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1 **Soft-bottom macrozoobenthos in semi-enclosed coastal systems of Morocco: a latitudinal**  
2 **and biogeographic analysis**

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24 **ABSTRACT**

25 Although soft-bottoms are the largest ecosystem on Earth in terms of area, only a small percentage  
26 of their macrobenthos has been studied and most of its species are not yet described. Herein, the  
27 most up-to-dated comprehensive inventory and the broad-scale baseline of the soft-sediment  
28 macrozoobenthos in semi-enclosed coastal systems (SECS) of the Moroccan Atlantic and  
29 Mediterranean coasts (3500 km) is presented. In total, 496 species (7 phyla, 21 classes, 65 orders  
30 and 201 families) were recorded among which 95 species were exclusively Mediterranean, 99  
31 species were Atlantico-Mediterranean SECS and 302 species exclusively Atlantic.

32 The best multivariate model, explaining 33% of the total variation observed in benthic  
33 assemblages' composition, included the type of the SECS (estuaries vs lagoons vs bay), the marine  
34 ecoregion (Atlantic vs Mediterranean), the surface of the SECS and the environmental features  
35 (minimal temperature, minimal and maximal salinity) as predictors of benthic macrofauna  
36 composition in the Moroccan SECS. In contrast to the general latitudinal diversity gradient (LDG)  
37 pattern, our results showed that species richness and taxonomic diversity showed no relationship  
38 with latitude. Such differences in benthic macrofaunal composition across a large scale could result  
39 from the fact that each ecosystem has its own specific characteristics, which implies an  
40 individualistic approach to ecosystem ecology.

41 The sample of the 12 SECS considered in this study covers most of the range of variation along  
42 the coasts of Morocco. The current compilation is relevant in such poorly known area at the global  
43 scale and fulfills a knowledge gap on benthic macrofauna in SECS of the Southern part of the  
44 North-Eastern Atlantic and Mediterranean ecoregions. However, the knowledge gained here is  
45 insufficient to address perceived shortfalls in knowledge of biodiversity, its importance to  
46 ecosystem function, and the threats and consequences of disturbance by anthropogenic activities.

47

48 **Key words:** Benthic macrofauna; Checklist; Latitudinal diversity gradient; North-East Atlantic;  
49 Mediterranean.

50

## 51 1. Introduction

52 Ecologists have long been intrigued by global patterns in biodiversity (Piacenza et al., 2015) and  
53 the understanding of the distribution of life on earth is a main goal in ecology and biogeography  
54 (Gaston, 2000; Hillebrand, 2004). The latitudinal diversity gradient, hereafter LDG (Hawkins,  
55 2001), with the highest numbers of species in the tropics and gradual decrease poleward, is the  
56 most famous large-scale biodiversity pattern (Hillebrand, 2004; Kinlock et al., 2018). Explanations  
57 for the LDG have been related to many potential mechanisms but no broad consensus on the causes  
58 of the LDG has emerged (Kinlock et al., 2018). The many explanations that have been proposed  
59 can be categorized broadly into ecological, evolutionary and historical processes (see Cruz-Motta  
60 et al., 2020 for recent summaries). Given the challenge of inferring process from pattern,  
61 disentangling these hypothesized drivers remains one of the great challenges in macroecology  
62 (Hurlbert & Stegen, 2014).

63 While the LDG is a well-recognized and long-established pattern in terrestrial ecology, the  
64 knowledge of global diversity patterns in marine ecosystems is limited to a small number of studies  
65 (Barboza & Defeo, 2015). For marine biota, the first suggestion of the latitudinal diversity cline  
66 was formulated in late 1950<sup>ies</sup> for hard bottom epifauna (Thorson, 1957) with pronounced decrease  
67 in the species richness of hard substratum epifauna towards arctic areas, whereas the number of  
68 soft-sediment infauna species was roughly the same in tropical, temperate and arctic areas.  
69 Latitudinal clines in benthic diversity of shallow waters have been also reported for gastropods  
70 (Roy et al. 1998), bivalve molluscs (Crame 2000; Roy, Jablonski & Valentine 2000), in shallow  
71 and deep-seas benthos (Sanders, 1968; Poore & Wilson 1993; Rex et al. 1993), and for pelagic  
72 taxa (Angel 1997; Pierrot-Bults 1997). Nevertheless, many studies have shown a deviation from  
73 the general LDG for the shallow-water marine fauna (Kendall & Aschan 1993; Boucher &  
74 Lamshead 1995). Furthermore, in the southern hemisphere the evidence of a latitudinal gradient  
75 of decreasing richness from the tropics to Antarctica is less convincing than in the northern  
76 hemisphere (Clarke 1992; Poore & Wilson 1993; Crame 2000). Recently, Kinlock et al. (2018)  
77 revisited the challenge of synthesizing individual LDGs and indicated that the phenomenon is not  
78 ubiquitous among habitats of the marine realm. More precisely, they indicated that the  
79 phenomenon is non-significant in the benthic habitat. However, Menegotto et al. (2019), in their  
80 comment on Kinlock et al. (2018), suggest that the marine habitat categories used by them (i.e.,

81 benthic, coral reefs, coastal, open ocean) are not independent and that reclassifying the studies  
82 significantly alters one of their main results. By assigning the studies into benthic and pelagic  
83 categories, and additionally into coastal or oceanic zones, they show that non-ambiguous,  
84 evolutionarily meaningful marine habitats display a significant latitudinal decline in species  
85 richness. Thus, there is no convincing evidence of a latitudinal cline across all taxa in the sea  
86 comparable to that seen on land (Clarke 1992; Clarke & Crame 1997).

87 Meta-analysis represents a suitable technique to analyse latitudinal gradients across different biota  
88 and regions and thus to generalize or not findings on the latitudinal distribution of species richness  
89 (Hillbrand, 2004; Kinlock et al., 2019). Therefore, Open science and the accumulation of spatially  
90 explicit biodiversity data are crucial to document LDG patterns better and to evaluate hypotheses  
91 broadly or for particular groups of organisms (Kinlock et al., 2018; 2019).

92 Soft-bottom substrates cover most of the world's ocean bottom and maintain a substantial part of  
93 the world's biodiversity (Snelgrove, 1998; Labrune et al., 2008). Assessing their biodiversity and  
94 latitudinal patterns, even though it is complicated by the difficulty in sampling and sharply  
95 delineating habitats in these systems, is thus of special importance (Labrune et al., 2008).  
96 Macrobenthos constitute the dominant organism biomass of marine soft sediments (Snelgrove,  
97 1998). All of the known non-symbiont phyla but one are found in the marine environment, with  
98 most being represented in marine sediments (Grassle et al., 1991). Soft bottom macrobenthos is a  
99 key biological component of marine ecosystems where it plays an important role in ecological  
100 processes such as nutrient cycling, pollutant metabolism or secondary production (Snelgrove,  
101 1998; Pratt et al., 2014). Although soft-bottoms are the largest ecosystem on Earth in terms of area,  
102 only a small percentage of their macrobenthos has been studied and most of its species are not yet  
103 described (Snelgrove, 1998). In this way, it is useful to improve our knowledge of its biodiversity  
104 (Ellingsen, 2002; Veiga et al., 2016).

105 Semi-enclosed coastal systems (SECS), such as lagoons and estuaries, are particular ecosystems  
106 of the coastal zone where the macrobenthos is a dominant biological component. The SECS are  
107 largely distributed worldwide under all the latitudes and are therefore ideal systems to study LDGs  
108 and their potential drivers because they (a) are easily accessible and (b) have very diverse,  
109 abundant, macrobenthic organisms belonging to various taxonomic groups.

