2-1, M2-2, and M2-3), station M3 twice (M3-1, M3-3), while stations M1 and M4 were sampled once (Table 1). During the sampling, station M3 was located north of the Polar Front, a major feature regulating the productivity of the region and primarily controlled by topography (Park et al., 2014; Rigual-Hernández et al., 2015); while the three other stations were permanently located south of the Polar Front (Pauthenet et al., 2018).

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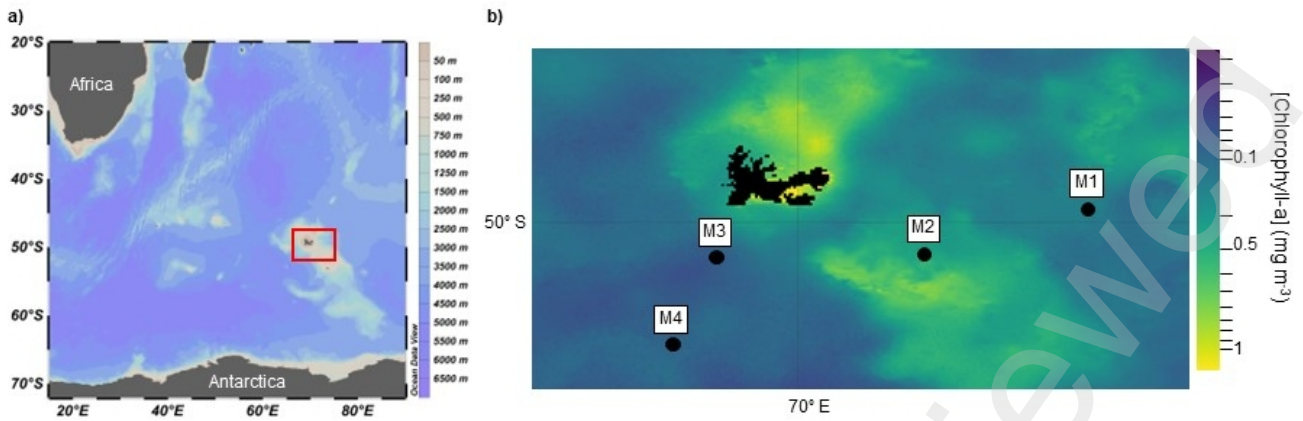
Fig 1 Map of the study region (a) indicating the location of the Kerguelen Islands (red box); and zoom in (b) showing the four stations (M1, M2, M3, M4) where sampling was conducted. The coloured shading in b indicates surface chlorophyll *a* concentration (mg m^{-3}) on the 7th of March 2018, obtained using the resolution Global Ocean Satellite Observations (Copernicus-Globcolour, Copernicus Marine Service, http://marine.copernicus.eu/).

Mesozooplankton samples were collected using a vertically hauled WP2 plankton net (2.5 m long, 57 cm diameter), fitted with 200 µm mesh and hauled vertically from 200 m depth) A first subsample of the net catch was used to estimate zooplankton abundance and identification (data available in Hunt *et al.*, 2021), while a second subsample was dedicated for FA analyses. The latter samples were size fractionated on board into five size classes (125 µm, 250 µm, 500 µm, 1000 µm and 2000 µm), and the content of each class was stored in separated cryovials. Additional zooplankton sampling was conducted using a WP3 plankton net (2 m long, 1.13 m diameter) fitted with 1000 µm mesh and targeted species (> 4000 µm in size) were collected and stored in cryovials for FA analyses. The species included: *Salpa thompsoni* Foxton, *Rhincalanus gigas* Brady, *Themisto gaudichaudii* Guérin, *Paraeuchaeta spp.*, *Euphausia vallentini* Stebbing. FA samples were stored at -80°C during the voyage, and subsequently shipped to inland laboratory facilities in dry ice where they were stored at -80°C until further analysis.

Table 1 Information of the stations sampled for fatty acid analysis during the MOBYDICK cruise at the Kerguelen Plateau in February-March 2018.

Station	Latitude (°S)	Longitude (°E)	Bottom depth (m)	Date of sampling	Visit
M1	49.9	74.9	2723	10/3/2018	M1
M2	50.6	72	520	27/02/2018	M2-1
				8/3/2018	M2-2
				17/03/2018	M2-3

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M3	50.7	68.1	1730	5/3/2018	M3-1
				19/03/2018	M3-3
M4	52.6	67.2	4731	3/3/2018	M4-1

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2.2. Fatty acid analyses

136 Total lipids were extracted using a modified method of Folch et al. (1957). A known amount of the

137 lipid extract (1-2 mL) was resuspended into chloroform:methanol (98:2; v/v). Neutral lipids (NL) and

138 polar lipids (PL) were then separated by adsorption chromatography on a silica gel micro-column.

