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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 Bouselham, 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.

#### 373 **References**

374 Achab, M., 2011. Les plages et les vasières des environs des embouchures des oueds Tahaddart et  
375 Gharifa (NW du Maroc) : dynamique morphosédimentaire et impact des aménagements sur leur  
376 évolution récente. Travaux de l'Institut Scientifique, Rabat. 6, 1-12.

377 Ait Mlik, K., 2009. Contribution à l'étude de l'évolution à long terme des structures benthiques de  
378 la lagune de Merja Zerga (Mémoire Master). Université Hassan II. Casablanca, 40pp.

379 Aksissou, M., 1997. Dynamique des populations d'*Orchestia gammarellus* (Pallas, 1766) -  
380 Crustacea, Amphipoda, Talitridae- du littoral méditerranéen du Maroc occidental et impact des  
381 aménagements (Thèse Doctorat d'Etat). Université Abdelmalek Essaâdi. Tétouan, 145pp.

382 Aller, J.Y., Aller, R.C., Green, M.A., 2002. Benthic faunal assemblages and carbon supply along  
383 the continental shelf/shelf break-slope off Cape Hatteras, North Carolina. Deep-Sea Res. Pt. II 49  
384 (20), 4599-4625. [http://dx.doi.org/10.1016/S0967-0645\(02\)00131-5](http://dx.doi.org/10.1016/S0967-0645(02)00131-5)

385 Alongi, D.M., 1990. The ecology of tropical soft-bottom benthic ecosystems. Oceanography and  
386 Marine Biology: An Annual Review. 28, 381-496.



- 387 Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: guide to  
388 software and statistical methods. University of Auckland and PRIMER-E, Plymouth.
- 389 Anderson, M.J., Millar, R.B., 2004. Spatial variation and effects of habitat on temperate reef fish  
390 assemblages in northeastern New Zealand. *J. Exp. Mar. Biol. Ecol.* 305, 191–221.  
391 <https://doi.org/10.1016/j.jembe.2003.12.011>
- 392 Angel, M.V., 1997. Pelagic diversity in “Marine Biodiversity. Patterns and Processes” (eds R.F.G.  
393 Ormond, J.D. Gage & M.V. Angel). Cambridge University Press, Cambridge, UK, 35-68. .  
394 <https://doi.org/10.1017/CBO9780511752360>
- 395 Attrill, M.J., Stafford, R., Rowden, A.A., 2001. Latitudinal diversity patterns in estuarine tidal  
396 flats: indications of a global cline. *Ecography*. 24, 318-324. <https://doi.org/10.1034/j.1600->  
397 [0587.2001.240309.x](https://doi.org/10.1034/j.1600-0587.2001.240309.x)
- 398 Azirar, A., 2006. Macrofaune benthique de l'estuaire d'Oum Rbia (Mémoire DESA). Université  
399 Mohammed V. Rabat, 64pp.
- 400 Barboza, F.R., Defeo, O., 2015. Global diversity patterns in sandy beach macrofauna: a  
401 biogeographic analysis. *Sci. Rep.* 5, 14515. <https://doi.org/10.1038/srep14515>
- 402 Basset, A., Abbiati, M., 2004. Challenges to transitional water monitoring: ecological descriptors  
403 and scales. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 14, S1-S3.  
404 <https://doi.org/10.1002/aqc.669>
- 405 Basset, A., Sabetta, L., Fonnesu, A., Mouillot, D., Do Chi, T., Viaroli, P., Giordani, G.,  
406 Reizopoulou, S., Abbiati, M., Carrada, G.C., 2006. Typology in Mediterranean transitional waters:  
407 new challenges and perspectives. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 16  
408 (5), 441-455. <https://doi.org/10.1002/aqc.767>
- 409 Battaglia, B., 1959. Final resolution of the symposium on the classification of brackish waters.  
410 *Archivio Di Oceanografia E Limnologia*. 11(suppl), 243-248.

