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1 **Distribution of modern dinocysts in surface sediments of southern**
2 **Brittany (NW France) in relation to environmental parameters:**
3 **implications for paleoreconstructions**

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13 Abstract

14 Dinoflagellate cyst assemblages from 15 modern surface sediment samples of the Bay of
15 Quiberon (Southern Brittany shelf) have been examined to assess their **potential as** marine
16 bio-indicators for paleoenvironmental reconstructions in a shallow coastal environment. **Some**
17 **discrepancies are** noted in the distribution of dinocyst **taxa in the study area**, and particularly
18 regarding **dinocyst concentration and diversity (26 different taxa identified in total) as well as**
19 **heterotrophic taxa percentages**. We suggest that the **proportion** of heterotrophic **taxa is**, in an
20 embayment of 15m deep in average, mainly attributed to bottom water oxygenation and
21 sediment granulometry, both acting on species-selective degradation after dinocyst deposition.
22 More precisely, higher heterotrophic abundances are found under lower oxic conditions and in
23 fine grain-size sediment samples, leading to caution about their use as productivity **indicators**
24 in coastal environments when these parameters are not fully addressed. **The** comparison of the
25 Bay of Quiberon data with surface sediment samples and top cores from **previously** published
26 data makes it possible to establish a transect of the modern dinocyst distribution from inshore
27 to offshore areas in the northern Bay of Biscay, allowing to identify different ecological
28 groups according to the hydrological and bathymetric contexts: i) an estuarine assemblage
29 strongly dominated by *Lingulodinium machaerophorum*, ii) a proximal coastal assemblage
30 dominated by *L. machaerophorum* and, to a lesser extent, *Spiniferites bentorii*, iii) a neritic
31 assemblage dominated by *L. machaerophorum*, *Spiniferites ramosus* and cysts of
32 *Pentapharsodinium dalei*, and iv) an oceanic group dominated by *Spiniferites mirabilis* and
33 *Operculodinium centrocarpum*.

34 Keywords: dinoflagellate cysts, marine palynology, taphonomic issues, southern Brittany
35 shelf, paleoenvironmental reconstructions

36 **1. Introduction**

37 Dinoflagellates (currently about 2,377 species known; *Gomez, 2012*) are eukaryotic
38 **unicellulars found** in most aquatic environments, mainly in marine waters and in the upper
39 part of the water column, **and play** an important role in the trophic network (*Dale, 1996*). Half
40 of them **are** heterotrophic and **feed** on other dinoflagellates, microalgae, diatoms and organic
41 debris in the water column (*Evitt, 1985; Dale, 1996*); **the** other half possesses chloroplasts
42 (*Gomez, 2012*). As the vegetative growth of heterotrophic dinoflagellates is likely to be
43 enhanced by prey availability (e.g. diatoms, autotrophic dinoflagellates, phytodetritus), they
44 are commonly used as : i) productivity tracers in the marine realm (i.e. upwelling areas, e.g.
45 *Radi and de Vernal, 2004; Penaud et al., 2016; Hardy et al., 2018*) as well as ii)
46 eutrophication tracers in coastal and estuarine areas (e.g. *Dale, 1999; Matsuoka, 1999;*
47 *Sangiorgi and Donders, 2004; Pospelova and Kim, 2010; Price et al., 2017, 2018; Garcìa-*
48 *Moreiras et al., 2018*).

49 Fossilizable **organic-walled** dinoflagellate cysts (i.e., resting cysts corresponding to “dormant
50 stages” mainly produced during sexual reproduction; e.g., *von Stosch, 1973*) show their
51 highest concentrations in neritic and coastal areas (i.e. where dinoflagellate blooms can occur;
52 *Taylor, 1987*). **Organic-walled** dinoflagellate cysts (dinocysts) thus represent an important
53 group of microfossils well preserved in sediments. Previous studies carried out on modern
54 marine sediments showed their worldwide distribution as being mainly driven by **sea-surface**
55 environmental parameters such as temperature (SST for **Sea-Surface** Temperature), salinity
56 (SSS for **Sea-Surface** Salinity), sea-ice cover duration in high latitudes, nutrient
57 concentrations and related primary productivity regimes, as well as inshore-offshore
58 gradients, allowing their use as powerful paleoceanographic tracers (e.g., *Dodge and Harland,*
59 *1991; Mudie et al., 2001; Marret and Zonneveld, 2003; de Vernal et al., 2013, 2020;*

60 *Zonneveld et al., 2013; Marret et al., 2020; Van Nieuwenhove et al., 2020*). However, studies
61 on the current dinocyst diversity, concentration and distribution in coastal environments are
62 scarce, especially for the French coasts. Along the Brittany's coasts, first steps towards
63 understanding of the modern distribution of coastal to oceanic dinocyst taxa were initiated by
64 *Reid (1972), Morzadec-Kerfourn (1977), Wall et al. (1977), Larrazabal et al. (1990)*, recently
65 complemented by *Ganne et al. (2016)* for the Loire estuary and *Lambert et al. (2017)* for the
66 Bay of Brest. A recent spatio-temporal (i.e. in space and time) Holocene study discussed the
67 nearshore-offshore dinocyst distribution on both sides of the freshwater front in the northern
68 Bay of Biscay shelf (*Penaud et al., 2020*). Dinocyst species were then classified in four
69 groups accounting for different hydrological contexts (i.e, estuarine; shallow bay to inner
70 neritic; Iroise Sea or neritic; outer neritic to full oceanic) due to a marine (i.e. distal or
71 offshore) to coastal (i.e. proximal or onshore) transect ranging from 2,174 m to 8 m water
72 depth (*Penaud et al., 2020*).

73 In this study, we investigated 15 new surface sediment samples collected in the Bay of
74 Quiberon (BQ), which will improve the discussion of the modern spatial dinocyst distribution
75 in a shallow bay environment, especially focusing on rarely addressed taphonomic processes.
76 Then, these data were compared to top cores retrieved in the southern Brittany shelf
77 (*Naughton et al., 2007; Zumaque et al., 2017; Penaud et al., 2020*) and to surface sediments
78 of the Loire estuary mouth (*Ganne et al., 2016*) in order to improve the understanding of the
79 modern spatial dinocyst distribution along a macro-regional inshore-offshore transect.

80

81 **2. Environmental and geographical settings of the Bay of** 82 **Quiberon**

83 The 'Mor Bras' (Fig. 1) is a bathymetric depression bordering the southern coast of Brittany.
84 It is partially isolated from the general oceanic circulation of the Bay of Biscay and from the
85 high energetic Atlantic swells **due** to a belt of shoals in the extension of the Quiberon
86 peninsula (Fig. 1). The Bay of Quiberon (BQ), which occupies the western part of the Mor
87 Bras, is a shallow coastal embayment (15 m depth in average) that has been submerged during
88 the Holocene (*Baltzer et al., 2014; Menier et al., 2014*). A vast network of flooded valleys
89 converges into the Teignouse Strait (TS on Fig. 1) which separates the Quiberon Peninsula
90 from the Houat Island (*Vanney, 1965; Menier et al., 2014; Fig. 1*). This strait is **burrowed** by
91 strong tidal currents joining the inlet of the Gulf of Morbihan and contributing to the partial
92 isolation of the BQ from the rest of the Mor Bras by the establishment of tidal gyres (yellow
93 arrows on Fig. 1; *Vanney, 1965; Lemoine, 1989; Tessier, 2006*).

94 Recent works carried out in the BQ, following high summer mortality of oysters (*Mazurié et*
95 *al., 2013a, b; Stanisière et al., 2013*), have shown that the shallower parts of the BQ (between
96 0 and 6 m deep) are mainly composed of sandy sediments, due to strong wind-forced water
97 column mixing, while the deepest parts of the BQ are covered **with** muddy sediments. This
98 sediment distribution is associated with a heterogeneous distribution of benthic foraminiferal
99 species, analyzed in the framework of the RISCO project ('*Comité régional de la*
100 *conchyliculture Bretagne Sud*' and Ifremer; 2010-2013; coord. J. Mazurié; *Mazurié et al.,*
101 *2013a, b; Stanisière et al., 2013*). Among the high foraminiferal diversity studied, some taxa
102 are characteristic of the deepest and fine grain-sized BQ areas (i.e. *Criboelphidium gerthi,*
103 *Elphidium earlandi, Gavelinopsis nitida, Lagena sulcata, Lagena semistriata, Lamarckina*
104 *haliotidea, Planorbulina mediterraneensis, Trifarina angulosa, and Textularia truncata*). They
105 form the 'deepest foraminiferal assemblage', noted 'DeepForam' hereafter.