139 NL were eluted with 10 mL of chloroform:methanol (98:2, v/v) and PL with 20 mL of methanol. A

140 known amount of the FA 23:0 was added to each sample as an internal standard. NL and PL fractions

141 were dried under vacuum using the evaporator Genevac. The FA methyl esters (FAME) of each

142 fraction, were obtained after acidic transesterification of the sample by the addition of a solution of

143 sulfuric acid/methanol (3.4%; v/v), and heated at 100°C for 10 min. The polar fraction FAME formed

144 were stored at -20°C until Gas Chromatography (GC) analysis, while neutral fraction FAME were

145 purified via High Performance Liquid Chromatography (HPLC), following the method of Marty et

146 al. (1999). The HPLC was equipped with two columns (LiChrospher Si 60 and LiChrospher 100

147 DIOL, both 5 μm) and a Dionex HPLC system (P680 pump AS-100 auto sampler, UVD170U UV

148 detector with deuterium lamp, Foxy fraction collector), and it was used to separate FAME from other

149 non-needed compounds (e.g., alcohols), which are formed after neutral lipid FAME formation. The

150 purified FAME were stored at -20°C until GC analysis.

151 FAME composition of each sample and fraction was determined using a Varian CP8400 GC equipped

152 with a ZBWAX column (30 m x 0.25 190 mm ID x 0.2 μm) and a flame ionisation detector, with

153 hydrogen as the carrier gas, housed at the LIPIDOCEAN facility in Brest, France. Samples were

154 injected in splitless mode. Peaks were identified by comparison with retention times of external

155 known standards (Supelco 37 Component FAME Mix, PUFA No.1 and No.3, and Bacterial Acid

156 Methyl Ester Mix from Sigma) using Galaxie 1.9.3.2 software (Varian). FA are reported using a

157 shorthand notation of A:Bn-*x*, where A indicates the number of carbon atoms, B is the number of

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158 double bonds and x indicates the position of the first double bond relative to the terminal methyl

159 group (Budge et al., 2006). FAME content was converted into FA (from neutral and polar lipids)

160 content based on 23:0 recovery. Data are reported as total FA (TFA) which is the sum of the polar

161 and neutral FA of each sample. TFA content was calculated as the sum of 55 identified FA, Poly-

162 unsaturated FA (PUFA) as the sum of 27 PUFA, Mono-unsaturated FA (MUFA) as the sum of 16

163 MUFA, and Saturated FA (SFA) as the sum of 13 SFA. Data are expressed in $\mu g\ mg^{-1}$ dry weight as

164 well as a proportion of the TFA (% of TFA). Amongst the common FA trophic markers (FATM), the

165 FA 16:1n-7, 16:2n-4, 16:2n-7, 16:3n-4, 16:4n-1 and 20:5n-3 (EPA) were used as diatom TM, while

166 the FA 18:1n-9, 18:3n-3, 18:4n-3 and 22:6n-3 (DHA) as non-diatom TM, following published

167 literature (Parrish et al., 2000; Cañavate, 2019; Jónasdóttir, 2019) and the work conducted on the

168 phytoplankton FA composition during the same cruise (Remize et al., 2022). EPA, DHA and 20:4n-

169 6 (arachidonic acid, ARA) are considered essential FA (EFA) in acquatic ecosystems (Parrish, 2013).

170 20:1n-11+22:1n-9 are indicative of zooplankton energy storage (Lee et al., 2006) and 18:1n-9 is used

171 to indicate carnivory (Graeve et al., 1994). Additionally, the nutritional quality of phytoplankton for

172 higher trophic levels was estimated using the FA-based nutritional quality index (NQI) calculated

173 following equation 1 of Cañavate (2019):

174 $$NQI = [(15DHA + 10EPA + 2ARA) * 0.8 + (\Sigma PUFA18) * 0.2] * \log(n - 3/n - 6)$$

175 where, DHA, EPA and ARA represent the % (of TFA) of 22:6n-3, 20:5n-3 and 20:4n-6, respectively.

176 $\Sigma PUFA18$ is the sum of 18:2n-6, 18:3n-3, 18:4n-3, % of TFA. n-3/n-6 is the ratio of Σn-3 FA to Σn-

177 6 FA.

178 **2.3.   Data Analyses**

179 A multivariate permutational analysis (PERMANOVA; Anderson & Clarke, 2008) was performed to

180 test for differences in the zooplankton TFA composition among the factors *Size Class* (n = 6; 125 μm,

181 250 μm, 500 μm, 1000 μm, 2000 μm, >4000 μm) and *Station* (n = 4). Further analyses were

182 performed to investigate differences among *Species* (n = 5; *Salpa thompsoni*, *Rhincalanus gigas*,

183 *Themisto gaudichaudii*, *Paraeuchaeta spp.*, *Euphausia vallentini*). Preliminary analysis indicated that

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184   the factor *time of sampling* did not have any significant effects on the zooplankton TFA composition

185   ($p > 0.05$), and it was thus not included in the subsequent analyses. Samples from different time of

186   sampling were used as replicates in the analyses. While stations were initially classified as LNHC

187   (M1, M2) and HNLC (M3, M4), we decided not to include this factor in the experimental design, in

188   order to investigate variation among stations without further constrains. The results are then discussed

189   within the framework of productivity of the stations/region.