- 411 Bayed, A., EL Agbani, M.A., Fekhaoui, M., Schouten, J.R., 1988. Benthos of soft substrates in the  
412 intertidal zone of the Khnifiss lagoon; in DAKKI M. & W. LIGNY (eds.): The Khnifiss lagoon  
413 and its surrounding environment (Province of Laayoune, Morocco). Trav. Inst. Sci., Mém. Hors-  
414 série. 71-80.
- 415 Bazairi, H., 1999. La faune macrobenthique de la lagune de Moulay Bousselham : Structure et  
416 successions spatio-temporelles (Thèse Doctorat). Université Mohammed V. Rabat, 199pp.
- 417 Bazairi, H., Bayed, A., 2006. L'écosystème benthique de l'estuaire de Tahaddart : biodiversité,  
418 fonctionnement et qualité écologique. Unpublished report, WADI Project, 75pp.
- 419 Bazairi, H., Gam, M., 2004. Diagnostic pour l'élaboration du plan de gestion: macroinvertébrés  
420 estuariens. Projet Gestion Intégrée du Complexe de Zones Humides du Bas Loukkos (Larache,  
421 Maroc), Deuxième phase (2004-2005): Actions opérationnels, 40pp.
- 422 Bazairi, H., Zourarah, B., 2001. Faune macrobenthique de l'estuaire d'Oum Rbia: biodiversité,  
423 distribution spatiale et état de la qualité écologique. Unpublished report, GREPEN, 25pp.
- 424 Bazairi, H., Zourarah, B., 2007. Faune macrobenthique de l'estuaire d'Oum Rbia: biodiversité,  
425 distribution spatiale et état de la qualité écologique. Unpublished report, GREPEN, 30pp.
- 426 Bazairi, H., Zourarah, B., El Kamcha, R., Boutoumit, S., 2017. Faune macrobenthique de l'estuaire  
427 d'Oum Rbia: biodiversité, distribution spatiale et état de la qualité écologique. Unpublished report,  
428 OMAZINE, 50pp.
- 429 Bekkali, R., 1987. Les ostracodes du lac Smir (Maroc nord-occidental) (Thèse Doctorat 3ème  
430 cycle). Université Mohammed V de Rabat, 165pp.
- 431 Boucher, G., Lamshead, P.J.D., 1995. Ecological biodiversity of marine nematodes in samples  
432 from temperate, tropical, and deep sea regions. Conservation Biology, 9, 1594–1604.  
433 <https://doi.org/10.1046/j.1523-1739.1995.09061594.x>

- 434 Bououarour, O., 2013. La Macrofaune benthiques des herbiers de *Zostera noltii* de la lagune de  
435 Moulay Bousselham (Merja Zerga) : Structure des communautés et état de la qualité écologique  
436 (Mémoire Master). Université Mohammed V. Rabat, 45pp.
- 437 Boussalwa, E., Douira, A., Mokhtar, N., 2000. Contribution à l'étude typologique d'une lagune  
438 exposée à la pollution, la lagune de Nador (Maroc): distribution des Crustacés. Cah. Biol. Mar. 41,  
439 255-263.
- 440 Boutahar, L., 2014. Evaluation à long terme de la macrofaune benthique dans la lagune de Oualidia  
441 (Atlantique, Maroc) entre 2006 et 2014 (Mémoire Master). Université Mohammed V. Rabat,  
442 105pp.
- 443 Chafik, A., Cheggour, M., Cossa, D., Benbrahim, S., Sifeddine, M., 2001. Quality of Moroccan  
444 Atlantic coastal waters: water monitoring and mussel watching. Aquat. Living Resour. 14, 239-  
445 249. [https://doi.org/10.1016/S0990-7440\(01\)01123-8](https://doi.org/10.1016/S0990-7440(01)01123-8)
- 446 Chaouti, A., Bayed, A., 2005. Diversité taxonomique et structure de la macrofaune benthique des  
447 substrats meubles de la lagune de Smir. In: Bayed A. & Felicita F. (Eds) – Ecosystèmes côtiers  
448 sensibles de la Méditerranée : cas du littoral de Smir. Trav. Inst. Sci. Série générale. 4, 33-42.
- 449 Chardy, P., Clavier, J., 1988. Biomass and trophic structure of the macrobenthos in the south-west  
450 lagoon of New Caledonia. Marine Biology. 99, 195-202. <https://doi.org/10.1007/BF00391981>
- 451 Chaudhary, C., Saeedi, H., Costello, M.J., 2016. Bimodality of Latitudinal Gradients in Marine  
452 Species Richness. Trends in Ecology & Evolution. 31, 670-676.  
453 <https://doi.org/10.1016/j.tree.2016.06.001>
- 454 Chbicheb, A., 1996. Organisation biogéologique d'un bassin paralytique : la lagune de Oualidia  
455 (côte atlantique marocaine) (Thèse Doctorat 3ème cycle). Université de Nantes, 167pp.
- 456 Cheggour, M., 1988. Contribution à l'étude d'un milieu paralytique : l'estuaire du Bou Regreg (Côte  
457 atlantique marocaine). Condition écologique globale. Etude de la contamination métallique (Thèse  
458 de 3ème cycle). ENS. Rabat, 337pp.

