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1 **Ecosystem spatial structure revealed by integrated survey data**

2

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11

12 **Abstract**

13 Integrated marine survey series such as PELGAS provide comprehensive geo-referenced data over
14 large sea areas in major ecosystem components with defined biological resolution and spatio-temporal
15 sampling scale. These data enable to develop product at different levels of biological organization and
16 spatial scale that are useful for ecosystem integrated assessments. Using the PELGAS integrated data
17 series, we applied a generic procedure made of several steps to identify and map ecologically coherent
18 ecosystem spatial units in the Bay of Biscay. First, the data were interpolated on a common spatial grid
19 and organized as a time series of matrices containing at each time the variables as columns and the
20 grid cell values as rows. The multi-table analysis method known as Multi-Factor Analysis (MFA) was
21 then applied on the series of matrices, thus separating in the analysis the spatial from the temporal
22 variability. Grouping the spatial grid cells based on their relative positions in the MFA space resulted
23 in mapping ecosystem spatial entities based on common spatial patterns across ecosystem
24 components. The result of the analysis is a map of ecosystem seascapes that are consistent over the
25 years together with a map of their inter-annual variability. The ecosystem sub-units were in agreement
26 with sub-regional production systems in the Bay of Biscay. This study thus highlights the possibility to
27 characterize and monitor ecosystem spatial structure and develop indicators thereof for their use in
28 ecosystem assessments. Also, it highlights the importance of identifying spatial limits of production
29 systems for ecosystem description, assessment and management.

30

31 **Keywords**

32 Integrated surveys, Ecosystems, Spatial structure, Multi-Factor Analysis, Bay of Biscay, Pelagic

33

34

35

36 **Contents**

37 1. Introduction

38 2. Sampling protocols and data

39 Multidisciplinary survey design

40 Hydrology and Phytoplankton

41 Zooplankton

42 Pelagic fish

43 Top predators

44 3. Methods

45 Gridding the data

46 Multi Factor Analysis (MFA)

47 Selection of variables in each ecosystem compartment

48 MFA applied on all ecosystem compartments

49 Summary of the procedure applied

50 4. Results

51 Selection of variables in each ecosystem compartment

52 Common spatial patterns across ecosystem compartments and their variability

53 5. Discussion

54 Data and methods for ecosystem description and assessment

55 From seascapes to production systems and meta-ecosystems

56 Towards spatially explicit management scenarios

57

58 **1. Introduction**

59 The ecosystem approach to fisheries management (Garcia et al., 2003) implies understanding stock
60 dynamics within ecosystems, conserving ecosystem structure and function, whilst considering multiple
61 pressures from fishing and other human activities as well as climate drivers. Clearly, the
62 implementation of an ecosystem approach to fisheries management requires the development of
63 integrated assessment procedures across different spatial and temporal scales relevant to the scale of
64 human pressures impacting upon various components of the marine ecosystems. In this context,
65 integrated ecosystem assessments have developed (Kenny et al., 2009; ICES, 2016) to i) characterize
66 past and present states of ecosystem components and functions, and ii) evaluate changes over time
67 and how these link with particular drivers. Fisheries surveys are naturally an important data source for
68 ecosystem description and identification of changes in ecosystem components over time. In effect,

69 fisheries surveys, which were previously dedicated to support stock assessments, are now increasingly
70 providing the basis for multidisciplinary integrated monitoring to assess the status and functions of
71 ecosystems (Doray et al., this issue; Eriksen et al., this issue; Shephard et al., 2015).

72 Two challenges need be addressed for using integrated surveys to characterize the status of
73 ecosystems: first, the technical ability to collect quasi-synoptically data in the main ecosystem
74 components without changing the original fisheries survey sampling design (Doray et al., this issue)
75 and secondly the spatio-temporal question of scale at which to collect meaningful data in the different
76 compartments (Kupschus, 2016; Huret et al., this issue). Parameters in lower trophic levels can be
77 expected to vary on different spatial and temporal scales in comparison to those at higher trophic
78 levels including fish. Accordingly, the design of a survey whilst addressing variation adequately for one
79 component may not be appropriate to make an assessment of all other ecosystem components of
80 interest, e.g. can plankton data and the physical properties of the sea, sampled as part of a fisheries
81 survey, be used jointly and inform appropriately ecosystem description and its assessment? The
82 present study aims to address this question.

83 The PELGAS survey series (Doray et al., this issue; ICES, in press) is an integrated pelagic survey that
84 collects data in the major components of the pelagic ecosystem (hydrology, phyto and zoo plankton,
85 fish, top predators) over a large sea region (Biscay French shelf) during one month, day and night. The
86 data collected are spatially resolved and thus offer the possibility to map ecosystem structure. The
87 objective of the paper is to characterize the spatial structure of the ecosystem using the end-to-end
88 data collected during the survey. First the different variables collected in the different ecosystem
89 components with different spatial resolutions are mapped at the same spatial scale. Then the time
90 series of multiple maps is analysed using a multi-table methodology, Multi-factor analysis (MFA:
91 Escoffier and Pagès, 1994; Dazy and Le Barzic, 1996; Abdi et al., 2013; Petitgas and Poulard, 2009). In
92 this approach, the same variables are evaluated at the same locations and repeatedly at different times
93 (years). The method quantifies, using Principal Components Analysis, the reproducibility in time of the
94 multivariate spatial structure among all the data. To our knowledge, maps of ecosystem structure are
95 seldom produced (ICES, 2016) while they are necessary for ecosystem assessments in the context of
96 an ecosystem approach to fisheries management. Using PELGAS survey data series in the Bay of Biscay,
97 this paper suggests a way forward for mapping ecosystem structure using geo-referenced
98 comprehensive data collected by integrated surveys.

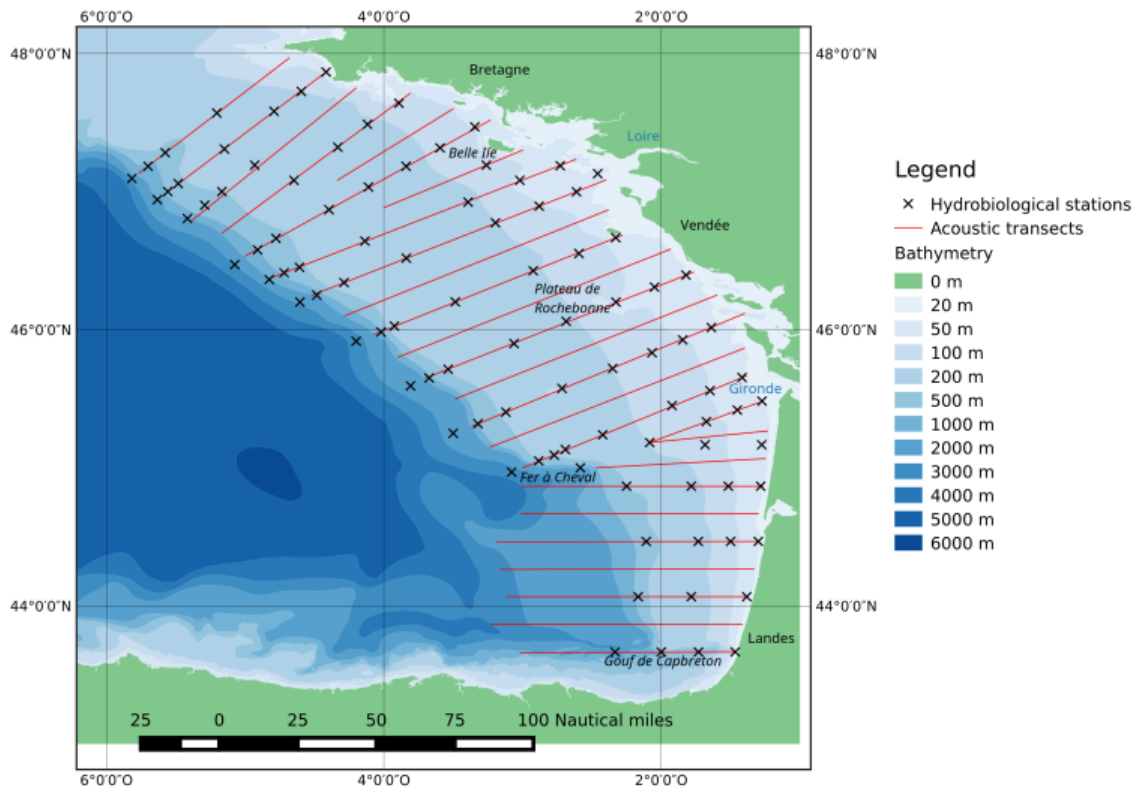
99

100 **2. Sampling protocols and data**

101 **2.1 Multidisciplinary survey design**

102 The PELGAS sampling design combines en-route with at-station data collection strategies (Doray et al.,
103 2014; ICES, in press; Doray et al., this issue). The survey takes place each year in May during spring and