190   Each term in the PERMANOVA analysis was tested using >9999 permutations as the relevant

191   permutable units (Anderson and Braak, 2003). In the event of significant results, PERMANOVA

192   pairwise tests were performed. Principle component analysis (PCA) was used to explore differences

193   in the zooplankton FA composition among factors. FA analyses were based on Euclidian

194   dissimilarities calculated from non-transformed percentage data. These analyses were conducted

195   using the PERMANOVA+ add-on package of PRIMER v6 (Anderson & Clarke, 2008).

196   We tested the effects of the factor *Size class* and *Station* on TFA, EPA and DHA zooplankton

197   concentrations and NQI, using a factorial analysis of variance (ANOVA). In the event of significant

198   results, Tukey HSD *post hoc* tests were conducted. Pearson correlation analyses were performed to

199   investigate possible relationships between the NQI and TFA, EFA, DHA and EPA of the zooplankton

200   size classes investigated. Analyses were performed using R version 3.6.3. (R Core Team, 2020).

201   PRIMER v6, Ocean Data View (OVD) and R software were used for visualisation of the data.

202

203   **3. RESULTS**

204   While no effects of *Station* were observed on the zooplankton TFA concentrations, significant effects

205   were observed among size classes with larger specimens generally having higher concentrations of

206   TFA than the smallest classes ($p<0.001$; Fig 2, Table S.1 a). Within the 4000 µm size class, which

207   was exclusively represented by single species, *S. thompsoni*, generally had low TFA concentrations,

208   similar to the smaller zooplankton size classes (5.7 ± 1.3 µg mg^{-1}), while *Paraeuchaeta* spp. and *E.*

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209 *vallentini* had the highest TFA recorded concentrations (135.7 ± 31.5 and 105 ± 11.3 µg mg^{-1}

210 respectively, Fig 3).
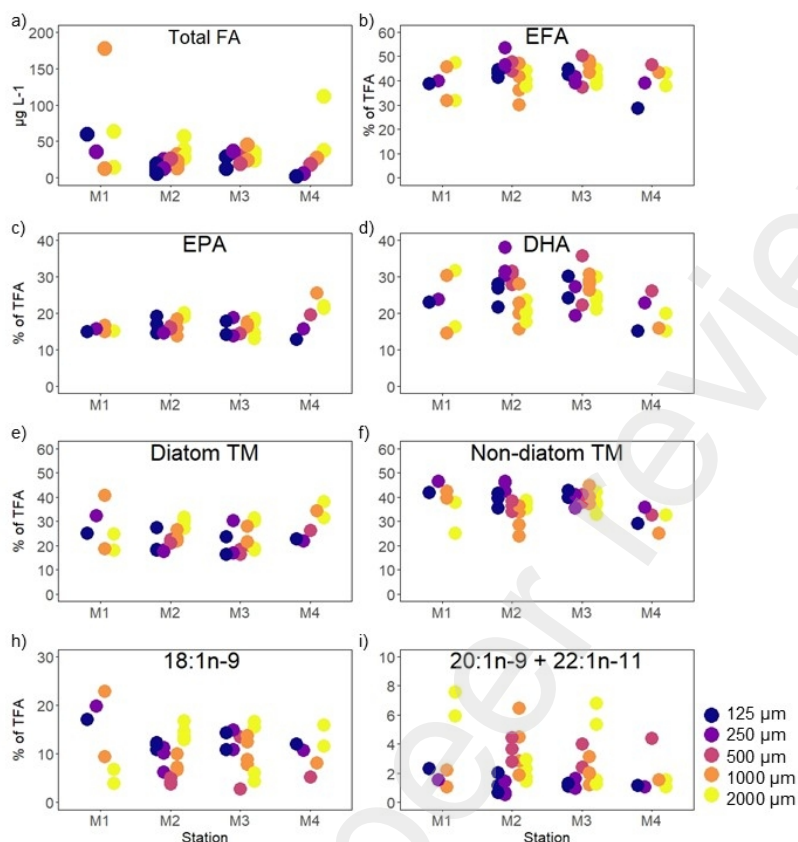
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212 **Fig 2** Fatty acid (FA) composition of zooplankton size classes (2000, 1000, 500, 250, 125 µm) of
213 samples collected in February-March 2018 at the proximity of the Kerguelen Plateau. a) Total FA
214 (dry weight µg mg^{-1}), b) Essential FA (20:4n-6, 20:5n-3, 22:6n-3), c) EPA (20:5n-3), d) DHA (22:6n-
215 3), e) diatom TM (Trophic Markers : 16:1n-7, 16:2n-4, 16:2n-7, 16:3n-4, 16:4n-1), f) non-diatom TM
216 (18:3n-3, 18:4n-3, 18:5n-3), g) zooplankton energy storage (20:1n-9+22:1n-11), h) carnivory (18:1n-
217 9). Panel b-g are expressed as % of Total FA (a). Each symbol represents a sample.