- 459 Cherkaoui, S., 2006. Structure et organisation des peuplements macrozoobenthiques de l'estuaire  
460 du Bou Regreg après la construction du barrage (Thèse Doctorat). Université Mohammed V.  
461 Rabat, 305 pp.
- 462 Clarke, A., 1992. Is there a latitudinal diversity cline in the sea? *Trends in Ecology and Evolution*.  
463 7, 286-287. [https://doi.org/10.1016/0169-5347\(92\)90222-W](https://doi.org/10.1016/0169-5347(92)90222-W).
- 464 Clarke, A., Crame, J.A., 1997. Diversity, latitude and time: patterns in the shallow sea. In "Marine  
465 Diversity: Patterns and Processes" (eds R.F.G. Ormond, J.D. Gage & M.V. Angel). Cambridge  
466 University Press, Cambridge, UK, 122-147. <https://doi.org/10.1017/CBO9780511752360>
- 467 Clarke, K.R., Gorley, R.N., 2006. PRIMER v.6: User Manual/Tutorial (Plymouth Routines in  
468 Multivariate Ecological Research). PRIMER-E, Plymouth.
- 469 Clarke, K.R., Warwick, R., 2001. Change in Marine Communities: An approach to statistical  
470 analysis and interpretation. PRIMER-E, Plymouth.
- 471 Coleman, N., Gason, A.S.H., Poore, C.B., 1997. High species richness in the shallow marine  
472 waters of south-east Australia. *Mar. Ecol. Prog. Ser.* 154, 17-26.  
473 <http://dx.doi.org/10.3354/meps154017>
- 474 Crame, J.A., 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from  
475 the composition of recent bivalve faunas. *Paleobiology*. 26, 188-241.  
476 [https://doi.org/10.1666/0094-8373\(2000\)026<0188:EOTDGI>2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)026<0188:EOTDGI>2.0.CO;2)
- 477 Cruz-Motta, J.J., Miloslavich, P., Guerra-Castro, E., Hernández-Agreda, A., Herrera, C., Klein,  
478 E., Barros, F., Navarrete, S.A., Sepúlveda, R., Glasby, T.M., Bigatti, G., Cárdenas-Calle, M.,  
479 Carneiro, P.B.M., Carranza, A., Flores, A., Gil-Kodaka, P., Gobin, J., Gutiérrez, J., Klein, E.,  
480 Krull, M., Lazarus, J.F., Londoño-Cruz, E., Lotufo, T., Macaya, E.C., Mora, E., Palomo, G.,  
481 Parragué, M., Pellizzari, F., Retamales, R., Rocha, R., Romero., 2020. Latitudinal patterns of  
482 species diversity on South American rocky shores: Local processes lead to contrasting trends in  
483 regional and local species diversity. *Journal of Biogeography*. 47, 1966-1979.  
484 <https://doi:10.1111/jbi.13869>

- 485 Cuvelier, J., Riviere, V., Bazairi, H., Benhoussa, A., Cerniaut, C., Charrier, M., Moulis, D., Pupier,  
486 P., Qninba, A., 2014. Plan de gestion ; Lagune de Nador – Cordon de la Bocana – partie 1 :  
487 Diagnostic socio-économique et écologique. Conservatoire du Littoral. O2TERRE ; AGIR  
488 écologique, 177p.
- 489 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E.,  
490 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science*. 344,  
491 296-299. <https://doi.org/10.1126/science.1248484>
- 492 El Amraoui, M., Salama, Y., El Amraoui, B., Lazrak, N., Mounkad, M., 2015. Evaluation of the  
493 physicochemical and some trace elements of the surface waters of the Moroccan Atlantic estuary:  
494 case of the estuary of the river Bouregreg. *Carpathian Journal of Earth and Environmental*  
495 *Sciences*. 10 (2), 189-198.
- 496 El Asri, F., 2019. Composition, organisation et dynamique des communautés zoobenthiques de  
497 deux écosystèmes côtiers : la lagune de Oualidia et la Baie de Dakhla (Atlantique Marocain)  
498 (Thèse Doctorat). Université Hassan II. Casablanca, 297 pp.
- 499 El Asri, F., Zidane, H., Errhif, A., Tamsouri, M.N., Maanan, M., Malouli Idrissi, M., Martin, D.,  
500 2017. Polychaete diversity and assemblage structure in the Oualidia Lagoon, Moroccan Atlantic  
501 coast. *J. Mar. Biol. Assoc. United Kingdom*. 98, 1337-1346.  
502 <https://doi.org/10.1017/S0025315417000388>
- 503 El Asri, F., Zidane, H., Maanan, M., Tamsouri, M., Errhif, A., 2015. Taxonomic diversity and  
504 structure of the molluscan fauna in Oualidia lagoon (Moroccan Atlantic coast). *Environmental*  
505 *Monitoring and Assessment*. 187, 545. <http://dx.doi.org/10.1007/s10661-015-4752-7>
- 506 El Houssaini, F., 2005. Composition et structure du macrozoobenthos associé à *Zostera noltii* de  
507 la lagune de Smir (Mémoire DESA). Université Hassan II Aïn Chock. Casablanca, 68 pp.
- 508 El Kamcha, R., Bououarour, O., Boutoumit, S., Bazairi, H., 2020. Occurrence of the invasive  
509 *Caprella scaura* Templeton, 1836 (Amphipoda: Caprellidae) in the Marchica coastal lagoon  
510 (Alboran Sea, Morocco). *BioInvasions Records*. 9. Article in press.