104 lasts one month. The en-route data concern higher trophic levels (fish and top predators) while the at-
 105 station data concern the hydrological water column structure and lower trophic levels (phyto- and
 106 zooplankton). En-route data are collected along a grid of regularly spaced transects 12 nautical miles
 107 (nm) apart, which extend from the coast (20m bottom depth) to the shelf break (250m). The survey
 108 lines are oriented perpendicular to the isobaths and are transited at 10 knots during day light hours.
 109 The grid is sampled annually at the same time of the year. Data collected simultaneously en-route are
 110 acoustic records of pelagic fish abundance, subsurface egg abundance pumped with CUFES
 111 (Continuous underway fish egg sampler) and visual counts of sea birds and mammals. At-station data
 112 are collected during hours of darkness, on a grid of stations positioned regularly along every second
 113 transect (10 to 20 nm apart). The same station positions are sampled annually. Data are collected
 114 simultaneously at each station by way of CTD vertical casts, which sample continuously and vertically
 115 temperature, salinity, and fluorescence. In addition Niskin bottles are used to measure chlorophyll a
 116 at depth (abundance by size class) and WP2 nets with 200 μm mesh size provide an integrated sample
 117 of the water column for zooplankton (abundance by size class). This minimum protocol (more variables
 118 can be sampled in a given year) has been performed since 2009 and covers the entire shelf of the
 119 French part of the Bay of Biscay from 43.6°N to 48°N (Fig.1). The data series available for the study
 120 extends from 2009 to 2014.



121
 122 Figure 1: Map of PELGAS survey design over the French shelf of the Bay of Biscay showing the transects
 123 (red lines) for collecting data on pelagic fish and top predators during day-light hours and the stations

124 (black crosses) for collecting depth-integrated data on hydrology and plankton during hours of
 125 darkness.

126
 127 To characterize the pelagic ecosystem, we considered a list of variables to represent the following
 128 compartments: hydrology, phytoplankton, zooplankton, pelagic fish, sea birds and mammals. For
 129 hydrology we considered surface and bottom temperature, surface salinity and indices characterizing
 130 water column stratification. For phytoplankton, we considered vertically integrated chlorophyll_a
 131 abundance and size fractionated chlorophyll_a at surface. For zooplankton, we considered vertically
 132 integrated total abundance and size fractionated abundance. While lower trophic levels were
 133 characterized by total and size fractionated abundance, higher trophic levels were characterized by a
 134 selection of species, which are most consistently found in the series of surveys (Table 1). The fish
 135 species were anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*),
 136 two mackerel species (*Scomber scombrus* and *Scomber japonicus*) and horse mackerel (*Trachurus*
 137 *trachurus*). Top predator species were aggregated in groups with common ecology: auks, gannets, gulls
 138 and terns, large and small delphinids.

139
 140 Table 1: List of variables characterizing the pelagic realm, which are derived from the PELGAS
 141 integrated survey design and protocol

Ecosystem compartment	Variable used
Hydrology	ST: Surface temperature (°C) BT: Bottom temperature (°C) SS: Surface salinity (psu) Heq: Height of equivalent freshwater depth (m) Depot: Deficit of potential energy ($\text{kg m}^{-1} \text{s}^{-2}$) Zpyc: Depth of pycnocline (m)
Phytoplankton	CHLint: Vertically integrated Chlorophyll a (mg m^{-2}) CHLS : Surface chlorophyll a (mg m^{-3}) CHLS1: Surface chlorophyll a in cells $< 3 \mu\text{m}$ (mg m^{-3}) CHLS2: Surface chlorophyll a in cells $3\text{-}20 \mu\text{m}$ (mg m^{-3}) CHLS3 : Surface chlorophyll a in cells $> 20 \mu\text{m}$ (mg m^{-3})
Zooplankton	Zmeso: Total dry weight of mesozooplankton (mg m^{-2}) Z200: Dry weight of zooplankton between $200\text{-}500 \mu\text{m}$ (mg m^{-2}) Z500: Dry weight of zooplankton between $500\text{-}1000 \mu\text{m}$ (mg m^{-2}) Z1000: Dry weight of zooplankton between $1000\text{-}2000 \mu\text{m}$ (mg m^{-2})

	Z2000: Dry weight of zooplankton > 2000 μm (mg m^{-2})
Fish	ENGRENK : Anchovy (10^3 kg nm^{-2}) SARDPIL : Sardine (10^3 kg nm^{-2}) SPRASPR : Sprat (10^3 kg nm^{-2}) SCOMSO : Atlantic mackerel (10^3 kg nm^{-2}) SCOMJAP : Chub mackerel (10^3 kg nm^{-2}) TRACTRU : Horse mackerel (10^3 kg nm^{-2})
Top predators	AUK: Auks (number km^{-2}) GAN: Gannets (number km^{-2}) GULT: Gulls and terns (number km^{-2}) DEL1: Small delphinids (number km^{-2}) DEL2: Large delphinids (number km^{-2})

142

143 **2.2 Hydrology and phytoplankton**

144 Sampling the water column for hydrology and phytoplankton parameters is performed at night at
 145 stations with a conductivity–temperature–depth (CTD, SeaBird SBE19+V2) probe instrumented with a
 146 Wetlab fluorimeter. Vertical casts provide temperature, salinity, density and fluorescence throughout
 147 the water column. In addition, Niskin bottles provided water samples at three different depths: below
 148 thermocline, within the chlorophyll maximum and at surface. Water samples were filtered for size-
 149 fractionated ($<3\mu\text{m}$, $3\mu\text{m} < <20\mu\text{m}$, $>20\mu\text{m}$) estimations of chlorophyll concentration performed by
 150 spectrophotometry in the laboratory. From the CTD profiles, several hydrological indices are computed
 151 following equations of Huret et al. (2013): Surface temperature and surface salinity (between 2 and
 152 7m), bottom temperature (with max depth set at 200m), equivalent water height and deficit of
 153 potential energy. The deficit of potential energy is an index of water column stratification
 154 corresponding to the energy that would be required to homogenize density over the column (with max
 155 depth set at 60m). The equivalent water height is an index of river plume influence on the shelf
 156 integrating over the water column the relative difference in salinity from a reference value set at 35.5.
 157 In comparison to surface salinity, this index relates better to the history of river run offs and vertical
 158 mixing. The integrated chlorophyll concentration is calculated by summing values over the water
 159 column profiles using a fluorimeter, after correcting for potential bias by comparison to laboratory
 160 measurements of chlorophyll. This is done by regressing the fluorimeter values on the chlorophyll
 161 values at depth, all depths pooled. This post-calibration is performed by year.