218
219 EFA accounted for 40.5 ± 0.8 % of TFA (Fig 4 a, Table S.1), with relative proportions of three EFA

220 (i.e., DHA, EPA, ARA) changing as a function of size class (p<0.001; Fig 2 and Fig 4b). EPA was

221 the most represented EFA for species > 4000 µm (19.6 ± 1.3 % of TFA, 51.6 ± 2.6 % of EFA), except

222 *S. thompsoni* which had a higher proportion of DHA vs. EPA (29.1 ± 1.0 vs. 16.5 ± 0.8 % of TFA for

223 DHA and EPA, respectively). DHA was the most represented EFA in the 125-2000 µm size classes

224 (24.7 ± 1.3 % of TFA, 58.0 ± 1.5 % of EFA). ARA represented only a small portion of TFA ($0.8 \pm$

225 0.2 %) and 1.9 ± 0.1 % of EFA (Fig 4b).

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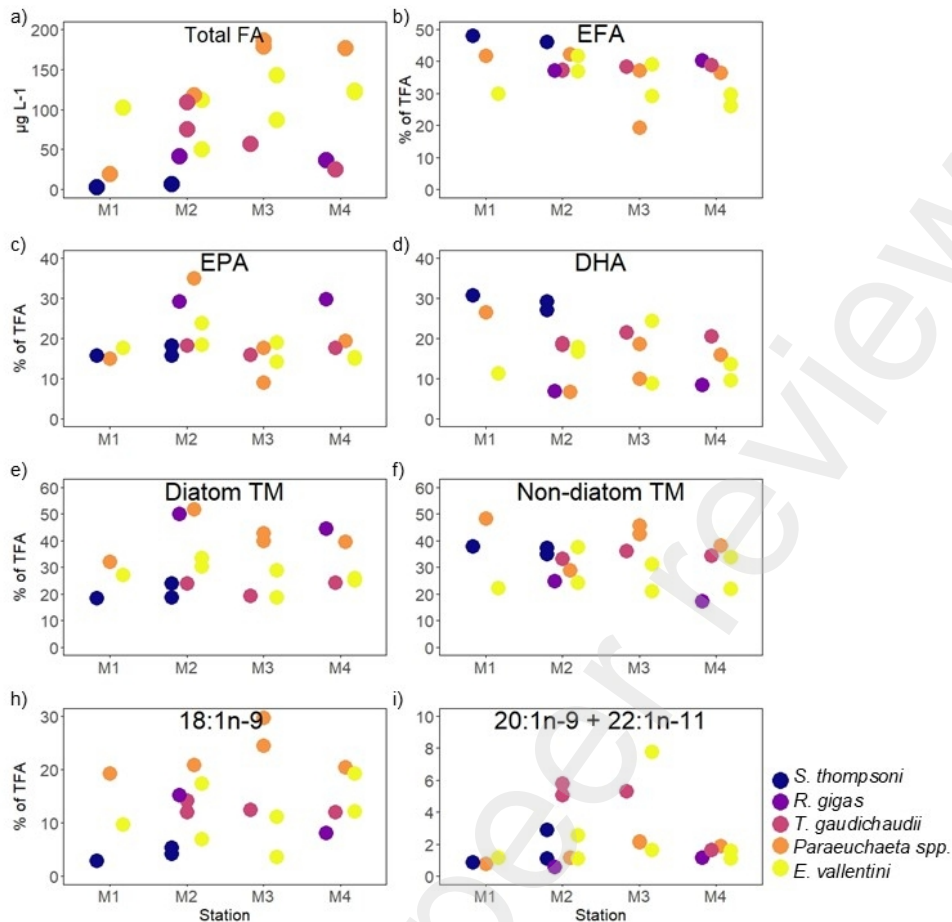
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Fig 3 Fatty acid (FA) composition of zooplankton species (*Salpa thompsoni*, *Rhincalanus gigas*,
Themisto gaudichaudii, Paraeuchaeta spp., *Euphausia vallentini*) collected in February-March 2018
at the proximity of the Kerguelen Plateau. a) Total FA (dry weight $\mu g \, mg^{-1}$), b) Essential FA (20:4n-6,
20:5n-3, 22:6n-3), c) EPA (20:5n-3), d) DHA (22:6n-3), e) diatom TM (Trophic Markers : 16:1n-7,
16:2n-4, 16:2n-7, 16:3n-4, 16:4n-1), f) non-diatom TM (18:3n-3, 18:4n-3, 18:5n-3), g) zooplankton
energy storage (20:1n-9+22:1n-11), h) carnivory (18:1n-9). Panel b-g are expressed as % of Total FA
(a). Each symbol represents a sample.

The only factor affecting FATM was *Size Class*. Diatom TM were more prominent in the largest size

classes and in the species *R. gigas* (47.3 ± 2.3 % of TFA, Table S.1), while non-diatom TM (e.g.,

dinoflagellate, haptophyte) were more abundant in small size classes (125-500 μm; Fig 2e, f). *S.*

thompsoni and *T. gaudichaudii* had higher amounts of non-diatom TM vs. diatom TM (20.4 ± 2.7 vs.

36.8 ± 2.1 % of TFA; 23.0 ± 1.7 vs. 34.3 ± 0.9 % of TFA, Fig 3e, f). Similar amounts of diatom and

non-diatom TM were observed in *Paraeuchaeta spp.* (41.2 ± 3.2, 40.7 ± 3.4 % of TFA respectively)

and *E. vallentini* (21.1 ± 3.2, 27.5 ± 4.5 % of TFA respectively, Table S.1).