- 511 Elkaïm, B., 1974. Contribution à l'étude écologique d'un estuaire atlantique marocain : l'estuaire  
512 du Bou Regreg (Thèse Doctorat d'Etat). Université de Bordeaux I- 2ème partie, 250 pp.
- 513 Ellingsen, K.E., 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to  
514 environmental variability. *Marine Ecology Progress Series*. 232, 15-27.  
515 <https://doi.org/10.3354/meps232015>
- 516 Galeron, J., Sibuet, M., Vanreusel, A., Mackenzie, K., Gooday, A., Dinet, A., Wolff, G., 2001.  
517 Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment  
518 geochemistry at an abyssal NE Atlantic site. *Progress in Oceanography*. 50 (1-4), 303-324 Sp. Iss.  
519 SI). [https://doi.org/10.1016/S0079-6611\(01\)00059-3](https://doi.org/10.1016/S0079-6611(01)00059-3)
- 520 Gam, M., de Montaudouin, X., Bazairi, H., 2010. Population dynamics and secondary production  
521 of the cockle *Cerastoderma edule*: A comparison between Merja Zerga (Moroccan Atlantic Coast)  
522 and Arcachon Bay (French Atlantic Coast). *Journal of Sea Research*. 63 (3-4), 191-201.  
523 <https://doi.org/10.1016/j.seares.2010.01.003>
- 524 Gaston, K.J., 2000. Global patterns in biodiversity. *Nature*. 405, 220-227.  
525 <https://doi.org/10.1038/35012228>.
- 526 Gauteur, M., 2006. Etablissement du diagnostic écologique d'un environnement lagunaire : la  
527 lagune de Oualidia (Côte atlantique, Maroc) (Mémoire Master). Université de Bordeaux 1, 60 pp.
- 528 Geawhari, M.A., Huff, L., Mhammdi, N., Trakadas, A., Ammar, A., 2014. Spatial-temporal  
529 distribution of salinity and temperature in the Oued Loukkos estuary, Morocco: using vertical  
530 salinity gradient for estuary classification. *Computational Statistics*. 3 (1), 1-9.  
531 <https://doi.org/10.1186/2193-1801-3-643>
- 532 Giangrande, A., Licciano, M., 2004. Factors influencing latitudinal pattern of biodiversity: An  
533 example using Sabellidae (Annelida, Polychaeta). *Biodiversity and Conservation* 13, 1633-1646.  
534 <https://doi.org/10.1023/B:BIOC.0000029327.63397.6b>