162

163 **2.3 Zooplankton**

164 Mesozooplankton samples are collected during the night by operating a WP2 net (mouth opening of
165 0.25 m² and mesh size of 200 µm). The net is hauled vertically from bottom (max depth set at 100 m)
166 to surface. When present macrozooplankton is eliminated by sieving the sample through a 5 mm mesh.
167 Four size-classes of mesozooplankton are obtained by successive filtrations (washed with distilled
168 water) on three sieves with mesh size 200, 500, 1000 and 2000 µm. Samples are frozen and stored at
169 -20°C until further analysis in the laboratory, where dry weight of size fractions are measured, the sum
170 of which estimates total dry wet.

171

172 **2.4 Pelagic fish**

173 Fish abundance by species is derived from combining the acoustic records interpreted as fish
174 echotraces with pelagic trawl haul samples following standard acoustic multi-species procedure
175 (Petitgas et al., 2003; Doray et al., 2014 and references there in). Acoustic data are recorded en-route
176 by day along transects at multiple frequencies, using Simrad ER60 hull-mounted calibrated
177 echosounders. Pelagic trawl hauls are undertaken adaptively depending on the echotraces to inform
178 on the species composition and their biological parameters (length, weight, age). Biomass estimation
179 is performed using the 38 kHz frequency data only while other frequencies are used to help isolate the
180 fish echotraces from other echoes (e.g., sound scattering layers). Echograms are manually corrected
181 for bottom detection errors then echo-integrated over standard depth layers (10 m) and one nautical
182 mile (nm) sailed distance (Elementary sampling distance unit: ESDU). Echograms are further scrutinized
183 by experts to allocate previous echo-integrals into several echo categories (echo-types). The resulting
184 data are Nautical area backscattering coefficients (NASC) by echo-type by nm along transects. For
185 species identification, the NASC value for each echo-type in each ESDU is associated by experts to one
186 identification trawl haul. The echo-type NASC value is then apportioned into a NASC per species using
187 standard acoustic multi-species equations (Doray et al., 2014 and references there in). Finally the
188 species-specific NASC values are further converted to biomass per species using the target strength
189 (TS) corresponding to the mean length and weight of the species in the catch. This procedure results
190 in estimating biomass per species (tonnes) for every nautical mile along transects.

191

192 **2.5 Top predators**

193 Sighting data of marine mammals and seabirds are collected en-route by day along transects by three
194 observers following a standard distance sampling protocol (Doray et al., 2014 and references there in).
195 The GPS location of each sighting is recorded. Two observers are positioned each on one side of the
196 vessel, on the upper bridge (16 m above sea level) or inside the bridge (14 m above sea level)
197 depending on weather conditions. Observations of megafauna is by eye within an angle of 90° from
198 the side to the bow. Binoculars are used for species identification following initial detection by eye.

199 Identification is carried out to the lowest possible taxonomic level. Photos are systematically taken to
200 validate species identification for cetaceans and seabirds. Every hour one observer is relieved from
201 duty by the third one to limit observer fatigue. Counts are estimated as number of individuals per km²
202 and located in the middle of 2 km segments (elementary sampling units) along transects.

203

204 **3. Data Analysis**

205 The method proposed to analyze the multivariate and spatio-temporal structure in the data combines
206 a gridding procedure with a multi-table analysis, in which spatial and temporal variability are
207 separated.

208

209 **3.1 Gridding the data**

210 The data were mapped using a grid and an automated gridding procedure. When multiple values of
211 the same variable were in the same grid cell these were averaged (Petitgas et al., 2009; ICES, in press).
212 The grid mesh size selected was 0.25 degrees in latitude and longitude with origin x_0 at 43°N and 6°W.
213 This choice resulted from a compromise between the number of variable values averaged in each grid
214 cell, and the grid spatial resolution. For each variable, the mean of the grid cell (i, j, x_0) was the average
215 of the data inside the grid cell, positioned at the grid cell center. The gridded data depended on the
216 grid origin. To decondition the gridded values from the grid origin, the point origin x_0 was randomized
217 in the lowest left corner grid cell one 100 times. The 100 values computed within each grid cell were
218 finally averaged to provide the grid cell value.

219

220 **3.2 Multi Factor Analysis (MFA)**

221 Multi Factor Analysis (MFA) is an extension of Principle Components Analysis (PCA) using multiple
222 tables for the analysis of 3-dimensionally structured data (Escoffier and Pagès, 1994; Dazy and Le
223 Barzic, 1996; Abdi et al., 2013). MFA is designed for situations where the same variables (matrix
224 columns) are measured in the same grid cells (data rows) at various times (tables). In the MFA analysis,
225 variability in time is explicitly differentiated from the correlation structure among the variables. This
226 allows an estimate of the correlation structure among the variables that is most consistent in time and
227 also to quantify the temporal variability around the average structure. In single PCA all sources of
228 variability are pooled and thus the spatial and temporal structures are less clearly identified than in
229 MFA. When using MFA, the data are structured as a time series of elementary tables. For a given survey
230 (year), the elementary table contains the variables in columns and the grid cell values in rows. The data
231 are organized as a time series of such tables, one per year. MFA proceeds as a double PCA. First, a PCA
232 is applied to each yearly table, where columns are centered and normed. Each table is then further
233 normalized by its first eigen value, which allows to compare all tables. For that, a second PCA is applied

234 on the global table made of the normalized tables appended by columns. In doing so MFA constructs
235 a factorial space that is a compromise between all elementary (normalized) tables, in which the 3-
236 dimensional structure of the data is represented. In particular, each grid cell (table row) is represented
237 by n points (n years) in the MFA space and so is each variable (table column). Further, the principal
238 components of the MFA are interpretable using their correlation with the variables. Each variable
239 having n point positions (n years) in the MFA space, the MFA principle components are interpreted
240 with those variables showing a good correlation with the components for a sufficiently large number
241 of years. Being based on PCA, MFA suffers the same limitations as PCA. In particular, all variables must
242 be valued in all grid cells and the correlation between variables may be affected by a large proportion
243 of zeroes and/or very high values. The gridding procedure reduces here these effects by smoothing.
244 Also transforming the grid cell means may reduce the effect of some high values on the correlations.
245 MFA has been applied in fisheries science to characterize seasonal and inter-annual variations in fish
246 community structures (Gaertner et al., 1998), fishing activities (Poulard and Léauté, 2002) or
247 monitoring in time the spatial structure in fish populations (Petitgas et al., 2009). Here to apply MFA,
248 we used the library ade4 in R language (Dray and Dufour, 2007) and in particular the function mfa()
249 with option 'lambda1'. The biological variables were $\log(x+1)$ transformed and the hydrological
250 variable were not.

251

252 **3.3 Selection of variables in each ecosystem compartment**

253 MFA was first applied to each ecosystem compartment using the variables characterizing that
254 compartment (Table 1). Variables were selected based on their repeated good correlation with the
255 MFA principal components for a sufficient number of years. In effect, variables selected on that criteria
256 carry the structure among the variables that is most consistent across the series of years (2009-2014).
257 The variables retained had correlation coefficients with at least one of the two first principal
258 components that were greater than 0.5 in absolute value and for which such (good) correlation
259 occurred with a frequency in time higher than 0.5. Correlation of variables with principal components
260 of higher order (>2) was often low or infrequent, meaning that these components were difficult to
261 interpret and this is why we used the first two principal components only. Some variables were
262 redundant as they showed similar correlation with the MFA principal components. In that case and in
263 order to select one variable only among the redundant ones, we analyzed the sensitivity of each of the
264 redundant variables in the global analysis. The full analysis was run considering each variable at a time
265 and without the other redundant ones. The variable selected was the one which allowed the most
266 clear-cut clustering among grid cell points (see below). This approach selected variables in one
267 ecosystem compartment that correlated well with other variables in other compartments. The
268 variables finally selected carried so to speak the correlation structure for their compartment that was

269 the most consistent over the years as well as across compartments. The selection procedure thus
270 reduces noise and allows to better identify the overall structure across ecosystem compartments.