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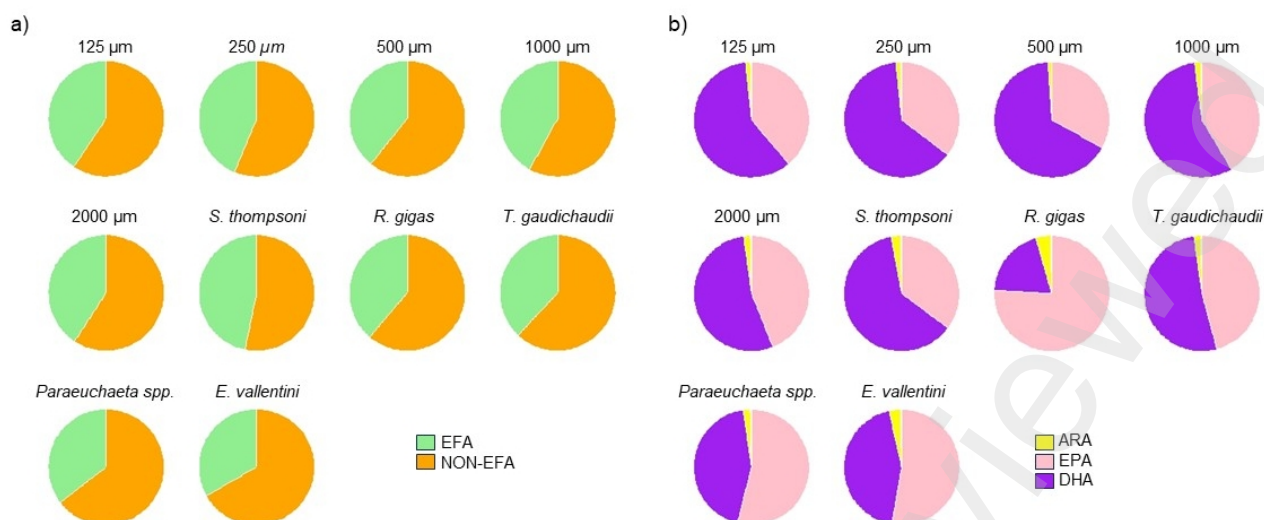
Fig 4 Relative contribution (%) of a) essential fatty acid (EFA) vs. non-EFA (% of total FA) and of b) the three EFA, ARA (20:4n-6), EPA (20:5n-3) and DHA (22:6n-3), of zooplankton samples collected in February-March 2018 the Kerguelen Plateau region. Each pie chart corresponds to a size class (125 µm, 250 µm, 500 µm, 1000 µm, 2000 µm) or species (>4000 µm; *Salpa thompsoni*, *Rhincalanus gigas*, *Themisto gaudichaudii, Paraeuchaeta spp., Euphausia vallentini*). Each pie represents average values for each class from all stations and replicates combined.

The zooplankton TM 20:1n-11 + 22:1n-9 accounted for a small portion of TFA (2.5 ± 0.1 %) and it varied among size classes ($p<0.05$) but without a clear pattern of variation (Fig 2g). The other zooplankton TM indicating carnivory, 18:1n-9, accounted for the 11.6 ± 0.7 % of TFA and showed variation among size classes ($p<0.001$). Specifically, the classes 125 µm, 250 µm, 1000 µm and *Paraeuchaeta spp.* from station M1 had the highest amounts of 18:1n-9 among stations (19.8 ± 1.2 % of TFA), with *Paraeuchaeta spp.* generally having a high amount of 18:1n-9 across all stations, accounting for up to 30 % of TFA (Fig 3 h).

The NQI of zooplankton ranged between 171 and 824, and it did not differ among stations, but there was a significant effect of size classes/species ($p<0.05$). The highest NQI was recorded for the 250 µm and 500 µm classes, and *S. thompsoni* (572 ± 53, 614 ± 38, 572 ± 11, respectively), whereas *R. gigas* had the lowest values (299 ± 6; Fig 5a, Table S.1).

A moderate negative correlation was observed for NQI-TFA ($r = 0.59$) with the highest NQI been associated to the lowest amount of TFA, which were usually observed in the smallest size classes (Fig 5b). Significantly high positive correlations were observed between NQI-EFA and NQI-DHA ($r = 0.91$ and 0.94; Fig 5c, d), while NQI-EPA were not significantly correlated ($r = 0.2$; Fig 5e).