110 The Moroccan coast stretches over 3500 km and 15° of latitude along both the Mediterranean Sea  
111 and the Atlantic Ocean. Moroccan low coasts offer an important succession of particular  
112 geomorphological forms (Chafik et al., 2001) among which several lagoons, estuaries and bays.  
113 Nador and Smir lagoons lie on the Mediterranean coast, whereas Moulay Bousselham, Sidi  
114 Moussa, Oualidia and Khnifiss are located in the Atlantic coast. The largest estuaries are located  
115 in the Atlantic coast: Tahaddart, Loukkos, Sebou, Bouregreg and Oum Rbia. Finally, Dakhla bay  
116 is the most important bay of the Atlantic coast of Morocco, it is unique in North Africa as a  
117 migration, wintering and nesting area for thousands of waterbirds (Qninba et al., 2003). Those  
118 ecosystems are heterogeneous, mainly due to their typology (bay, estuaries, lagoons),  
119 geomorphology, catchment geology and the spatio-latitudinal variation in different environmental  
120 factors along the Moroccan coasts

121 Up-to-now, there is no synthesis of the benthic species of the Moroccan SECS, despite several  
122 studies conducted in the last decades (e.g. Elkaïm, 1974; Lacoste, 1984; Bekkali, 1987; Guelorget  
123 et al., 1987; Bayed et al., 1988; Cheggour, 1988; Zine, 1989; Chbicheb, 1996; Bazairi, 1999;  
124 Mergaoui, et al., 2003; Chaouti and Bayed, 2005; Zine, 2005; Azirar, 2006; Cherkaoui, 2006;  
125 Gauteur, 2006; Lefrere, 2012; Joulami, 2013; Bazairi et al., 2014; Boutahar, 2014; El Asri et al.,  
126 2015; El Asri et al., 2017; Touhami, 2018; El Asri, 2019). This was a stimulating fact to provide  
127 a first baseline meta-data on such ecosystems in such poorly known area at the global scale and to  
128 fulfill a knowledge gap on benthic macrofauna in SECS of the Southern North-East Atlantic and  
129 Mediterranean ecoregions.

130 The overall objectives of this study were (1) to provide the first national and comprehensive  
131 checklist of the soft bottom macrozoobenthic species in semi-enclosed coastal systems of  
132 Morocco, (2) to test for the presence of a latitudinal diversity gradients in soft bottom  
133 macrozoobenthic species of semi-enclosed coastal systems of Morocco and (3) to understand their  
134 drivers by comparing the benthic assemblages between the different sites according to their  
135 ecoregion, their latitudinal position, the type of ecosystem (lagoon, estuary or bay), the site surface  
136 area, temperature and salinity. Additionally, we identified the current knowledge and gaps and  
137 make recommendations on respective research in future years.

138

## 139 2. Materials and methods *Study sites*

140 12 SECS were considered in this study based of data availability (Fig. 1). There are distributed  
141 along a large latitudinal gradient and are situated both in the Mediterranean coast of Morocco (two  
142 lagoons) and the Atlantic coast of Morocco (four lagoons, five estuaries and one bay). These SECS  
143 differ in terms of configuration, surface area and environmental conditions (Table 1). These sites  
144 have a very important ecological interest; most of them have been listed to the RAMSAR  
145 Convention as wetlands of international importance. They represent the most important Moroccan  
146 wetlands for the migration and wintering of birds.

147 These SECS are contrasting in the climate: Mediterranean semi-arid to temperate variant at the  
148 level of Nador lagoon to a desert climate at Dakhla bay. On the other hand, anthropogenic activities  
149 differ from one site to another: traditional fishing (all sites), aquaculture (Oualidia and Dakhla),  
150 thermal power station (Tahaddart), intensive agriculture (Moulay Bousselham, Sidi Moussa and  
151 Oualidia), port's activities (Nador, Loukkos, Sebou, Bouregreg, and Dakhla), dredging activities  
152 (Sebou and Oum Rbia,), mining (Nador, Sidi Moussa, Oualidia and Khnifiss) and industrial  
153 effluents (Nador, Sidi Moussa and Dakhla).

### 154 2.2. *Data sources*

155 The checklist was based on published data from 1974 to 2020 as well as co-authors unpublished  
156 data (see Table S1 and Table 4 for references' details). The list of benthic macrofauna species and  
157 total species richness were compiled for each SECS. Species names were checked and updated to  
158 current nomenclature according to World Register of Marine Species  
159 (<http://www.marinespecies.org>) (consulted January 14, 2020). Only few species were not included  
160 in WORMS. Taxa identified at a higher taxonomic level than the species were removed from the  
161 checklist. Only the taxa sp. and cf. were retained if cited only once.

162 The heterogeneity and incompleteness of available information led to the selection of a subset of  
163 the SECS environment descriptors which fulfilled the criteria of data reliability (i.e. information  
164 coming from published sources), homogeneity (i.e. available for all the lagoons), and  
165 comparability (i.e. data which can be expressed with a shared measurement unit). Nine different  
166 SECS variables were included: type of aquatic system (1 = lagoon; 2 = estuary; 3 = bay), latitude



167 (LAT), longitude (LON), surface area, maximum annual water temperature (M Temp, °C),  
168 minimum annual water temperature (m Temp, °C), maximum annual water salinity (M Sal),  
169 minimum annual water salinity (m Sal).

### 170 2.3. Biological data

171 Biotic parameters including the species richness (S), average taxonomic distinctness with  
172 presence/absence data ( $\Delta^+$ ), total taxonomic distinctness ( $S\Delta^+$ ), average phylogenetic diversity  
173 ( $\Phi^+$ ) and variation in taxonomic distinctness ( $\Lambda^+$ ), total phylogenetic diversity ( $S\Phi^+$ ) were  
174 calculated.

175 Sampling effort leading to the compilation of the species lists was also measured by the total  
176 number of samples collected in each SECS (calculated as number of sampling sites x sampling  
177 frequency).

### 178 2.4. Data analysis

179 The relation between SECS characteristics (independent variables) on species richness and  
180 taxonomic diversity indices (dependent variables) was tested using multiple linear regressions after  
181 testing the collinearity between independent variables. The possible effect of sampling effort on  
182 biotic parameters was previously tested by univariate regression. Then, residuals of the univariate  
183 regression with sampling effort were considered instead of the original data in multiple regression  
184 analysis. Moreover, the effect of the types of SECS (lagoon vs estuary) was tested using univariate  
185 PERMANOVA (Anderson et al., 2004).

186 Differences in the structure of the taxonomic assemblages between Moroccan SECS were explored  
187 using a cluster analysis based on a Bray-Curtis coefficient. Similarities (Bray-Curtis coefficient)  
188 among Moroccan SECS were calculated based on the taxonomical composition (Bray-Curtis  
189 coefficient calculated on (0, 1) species presence-absence data corresponding to Sorensen  
190 coefficient (Clarke and Warwick, 2001) (Table S2). Affinity groups differences were visualized  
191 through Principal Coordinates Ordination analysis (PCO) (Clarke and Warwick, 2001). The abiotic  
192 variables that were correlated (Spearman  $\rho > 0.5$ ) to samples ordination were represented as  
193 superimposed vectors in the PCO graph.

194 The best subset of SECS characteristics explaining the observed variability in benthic macrofauna  
195 assemblages was selected by means of distance-based linear models (DISTLM) (Anderson et al.,  
196 2008), using appropriate permutation (9999 permutations) and with Adjusted R<sup>2</sup> criterion and  
197 stepwise procedure for the model selection. Distances among aquatic systems were visualized  
198 through a dbRDA plot. Predictors variables were partitioned to four sets of predictor variables:  
199 environmental variables (surface area, maximum annual water temperature (minimum annual  
200 water temperature, maximum annual water salinity, minimum annual water salinity), type of SECS  
201 (lagoon, estuary, bay), province (Mediterranean and Atlantic) and geographical variables (latitude  
202 and longitude).

203 All multivariate analyses were conducted in the Primer 7 space (Clarke and Gorley, 2006), while  
204 correlation and regressions tests were carried out in Statistica 12.0 (Statsoft, 2017).