271

272 **3.4 MFA applied on all ecosystem compartments**

273 MFA was then applied to all selected variables representing best their ecosystem compartment. Those
274 variables, which had with the MFA principal components correlation coefficients greater than 0.5 in
275 absolute value for more than half of the years, were identified as those carrying the main structure of
276 the ecosystem. The positions of the grid cells in the MFA space served to map ecosystem structure and
277 characterized variability between years around the average map. A hierarchical clustering (function
278 `hclust` in R language) was performed on the average grid points. Cutting the hierarchical tree at
279 appropriate level allowed to group the grid cell points into a few classes, which were then mapped.
280 The clusters of grid cell points represented particular regions in the Bay of Biscay, thus revealing sub-
281 systems or seascapes. For each grid cell, the squared distance in the MFA space between its annual
282 position and its mean position summed over the years represented the inertia of that grid cell and
283 characterized inter-annual variability, which was also mapped. The inertia at geographical location x
284 writes:

$$285 \quad I(x) = \sum_{k=1}^n dist^2(p(x,k), pm(x))$$

286 Where x is a grid cell center, k the index of the years, $p(x,k)$ the point in the MFA space representing
287 grid point x in year k and pm the point in the MFA space representing the average grid point. The
288 squared distance $dist^2$ was computed using coordinates of points $p(x,k)$ and $pm(x)$ on the two first
289 MFA principal components. Similarly, the inertia for each variable was computed to quantify inter-
290 annual variability in each of the variables.

291

292 **3.5 Summary of the procedure applied**

293 In summary we suggest here a procedure to analyze data from fisheries integrated surveys. The data
294 are geo-referenced and correspond to repeated measurements in time (e.g., each year) of the same
295 variables in major ecosystem compartments. The different steps of the procedure are the following:

- 296 • Data gridding. The data are mapped on the same grid providing a series of maps. There are as
297 many maps as years. Each map is a table where the rows are the grid cell values and the
298 columns the variables measured;
- 299 • Selection of variables in each ecosystem compartment. This step results is a list of variables,
300 which carry the multivariate structure that is most consistent in time in each ecosystem
301 compartment and also across compartments;

302 • MFA on all ecosystem compartments using selected variables. This provides a description of
303 the ecosystem multivariate and spatial structure that is consistent in time as well as a
304 quantification of the temporal variability around the average structure. Hierarchical clustering
305 of the grid cell points in the MFA space allows to map ecosystem structure. And computing in
306 the MFA space the inertia in time allows to map ecosystem variability around the average
307 structure.

308 An example R script is provided as supplementary material together with gridded data from the Pelgas
309 survey series, allowing to apply MFA on this example data set to perform the last step of the above
310 procedure.

311

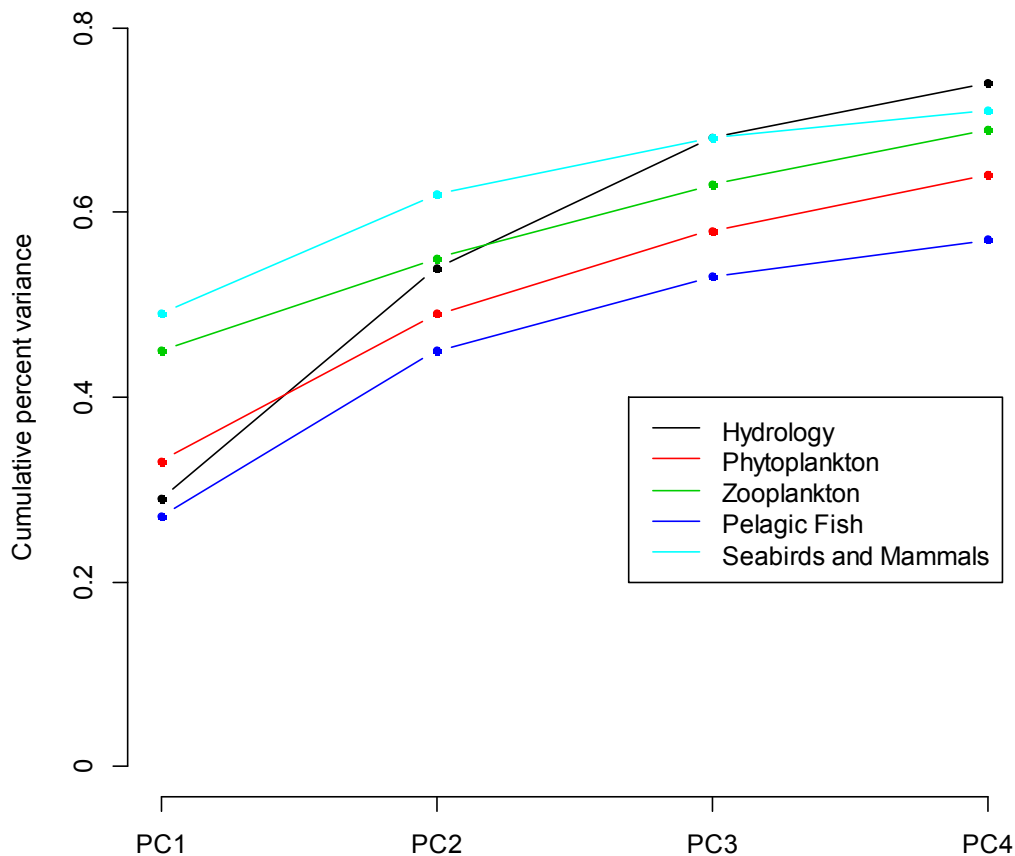
312 **4. Results**

313 **4.1 Selection of variables in each ecosystem compartment**

314 MFA was applied in each ecosystem compartment on the series 2009-2014 (see Table 1 for the list of
315 variables by compartment). The first two principal components in each compartment explained
316 between 45-62 percent of the space-time variability, Phytoplankton and Pelagic Fish compartments
317 showing the less explained variability (Figure 2).

318

319



320

321 Figure 2: Cumulated percent variance explained by the first four MFA principal components, when
 322 applying MFA in each ecosystem compartment on the series 2009-2014 of the gridded data.

323

324 The frequency in time of the correlation of the variables with the MFA components (Table 3) allowed
 325 to select those variables representing best the space-time variability in their ecosystem compartment.
 326 For a few variables only, we considered their sensitivity in the global analysis. In the Phytoplankton
 327 compartment, Total surface chlorophyll and Chlorophyll in cells greater than 20 μm were redundant
 328 but we finally selected Total surface chlorophyll, which was also less statistically variable. Similarly in
 329 the Zooplankton compartment, biomasses in the fractions greater than 1000 μm and 2000 μm were
 330 redundant and we selected the fraction greater than 1000 μm , which was also less statistically variable.
 331 In the Seabirds and Mammals compartment Gannets and Gulls were redundant and neither was
 332 selected. These species were largely distributed on the entire shelf, which decreased the efficiency of
 333 the clustering in the global analysis. Chub mackerel in the Fish compartment was close to be selected
 334 using the correlation criteria. This variable was mainly distributed in the South ($<45.5^\circ$) but with high
 335 variability among years in its location. When selected, it also decreased the efficiency of the clustering
 336 in the global analysis. Finally 13 variables were retained (Table 4), which summarized spatial patterns

337 in their compartments that were consistent in time: 3 for Hydrology, 2 for Phytoplankton, 2 for
 338 Zooplankton, 3 for Fish and 3 for Top predators.

339

340 Table 3: Number of years, in which the variables were correlated with the first four principal
 341 components of (partial) MFA applied in each ecosystem compartment. The time series was from 2009
 342 to 2014. The notation “n+|k-” indicates n positive and k negative correlations. Correlations with
 343 absolute value greater than 0.5 were considered only. Acronyms of variable are defined in Table 1.
 344 The column Selection indicates whether or not the variable was selected for applying MFA on all
 345 ecosystem compartments.