106 **3. Methods**

107 **3.1. Sampling and environmental parameters**

108 **3.1.1. Data collection**

109 The sampling campaign was carried out in 2010 in the framework of the RISCO project in 15
110 sites within the BQ using a 50 x 50 cm Van Veen grab for the optimal preservation of surface
111 sediments (*Mazurié et al., 2013a, b; Stanisère et al., 2013; Fig. 1*). The **first cm** of each site
112 was sampled (Table 1) for grain-size and microfossil analyses. All samples were stored in
113 sealed vials with ethanol.

114 For grain-size analyses, sediments were passed through a column of sieves with different
115 sizes of apertures (i.e. 2 mm, 500 µm, 125 µm and 45 µm). Averaged percentages of the fine
116 sediment fraction (i.e. <125 µm, referred to as ‘granulo<125’ hereafter; Table 2) **were**
117 considered in this study (*Mazurié et al., 2013a, b; Stanisère et al., 2013*).

118 In addition, we compiled the monthly measurements of the bottom water physico-chemical
119 parameters measured at each station to obtain averaged values for the year 2010 (Table 2).
120 Bottom water temperature (referred to as ‘Temp’ hereafter), bottom water salinity (‘Sal’),
121 dissolved oxygen concentration in bottom waters (‘O2’), bottom water turbidity (‘Turb’) and
122 Chlorophyll a concentration in bottom water (‘Chla’) were measured with an MP6 probe
123 (NKE). **In addition**, bottom water samples were taken from each station to calculate the
124 suspended matter concentration (‘SM’) using vacuum pump filtration. Annual averaged
125 values will be considered in this study (Table 2).

126

127 **3.1.2. Correlation matrix of variables**

128 A correlation matrix of variables was performed with the “Analysis Toolpack” of Microsoft
129 Excel 2016, to assess the relationship between: i) sedimentological (‘granulo<125’,
130 subsection 3.1.1) and foraminiferal (‘DeepForam’, section 2) data, ii) dinocyst data (‘Cdino’,
131 subsection 3.2.1.; and ‘Srdino’, ‘Hdino’, subsection 3.2.2.) and iii) the measured
132 environmental variables (‘Depth’, ‘Temp’, ‘Sal’, ‘O2’, ‘Chla’, ‘Turb’, ‘SM’, subsection
133 3.1.1).

134 The matrix consists of Pearson correlation coefficients (r) between each variable that range
135 from -1 to 1. If r=0, no linear correlation exists between compared variables. The greater the
136 absolute value of r, the stronger the correlation: positive when approaching 1 and negative
137 when approaching -1. Statistical significance is expressed by the p-value. P-value < 0.05
138 indicates a strong presumption against the null hypothesis and a good confidence in the
139 statistical correlation expressed by the Pearson coefficients.

140

141 **3.2. Dinoflagellate cyst analysis**

142 **3.2.1. Laboratory procedure for palynological slides**

143 Dinocyst extraction was performed at the UMR 6538 CNRS (LGO-*Laboratoire Géosciences*
144 *Océan*, UBO-University of Brest) from the 10–150 µm sediment fraction. Three cm³ of
145 fifteen BQ surface sediment samples (samples from December 2010) were analyzed following
146 a standard protocol described by *de Vernal et al. (1999)* that includes 10% cold HCl and 70%
147 cold HF to remove carbonate and siliceous fractions, respectively. The final residues were
148 mounted between slides and coverslips with glycerol. Dinocyst concentrations (‘Cdino’;
149 Table 2), expressed in number of cysts per cm³ of dry sediments (cysts/cm³) were calculated
150 thanks to the marker grain method (*Stockmarr, 1971; de Vernal et al., 1999; Mertens et al.,*
151 *2009*). This method consists in adding aliquot volumes of *Lycopodium* spores before the

152 palynological treatment, these exotic spores being counted in parallel with fossilized
153 palynomorphs.

154

155 **3.2.2 Dinocyst identification, diversity indexes and statistical analysis**

156 For each analyzed sample, except BQ sample n°3 (cf. Fig. 1), a minimum of 150 dinocysts
157 was reached, using an Olympus CH-2 optical microscope (at magnifications $\times 630$ and
158 $\times 1000$), in order to provide robust assemblages from a statistical point of view. The threshold
159 of 100 individuals is indeed required to identify 99% of major ($>5\%$) species (*Fatela and*
160 *Taborda, 2002*) and thus robust to discuss the proportion of the two large groups of dinocysts
161 (i.e. the strict heterotrophic taxa vs. the other dinocysts). The BQ sample n°3, mainly
162 characterized by coarse sediments (i.e. 63% of grain sizes exceed $125\mu\text{m}$), must be interpreted
163 with caution since only 13 specimens were counted. Taxa identification followed *Rochon et*
164 *al. (1999)*, *Zonneveld & Pospelova (2015)* and *Van Nieuwenhove et al. (2020)*. Dinocyst
165 percentages were calculated for each taxon (list of identified taxa in Table 3), on a main sum
166 including all taxa and excluding non-identified ones (always less than three undetermined
167 specimens per analyzed level).

168 We use the Shannon Diversity index to estimate the dinocyst diversity as an additional
169 ecological indicator (noted 'Srdino' hereafter for Species Richness; Table 2). The Shannon
170 index provides information both on specific richness and on the structure of populations. The
171 higher the value, the greater the taxa diversity and the more homogeneous the relative
172 abundances. In addition, we calculated the total percentages of brown cysts from
173 heterotrophic dinoflagellates, or heterotrophic dinocysts ('Hdino'; Table 2). Cluster analysis
174 was also conducted on the 15 samples, using PAST v.1.75b (*Hammer et al., 2001*), according

175 to dinocyst assemblages to better highlight similarities and differences between analyzed
176 samples.

177

178 **3.2.3 Inshore-offshore transect**

179 In order to discuss dinocyst diversity changes along an inshore-offshore gradient on a larger-
180 scale, we also compared dinocyst assemblages from surface sediments and core tops taken in
181 the northern Bay of Biscay, in different environmental and bathymetric contexts: i) two
182 samples taken in the downstream Loire Estuary (*Ganne et al., 2016*) are representative of the
183 Loire river mouth, ii) the averaged 15 surface samples of this study account for the shallow
184 coastal BQ, iii) a sample from the top core section (level 47 cm) of the CBT-CS11 core (73 m
185 water depth) is representative of the shelf under mixed oceanic and winter fluvial influences
186 (*Penaud et al., 2020*), iv) a sample from top core section (level 4 cm) of the VK03-58bis core
187 (97 m water depth) is representative of the deeper shelf (*Naughton et al., 2007*). Regarding
188 these last two sites, we targeted the two “modern” samples on the basis of palynological
189 evidence unambiguously **signaling** for their contemporaneity (i.e., presence of pollen grains of
190 *Zea mays*). The distal MD95-2002 core, taken off the Armorican margin at 2,200 m deep, has
191 finally been added to the transect (*Zumaque et al., 2017*). The top core sample (0 cm) is
192 estimated at ca. 1,000 Cal. years BP and is therefore representative of late Holocene
193 conditions (*Zumaque et al., 2017*). Such a gradient in dinocyst distribution as a function of the
194 distance to the coast therefore provides a baseline reference for inferring dinocyst-derived
195 past environmental changes on the temperate north-eastern Atlantic margin.

196

197

198 **4. Results**

199 **4.1. Cluster analysis between study samples**

200 All studied stations are represented within the BQ with a colour code corresponding to the
201 result of the cluster analysis (Figs. 2a, b).

202 Station n°3 stands out from the others with a low similarity coefficient (i.e. around 0.65; Fig.
203 2a). The coarse grain size (Fig. 2h) and the related very low dinocyst concentration (Figs. 2c
204 and 3a) characterizing this station set it apart from the others. **With the exception of** station
205 n°5, all stations located **below** the 6 m isobath (n°2, 10, 15, 11, 13, 12, 8, and 14) are grouped
206 together in a same cluster (brown colour, Figs. 2a,b) with a high coefficient of similarity (>
207 0.825; Fig. 2a), **and** stations located above the 6 m bathymetric threshold (n°4, 6, and 9) are
208 grouped in a same cluster (green colour, Figs. 2a,b) with the additional sites n°7 and 1. All
209 these shallowest sites are characterized by generally coarser grain-size values (Fig. 2h).