### 205 **3. Results**

#### 206 *3.1. Checklist*

207 36 sets of both published and unpublished data were compiled to obtain the checklist of benthic  
208 macrofauna of SECS of Morocco (Table S1). Most of them focused on a single SECS. There were  
209 496 species recorded from the Moroccan SECS. They belong to 7 phyla, 21 classes, 65 orders and  
210 201 families. Molluscs are the richest phylum with 179 species belonging to 5 classes, 31 orders  
211 and 71 families. Arthropods is the second richest phylum with 164 species belonging to 5 classes,  
212 12 orders and 72 families. 120 species of Annelida were reported, with 2 classes, 7 orders and 33  
213 families. Chordata presented 15 species, from 1 class, 5 orders and 9 families. The phylum of  
214 Echinodermata, Cnidaria, and Nemertea were represented by 8, 6 and 4 species respectively.

215 Among the 496 species reported in this study, 95 species showed an exclusive Mediterranean  
216 distribution (M), 99 species have an Atlantico-Mediterranean distribution (AM) and 302 have an  
217 Atlantic distribution (A) (Fig. 2).

#### 218 *3.2. Species composition and taxonomic diversity*

219 Values estimated for the different indices are summarised in Table 2. The number of taxa compiled  
220 by site fluctuated between 32 (Loukkos estuary) and the 161 (Moulay Bouselham lagoon) (Table

221 3). Sampling effort showed a wide variability among the studied sites, with the maximal value in  
222 Moulay Bouselham lagoon and the minimum in Loukkos estuary (Table 4). With the exception  
223 of average phylogenetic diversity ( $\Phi+$ ) and variation in taxonomic distinctness ( $\Lambda+$ ), all the other  
224 indices showed significant dependence with the sampling effort ( $p < 0.05$ ). Moreover, all the  
225 taxonomic indices were significantly ( $p < 0.05$ ) related to species richness except the average  
226 taxonomic distinctness ( $\Delta+$ ). In the majority of the SECS, both average taxonomic distinctness  
227 ( $\Delta+$ ) and variation in taxonomic distinctness ( $\Lambda+$ ) were within the 95% confidence funnel  
228 ( $p \geq 0.05$ ). Only the Oum Rbia and the Sebou estuaries as well as the Khnifiss lagoon appeared out  
229 of the confidence funnels (Fig. 3).

230 Multiple regression analysis ( $p > 0.05$ ) revealed that none of the SECS features considered here are  
231 structural abiotic features regarding the species richness and the taxonomic diversity indices.  
232 Moreover, permutational multivariate analysis of variance (PERMANOVA) showed no  
233 interactions between type of SECS ( $p > 0.05$ ) (Table 3) in terms of species richness (S) and all  
234 taxonomic diversity indices (Table 4).

### 235 3.3. *Macrobenthic assemblages' affinity*

236 Cluster analysis, at a similarity distance of 40%, allowed to distinguish three affinity groups (Fig.  
237 4): G1 (40% of similarity) composed by Bouregreg estuary and Moulay Bouselham lagoon, G2  
238 (50% of similarity) composed by Tahaddart, Loukkos and Oum Rbia estuaries and G3 (60% of  
239 similarity) composed by Oualidia and Sidi Moussa lagoons; the others SECS (Nador and Smir  
240 lagoons on the Mediterranean coast; Khnifiss lagoon and Dakhla bay on the Atlantic coast) remain  
241 individually separated from the previous groups with similarity fluctuating between 20% and 30%.

242 The obtained affinity groups as well as the other sites were represented on the PCO ordination  
243 graph (Fig. 5). The first two ordination axes explained 36% (all sites considered) of the total  
244 variance in benthic macrofauna assemblages. The two-dimensional plots show a clear separation  
245 between lagoons and estuaries systems.

246 Through the DistLM analysis, only the SECS-type set of predictor variables had a significant  
247 relationship (type-estuary and type-lagoon) with species-derived multivariate cloud ( $p < 0.01$ ),  
248 explaining 27% of the total variation. However, the best model obtained through the DistLM

249 procedure included height variables (Type-estuary, Type-lagoon, Type-bay, Province-Atlantic  
250 Surface, m-Temp, m-Sal and M-Sal) as predictors of benthic macrofauna composition, explaining  
251 33% of the total variation (Adjusted  $R^2=0.33$ ). When transposed to the dbRDA plot, the first two  
252 axes captured nearly 62% of the variability in the fitted model and 47% of the total variation in the  
253 data cloud (Fig. 6). Axis 1 (representing 20% of total variation) was negatively correlated to Type-  
254 estuary ( $r = -0.58$ ) and to M-Sal ( $r = -0.52$ ). Axis 2 (representing 14% of total variation) was  
255 negatively correlated to Surface ( $r = -0.53$ ). The axis 3 (representing 13% of total variation) was  
256 negatively correlated to Province-Atl ( $r = -0.52$ ) and Type-bay ( $r = -0.55$ ).

### 257 3.4. Gaps and knowledge gained

258 Table 4 showed that there is a scarcity of studies and that there is no regular spatio-temporal  
259 monitoring. Sampling techniques, effort and objectives differ between sites and studies. Although  
260 all the existing studies are quantitative, most of them were single spot studies, had limited  
261 geographic scope (Mergaoui et al., 2003; Ait Mlik, 2009; Bououarour, 2013; Joulami, 2013),  
262 focused only on single taxonomic groups (e.g. Annelida: El asri et al., 2017; Arthropoda: Aksissou,  
263 1997; Boussalwa et al., 2000), or on habitats (intertidal, subtidal, meadows). On the other hand,  
264 few studies have been carried out on benthos-predator interactions (Joulami, 2013; Touhami et al.,  
265 2019). Moreover, while few studies have considered biomass, there is no evaluation of secondary  
266 production and productivity in all the Moroccan SECS. As a result, the studies that can be  
267 considered as references for soft sediments benthic assemblages are those of Guelorget et al.  
268 (1987), Zine (1989) and El Kamcha (unpublished data) for the lagoon of Nador, Bazairi & Gam  
269 (2004) for the Loukkos estuary, Bazairi (1999) and Boutoumit (unpublished data) for the Moulay  
270 Bousselham lagoon, Elkaïm (1974) and Cherkaoui (2006) for the Bouregreg estuary, Gauteur  
271 (2006), Boutahar (2014) and El asri (2019) for the Oualidia lagoon, Bazairi & Zourarah (2001,  
272 2007) and Bazairi et al. (2017) for the Oum Rbia estuary and finally El asri (2019) for Dakhla bay.

## 273 4. Discussion

274 Checklists of marine species at regional scale have multiple uses. In addition to offering  
275 comparative facts for biodiversity studies, they serve as a crucial device in spotting and delimiting  
276 regions in need of protection, inferring the capacity effect of anthropogenic interest, assessing the

277 complexity of organic communities, and estimating the provision of dwelling resources  
278 (Hendrickx and Harvey, 1999).

279 The sample of SECS considered in this study covers most of the range of variation along the coasts  
280 of Morocco. Therefore, the current compilation represents the first comprehensive annotated  
281 checklist that gives an overall view on soft-bottom benthic macrofauna of the semi-enclosed  
282 coastal systems within the Atlantic and Mediterranean oceanographic regions of Moroccan waters,  
283 which is relevant in such poorly known area at the global scale. Moreover, it fulfilled a knowledge  
284 gap on benthic macrofauna in SECS of the Southern part of the Northeastern Atlantic and  
285 Mediterranean ecoregions. While all the existing inventories on Moroccan marine fauna focused  
286 on single taxonomic group and have large scope, our ecosystem-based checklist is more than a  
287 simple list of species inhabiting comparable ecosystems and constitutes a synthetic illustration of  
288 the relationships that species have with each other and with their environment. Furthermore, the  
289 resulting metadata, available in open access, will serve in comparing the soft-bottom macrobenthos  
290 assemblages at a large scale.

291 This study revealed a diverse benthic macrofauna for the Moroccan SECS with overall 496 species  
292 dominated by Molluscs, Arthropods and Annelids. It represents almost 46% of the known marine  
293 fauna of marine waters of Morocco (1068 taxa, all groups combined) (ONEM, 1998). However,  
294 comparison of diversity results between Moroccan SECS may be done with caution since the  
295 sampling methods, units and scales are often different, and moreover the diversity of habitats in  
296 such ecosystems are high (Chardy and Clavier, 1988; Alongi, 1990).