	Variables	Corr. PC1	Corr. PC2	Corr. PC3	Corr. PC4	Selection
Hydrology	ST	0+ 0-	3+ 0-	3+ 0-	0+ 1-	No
	BT	4+ 0-	3+ 0-	0+ 0-	0+ 0-	Yes
	SS	0+ 4-	3+ 0-	0+ 1-	0+ 0-	Yes
	Heq	3+ 0-	0+ 3-	2+ 0-	0+ 0-	No
	Depot	0+ 4-	0+ 0-	4+ 0-	0+ 0-	Yes
	Zpyc	0+ 4-	0+ 1-	0+ 0-	0+ 0-	No
Phytoplankton	CHLint	1+ 0-	5+ 0-	0+ 0-	0+ 0	Yes
	CHLS	0+ 5-	1+ 0-	1+ 0-	0+ 0-	Yes
	CHLS1	0+ 2-	0+ 0-	0+ 1-	0+ 0-	No
	CHLS2	0+ 3-	1+ 0-	0+ 0-	1+ 0-	No
	CHLS3	0+ 5-	1+ 0-	0+ 0-	0+ 0-	No
Zooplankton	Zmeso	0+ 6-	0+ 1-	0+ 1-	1+ 0-	Yes
	Z200	0+ 0-	1+ 1-	0+ 1-	0+ 1-	No
	Z500	0+ 5-	0+ 1-	0+ 0-	0+ 0-	No
	Z1000	0+ 6-	0+ 0-	0+ 0-	0+ 0-	Yes
	Z2000	0+ 6-	0+ 0-	0+ 0-	0+ 0-	No
Pelagic Fish	ENGRENC	0+ 5-	0+ 0-	0+ 1-	0+ 0-	Yes
	SARDPIL	0+ 6-	0+ 0-	0+ 0-	0+ 0-	Yes
	SPRASPR	0+ 4-	0+ 2-	0+ 0-	0+ 0-	Yes
	SCOMSO	1+ 0-	1+ 0-	0+ 0-	0+ 1-	No
	SCOMJAP	0+ 0-	3+ 0-	0+ 0-	0+ 0-	No
	TRACTRU	2+ 0-	1+ 0-	0+ 0-	0+ 0-	No
Seabirds and Mammals	AUK	0+ 6-	5+ 0-	1+ 0-	0+ 0-	Yes
	GAN	0+ 5-	0+ 0-	0+ 0-	0+ 1-	No

	GULT	0+ 6-	0+ 0-	0+ 0-	0+ 0-	No
	DEL1	5+ 0-	6+ 0-	0+ 0-	0+ 0-	Yes
	DEL2	6+ 0-	0+ 0-	0+ 0-	0+ 0-	Yes

346

347

348 4.2 Common spatial patterns across ecosystem compartments and their variability

349 MFA was applied on all ecosystem compartments using the 13 variables selected in section 4.1 (Table
 350 3). The summed percent variance explained by the four first principal components were 0.31, 0.51,
 351 0.59 and 0.65 respectively, which is close to what MFA explained in each compartment (Fig. 2),
 352 meaning that the spatial structures in the different compartments had broad similarities at the scale
 353 and resolution of this study. This is confirmed by the fact that 3 variables only (integrated chlorophyll,
 354 total mesozooplankton and small delphinids) were not well correlated with the principal components
 355 (Table 4).

356

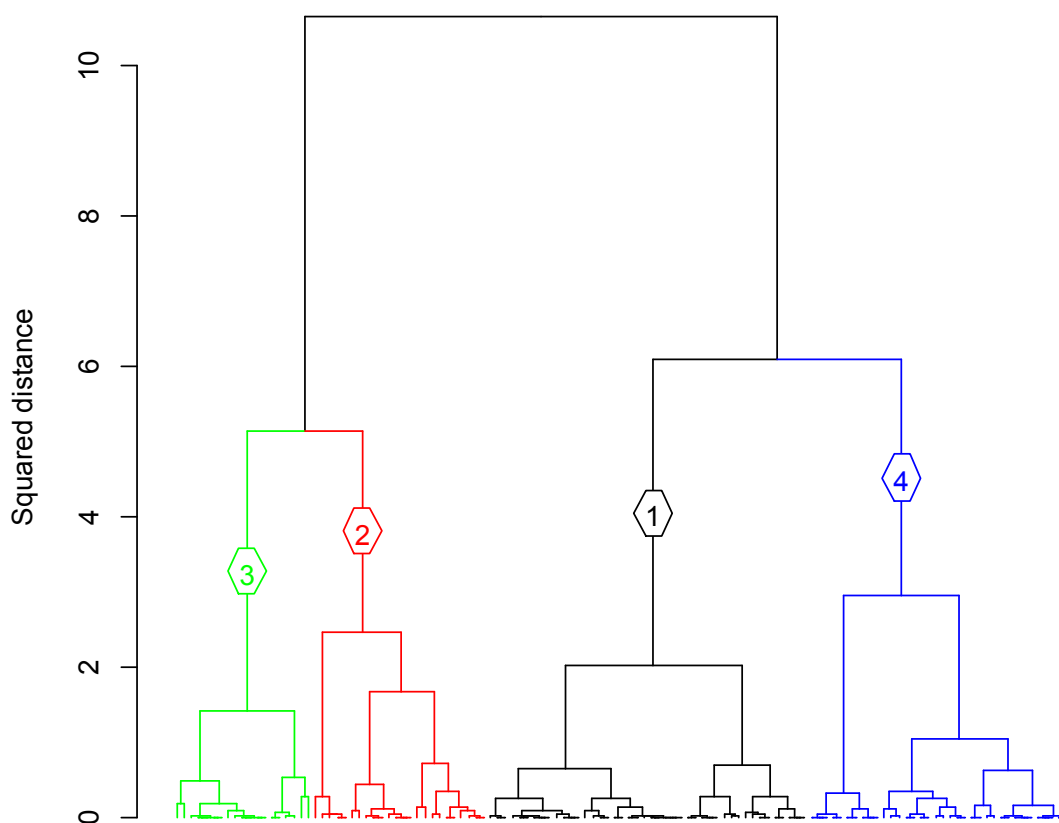
357 Table 4: MFA on all ecosystem compartments using the 13 selected variables. Number of years, in
 358 which the variables were correlated with the MFA four first principal components. The time series was
 359 from 2009 to 2014. The notation “n+|k-” indicates n positive and k negative correlations. Correlations
 360 with absolute value greater than 0.5 were considered only. Acronyms of variable are defined in Table
 361 1.

	Variables	Corr. PC1	Corr. PC2	Corr. PC3	Corr. PC4
Hydrology	BT	0+ 1-	6+ 0-	0+ 0-	0+ 0-
	SS	0+ 6-	0+ 0-	0+ 0-	0+ 0-
	Depot	0+ 0-	0+ 4-	3+ 0-	0+ 0-
Phytoplankton	CHLint	0+ 2-	0+ 0-	0+ 1-	0+ 1-
	CHLS	4+ 0-	0+ 0-	0+ 1-	0+ 0-
Zooplankton	Zmeso	0+ 3-	0+ 3-	0+ 0-	0+ 0-
	Z1000	0+ 6-	0+ 3-	0+ 0-	0+ 0-
Pelagic Fish	ENGRENC	1+ 0-	5+ 0-	0+ 0-	0+ 1-
	SARDPIL	6+ 0-	0+ 0-	0+ 0-	0+ 0-
	SPRASPR	5+ 0-	0+ 0-	0+ 0-	0+ 0-
Seabirds and Mammals	AUK	6+ 0-	0+ 0-	0+ 0-	0+ 0-
	DEL1	0+ 0-	1+ 0-	0+ 0-	0+ 1-
	DEL2	0+ 5-	2+ 0-	0+ 0-	0+ 0-

362

363 The spatial grid cells were grouped by applying hierarchical clustering in the MFA space. The similarity
364 distance considered for grouping grid cells was the squared Euclidian distance between cells and it was
365 computed using their average scores on the two first principal MFA components. Four groups were
366 identified visually corresponding to a clear decline in dissimilarity (Fig. 3).