210

211 **4.2. Dinoflagellate cyst results**

212 Dinocyst concentrations of the 15 surface sediment **samples range** from ca. 300 to 18,300
213 cysts/cm³ with a mean of ca. 8,100 cysts/cm³ (standard deviation of ca. 5,300 cysts/cm³) (Fig.
214 **3a**). The lowest values correspond to the shallowest sites located to the north and west of the
215 BQ whereas the highest ones are recorded at the deepest sites, **below** the 6 m isobath (Figs. 2c
216 and 3a).

217 A total of 26 different dinocyst taxa was identified (12 autotrophic and 14 heterotrophic taxa;
218 cf. Table 3) with an average of 14 different taxa per sample (Fig. 3a). Assemblages (Figs.
219 3a,b) are largely dominated by *Lingulodinium machaerophorum* (45 % in average; Fig. 3b),
220 commonly found dominant in areas with strong fluvial influences (*Morzadec-Kerfourne*,

221 1977; Ganne et al., 2016; Lambert et al., 2017; Penaud et al., 2020). The other major
222 autotrophic taxa are *Spiniferites bentorii* (11 % in average; Fig. 3b), *Spiniferites*
223 *membranaceus* (6 % in average; Fig. 3b) and cysts of *Pentapharsodinium dalei* (5 % in
224 average; Fig. 3b).

225 The heterotrophic rate is on average 20 % over the whole BQ (Fig. 3b) and is particularly
226 represented by *Brigantedinium* spp. species (i.e. “round brown” cysts produced by
227 *Protoperidinium* dinoflagellate species) (12 % in average; Fig. 3b). The highest relative
228 abundances of heterotrophic cysts (Figs. 2e, 3a) are generally observed in the deepest areas of
229 the BQ (Fig. 2), between 6 and 10 m, which are characterized by the lowest bottom water
230 oxygen concentrations (Fig. 2g) and the lowest sediment grain-size values (Fig. 2h). The total
231 dinocyst concentrations (Figs. 2c, 3a) and in a lesser extent the specific richness (Fig. 2d)
232 follow the same trend. The 6 m isobath therefore seems to constitute a limit below which
233 dinocyst concentrations are greater.

234

235 4.3. Correlation matrix of variables

236 The correlation matrix of variables (Fig. 4) shows strong correlations between the different
237 variables here used to explain the dinocyst distribution. Among these, a good positive
238 correlation ($r > 0.5$) is noted between ‘Hdino’ and three variables: ‘depth’, ‘granulo<125’ and
239 ‘DeepForam’ (Fig. 4). Heterotrophic dinocysts therefore increase with the bathymetry, in
240 parallel with finer sediments and increasing occurrences of the deepest foraminiferal taxa.
241 Also, a similar correlation with ‘depth’, ‘granulo<125’ and ‘DeepForam’ is observed with
242 ‘Cdino’ and ‘Srdino’ (Fig. 4), likely caused by the greater occurrences of heterotrophics in the
243 deepest zones of the BQ (> 6 m). Finally, a good positive correlation is noted between

244 ‘Srdino’, ‘Cdino’, and to a lesser extent ‘Hdino’, and on the other hand ‘O2’, while ‘Hdino’ is
245 little or not correlated with “Chla” (Fig. 4).

246 **5. Discussion**

247 **5.1. Taphonomic issues and dinocyst preservation in the Bay of Quiberon**

248 **Some discrepancies** in dinocyst distribution **are** observed within the BQ, especially for the
249 heterotrophic taxa, **showing slightly higher occurrences** in the deepest areas (below the 6 m
250 bathymetric threshold; Figs. 2e and 3a; Fig. 4). Furthermore, we assume that the small BQ
251 (i.e. 40 km²), characterized by strong tidal currents (cf. gyrotory circulation in Fig. 1) which
252 homogenize surface water properties including nutrients (Tessier, 2006), cannot explain the
253 differential distribution of heterotrophic dinocysts in the BQ (Figs. 2e and 3a).
254 *Brigantedinium* species, which dominate the heterotrophic assemblages (Fig. 3), as well as
255 *Echinidinium* species, are sensitive to oxidation (Zonneveld *et al.*, 1997; Kodrans-Nsiah *et al.*,
256 2008; Bogus *et al.*, 2014). Their occurrences even decrease logarithmically with increasing
257 bottom water oxygen concentrations (Zonneveld *et al.*, 2001, 2007, 2008). Double-walled
258 organic dinocysts (i.e. dormant resting stages with a mandatory dormancy period; Anderson
259 and Wall, 1978) are composed of a macromolecule, whose chemical composition consists in a
260 cellulose-like glucan in autotrophic, and a nitrogen-rich glycan in heterotrophic forms (Bogus
261 *et al.*, 2014). This difference in dinocyst chemical composition explains the greater
262 vulnerability of heterotrophics to oxidation and a differential preservation during diagenetic
263 processes (Bogus *et al.*, 2014).

264 In our study, statistical correlation between the percentages of heterotrophic dinocysts and
265 measured environmental parameters allowed us to discuss the significance of the
266 heterotrophic signature in the BQ (Fig. 4). A lack of correlation between ‘Chla’ and ‘Hdino’
267 ($r = -0.06$; Fig. 4) suggests that productivity is not a main factor explaining differences in the

268 BQ spatial distribution of heterotrophic dinocysts. The weak negative correlation observed
269 between heterotrophic cysts ('Hdino') and 'O₂' ($r = -0.25$; Fig. 4) is mitigated by a non-
270 obvious statistical correlation ($p\text{-value}=0.369$; Fig. 4). Moreover, dissolved oxygen values
271 ('O₂'), are derived from occasional measurements and are not representative of an averaged
272 state of the BQ bottom water oxygenation. Indeed, seasonal hypoxia have been recognized in
273 the deepest areas of the BQ and related to the establishment of a seasonal water column
274 stratification, with oyster mortality below the bathymetric threshold of 6 m (*Stanisière et al.,*
275 *2013*). Therefore, to test the effect of heterotrophic degradation(/preservation) under
276 oxic(/anoxic) conditions, benthic foraminiferal data have been additionally considered. The
277 deepest benthic foraminiferal assemblage considered ('DeepForam'; Fig. 2f) is mainly
278 constituted by opportunistic species and characterize areas subjected to seasonal hypoxia,
279 confirming the modern environmental assessment (*Stanisière et al., 2013*). It is also worth
280 noting that the water column stratification, and its effects on the seasonal bottom water
281 oxygen depletion from the 6 m isobath, is also confirmed by i) the negative correlation
282 between 'depth' and 'Temp' ($r = -0.79$; Fig. 4), as well as between 'depth' and 'O₂' ($r = -0.70$;
283 Fig. 4), and ii) the positive correlation between 'depth' and 'DeepForam' ($r = 0.95$; Fig. 4).
284 The positive correlations we observed between 'DeepForam' and 'Hdino' ($r = 0.76$; Fig. 4),
285 'DeepForam' and 'Srdino' ($r = 0.49$; Fig. 4) and 'DeepForam' and 'Cdino' ($r = 0.57$; Fig. 4)
286 therefore suggest that depleted oxygen concentrations may be involved in the higher dinocyst
287 preservation by increasing heterotrophic taxa percentages and dinocyst concentrations. The
288 heterotrophic signature also seems to be correlated with grain-size values. The distribution
289 map (Fig. 2h) and the Pearson correlation coefficient (Fig. 4) show that the proportion of the
290 finest sediments increases with depth. A significant correlation is highlighted between
291 'granulo<125' and 'Hdino' ($r = 0.56$; Fig. 4), 'granulo<125' and 'Srdino' ($r = 0.61$; Fig. 4)
292 and 'granulo<125' and 'Cdino' ($r = 0.75$; Fig. 4). It is well-known that coarser sediments are

293 not conducive to a good preservation of palynomorphs (cf. example of sampling site n°3 in
294 the BQ; Fig. 3a) due to interstitial fluid circulation and higher oxygenation in a porous
295 sediment. The coarser the sediment, the lower the proportion of heterotrophics (Figs. 2e, h).
296 Variations in the proportions of heterotrophics may thus be related to the effect of oxidation
297 processes acting on species-selective degradation after cyst deposition in the BQ.