297 Patterns in diversity are often related to latitude, a phenomenon known as the latitudinal diversity  
298 gradient (LDG), whereby a decrease with increasing latitude is found (Roy et al., 1998; Rex et al.,  
299 2000; Attrill et al., 2001; Willig et al., 2003; Hillebrand, 2004). Several hypotheses for the  
300 underlying causes for such pattern are suggested, yet none of them is solely sufficiently convincing  
301 (Willig et al., 2003; Hillebrand, 2004), although solar energy input (and for the marine territory,  
302 the sea surface temperature as its proxy) is most often mentioned as the main acting principle  
303 (Rohde, 1992; Roy et al., 1998). Species richness is the most elementary, easy to interpret and  
304 widely used measure of biodiversity (e.g. Dornelas et al., 2014). It has been shown to follow a –  
305 generally unimodal – large-scale (>45°) latitudinal gradient for marine benthic invertebrates with

306 a peak in equatorial regions (Chaudhary et al., 2016). In contrast to the general LDG pattern, our  
307 results showed that species richness and taxonomic diversity indices showed no relationship with  
308 latitude. Deviations from the general LDG pattern have also been reported before for European  
309 marine benthos by Renaud et al. (2009) who found no or weakly positive relationships. The  
310 explanation for this kind of diverting trend is that the impact of local variation in environmental  
311 factors is stronger than that of latitude related factors (Gaston, 2000; Renaud et al., 2009). Marine  
312 diversity might not follow a strict latitudinal gradient as the drivers of marine diversity themselves  
313 are not usually correlated with latitude (Piacenza et al., 2015).

314 In terms of assemblages composition, the best multivariate model, explaining 33% of the total  
315 variation observed in benthic assemblages, included the type of the SECS (estuaries vs lagoons vs  
316 bay), the marine ecoregion (Atlantic vs Mediterranean), the surface of the SECS and the  
317 environmental features (minimal temperature, minimal and maximal salinity) as predictors of  
318 benthic macrofauna composition in the Moroccan SECS. Such differences in benthic macrofaunal  
319 composition across a scale could result from the fact that each ecosystem has its own specific  
320 characteristics, which implies an individualistic approach to ecosystem ecology. Indeed, all  
321 ecosystems are subject to climatic and environmental forces and it is assumed that their variations  
322 induce a response from communities (Möllmann and Diekmann, 2012). The diversity and  
323 distribution of organisms can be influenced by the stochastic, ecological and evolutionary  
324 processes at local and regional scales (Hubbell, 2001), the limits of dispersion and recruitment of  
325 macroinvertebrate taxa (Hurtt & Pacala, 1995), the structural heterogeneity of the transitional  
326 waters (Basset & Abbiati, 2004) and the consequent selection of macroinvertebrate taxa according  
327 to their functional traits and niche needs (MacArthur, 1970).

328 Variations in species richness and taxonomic composition of benthic macrofauna depends on local  
329 oceanographic processes (Aller et al., 2002; Coleman et al., 1997; McCallum et al., 2015), as well  
330 as on physiographic characteristics, such as surface area and outlet length (Basset et al., 2006).  
331 Variations might be related to ecosystem morphology, substrate type, organic residues (Galeron et  
332 al., 2001), salinity (Battaglia, 1959), degree of confinement (Guelorget and Perthuisot, 1983;  
333 Guelorget et al., 1983), changes in nutrient concentrations and changes in primary productivity  
334 (Galeron et al., 2001).

335 According to Spalding et al. (2007), the vast marine region of Morocco can be subdivided into two  
336 provinces, the Mediterranean Sea (Alboran Sea Ecoregion) and the Lusitanian (Saharan Upwelling  
337 Ecoregion). In corroboration to this subdivision, the type of province (Atlantic vs Mediterranean)  
338 was shown to be a significant predictor factor of the composition of the soft-bottom benthic fauna  
339 of the Moroccan SECS. Therefore, the currently described marine biogeographic boundaries in  
340 Morocco seem to apply to soft-bottom macrofauna of SECS and which environmental drivers were  
341 most associated with species differences among these two provinces. Significant differences have  
342 been found on the structure of the communities between the marine ecoregions, a fact which may  
343 be correlated with the specificities of the ecoregion's physiographical characteristics, as shown by  
344 Kong et al. (2013), which emphasizes that the distribution of the macroinvertebrate is correlated  
345 with ecoregional characteristics. Moreover, these marine ecoregions are affected by environmental  
346 factors (Lara-Lara et al., 2008).

## 347 **5. Conclusion**

348 Our results provide the first broad-scale baseline of composition and diversity patterns of soft-  
349 bottom macrozoobenthos in semi-enclosed coastal systems of Morocco and elucidate the main  
350 environmental factors that shape their latitudinal and biogeographic patterns. To our knowledge,  
351 the presently reviewed meta-data would be considered as most up-to-dated checklist of the soft-  
352 sediment macrozoobenthos in Moroccan SECS. This checklist is relevant in such poorly known  
353 area and fulfills a knowledge gap on SECS in the Northeastern Atlantic and Mediterranean  
354 ecoregions. However, the knowledge gained here is insufficient to address perceived shortfalls in  
355 knowledge of biodiversity, its importance to ecosystem function, and the threats and consequences  
356 of disturbance by anthropogenic activities.

357

358

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#### 364 **Authors' Contributions**

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366 **El Kamcha:** Investigation, Data curation, Writing – Original Draft, Visualisation. **Oussama**  
367 **Bououarour:** Investigation, Data curation, Writing – Original Draft, Visualisation. **Latifa**  
368 **Joulami:** Investigation, Data curation, Review. **Boutahar Loubna:** Investigation, Data curation,  
369 Review. **Abdelaziz Benhoussa:** Resources, Funding acquisition. **Mohamed Maanan:** Review  
370 & Editing, Supervision. **Laurent Godet:** Writing-Review & Editing, Validation. **Abdellatif**  
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372 Original Draft, Review & Editing, Supervision.

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700 **Table 1**

701 Environment descriptors of the semi-enclosed coastal systems of Morocco in terms of aquatic system type (1 = lagoon; 2 = estuary; 3  
 702 = bay), latitude (LAT, N), longitude (LON, W), surface area (km<sup>2</sup>), maximum annual water temperature (M Temp, °C), minimum  
 703 annual water temperature (m Temp, °C), maximum annual water salinity (M Sal), minimum annual water salinity (m Sal). NA: Nador,  
 704 SM: Smir, TA: Tahaddart, LO: Loukkos, MB: Moulay Bouselham, SE: Sebou, BR: Bouregreg, OR: Oum Rbia, SI: Sidi Moussa, OU:  
 705 Oualidia, KH: Khnifiss, DA: Dakhla.

| System                       | Type | LAT    | LON     | Surface Area | M Temp | m Temp | M Sal | m Sal | Reference                               |
|------------------------------|------|--------|---------|--------------|--------|--------|-------|-------|---|
| <b>Nador (NA)</b>            | 1    | 35°10' | 02°51'  | 115          | 28     | 14     | 38    | 32    | El Kamch et al. (2020)                  |
| <b>Smir (SM)</b>             | 1    | 35°42' | 05°20'  | 0.3          | 32     | 12     | 41    | 7.8   | Chaouti & Bayed 2005                    |
| <b>Tahaddart (TA)</b>        | 2    | 35°46' | 05°42'  | 10           | 26     | 13     | 41    | 21    | Achab 2011                              |
| <b>Loukkos (LO)</b>          | 2    | 35°07' | 06°00'  | 72           | 27     | 15     | 34    | 22    | Geawhari et al., 2014                   |
| <b>Moulay Bouselham (MB)</b> | 1    | 34°51' | 06°16'  | 27           | 28     | 11     | 35    | 27    | Gam et al., 2010                        |
| <b>Sebou (SE)</b>            | 2    | 34°16' | 06°39'  | 17.5         | 30     | 16     | 35    | 12    | Haddout et al., 2015                    |
| <b>Bouregreg (BR)</b>        | 2    | 34°    | 06° 50' | 4000         | 45     | 14     | 30    | 10    | Cherkaoui 2006; El Amraoui et al., 2015 |
| <b>Oum Rbia (OR)</b>         | 2    | 33°28' | 08°34'  | 1.5          | 25     | 15     | 35    | 30    | Khalki & Moncef 2007                    |
| <b>Sidi Moussa (SI)</b>      | 1    | 32°54' | 08°49'  | 4.2          | 27     | 15     | 33    | 22    | Maanan et al., 2004                     |
| <b>Oualidia (OU)</b>         | 1    | 32°45' | 08°30'  | 3.0          | 21     | 16     | 36    | 28    | Hilmi et al., 2005                      |
| <b>Khnifiss (KH)</b>         | 1    | 28°03' | 12°15'  | 65           | 22     | 16     | 38    | 34    | Semlali et al., 2012                    |
| <b>Dakhla (DA)</b>           | 3    | 23°45' | 15°50'  | 400          | 26     | 14     | 40    | 37    | Zidane et al., 2018                     |