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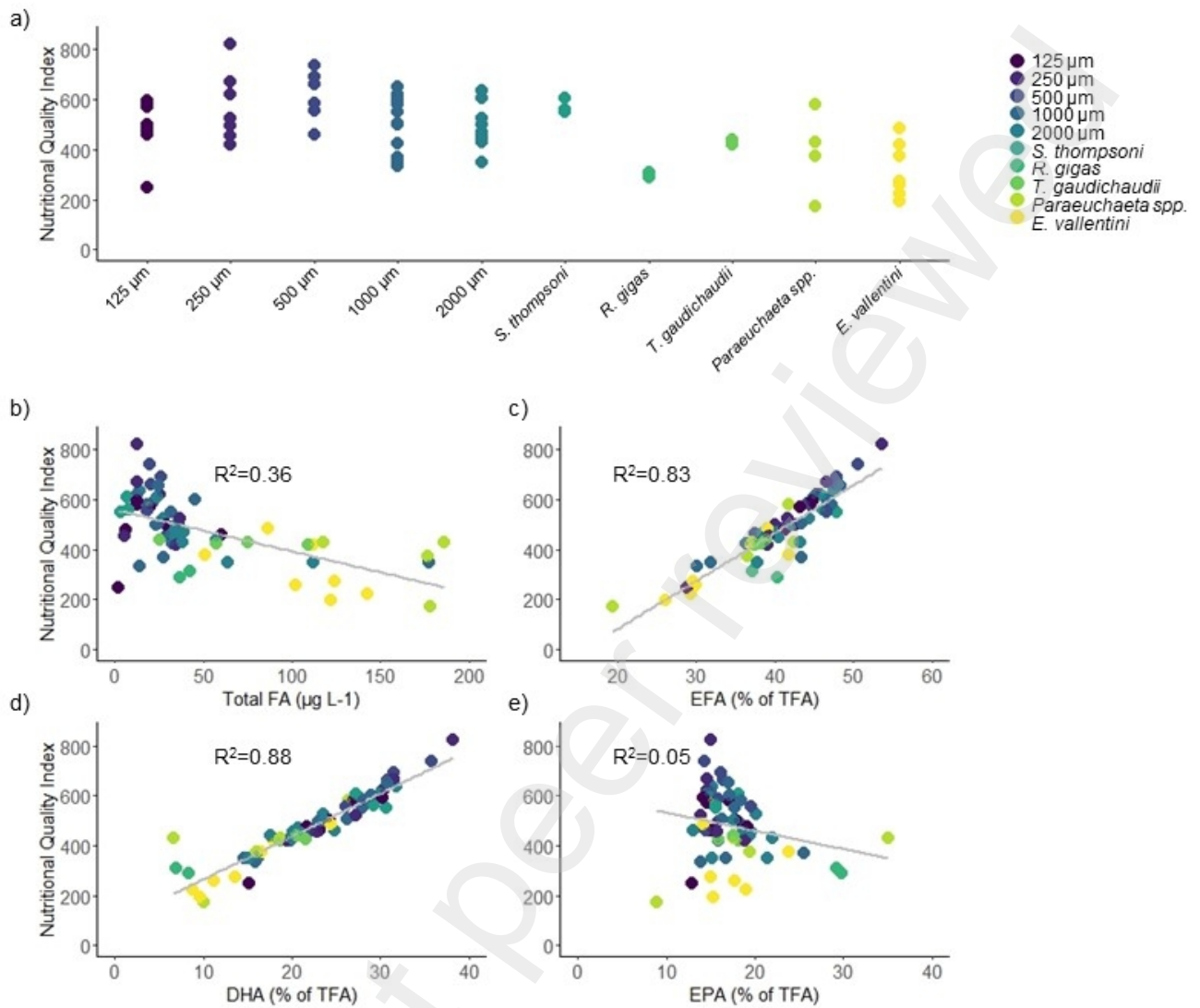
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268 **Fig 5** Nutritional quality index (NQI) of zooplankton collected in February-March 2018 in the
269 proximity of the Kerguelen Plateau a) plotted as a function of the size classes/species. Regressions of
270 NQI vs. b) the amount of total fatty acid (TFA), c) essential FA (EFA), d) DHA and e) EPA.
271

272 Regardless of the size class/species investigated, zooplankton samples had overall a higher NQI than

273 phytoplankton samples collected concurrently to our sampling (total average from all stations and

274 size classes: 477 ± 16.7 vs. 398 ± 8.8; Fig 6).

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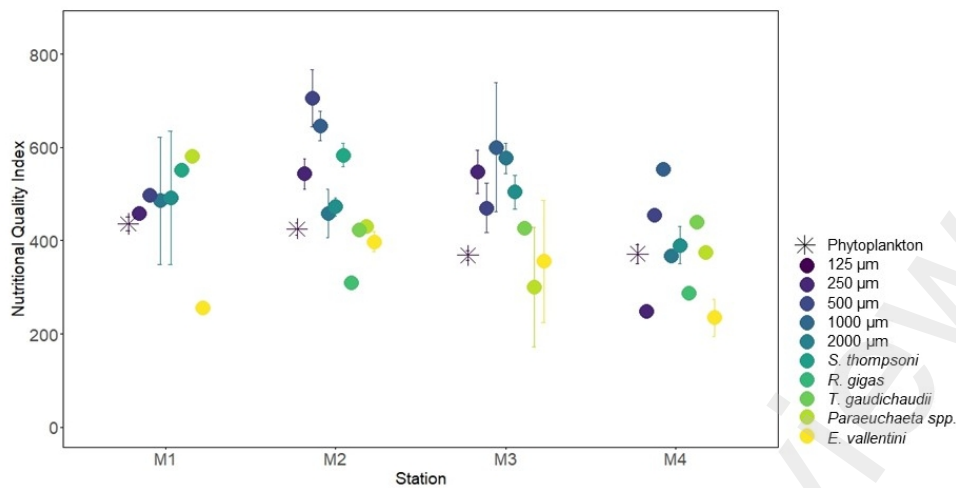
Fig 6 Average value (mean ± standard error) of the nutritional quality index (NQI) of phytoplankton and zooplankton, from samples collected in February-March 2018 in the proximity of the Kerguelen Plateau. Phytoplankton data were obtained from Remize et al. (2022).