298 A conceptual model allows gathering environmental conditions prevailing in the BQ to
299 explain the differential dinocyst distribution pattern (Fig. 5). At the scale of the study area, we
300 postulate that “autotrophic/heterotrophic” dinocyst fluxes to the sediments are almost
301 identical at all points of the BQ (red arrows on Fig. 5), due to a bay-wide homogenization of
302 sea-surface properties through tidal currents. Beyond 6 m deep, the water column
303 stratification results in an oxygen bottom-water consumption which exceeds its renewal and
304 thus in seasonal bottom-water hypoxia. Because of this stratification, the weakening of coastal
305 and tidal currents in the deepest areas of the BQ enhanced the sedimentation of finer
306 sediments. The combination of seasonal bottom-water oxygen depletion and higher proportion
307 of finer sediments may explain the greater occurrences of heterotrophics below the 6 m
308 isobath.

309 Such considerations lead us to consider with great caution, in shallow-bay paleoecological
310 reconstructions, the use of heterotrophic-derived productivity indexes. In this context,
311 *Zonneveld et al. (2007)* suggested the use of the absolute concentrations of autotrophic
312 dinocysts rather than total or heterotrophic concentrations to discuss varying productivity
313 conditions. Also, since the sediment granulometry plays a crucial role in the dinocyst
314 preservation, it appears essential to carry out grain-size analyses along core or to work in
315 homogeneous sediment contexts.

316

317 **5.2. Inshore-Offshore dinocyst assemblages across the Southern Brittany** 318 **shelf**

319 The influence of environmental parameters on the dinocyst distribution is increasingly
320 understood thanks to the gradual **improvement** of the world marine current databases and
321 atlases (e.g. *Zonneveld et al., 2013; Marret et al., 2020; de Vernal et al., 2020; Van*
322 *Nieuwenhove et al., 2020*). However, although the highest dinocyst concentrations are
323 observed in neritic and coastal areas, studies on current dinocyst distributions in French
324 coastal environments are still scarce (e.g. *Morzadec-Kerfourn, 1977; Larrazabal et al., 1990;*
325 *Ganne et al., 2016; Lambert et al., 2017*). From previous studies (e.g. *Williams, 1971;*
326 *Morzadec-Kerfourn, 1977; Penaud et al., 2020*), dinocyst groups have been established: i) the
327 oceanic zone (>100-150 m water depth, outer-neritic assemblage) appears characterized by
328 *Impagidinium aculeatum*, *O. centrocarpum*, *S. mirabilis*, and *S. elongatus* (with *S. ramosus*
329 and *S. bulloideus* in addition), *I. aculeatum* being restricted to full-oceanic waters, ii) the
330 coastal zone (inner-neritic) is characterized by the association *S. ramosus-S. bulloideus-S.*
331 *bentorii*, and iii) the estuarine-coastal zone, under fluvial-derived major influence, is
332 characterized by *L. machaerophorum*, a species tolerant to large drops in salinity and mainly
333 proliferating in brackish environments (*Reid, 1975; Morzadec-Kerfourn, 1977, 1997; Mudie*
334 *et al., 2017; Penaud et al., 2020*).

335 Along the inshore-offshore gradient (Fig. 6a), estuarine to inner-neritic samples under strong
336 fluvial influences exhibit an almost monospecific assemblage of *L. machaerophorum* (more
337 than 80 %; Fig. 6b). *L. machaerophorum* is becoming less and less abundant with the distance
338 from the coast and is rarely observed in the full-oceanic environment (i.e. around 0.3% in the
339 MD95-2002 core; Fig. 6b). The offshore **sea-surface** conditions are indeed influenced by the
340 North Atlantic general circulation, while the circulation on the continental shelf is influenced

341 by a mixed river / tidal current limited to the coast (Penaud et al., 2020). In shelf sediments
342 (CBT-CS11 and VK03-58bis cores), the prevalence of the *L. machaerophorum* species over
343 neritic to oceanic cyst taxa thus suggests seasonally coastal stratified waters subjected to
344 strong continental influence (Penaud et al., 2020). Indeed, from mid-autumn to early spring,
345 strong river flows (i.e. Gironde, Loire, Vilaine) associated with sustained northeastward wind
346 activity maintain this region under the influence of northward freshwater plumes and
347 associated low salinities between the coast and the 100 m isobath (Lazure et al., 2008;
348 Charria et al., 2013; Costoya et al., 2015, 2016). The resulting density gradients explain
349 water mass stratification and thermohaline front at the 100 m isobath, and thus the prevalence
350 of *L. machaerophorum* until this limit (Penaud et al., 2020).

351 **The** transect confirms the ecological preferences of *S. bentorii* and *S. ramosus* for the coastal
352 environments. However, while *S. bentorii* seems to be a good marker of the strict proximal
353 domain (i.e. strong occurrence in BQ: 11.5 %; Fig. 6b), being almost absent from the shelf
354 (i.e. VK03-58bis and CBT-CS11 cores: 0.3 and 2 %, respectively), *S. ramosus* exhibits an
355 inverse distribution and becomes more and more present away from the coast (Fig. 6b): *S.*
356 *ramosus* reaches 5% in the full-oceanic domain (MD95-2002 core) while *S. bentorii* is totally
357 absent. *S. ramosus* and *S. bentorii* can therefore be considered as excellent markers of the
358 proximal neritic environment under moderate fluvial influences. Cysts of *P. dalei* show a
359 fairly homogeneous distribution and low percentages all along the transect (i.e. 3 to 10%; Fig.
360 6b), being more dominant in northern latitudes of the North Atlantic Ocean and in fjords
361 (Mudie and Rochon, 2001; Zonneveld et al., 2013; Heikkilä et al., 2014; Marret et al., 2020).
362 This species also occurs in environments where upper water salinities are reduced as a result
363 of meltwater or river inputs (Zonneveld et al., 2013). The neritic zone of the southern Brittany
364 shelf, marked by a winter salinity front, may explain its greater occurrence in the proximal
365 zone of the continental shelf (i.e. CBT-CS11 and BQ; 12 % and 5 %, respectively). In

366 temperate waters, cysts of *P. dalei* may likely be used as indicators of cooling and/or
367 continental influences. *S. mirabilis* and *O. centrocarpum* are not significant in the Loire
368 Estuary and in the other three coastal sites (i.e. BQ, CBT-CS11 and VK03-58bis; Fig. 6b),
369 whereas both taxa respectively reach 53 and 21% in the deepest site (i.e. MD95-2002; Fig.
370 6b). These results confirm their affinity for full-oceanic North Atlantic areas. The distribution
371 of heterotrophic dinocysts along this transect is more difficult to interpret. Although we
372 cannot exclude an influence of productivity conditions on heterotrophics, their virtual absence
373 from the Loire Estuary (LE; Fig. 6b) raises questions as it is the most productive area of the
374 transect (Gohin *et al.*, 2019). As previously mentioned in section 5.1, conditions of
375 oxygenation may result in differences between heterotrophic preservation. Comparing
376 heterotrophics would also require to consider mean bottom oxygen conditions and grain-size
377 values for each analyzed site.

378

379 **6. Conclusion**

380 The Bay of Quiberon (BQ), characterized by seasonal hypoxia, appears appropriate to
381 investigate the effects of the different degrees of bottom water oxygenation on dinocyst
382 taphonomic processes (i.e. species-selective degradation after cyst deposition). Among
383 dinocyst assemblages, heterotrophic taxa, well-known to be sensitive to degradation
384 processes, here show a spatial distribution that appears mainly controlled by bottom-water
385 oxygen conditions and sediment granulometry; lower heterotrophic percentages and dinocyst
386 diversity are observed under “higher O₂-coarser sediments”. Heterotrophic occurrences in
387 coastal sediments are here mainly associated to oxidation processes, leading to caution about
388 their use as productivity indexes in paleoecological reconstructions carried out in these kinds

389 of shallow environments, unless high-resolution grain-size analyses are at least conducted in
390 parallel with palynological studies to avoid misinterpretations.