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708 **Table 2**

709 Species richness (S) and taxonomic distinctness indices values in the semi-enclosed coastal  
 710 ecosystems of Morocco.  $\Delta^+$ : taxonomic distinctness,  $S\Delta^+$ : total taxonomic distinctness,  $\Phi^+$ :  
 711 average phylogenetic diversity,  $\Lambda^+$ : variation in taxonomic distinctness,  $S\Phi^+$ : total phylogenetic  
 712 diversity. NA: Nador, SM: Smir, TA: Tahaddart, LO: Loukkos, MB: Moulay Bouselham, SE:  
 713 Sebou, BR: Bouregreg, OR: Oum Rbia, SI: Sidi Moussa, OU: Oualidia, KH: Khnifiss, DA:  
 714 Dakhla.

| Sites | Sampling effort | S   | $\Delta^+$ | $S\Delta^+$ | $\Lambda^+$ | $\Phi^+$ | $S\Phi^+$ |
|-------|-----------------|-----|------------|-------------|-------------|----------|-----------|
| NA    | 366             | 158 | 90         | 14232       | 279.9       | 47.7     | 7533.3    |
| SM    | 123             | 53  | 89.6       | 4748.1      | 293.3       | 56.3     | 2983.3    |
| TA    | 99              | 40  | 88.7       | 3549.6      | 311.6       | 55.0     | 2200.0    |
| LO    | 134             | 32  | 89.1       | 2852.7      | 300.5       | 60.4     | 1933.3    |
| MB    | 599             | 161 | 90.5       | 14569.2     | 268.7       | 47.8     | 7700.0    |
| SE    | 7               | 94  | 87.8       | 8162.0      | 275.5       | 52.9     | 4916.7    |
| BR    | 120             | 101 | 89.9       | 9075.7      | 278.3       | 51.7     | 5216.7    |
| OR    | 39              | 48  | 88.5       | 4247.5      | 328.8       | 51.4     | 2466.7    |
| SI    | 117             | 57  | 90.2       | 5141.7      | 271.3       | 56.4     | 3216.7    |
| OU    | 43              | 105 | 89.8       | 9428.2      | 268.2       | 48.6     | 5100.0    |
| KH    | 29              | 62  | 88.6       | 5491.8      | 333.7       | 51.9     | 3216.7    |
| DA    | 100             | 105 | 89.7       | 9414.4      | 255.7       | 50.6     | 5316.7    |

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720 Table 3. Results of PERMANOVAs testing for the effect of the type of ecosystem (Lagoon -  
 721 Estuary) on species richness and taxonomic.

| Source   | <i>df</i> | MS  | Pseudo-F | P (perm) | <i>df</i> | MS   | Pseudo-F | P (perm) |
|----------|-----------|---|----------|----------|-----------|--|----------|----------|
|          |           | <i>Species richness (S)</i>                                 |          |          |           | <i>Taxonomic distinctness (A+)</i>                         |          |          |
| Type     | 1         | 312,26  | 1,9692   | 0,1845   | 1         | 0,20702  | 5,188    | 0,0528   |
| Residual | 9         | 158,57  |          |          | 9         | 3,99E-02   |          |          |
| Total    | 10        |   |          |          | 10        |  |          |          |
|          |           | <i>Total taxonomic distinctness (SA+)</i>                   |          |          |           | <i>Variation in taxonomic distinctness (A+)</i>            |          |          |
| Type     | 1         | 330,52  | 2,076    | 0,1825   | 1         | 3,5385   | 0,87669  | 0,3505   |
| Residual | 9         | 159,21  |          |          | 9         | 4,0363   |          |          |
| Total    | 10        |   |          |          | 10        |  |          |          |
|          |           | <i>Average phylogenetic diversity (<math>\Phi^+</math>)</i> |          |          |           | <i>Total phylogenetic diversity (<math>S\Phi^+</math>)</i> |          |          |
| Type     | 1         | 5,0236  | 1,4911   | 0,2565   | 1         | 251,47   | 2,0287   | 0,1876   |
| Residual | 9         | 3,3689  |          |          | 9         | 123,95   |          |          |
| Total    | 10        |   |          |          | 10        |  |          |          |

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725 **Table 4**

726 Gaps and knowledge gained from studies performed on soft-bottom zoomacro-benthos of the  
 727 Moroccan SECS. NA: Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bousselham.  
 728 SE: Sebou. BR: Bouregreg. OR: Oum Rbia. SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA:  
 729 Dakhla. **I** = Intertidal **S**= Subtidal. **B** = Biomass. References (Numbers 1-36): **(1)** Elkaïm (1974);  
 730 **(2)** Lacoste (1984); **(3)** Bekkali (1987); **(4)** Guelorget et al. (1987); **(5)** Bayed et al. (1988); **(6)**  
 731 Cheggour (1988); **(7)** Zine (1989); **(8)** Chbicheb (1996); **(9)** Aksissou (1997); **(10)** Bazairi (1999);  
 732 **(11)** Boussalwa et al. (2000); **(12)** Bazairi & Zourarah (2001); **(13)** Mergaoui et al. (2003); **(14)**  
 733 Bazairi & Gam (2004); **(15)** Chaouti & Bayed (2005); **(16)** El Houssaini (2005); **(17)** Zine (2005);  
 734 **(18)** Azirar (2006); **(19)** Bazairi & Bayed (2006); **(20)** Cherkaoui (2006); **(21)** Gauteur (2006);  
 735 **(22)** Bazairi & Zourarah (2007); **(23)** Ait Mlik (2009); **(24)** Lefrere (2012); **(25)** Bououarour  
 736 (2013); **(26)** Joulami (2013); **(27)** Boutahar (2014); **(28)** Cuvelier et al. (2014); **(29)** El Asri et al.  
 737 (2015); **(30)** Bazairi et al. (2017); **(31)** El Asri et al. (2017); **(32)** Touhami (2018); **(33)** El Asri  
 738 (2019); **(34)** Bououarour (unpublished data); **(35)** Boutoumit (unpublished data); **(36)** El Kamcha  
 739 (unpublished data). Grey colour indicates studies that can be considered as references for  
 740 respective sites.  
 741