4. DISCUSSION

This study aimed to investigate the FA composition of mesozooplankton at the Kerguelen Plateau and assess variations in the FA content and composition across stations and size classes/species composition. Our findings revealed no significant differences in the FA composition of zooplankton among stations, however significant differences were observed across size classes/species.

In this study, smaller zooplankton size classes had the lowest FA concentrations, whereas total FA content increased with size except for *S. thompsoni* (Table S.1). Concurrently, the smallest size classes (125-500 μm) had the highest proportion of non-diatom TM and DHA, while proportions of diatom TM and EPA were higher in the largest size class (>4000 μm; Figs 2, 3), with the zooplankton carnivory marker (18:1n-9), accounting for up the 20 % of TFA in the classes 125 μm, 250 μm, 1000 μm and 30 % is *Paraeuchaeta spp*. Zooplankton of different sizes can vary significantly in trophic level, as different species or conspecific of varying sizes and/or ontogenetic stages can exhibit herbivory, carnivory or omnivory feeding behaviours (Décima, 2022; McLaskey et al., 2024), and even with large species as salp, can have a relative low trophic position (Pakhomov et al., 2019). These dietary differences can then be reflected in the FA profiles of those groups (Zhang et al., 2024). During the investigation, *Oithona* and calanoids were the main contributors to mesozooplankton

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abundance, numerically accounting for more than 80 % (Hunt et al., 2021). *Oithona sp.* are small-sized omnivorous copepods, with diatoms and microzooplankton representing a significant component of their diet, especially in the Southern Ocean (Atkinson, 1996; Lonsdale et al., 2000; Pond and Ward, 2011). In contrast, the calanoid *Paraeuchaeta spp.* exhibits predatory feeding behaviors feeding on other copepods (Carlotti et al., 2015). Among the other species investigated, *T. gaudichaudii* is mostly a carnivorous zooplankton, *R. gigas,* is rather large-sized herbivorous copepod, while *E. vallentini*, can display a variable diet, switching from omnivory to predation depending on ontogenetic stage and season (Carlotti et al., 2015; Polito et al., 2013; Tarling et al., 2007; Zhang et al., 2017). These species can be large enough to potentially represent important prey for top predators, including fish and seabirds, in the Southern Ocean (Bocher et al., 2002, 2001; Padovani et al., 2012). Despite its generally large body size, *S. thompsoni* exhibited a FA profile similar to smaller mesozooplankton size classes that exhibit herbivorous feeding behaviour consuming primarily small phytoplankton (Hunt et al., 2021). The gelatinous nature of *S. thompsoni* largely composed of water and proteins (Dubischar et al., 2012; Madin et al., 1981), can thus explain their low FA content. These results suggest that variations in the zooplankton community composition are clearly reflected in their respective FA profiles, highlighting intricate relationships between species-specific feeding behaviours and size-related dietary preferences.

While the stations selected were distributed over the HNLC and LNHC areas, our results indicated that there were no statistical differences in the FA composition of zooplankton size classes and species across stations. This lack of variation is likely explained by the progression of the plankton blooms. Chlorophyll *a* collected during the cruise indicated that the sampling was conducted post phytoplankton bloom with generally low chlorophyll *a* values both on the plateau (<0.6 μg L^{-1}) and in the upstream regions (<0.22 μg L^{-1}) (Hunt et al., 2021; Irion et al., 2020). Phytoplankton abundance, community and FA compositions did not vary between HNLC and LNHC stations (Irion et al., 2020; Remize et al., 2022), which were mostly characterized by small phytoplankton particularly prymnesiophytes and prasinophytes accounting for 53–58% of total chlorophyll *a*.

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322   Similarly, the mesozooplankton community composition and biomass was comparable across stations

323   (4.4–5.6 mg C m^{-3}), with copepods contributing largely to the total mesozooplankton abundance in

324   the region (Hunt et al., 2021). The similarity in the overall community composition, including larger

325   specimens, across stations was thus reflected in the similar FA composition. A different pattern might

326   have been observed prior, during or just after the bloom. Previous cruises conducted in the region in

327   spring and summer indicated that blooms are diatom-dominated especially over the plateau (Irion et

328   al., 2020). The main factor affecting phytoplankton FA profiles is the community composition

329   (Cañavate, 2019; Galloway and Winder, 2015) and diatoms are known to have a particular FA profile,

330   which is different from haptophyte or dinophyte profiles (Cañavate, 2019; Galloway and Winder,

331   2015; Puccinelli et al., 2023). Phytoplankton FA turnover rate can be rather fast (days) if there are

332   the conditions for the proliferation of a given community (Puccinelli et al., 2023), as during a bloom.