- 535 Grassle, J.F., Lasserre, P., McIntyre, A.D., Ray, G.C., 1991. Marine Biodiversity and Ecosystem  
536 Function: A proposal for an international program of research. *Biology International Special Issue*.  
537 23, 19p.
- 538 Guelorget, O., Frisoni, G.F., Perthuisot, J.P., 1983. Zonation biologique des milieux lagunaires:  
539 définition d'une échelle de confinement dans le domaine paralique méditerranéen. *Journal de*  
540 *Recherche océanographique*. 8, 15-35.
- 541 Guelorget, O., Perthuisot, J.P., 1983. Le domaine paralique. Expressions géologiques, biologiques  
542 et économiques du confinement. *Travaux du laboratoire de géologie*. 16, 1-136.
- 543 Guelorget, O., Perthuisot, J.P., Frisoni, G.F., Monti, D., 1987. Le rôle du confinement dans  
544 l'organisation biogéographique de la lagune de Nador (Maroc). *OceanolActa*. 10 (4), 435-444.
- 545 Haddout, S., Maslouhi, A., Magrane, B., Igouzal, M., 2015. Study of salinity variation in the Sebou  
546 River Estuary (Morocco). *Desalination and Water Treatment*. 57 (36), 17075-17086.  
547 <https://doi.org/10.1080/19443994.2015.1091993>
- 548 Hawkins, B.A., 2001. Ecology's oldest pattern? *Trends Ecol. Evol.*, 16, 470.  
549 [https://doi.org/10.1016/S0160-9327\(00\)01369-7](https://doi.org/10.1016/S0160-9327(00)01369-7)
- 550 Hendrickx, M., Harvey, A.W., 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the  
551 Eastern Tropical Pacific. *Belgian Journal of Zoology*. 129 (2), 363-389.
- 552 Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. *The American*  
553 *Naturalist*. 163, 192-211. <https://doi.org/10.1086/381004>
- 554 Hilmi, K., Koutitonsky, V.G., Orbi, A., Lakhdar, J.I., Chagdali, M., 2005. Oualidia lagoon,  
555 Morocco: An estuary without a river. *African Journal of Aquatic Science*. 30 (1), 1-10.  
556 <https://doi.org/10.2989/16085910509503828>
- 557 Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton  
558 University Press, Princeton, 448 pp.

- 559 Hurlbert, A.H., Stegen, J.C., 2014. On the processes generating latitudinal richness gradients :  
560 identifying diagnostic patterns and predictions. *Evol Popul Genet.* 5: 420.  
561 <https://doi.org/10.3389/fgene.2014.00420>
- 562 Hurtt, G.C., Pacala, S.W., 1995. The consequences of recruitment limitation. Reconciling chance,  
563 history and competitive differences between plants. *Journal of Theoretical Biology.* 176, 1-12.  
564 <https://doi.org/10.1006/jtbi.1995.0170>
- 565 Joulami, L., 2013. Interactions entre les conditions écologiques, le benthos et les communautés  
566 des limicoles dans un écosystème côtier du Nord-Ouest de L'Afrique (Lagune de Sidi Moussa,  
567 Maroc) (Thèse Doctorat.) Université Hassan II. Casablanca, 129 pp.
- 568 Kendall, M.A., Aschan, M., 1993. Latitudinal gradients in the structure of macrobenthic  
569 communities: a comparison of Arctic, temperate and tropical sites. *Journal of Experimental Marine*  
570 *Biology and Ecology.* 172, 157–169. [https://doi.org/10.1016/0022-0981\(93\)90095-6](https://doi.org/10.1016/0022-0981(93)90095-6)
- 571 Khalki, A.E., Moncef, M., 2007. Etude du peuplement de copépodes de l'estuaire de l'Oum Er  
572 Rbia (côte Atlantique du Maroc): Effets des marées et des lachers de barrages. *Lebanese Science*  
573 *Journal.* 8 (1), 3-18.
- 574 Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajiye, M., Bender, N., Umarani,  
575 M., Ryu, H.Y., Şen, B., Gurevitch, J., 2018. Explaining global variation in the latitudinal diversity  
576 gradient: Meta-analysis confirms known patterns and uncovers new ones. *Global Ecology and*  
577 *Biogeography.* 27, 125-141. <https://doi.org/10.1111/geb.12665>.
- 578 Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajiye, M., Bender, N., Umarani,  
579 M., Ryu, H.Y., Şen, B., Gurevitch, J., 2019. Open science and meta-analysis allow for rapid  
580 advances in ecology: A response to Menegotto et al. (2019). *Global Ecology and Biogeography.*  
581 28, 1533-1534. <https://doi.org/10.1111/geb.12964>
- 582 Kong, W.J., Meng, W., Zhang, Y., Christopher, G., Qu, X.D., 2013. A freshwater ecoregion  
583 delineation approach based on freshwater macroinvertebrate community features and spatial