391 The comparison of the averaged dinocyst results acquired in the BQ with surface sediments
392 and top cores, **issued** from already published data, made it possible to improve our knowledge
393 regarding the dinocyst distribution along a northern Bay of Biscay (southern Brittany)
394 inshore-offshore gradient. We **highlighted clear** different ecological groups according to the
395 hydrological and bathymetric contexts: i) an estuarine assemblage at the outlet of the Loire
396 river strongly dominated by *L. machaerophorum*, ii) a proximal coastal assemblage in the
397 shallow BQ still dominated by *L. machaerophorum* with, to a lesser extent, *S. bentorii* and *S.*
398 *membranaceus*, iii) a neritic assemblage dominated by *L. machaerophorum*, *S. ramosus* and
399 cysts of *P. dalei*, and iv) an oceanic group dominated by *S. mirabilis* and *O. centrocarpum*
400 and in which *L. machaerophorum* is rare or absent.

401

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410 context of the LEFE-IMAGO research axis.

411

412 **8. Data availability**

413 The dinocyst dataset related to this article (dinocyst counts on the 15 samples collected in the
414 Bay of Quiberon) can be found in the supplementary material.

415

416 **9. Declaration of competing interest**

417 The authors declare that they have no competing interests.

418

419 **10. References**

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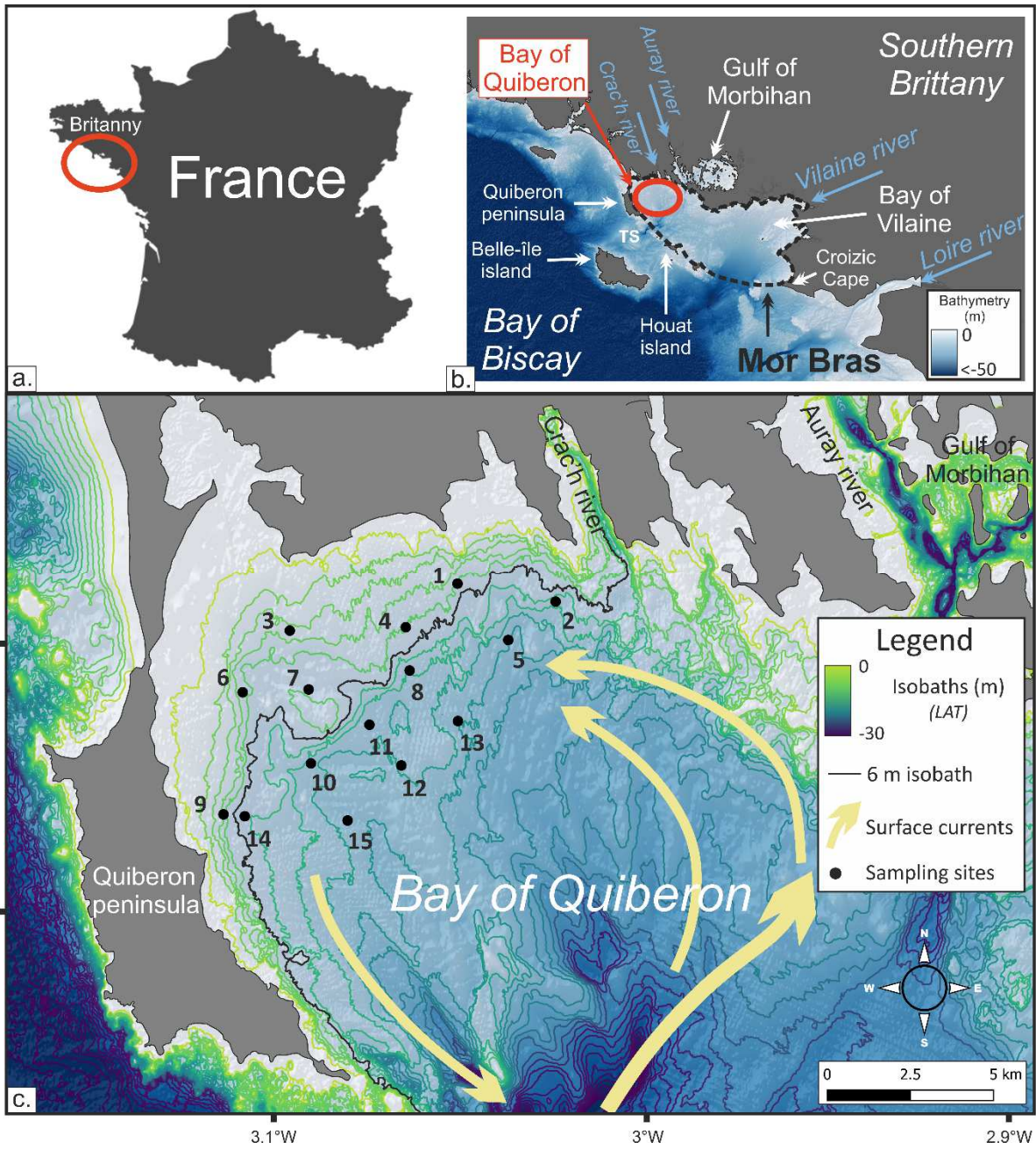
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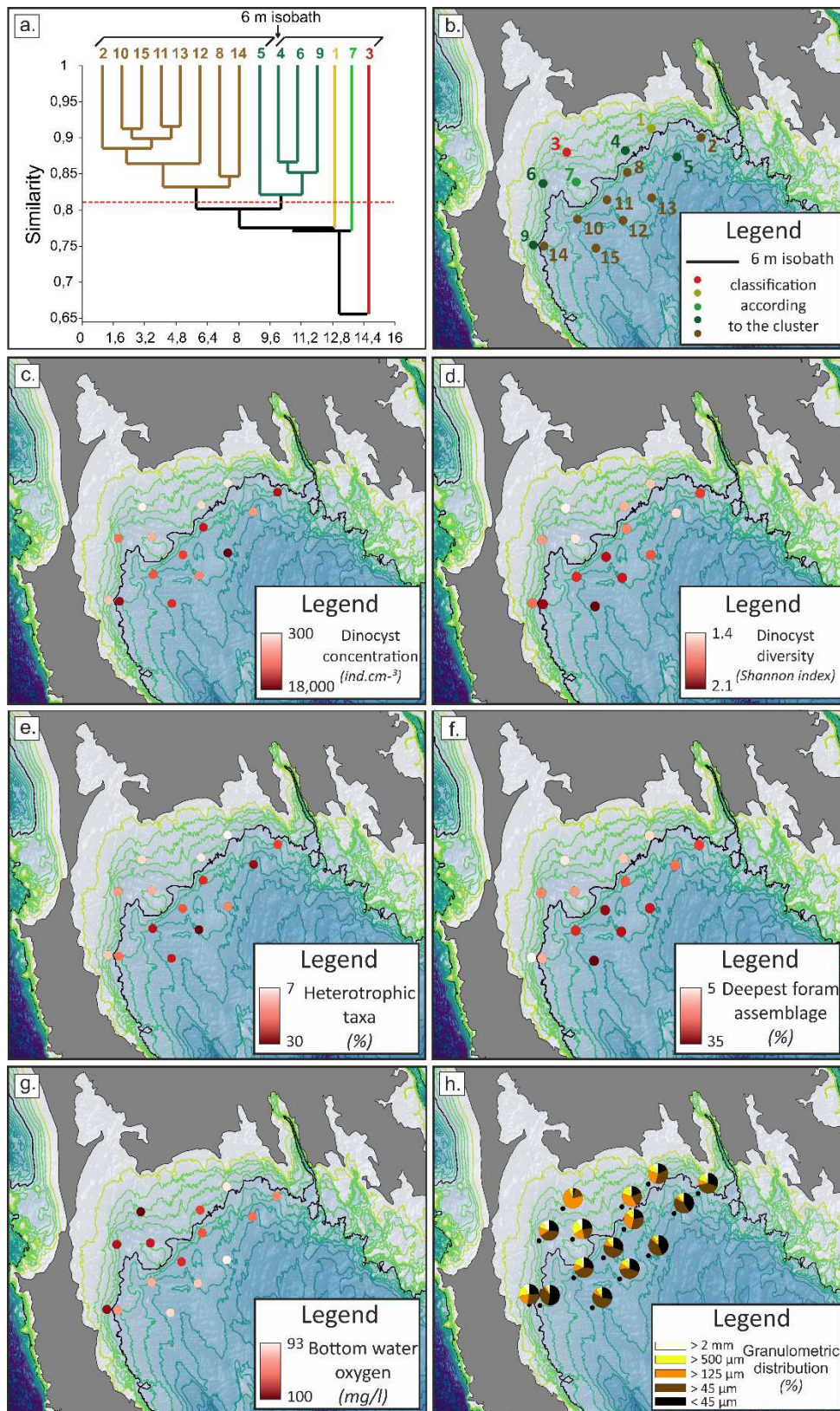
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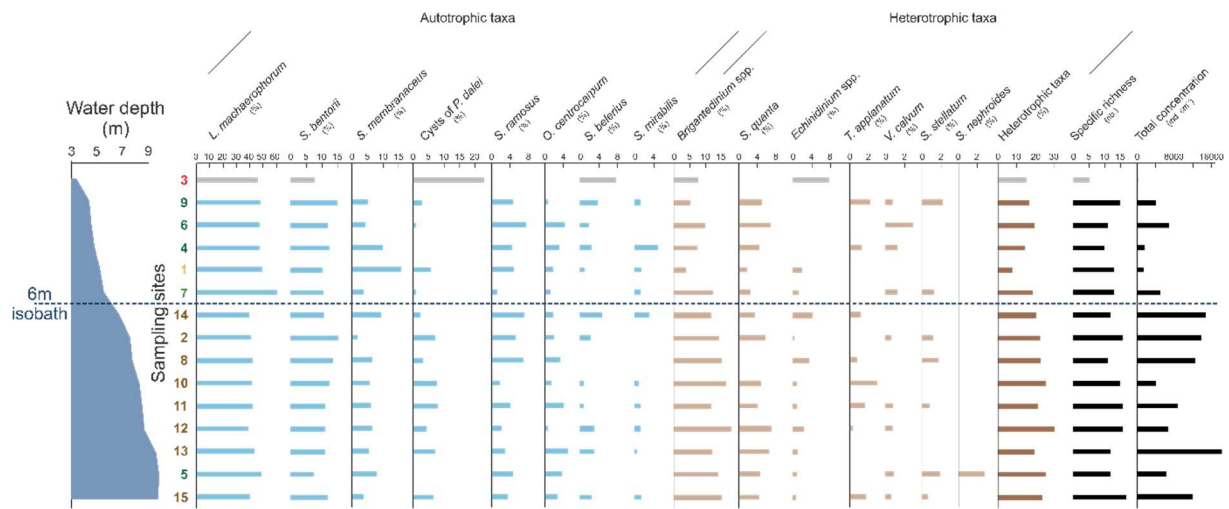
639 **Figure 1**