367



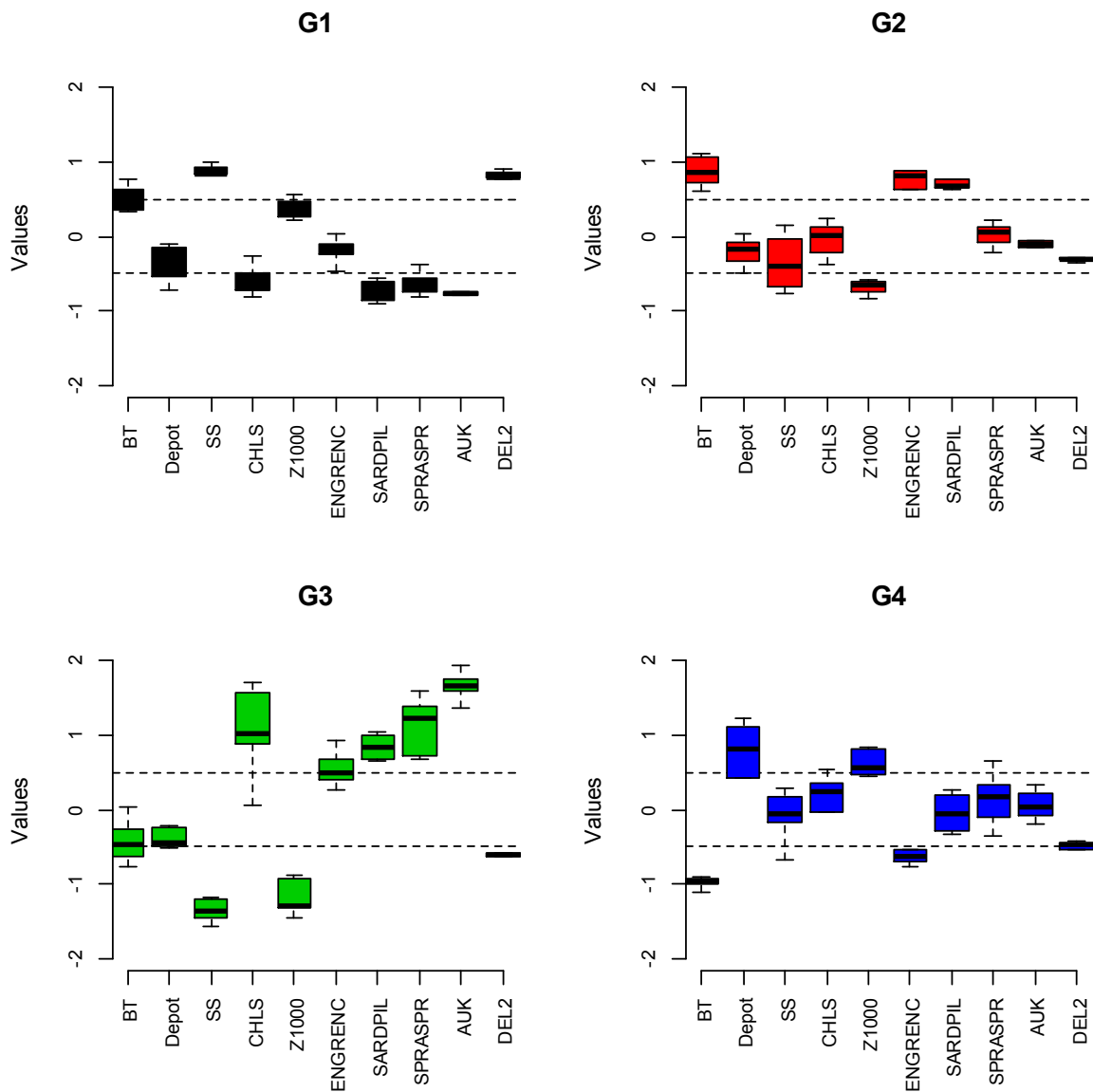
368
369 Figure 3: Cluster dendrogram of grid cells obtained by their hierarchical clustering in the MFA space.
370 The distance considered is the squared Euclidian distance between average grid cell points in the MFA
371 plane made of the first two principal components. Four clusters were retained, which are shown in
372 different colors.

373

374 The four (spatial) groups of grid cells were interpreted by identifying the variables, which characterized
375 them best. For that we computed in each group the average variable value per year and looked for
376 higher/lower values. In the analysis the variables are centered and normed. Thus the average per group
377 per year is a residual variation for that group and year (Fig. 4). Group G1 was characterized by higher
378 salinity and higher abundance of large delphinids and lower abundance of surface chlorophyll, sprat,
379 sardine and auks. In contrast to G1, group G3 was characterized by lower salinity, higher abundance
380 of surface chlorophyll, sprat, sardine and auks and lower abundance of large zooplankton and

381 delphinids. Group G2 was characterized by higher bottom temperature, higher abundance of anchovy
 382 and sardine and lower abundance of large zooplankton. In contrast to G2, group G4 was characterized
 383 by lower bottom temperature, lower anchovy abundance and greater water column stratification and
 384 greater abundance of large zooplankton.

385



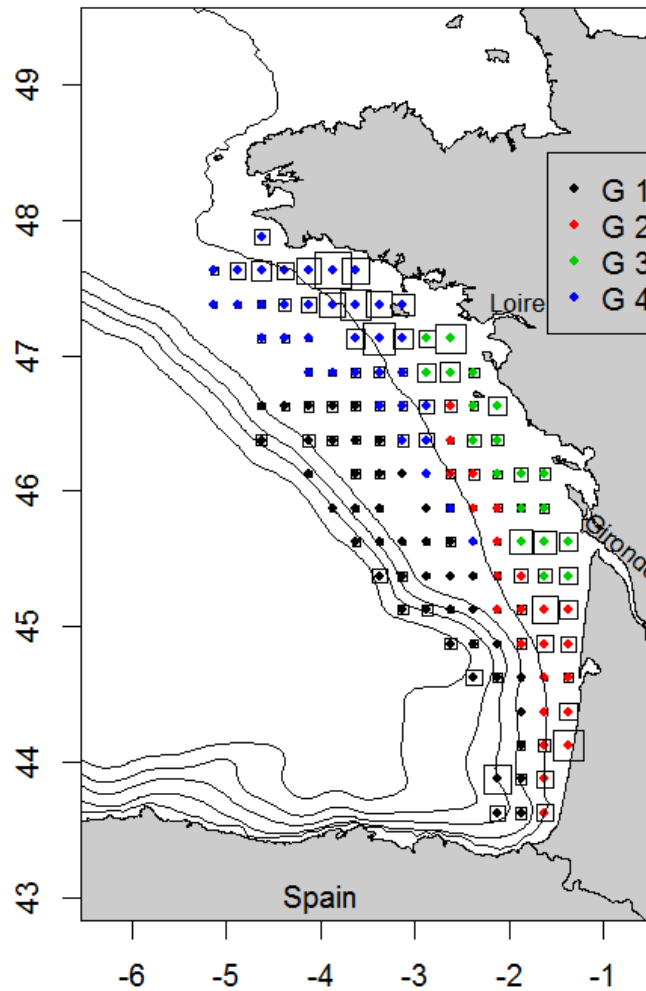
386

387 Figure 4: Variables values in each group (G1 to G4) of the spatial grid cells identified by hierarchical
 388 clustering. There is one average value per year per group for each variable allowing the inter-annual
 389 variability to be represented in boxplots. The variables being centered and normed, the horizontal dash
 390 lines are drawn for -0.5 and +0.5 standard deviation. Acronyms of variables are defined in Table 1.

391

392 The clusters of grid cells were mapped, showing a strong spatial pattern revealing the Bay of Biscay
393 seascapes (Fig. 5), which corresponded to the common spatial structure across ecosystem
394 compartments.