|      | Mediterranean |       | Atlantic |           |          |           |        |           |          |          |          |          |
|------|---------------|-------|----------|-----------|----------|-----------|--------|-----------|----------|----------|----------|----------|
|      | NA            | SM    | TA       | LO        | MB       | SE        | BO     | OR        | SI       | OU       | KH       | DA       |
| 1974 |               |       |          |           |          |           | 1, IS  |           |          |          |          |          |
| 1984 |               |       |          |           | 2, I     |           |        |           |          |          |          |          |
| 1987 | 4, S, B       | 3, S  |          |           |          |           |        |           |          |          |          |          |
| 1988 |               |       |          |           |          |           | 6, I   |           |          |          | 5, I     |          |
| 1989 | 7, S          |       |          |           |          |           |        |           |          |          |          |          |
| 1995 |               |       |          |           |          |           |        |           |          |          |          |          |
| 1996 |               |       |          |           |          |           |        |           |          | 8, I     |          |          |
| 1997 |               | 9, I  |          |           |          |           |        |           |          |          |          |          |
| 1999 |               |       |          |           | 10, IS   |           |        |           |          |          |          |          |
| 2000 | 11, S         |       |          |           |          |           |        |           |          |          |          |          |
| 2001 |               |       |          |           |          |           |        | 12, IS, B |          |          |          |          |
| 2003 |               |       |          |           |          | 13, S     |        |           |          |          |          |          |
| 2004 |               |       |          | 14, IS, B |          |           |        |           |          |          |          |          |
| 2005 |               | 15, I | 16, I    |           |          | 17, IS    |        |           |          |          |          |          |
| 2006 |               |       | 19, IS   |           |          |           | 20, IS |           |          | 21, IS   |          |          |
| 2007 |               |       |          |           |          |           |        | 22, IS, B |          |          |          |          |
| 2009 |               |       |          |           | 23, IS   |           |        |           |          |          |          |          |
| 2012 |               |       |          |           |          |           |        |           |          |          | 24, I    |          |
| 2013 |               |       |          |           | 25, I    |           |        |           | 26, I, B |          |          |          |
| 2014 | 28, S         |       |          |           |          |           |        |           |          | 27, IS   |          |          |
| 2015 |               |       |          |           |          |           |        |           |          | 29, IS   |          |          |
| 2016 |               |       |          |           |          |           |        |           |          |          |          |          |
| 2017 |               |       |          |           |          |           |        | 30, IS, B |          | 31, IS   |          |          |
| 2018 |               |       |          |           | 32, I, B |           |        |           |          |          |          |          |
| 2019 |               |       |          |           |          |           |        |           |          | 33, IS   |          | 33, IS   |
| 2020 | 36, S, B      |       |          | 34, I, B  | 34, I, B | 35, IS, B |        |           | 34, I, B | 34, I, B | 34, I, B | 34, I, B |

742

743 **Figure Captions:**

744 **Figure 1.** Map showing the geographical position of the semi-enclosed coastal systems of  
745 Morocco considered in this study. ★: lagoon; ▲: estuary; ■: bay.

746 **Figure 2.** Species richness by biogeographical repartition in the semi-enclosed coastal systems of  
747 Morocco. A: Atlantic. AM: Atlantico-Mediterranean. and M: Mediterranean. NA: Nador. SM:  
748 Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR: Bouregreg. OR:  
749 Oum Rbia. SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA: Dakhla.

750 **Figure 3.** Confidence funnel (mean and 95% confidence interval) of the variation in taxonomic  
751 distinctness (A) and taxonomic distinctness (B) in the Moroccan Semi-enclosed coastal systems.  
752 NA: Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR:  
753 Bouregreg. OR: Oum Rbia. SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA: Dakhla.

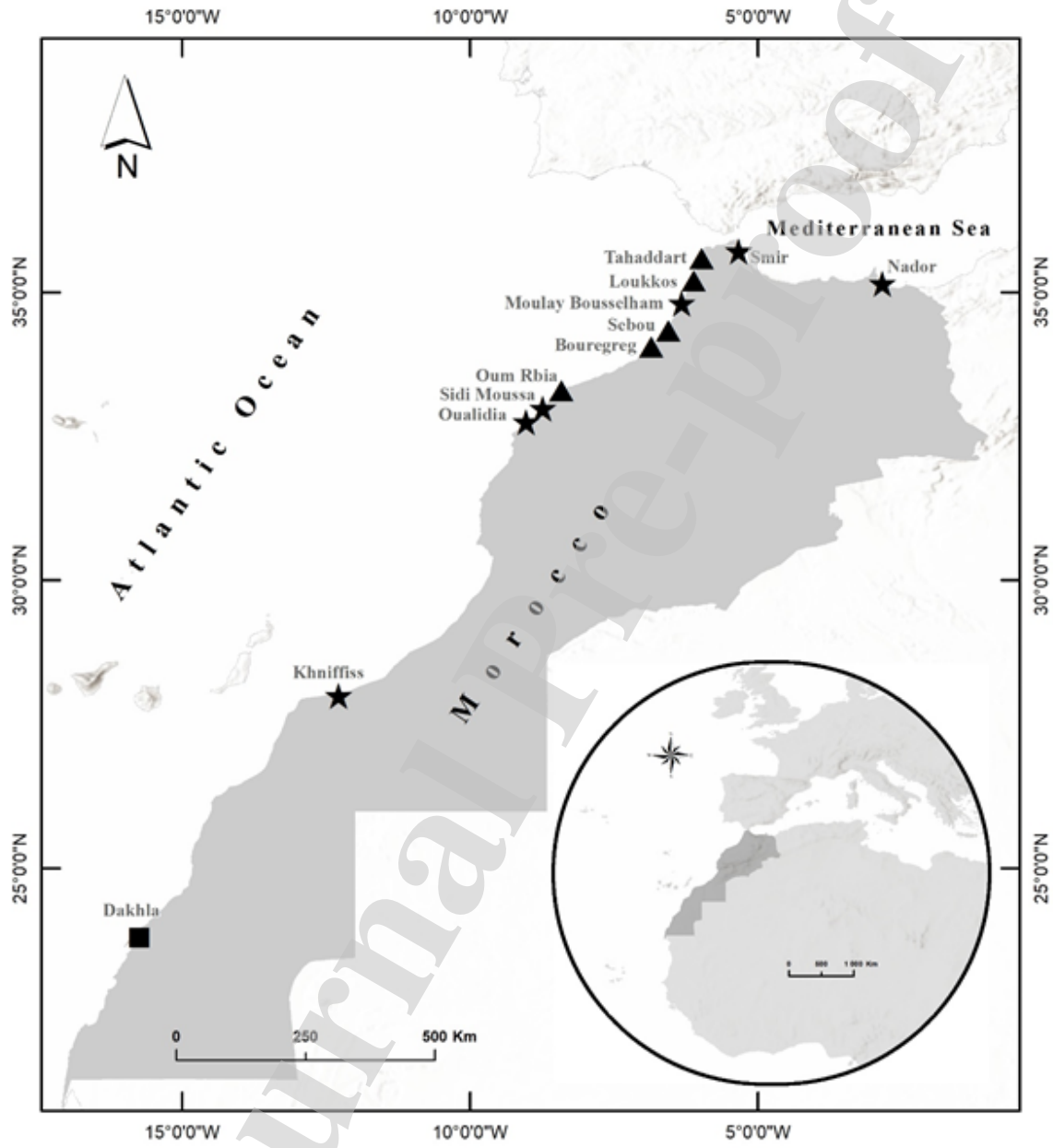
754 **Figure 4.** Dendrogram of cluster analysis using group-average linkage of Bray-Curtis similarities  
755 based on benthic macrofauna composition in the semi-enclosed coastal systems of Morocco. NA:  
756 Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR:  
757 Bouregreg. OR: Oum Rbia. SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA: Dakhla.

758 **Figure 5.** Ordination of the semi-enclosed coastal systems using the Principal coordinates  
759 ordination (PCO) with vectors (longer than 0.7) and clusters overlay. NA: Nador. SM: Smir. TA:  
760 Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR: Bouregreg. OR: Oum Rbia.  
761 SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA: Dakhla.

762 **Figure 6.** Distance-based redundancy analysis plot and the correlated variables that explained  
763 the semi-enclosed coastal systems distribution based on benthic macrofauna composition. NA:  
764 Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR:  
765 Bouregreg. OR: Oum Rbia. SI: Sidi Moussa. OU: Oualidia. KH: Khnifiss. DA: Dakhla.