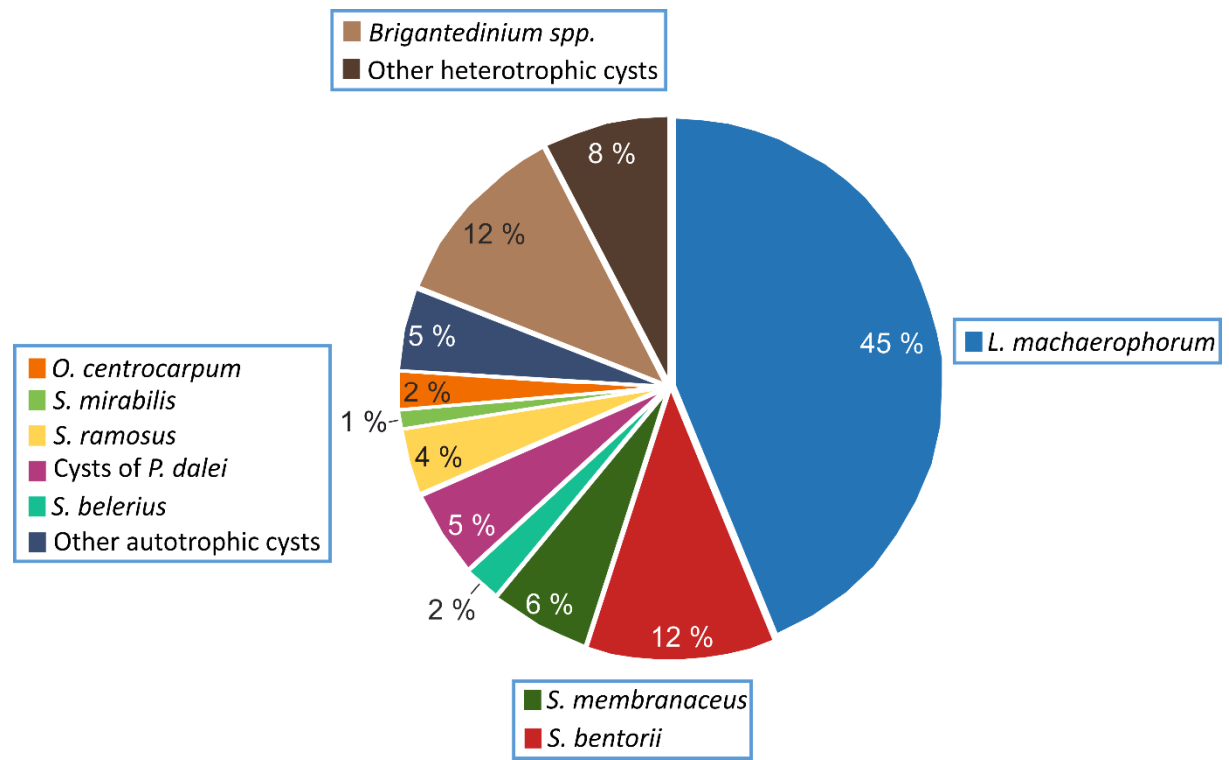
640

641 Figure 2

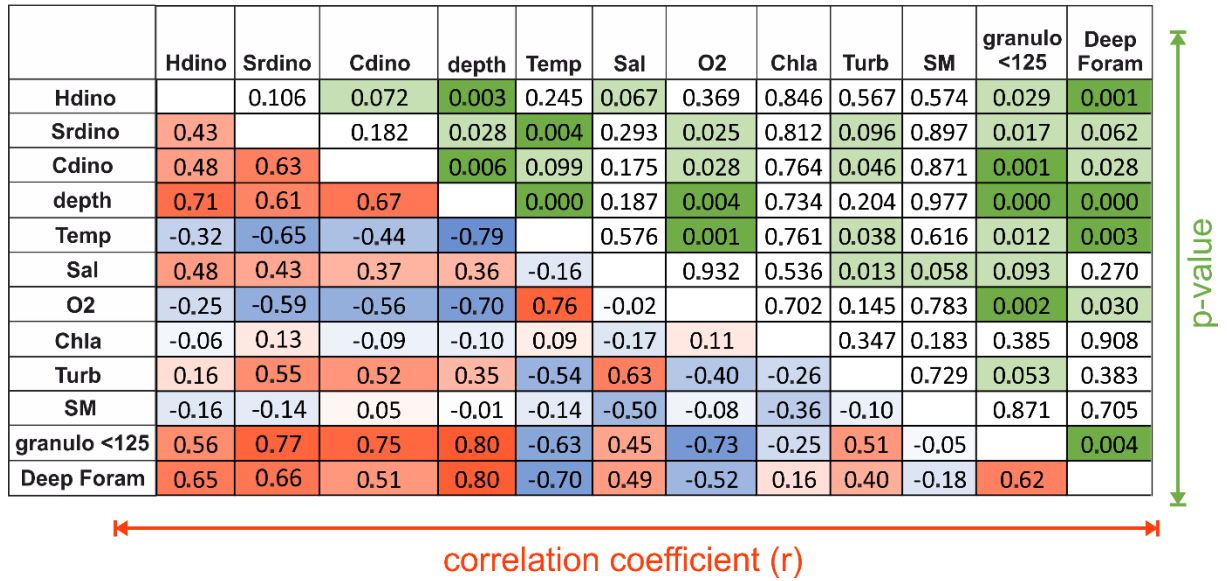
642



643



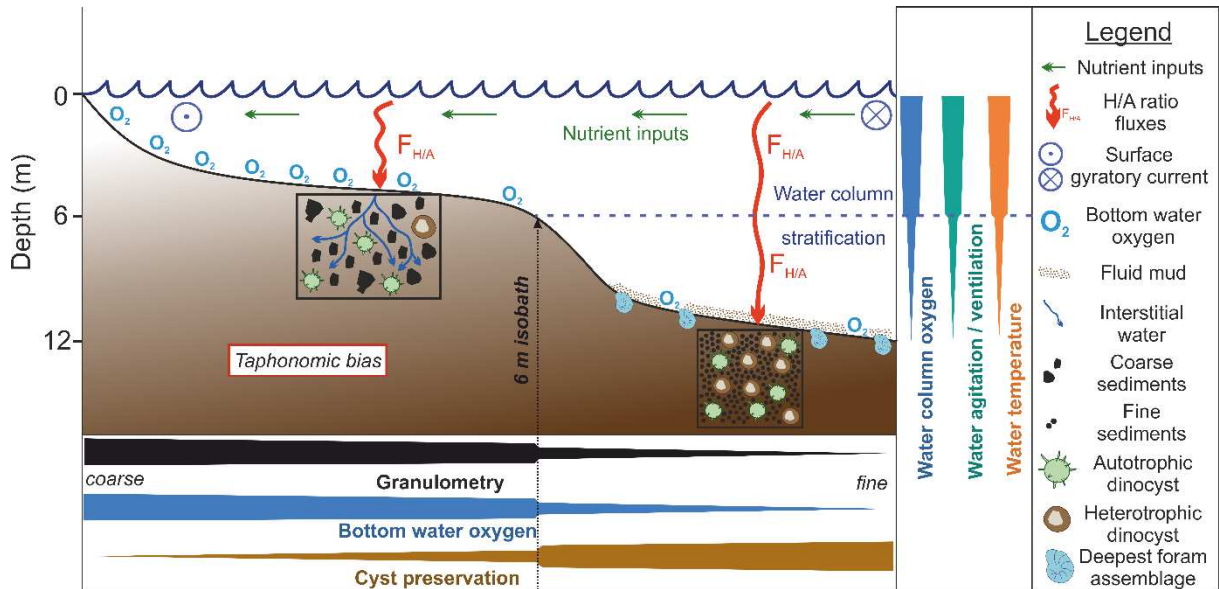
644 **Figure 3**



645

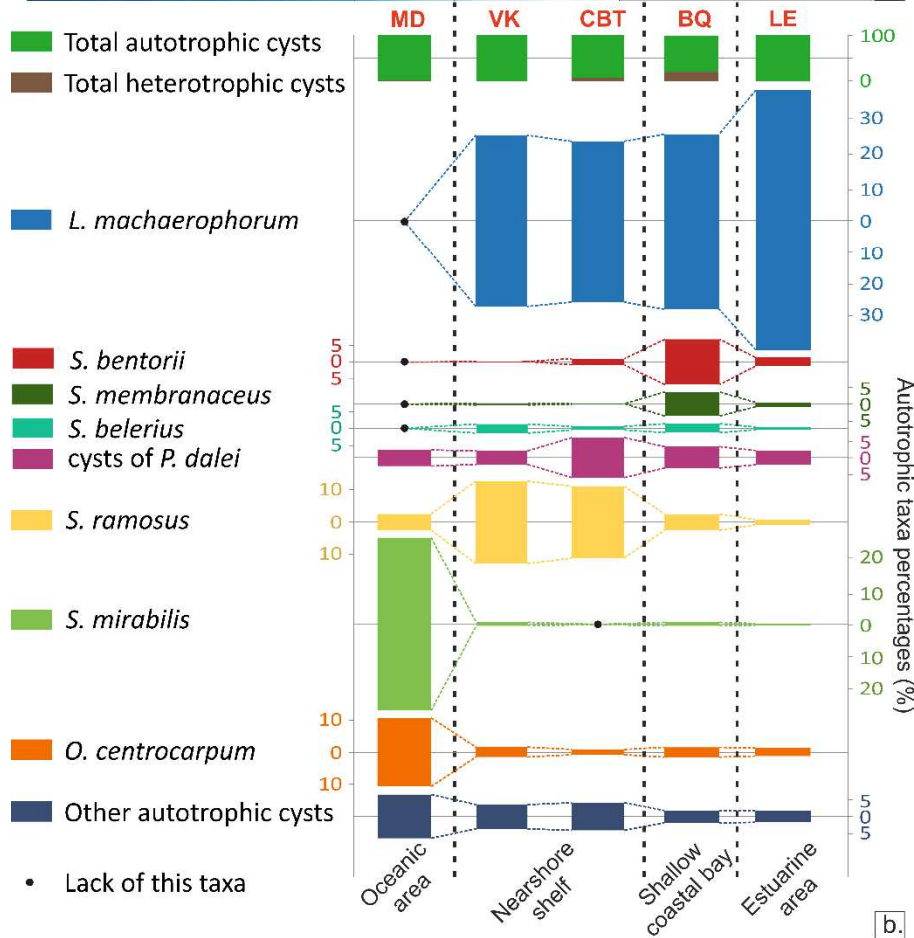
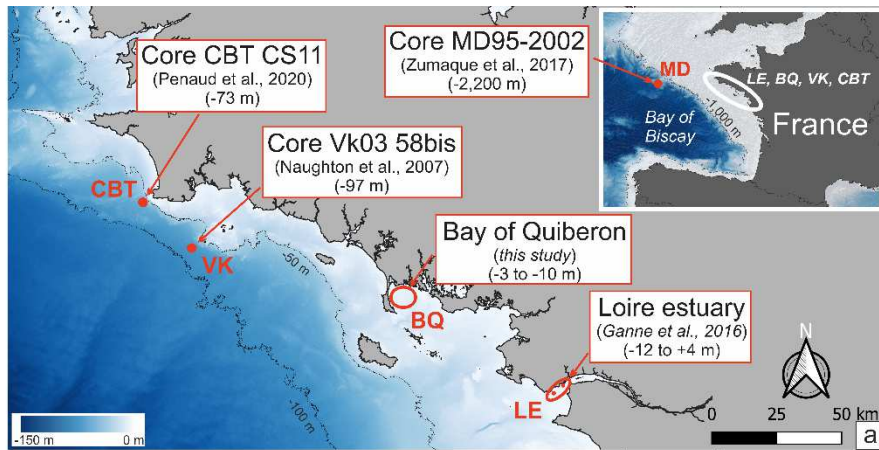
646 Figure 4

647



648

649 Figure 5:



650

651 **Figure 6**

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653

Site	Longitude	Latitude	Sampling depth (m)
1	-3.0501	47.5592979	5.24
2	-3.02359375	47.5560063	7.57
3	-3.09542143	47.5507071	3.37
4	-3.06407917	47.5513313	4.82
5	-3.03639167	47.5489833	9.83
6	-3.10814524	47.5394214	4.58
7	-3.09032917	47.5399396	5.55
8	-3.0630375	47.5434083	7.77
9	-3.11331927	47.5170971	4.4
10	-3.08969323	47.5264333	8.3
11	-3.0739	47.5334896	8.52
12	-3.06528125	47.52605	8.69
13	-3.04997917	47.5341708	9.6
14	-3.10756875	47.5167521	6.75
15	-3.07979245	47.5159747	9.74

655 Table 1

Site	depth (m)	Srdino	Cdino (nb./cm ³)	Hdino (%)	Temp (°C)	Sal (‰)	O2 (mg/l)	Chla (µg/l)	Turb (NTU)	SM (mg/l)	DeepF oram (%)	granulo <125 (%)