395



396

397 Figure 5: Map of Bay of Biscay seascapes as identified by applying MFA on all ecosystem compartments.
398 Map of grid cell clusters and their variability in time over the years 2009-2014. Colors are that of the
399 clusters (Fig. 3). Squares are proportional to the variability in time at each grid point (inertia). The
400 isobaths are 100, 200, 500, 1000, 2000 m.

401

402 Group G1 is located (Fig. 5) on the shelf-break and outer-shelf (bottom depth > 120 m) while group G3
403 is located in the coastal and inner-shelf waters (bottom depth < 80 m) from the Gironde to the Loire
404 estuaries occupying the mid-latitudes in Biscay. Group G2 is located mainly over the southern shelf
405 (latitude < 45°N) while Group G4 is a northern Biscay group (latitude > 46°N) centered on isobath 100m.

406 The spatial organization and multivariate characteristics of the groups identified are summarized in
 407 Table 5. Some variables showed opposition across groups: surface salinity, large zooplankton, anchovy
 408 and sprat have higher values in particular groups and lower in others.

409

410 Table 5: Summary of the multivariate characteristics of the spatial clusters. Acronyms of variables are
 411 defined in Table 1.

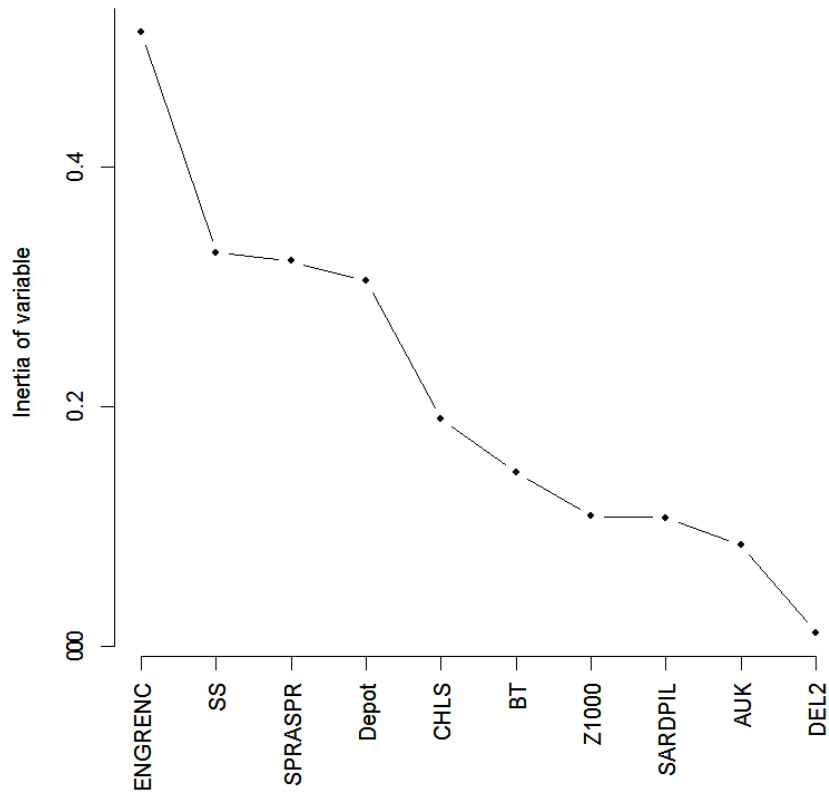
Group	Higher than mean	Lower than mean
G1 (shelf-break)	SS DEL2	CHLS SARDPIL, SPRASPR AUK
G3 (coastal at mid-latitude)	CHLS SARDPIL, SPRASPR AUK	SS Z1000 DEL2
G2 (southern shelf)	BT ENGRENC, SARDPIL	Z1000
G4 (northern shelf)	Depot Z1000	BT ENGRENC

412

413 In the MFA space, each variable and each point (grid cell) are represented by an average (compromise)
 414 position as well as by a position per year. When grouping the grid cells by hierarchical clustering, we
 415 used their average positions. We now consider the inertia around the average positions. The inertia
 416 in time for each grid cell showed a clear spatial pattern also (Fig. 5), where the variability is mostly
 417 located in the coastal areas and close to the limits of groups G2, G3 and G4. Such variability can be
 418 interpreted by analyzing the variability in time of the variables. The variables showing the largest
 419 variability in time (Fig. 6) are anchovy, surface salinity, sprat and water column stratification (Depot).
 420 They are characteristic of different spatial groups (Table 5) and therefore key in explaining the spatial
 421 pattern in the temporal variability (Fig. 5). These variables are correlated: salinity and sprat, and
 422 anchovy and water column stratification are opposed on MFA principal axis 1 and 2, respectively (Fig.
 423 7). The bi-plot representation, where both variables and grid cell points are superposed (Fig. 7) allows
 424 to identify what generates the spatial pattern in the temporal variability. Surface salinity, water column
 425 stratification and sprat in 2010 and 2012, and anchovy and sprat in 2011 show largest deviations from
 426 the average pattern and are thus responsible for the inertia observed on the map of ecosystem

427 structure (Fig. 5). It is noteworthy that the major source of variability lies in variables related to river
428 plume dynamics.