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768 **Figure 1**

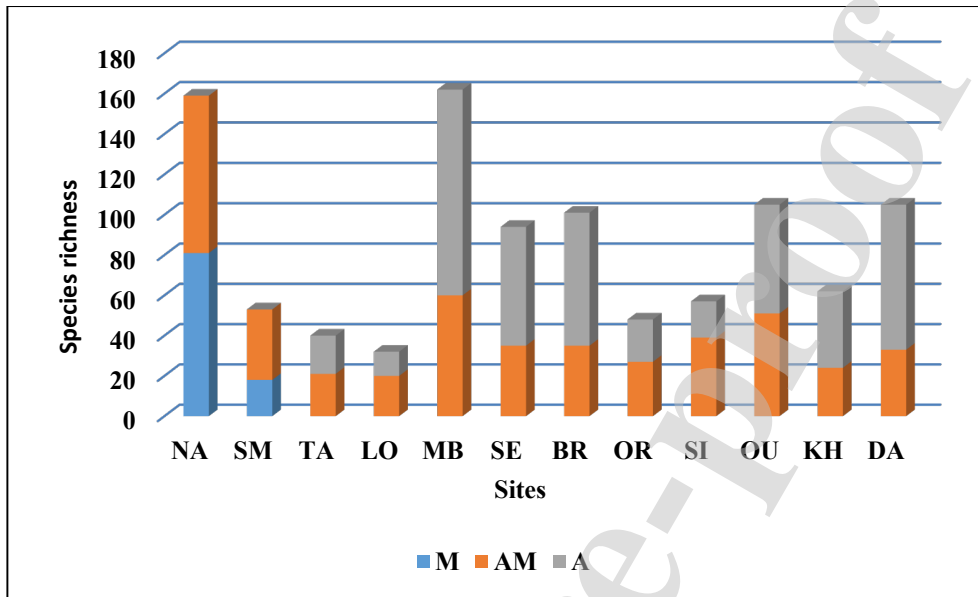


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773 **Figure 2**

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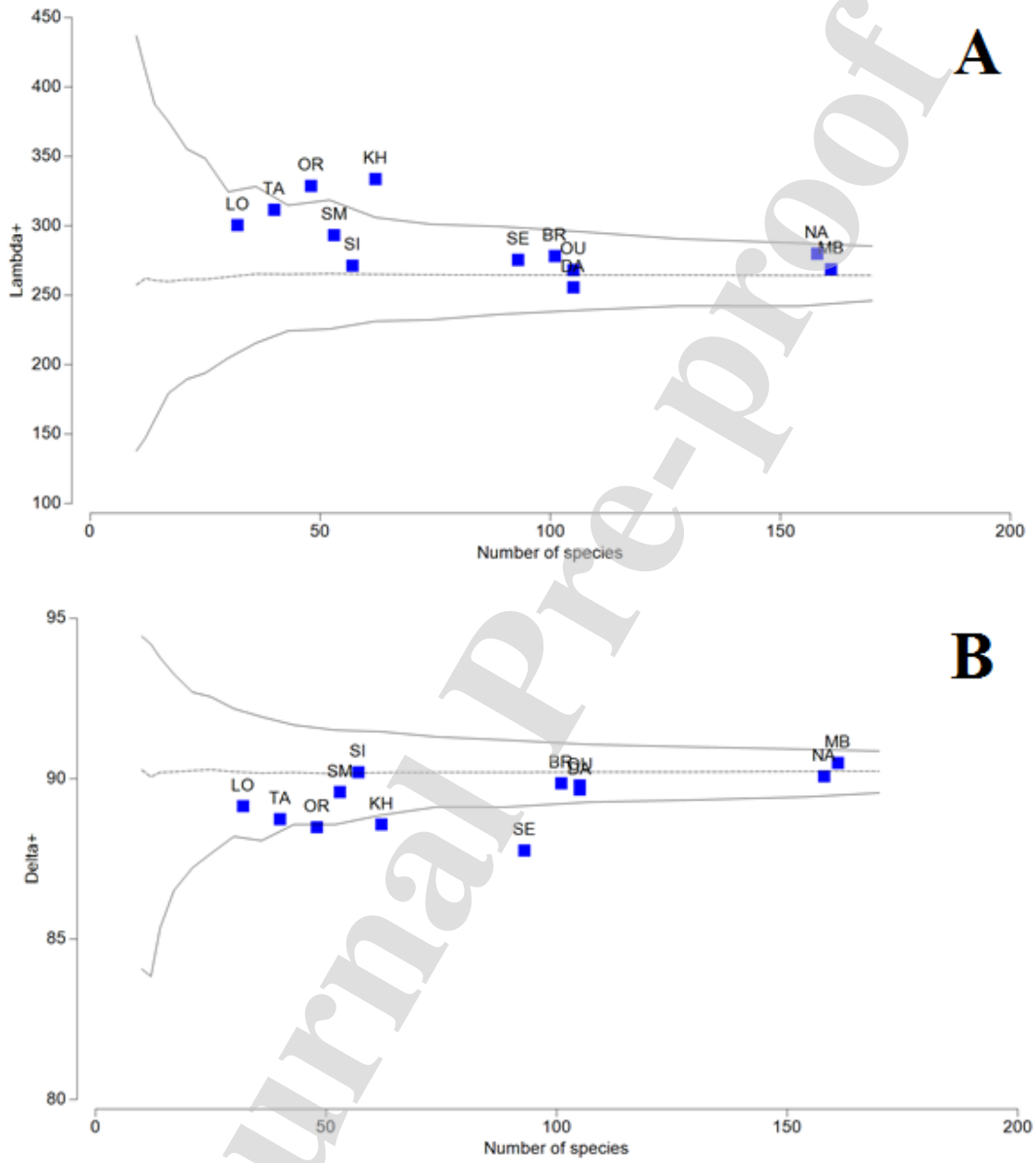
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785 **Figure 3**

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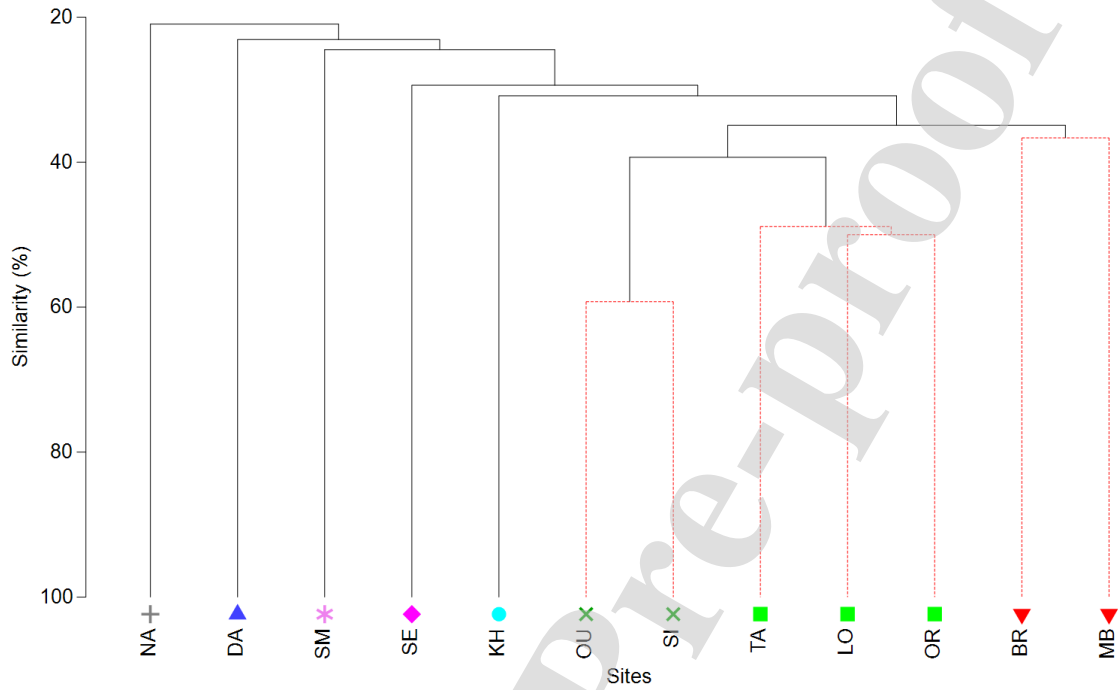
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790 **Figure 4**