333   Such effects can be reflected in the zooplankton population within days/weeks (Graeve et al., 2005).

334   As a result, if diatoms were dominant on the plateau for a sufficient amount of time prior our

335   sampling, a different FA composition of zooplankton between HNLC and LNHC stations could have

336   been expected.

337   The NQI of zooplankton revealed an interesting result. Regardless of the size class/species

338   investigated, the NQI of zooplankton was higher than the phytoplankton NQI collected at the same

339   time (477 ± 16.7 vs. 398 ± 8.8; Fig 6). This phytoplankton-NQI was already considered particularly

340   high in comparison to the phytoplankton NQI in other ocean systems (Puccinelli et al., 2023; Remize

341   et al., 2022), indicating that zooplankton food was of a rather high quality. The NQI is based on the

342   proportion of selected FA including EFA, which are largely produced by phytoplankton, and

343   zooplankton cannot synthetize them in sufficient quantity to support organism health requirements

344   (Bi and Sommer, 2020; Litzow et al., 2006). As such, it was plausible to expect the NQI of

345   zooplankton to be lower than the NQI of their food source. Such discrepancy could be linked to the

346   fact that the sampling was conducted in late austral summer, just before the long winter period.

347   Zooplankton is known to store lipid reserve during the summer to be used during the winter when

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phytoplankton production is at its lowest, with lipids playing a critical role on the overwinter success of this group (Hagen et al., 1996; Hagen and Schnack-Schiel, 1996).

When focusing on the differences in NQI among classes/species, we observed that the 250 µm and 500 µm classes and *S. thompsoni* had the highest NQI with significant high positive correlations between NQI and DHA, indicating that the NQI was mostly driven by DHA. In contrast, the largest size classes (1000 and 2000 µm) had generally lower values and negatively correlated with TFA (Fig 5). Such variability could also be linked to different feeding behaviour and consequent different trophic levels of the size class/species investigated as explained above, and to the fact that energy/biomass may be lost moving upper onto higher trophic levels. Alternatively, the dissimilarities observed among size classes could also reflect difference in their metabolic ability, with some smaller size groups preferentially taking up some EFA to cope with physiological requirements/needs (Kainz et al., 2004). *S. thompsoni* showed a rather interesting pattern, being the species with the lowest total FA amount (µg mg^{-1}) but having amongst the highest NQI. NQI is based on FA proportions, and thus the results should be considered with caution, but our results highlight the nutritional value of this group, at least of specimens collected during late austral summer in the Southern Ocean and support recent studies that have also indicated that salps can represent a valuable food source for higher trophic levels (Cavallo et al., 2018; Thiebot et al., 2017) while ingested in high amount. Although we observed differences among size class/species, overall our results indicate that zooplankton from the Kerguelen region collected in late austral summer represented a high-quality food source for higher trophic levels that feed directly on them.

Under projected climate warming scenarios it is predicted that zooplankton community composition will change from omnivorous copepods and euphausiids to gelatinous filter-feeding zooplankton domination, and that will result in a decline in the food quality available to higher trophic levels (Heneghan et al., 2023). The results of our work become even more relevant under these climate warming scenarios, that despite we observed no significant differences in the FA composition of mesozooplankton size classes and species among HNLC and LNHC stations, the nutritional quality

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374 of zooplankton was generally high with the gelatinous species salp representing a high nutritional

375 source of food (if ingested in large quantity). Indeed this work was conducted in late Southern Ocean

376 summer where the energy content of overwintering organisms is at its highest, and our results may

377 not necessarily reflect the average annual conditions, but it provides novel results that may aid to

378 further understand potential long term global warming effects on the nutritional role of

379 mesozooplankton. Such information is timely and essential to further understand potential cascading

380 effects on higher trophic levels, with implications for overall marine biodiversity and ecosystem

381 stability.

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398 **Author contribution: CRediT**

399 EP: Conceptualization; Data curation; Methodology; Formal analysis; Visualization; Roles/Writing -

400 original draft; Writing – review and editing

401 BE: Conceptualization; Investigation; Writing – review and editing

402 BH: Conceptualization; Funding acquisition; Methodology; Resources; Writing – review and editing

403 FLG: Methodology; Data curation; Formal analysis; Writing – review and editing

404 EPa: Conceptualization; Methodology; Resources; Writing – review and editing

405 FP: Conceptualization; Funding acquisition; Investigation; Resources

406 MR: Investigation; Formal analysis; Data curation

407 PS: Conceptualization; Methodology; Funding acquisition; Data curation; Formal analysis;

408 Roles/Writing - original draft; Resources; Writing – review and editing

409 **Conflict of interest**

410 The authors declare that they have no known competing financial interests or personal relationships

411 that could have appeared to influence the work reported in this paper.

412 **Data statement**

413 The authors declare that all data relative to this work are available in the public repository Data

414 Archive System (DAS) of NIOZ at the link https://dataportal.nioz.nl/doi/10.25850/nioz/7b.b.uh.

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