1	5.24	1.78	1504.49	7.6	14.5	34.3	93.55	1.95	2.04	6.23	6	54
2	7.57	1.94	13979.95	22.7	14.5	34.4	94.77	1.56	2.40	7.06	12	72

3	3.37	1.48	332.14	15.4	14.8	34.5	100.53	1.94	1.77	5.34	5	21
4	4.82	1.78	1704.96	14.6	14.6	34.4	95.56	1.94	2.09	4.16	8	42
5	9.83	1.77	6313.97	25.9	14.5	34.5	94.84	1.48	1.97	5.29	17	84
6	4.58	1.84	6949.33	19.4	14.7	34.5	96.31	1.89	2.30	4.51	8	66
7	5.55	1.53	5066.16	18.2	14.7	34.5	96.09	1.76	2.03	4.62	10	47
8	7.77	1.87	12657.71	22.7	14.6	34.4	95.25	2.23	1.81	5.17	14	54
9	4.4	1.93	4067.19	16.5	14.6	34.6	97.84	1.81	2.80	4.68	6	52
10	8.3	1.96	8749.84	25.3	14.5	34.5	94.58	2.11	2.17	4.02	14	67
11	8.52	2.03	8831.44	21.3	14.5	34.5	96.02	2.22	2.06	4.63	17	78
12	8.69	2.02	6781.88	30.0	14.5	34.6	94.50	2.00	2.55	5.05	16	74
13	9.6	1.94	18287.72	19.5	14.4	34.6	93.23	1.83	3.30	4.90	17	87
14	6.75	2.03	14767.33	20.6	14.7	34.6	94.67	1.83	2.28	4.51	9	89
15	9.74	2.10	12019.51	23.3	14.4	34.7	93.61	1.76	2.74	4.48	15.08	82