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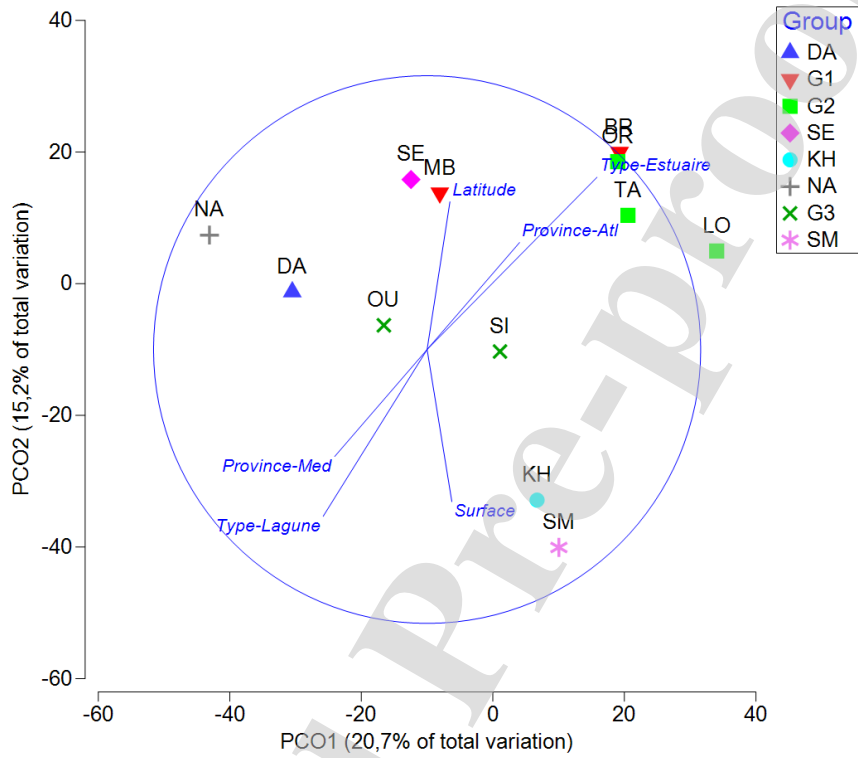
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801 **Figure 5**

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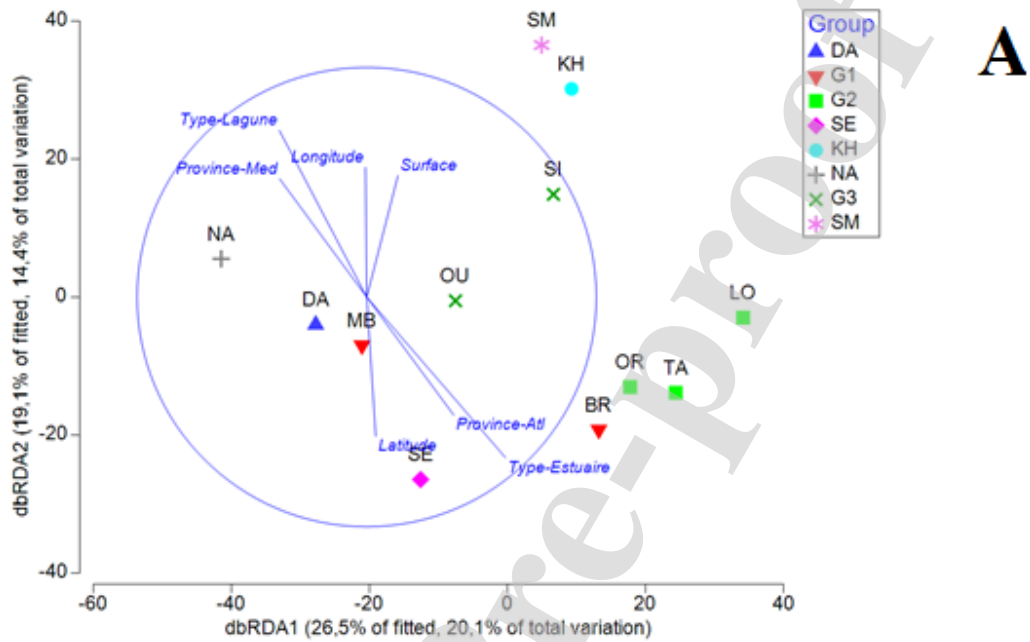
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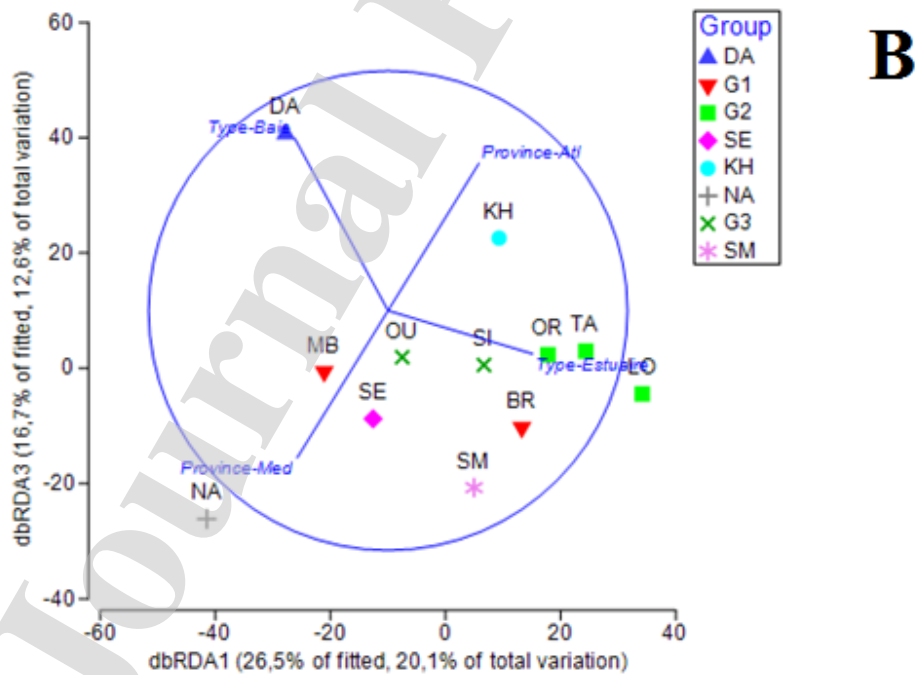
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814 **Figure 6**

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- The first broad-scale baseline of soft-bottom macrozoobenthos in semi-enclosed coastal systems (SECS) of Morocco is presented
- 496 species were recorded from the Moroccan SECS and belong to 7 phyla, 21 classes, 65 orders and 201 families
- Species richness and taxonomic diversity indices showed no relationship with SECS features including latitude
- The type of the SECS (estuaries vs lagoons vs bay), the marine ecoregion (Atlantic vs Mediterranean), the surface of the SECS and the environmental features (minimal temperature, minimal and maximal salinity) are the most predictors of benthic macrofauna composition in the Moroccan SECS

**Author statement file:**

**Soilam Boutoumit:** Investigation, Data curation, Writing – Original Draft, Visualisation. **Reda El Kamcha:** Investigation, Data curation, Writing – Original Draft, Visualisation. **Oussama Bououarour:** Investigation, Data curation, Writing – Original Draft, Visualisation. **Latifa Joulami:** Investigation, Data curation, Review. **Boutahar Loubna:** Investigation, Data curation, Review. **Abdelaziz Benhoussa:** Resources, Funding acquisition. **Mohamed Maanan:** Review & Editing, Supervision. **Laurent Godet:** Writing-Review & Editing, Validation. **Abdellatif Bayed:** Resources, Validation. **Hocein Bazairi:** Conceptualization, Methodology, Writing – Original Draft, Review & Editing, Supervision.

**Declaration of interests**

The authors (Soilam Boutoumit, Reda El Kamcha, Oussama Bououraour, Latifa Joulami, Loubna Boutahar, Abdelaziz Benhoussa, Mohamed Maanan, Laurent Godet, Abdellatif Bayed and Hocein Bazairi) declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the paper entitled **“Soft-bottom macrozoobenthos in semi-enclosed coastal systems of Morocco”**

In behalf of all authors: Hocein Bazairi



Laboratoire de Biodiversité,  
Ecologie et Génome

A handwritten signature in blue ink, appearing to read 'Hocein'.

Pr Hocein Bazairi