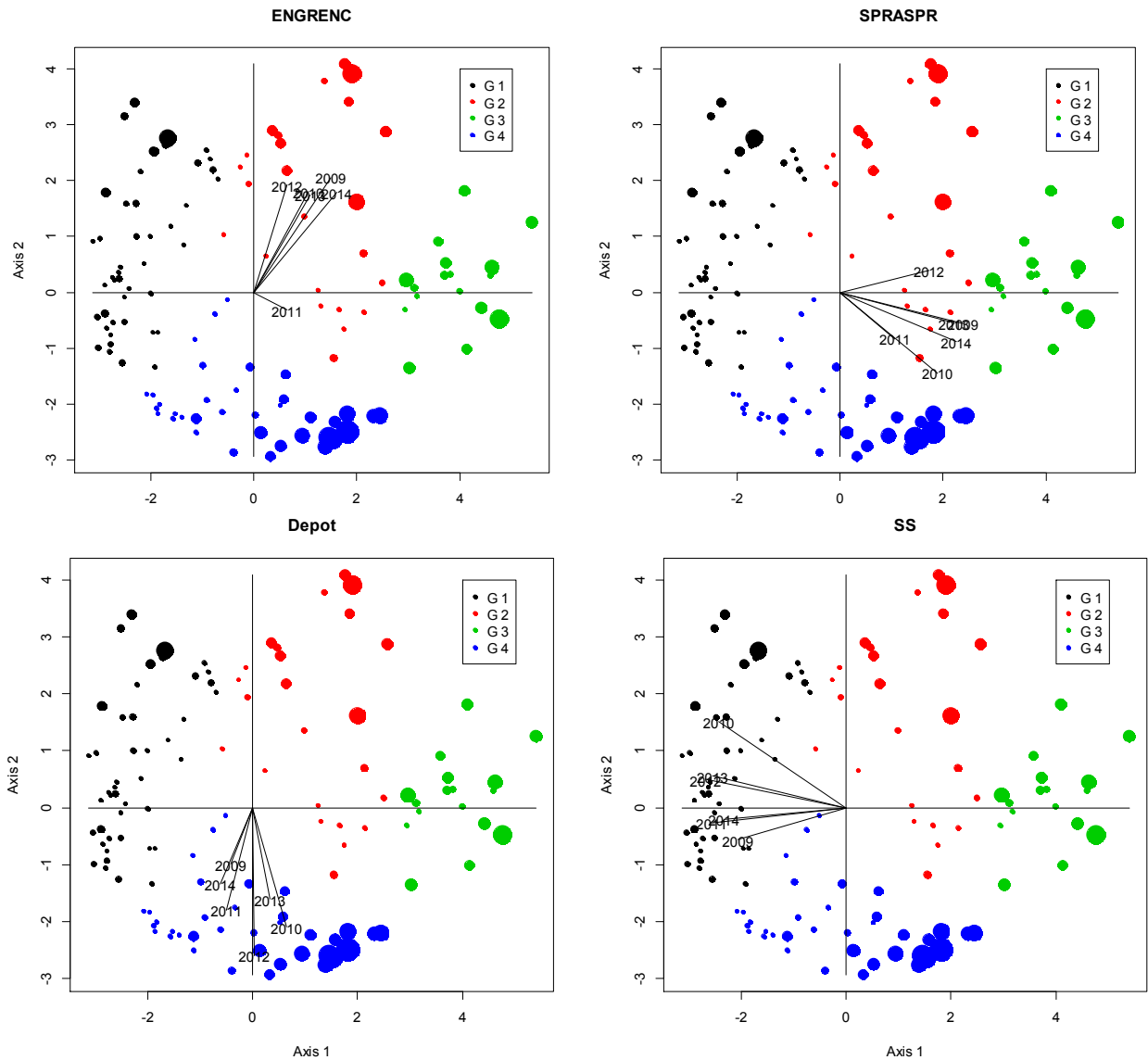
429



430

431 Figure 6: MFA applied on all ecosystem compartments. Inertia of the variables (Table 5) that are most
432 correlated to the principal components. Acronyms of variables are defined in Table 1.

433



434

435 Figure 7: Bi-plot in the MFA plane (two first principal axis) of the four variables showing greatest
 436 variability in time superposed on the (spatial) grid cells. The segments represent the variable-vectors
 437 in the different years. The circles are proportional to the inertia in time around the average grid points.
 438 The colors correspond to the four groups identified by hierarchical clustering. Acronyms of variables
 439 are defined in Table 1.

440

441 5. Discussion

442 5.1 Data and methods for ecosystem description and assessment

443 Integrated survey series such as PELGAS provide end-to-end georeferenced data over large sea areas
 444 in major ecosystem compartments with defined biological resolution and spatio-temporal scale. We

445 applied a generic procedure made of several steps to identify and map ecosystem spatial entities. First,
446 the data were interpolated on a common spatial grid and organized as a time series of tables containing
447 at each time the variables as columns and the grid cells as rows. The multi-table analysis method known
448 as Multi-Factor Analysis (MFA) was then applied on the series of tables. This allowed a description of
449 the correlation among the variables over space and time. Grouping the grid cells based on their relative
450 positions in the MFA space resulted in mapping grid cells of similar state over time. We developed a
451 procedure to select variables in each ecosystem compartment that facilitated the identification of
452 common spatial patterns across compartments. The result of the analysis is a map of ecosystem
453 seascapes that are consistent over the years together with a map of their inter-annual variability. Our
454 analysis demonstrated the possibility of analyzing data from integrated survey series with appropriate
455 space-time methodology to characterize and monitor ecosystem spatial structure at meso-scale over
456 large sea areas. Survey products characterizing ecosystem spatial organization are seldom considered
457 as yet (ICES, 2016). This study highlights the value in monitoring ecosystem spatial structure and
458 developing indicators for their use in ecosystem assessment. The space-time analysis performed here
459 served for ecosystem description but it could also be used for ecosystem assessment. In particular, the
460 inertia in time measures departure from a mean or a reference state and thus can serve to assess
461 changes in the ecosystem with defined statistical significance. For instance, Petitgas and Poulard
462 (2009) combined MFA and decision-CUSUM methods to statistically evidence changes in spatial
463 distributions.

464

465 **5.2 From seascapes to production systems and meta-ecosystems**

466 Though lower trophic level parameters are expected to vary during the survey on a shorter time scale
467 than the survey duration, the study revealed that many parameters showed strong spatial patterns at
468 the scale of the survey, such as gradients in bottom temperature, salinity or biomass in chlorophyll or
469 large zooplankton. These patterns were spatially coherent with that in the higher trophic levels.
470 Patterns in higher trophic levels corresponded to gradients in the abundance of particular species. We
471 were thus able to map the overall coherence in the spatial organization across the ecosystem
472 compartments. The spatial patterns identified were typically meso-scale (tens to hundreds of
473 kilometers). Ecosystem mapping at a lower spatial resolution would perhaps be difficult to attain
474 because of the biological resolution of the data and the space-time scale of the sampling.

475 The ecosystem spatial units identified are similar to seascapes (Wiens, 2005). Further, we now argue
476 that they correspond to production systems. The four ecosystem spatial units identified agree with
477 previous descriptions of the dynamics of hydrology and plankton in the Bay of Biscay. The river plumes
478 from Loire and Gironde influence in terms of salinity, turbidity and nutrients the coastal and shelf
479 waters extending to the mid-shelf as indicated by the 100m isobath (Castaing et al., 1999). In late

480 winter, phytoplankton blooms (diatoms) occur on mid-shelf at the distal end of the river plumes and
481 in spring nutrients are depleted in these areas, where the microbial loop is active (Guillaud et al., 2008).
482 In spring the nutrient-rich river plumes sustain phytoplankton production in coastal waters only. In
483 contrast at the shelf break, the production system is different. There, incoming spring tides interact
484 with the shelf-break topography and generate internal waves of the pycnocline, which result in regular
485 vertical mixing and a sustained phytoplankton production. Differences between coast, mid-shelf and
486 shelf-break areas was also reported for zooplankton communities (Albaina and Irigoien, 2004). In
487 addition, Vandromme et al. (2015) evidenced larger zooplankton in northern Biscay, probably because
488 of the seasonal evolution of stratification, the timing of phytoplankton blooms and the distribution of
489 small pelagic fish. These production systems agree with the four groups identified and in particular the
490 shelf-break and the coastal groups (G1 and G3). The difference between the southern and northern
491 shelf groups (G2 and G4) could be explained by the seasonal dynamics in water warming, the timing of
492 phytoplankton blooms and the distribution of small pelagic fish during their life cycles.

493 In a recent review of worldwide biological production systems that sustain fisheries, Fogarty et al.
494 (2016) considered the consequence of different trophic pathways on fisheries production. Here the
495 Bay of Biscay (a large marine ecosystem) is patchy with different production systems at meso-scale
496 each having its particular temporal dynamics (Koutsikopoulos and Le Cann, 1996; Planque et al., 2004)
497 and corresponding trophic pathways (Guillaud et al., 2008). Thus the Bay of Biscay could be seen as a
498 meta-ecosystem (Loreau et al., 2003; Massol et al., 2011) made of connected local production systems.
499 The major connectivity pathways could be seasonal migration patterns in the higher trophic levels and
500 seasonal hydrodynamic regimes. The understanding of the ecology of the Bay of Biscay as a meta-
501 ecosystem would require to identify and map the sub-units (as in the present study), but also
502 understand their production dynamics and the connectivity between them. An ecosystem assessment
503 would need to consider how all these elements depart from a reference situation. The present analysis
504 defines the areas and limits of ecosystem sub-units to be considered in ecosystem assessment and
505 management.

506

507 **5.3 Towards spatially explicit management scenarios**

508 The ecosystem sub-units identified related to production systems, which could be considered as
509 elementary units for designing ecosystem-based management scenarios. Such scenarios would then
510 need to consider the production systems that stocks visit at different seasons during their life cycles
511 (ICES, 2010). This will require spatially explicit end-to-end models to assemble knowledge and evaluate
512 by simulations management scenarios in space and time. Thus, in addition to ecosystem monitoring,
513 description and assessment, integrated survey data series are also useful to validate the capability of
514 models to simulate realistically spatial patterns in ecosystems (Travers-Trolet et al., 2014). Thus the

515 importance of novel survey products based on mapping (e.g., ICES, in press), such as maps of
516 ecosystem units as produced here. In effect, they provide information on the spatial scales and areas
517 that need be considered.

518

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526

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