656 Table 2

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658

Abbreviation	Cyst-based taxonomy	Motile stage-based taxonomy	Autotrophic or Heterotrophic	Mean %
ACHO	<i>Ataxodinium choane</i>	<i>Gonyaulax</i> spp. ?	A	0.3
ISPH	<i>Impagidinium sphaericum</i>	<i>Gonyaulax</i> spp. ?	A	< 0.1
LMAC	<i>Lingulodinium machaerophorum</i>	<i>Lingulodinium polyedra</i>	A	45.3
OCEN	<i>Operculodinium centrocarpum</i>	<i>Protoceratium reticulatum</i>	A	2.5

OISR	<i>Operculodinium israelianum</i>	<i>Protoceratium</i> spp. ?	A	< 0.1
PDAL	Cyst of <i>Pentapharsodinium dalei</i>	<i>Pentapharsodinium dalei</i>	A	5.4
SBEL	<i>Spiniferites belerius</i>	Unknown	A	2.3
SBEN	<i>Spiniferites bentorii</i>	<i>Gonyaulax digitale</i> ?	A	11.5
SDEL	<i>Spiniferites delicatus</i>	<i>Gonyaulax</i> spp. ?	A	0.6
SMEM	<i>Spiniferites membranaceus</i>	<i>Gonyaulax</i> spp. (<i>membranacea</i> ?)	A	6.3
SMIR	<i>Spiniferites mirabilis</i>	<i>Gonyaulax spinifera</i> ?	A	1.1
SRAM	<i>Spiniferites ramosus</i>	<i>Gonyaulax</i> spp. ?	A	4.1
BSPP	<i>Brigantedinium</i> spp.	<i>Protoperidinium</i> spp. ?	H	11.8
ESPP	<i>Echinidinium</i> spp.	<i>Protoperidinium</i> spp. ?	H	1.7
GCAT	Cyst of <i>Gymnodinium catenatum</i>	<i>Gymnodinium catenatum</i>	H	0.1
GSPP	Cyst of <i>Gymnodinium</i> spp.	<i>Gymnodinium</i> spp.	H	< 0.1
LSAB	<i>Lejeunecysta sabrina</i>	<i>Protoperidinium leonis</i> ?	H	0.1
PAME	Cyst of <i>Protoperidinium</i>	<i>Protoperidinium americanum</i>	H	0.1
	<i>americanum</i>			
PSPP	Cyst of <i>Protoperidinium</i> spp.	<i>Protoperidinium</i> spp.	H	< 0.1
SNEP	<i>Selenopemphix nephroides</i>	<i>Protoperidinium subinermis</i>	H	0.2
SQUA	<i>Selenopemphix quanta</i>	<i>Protoperidinium conicum</i>	H	4.2
STEL	<i>Stelladinium stellatum</i>	<i>Protoperidinium compressum</i>	H	0.6
TAPP	<i>Trinovantedinium applanatum</i>	<i>Protoperidinium pentagonum</i>	H	0.8
VCAL	<i>Votadinium calvum</i>	<i>Protoperidinium oblongum</i> ?	H	0.7
VSPI	<i>Votadinium spinosum</i>	<i>Protoperidinium claudicans</i>	H	< 0.1
XAND	<i>Xandarodinium xanthum</i>	<i>Protoperidinium divaricatum</i>	H	0.1

659 Table 3

660

661 **Figure captions:**

662 **Figure 1:** a) Location of the study area in NW France. b) Zoom on the S Brittany area
663 identified in a): main bays and rivers are highlighted in the map, as well as the investigated
664 Bay of Quiberon (BQ). The ‘Mor Bras’ is a bathymetric depression bordering the southern
665 coast of Brittany. c) Distribution of the 15 sampling sites within the BQ. The yellow arrows
666 represent the residual gyrotory tidal currents (*Vannev, 1965; Lemoine, 1989; Tessier, 2006*).
667 Maps are performed using the SHOM bathymetric data (SHOM, 2015. ‘*MNT Bathymétrie*
668 *de façade Atlantique*’ (Homonim Project).
669 http://dx.doi.org/10.17183/MNT_ATL100m_HOMONIM_WGS84). LAT = “Lowest
670 Astronomical Tides”, chart datum.

671 **Figure 2:** Distribution maps of various palynological and environmental parameters within
672 the BQ. a) Clustering of sampling stations according to the relative abundances of dinocyst
673 taxa (using PAST v.1.75b; Hammer et al., 2001); b) Colorization of sampling stations
674 according to their membership group in the cluster; c) Dinocyst concentrations (number of
675 specimens/cm³); d) Dinocyst diversity (Shannon diversity index); e) Heterotrophic dinocyst
676 taxa percentages; f) Proportion of the ‘deep foraminiferal assemblage’ regarding the total
677 benthic foraminifera taxa (as described in section 2.); g) Bottom water oxygen concentrations;
678 h) Percentages of grain-size classes.

679 **Figure 3:** a) Diagram representing the percentages of the main dinocyst taxa (greater than 2%
680 on at least one study site), as well as the number of taxa and the total dinocyst concentration,
681 for each BQ study sample. Sampling sites are classified according to water depth. Sample n°3
682 (with only 13 individuals counted) is highlighted in grey. The station numbers (to the left of

683 the diagram) are **highlighted** with the colors identified in the cluster (Fig. 2). b) Averaged
684 percentages of the dominant dinocyst taxa recorded in the fifteen BQ samples.

685 **Figure 4:** Correlation matrix of the different environmental, foraminiferal and dinocyst taxa
686 presented in Tables 2 and 3. A color gradient from blue to red is used to represent the
687 correlation coefficients (blue is used for negative values and red for positive ones; the higher
688 the absolute value (i.e. when it tends to 1), the darker the color). Regarding the other half of
689 the matrix, only p-values below 0.1 are highlighted in light ($0.1 < p\text{-value} < 0.01$) and dark ($p\text{-value} < 0.1$) green.

691 **Figure 5:** Conceptual model presenting the taphonomic preservation bias impacting dinocysts
692 (especially heterotrophics and dinocyst concentrations) in the shallow Bay of Quiberon, on
693 either side of the 6 m bathymetric threshold. The red arrows represent dinocyst fluxes to the
694 sediments. H/A: ratio Heterotrophic to Autotrophic dinocysts. Due to homogenized
695 hydrological parameters of the surface waters within the BQ, we consider that the H/A ratio
696 and nutrient concentrations remain stable at the BQ scale. Gradients for particle size, oxygen
697 concentration, and dinocyst preservation are highlighted under the figure with horizontal
698 thicker or thinner lines on either side of the 6m isobath, and gradients for oxygen
699 concentration, sea-surface temperature and water column mixing are highlighted to the right
700 of the figure with vertical thicker or thinner lines according to the BQ water depth.

701 **Figure 6:** a) Location of modern samples and core tops used in the inshore-offshore transect
702 at the southern Brittany-scale. Map performed using the SHOM bathymetric data (SHOM,
703 2015. '*MNT Bathymétrie de façade Atlantique*' (Homonim Project).
704 http://dx.doi.org/10.17183/MNT_ATL100m_HOMONIM_WGS84) and depths are given
705 according to the chart datum. b) Selected dinocyst taxa percentages: heterotrophics vs.
706 autotrophics for the first line and percentages of the major taxa based on a main autotrophic
707 sum (i.e. excluding heterotrophics). Sites are presented, from right to left, according to their

708 distance from continental influences: LE for 'Loire estuary', BQ for 'Bay of Quiberon', CBT
709 for 'Core CBT-CS11', VK for 'Core VK03-58bis' and MD for 'Core MD95-2002').

710 **Table 1:** Geographic coordinates of sampling sites. Sampling depths ('depth' in the
711 correlation matrix of variables) are provided according to the chart datum ('lowest
712 astronomical tides').

713 **Table 2:** Values of the environmental quantitative parameters used in the correlation matrix of
714 variables for each sampling station (cf. Fig. 4).

715 **Table 3:** List of dinocyst taxa (and their thecate name) identified in this study, abbreviations
716 and percentages recorded in the averaged fifteen BQ surface sediment samples.

717