- 584 environmental data in Taizi River Basin, northeastern China. *Ecol. Res.* 28, 581-592.  
585 <http://dx.doi.org/10.1007/s11284-013-1048-7>
- 586 Labrune, C., Grémare, A., Amouroux, J.M., Sardá, R., Gil, J., Taboada, S., 2008. Structure and  
587 diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean).  
588 *Helgol Mar Res.* 62, 201-214. <https://doi.org/10.1007/s10152-008-0108-9>
- 589 Lacoste, M., 1984. Contribution à l'étude écologique de la lagune de Moulay Boussalham (Maroc)  
590 (Thèse Doctorat 3ème cycle). Université Paul Sabatier. Toulouse, 207 pp.
- 591 Lara-Lara, J., Arreola, J., Calderon, L., Camacho, V., De la Lanza, G., Escofet, A., Espejel, M.,  
592 Guzman, M., Ladah, L., Lopez, M., Meling, E., Moreno, P., Reyes, H., Rios, E., Zertuche, J., 2008.  
593 Los ecosistemas costeros, insulares y epicontinentales. In: Capital natural de México Vol. I :  
594 Conocimiento actual de la biodiversidad. Mexico City : CONABIO, 109-134.
- 595 Lefrere, L., 2012. Contribution à l'étude de deux lagunes atlantiques marocaines, Khnifiss et  
596 Oualidia: faune malacologique, biologie de trois mollusques bivalves et contamination métallique  
597 (Thèse Doctorat). Université Ibn Zohr. Agadir, 180 pp.
- 598 Maanan, M., Zourarah, B., Carruesco, C., Aajjane, A., Naud, J., 2004. The distribution of heavy  
599 metals in the Sidi Moussa lagoon sediments (Atlantic Moroccan Coast). *Journal of African Earth*  
600 *Sciences.* 39 (3-5), 473-483. <https://doi.org/10.1016/j.jafrearsci.2004.07.017>
- 601 MacArthur, R.H., 1970. Species packing and competitive equilibrium for many species.  
602 *Theoretical Population Biology.* 1, 1-11.
- 603 McCallum, A.W., Woolley, S., Błażewicz-Paszkowycz, M., Browne, J., Gerken, S., Kloster, R.,  
604 Poore, G.C.B., Staples, D., Syme, A., Taylor, J., Walker-Smith, G., Williams, A., Wilson, R.S.,  
605 2015. Productivity enhances benthic species richness along an oligotrophic Indian Ocean  
606 continental margin. *Global Ecol. Biogeogr.* 24 (4), 462-471. <http://dx.doi.org/10.1111/geb.12255>

- 607 Menegotto, A., Kurtz, M.N., Lana, P., 2019. Benthic habitats do show a significant latitudinal  
608 diversity gradient: a comment on Kinlock et al. (2018). *Global Ecology and Biogeography*. 28,  
609 1712–1717. <http://doi.org/10.5281/zenodo.3245484>
- 610 Mergaoui, L., Fekhaoui, M., Bouya, D., Gheit, A., Stambouli, A., 2003. Qualité des eaux et  
611 macrofaune benthique d'un milieu estuarien du Maroc ; Cas de l'estuaire de Sebou. *Bulletin de*  
612 *l'Institut Scientifique*. 25, 67-75.
- 613 Möllmann, C., Diekmann, R., 2012. Marine ecosystem regime shifts induced by climate and  
614 overfishing a review for the northern hemisphere. *Advances in Ecological Research*. 47, 303-347.  
615 <https://doi.org/10.1016/B978-0-12-398315-2.00004-1>
- 616 Observatoire National de l'Environnement au Maroc (ONEM)., 1998. Rapport National sur la  
617 biodiversité : faune marine, 105pp.
- 618 Piacenza, S. E., Barner, A. K., Benkwitt, C. E., Boersma, K. S., Cerny-Chipman, E. B., Ingeman,  
619 K. E., Kindinger, T.L., Lee, J.D., Lindsley, A.J., Reimer, J.N., Rowe, J.C., Shen, C., Thompson,  
620 K.A., Thurman, L.L., Heppell, S.S., 2015. Patterns and variation in benthic biodiversity in a large  
621 marine ecosystem. *PLOS One*. 10(8): e0135135. <https://doi.org/10.1371/journal.pone.0135135>
- 622 Pierrot-Bults, A.C., 1997. Biological diversity in oceanic macrozooplankton: more than counting  
623 species in "Marine Biodiversity: Patterns and Processes" (eds R.F.G. Ormond, J.D. Gage & M.V.  
624 Angel), pp. 69–93. Cambridge University Press, Cambridge, UK.  
625 <https://doi.org/10.1017/CBO9780511752360>
- 626 Poore, G.C.B., Wilson, G.D.F., 1993. Marine species richness. *Nature*. 361, 597-598.  
627 <https://doi.org/10.1038/361597a0>
- 628 Pratt, D.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., 2014. The effects of short-term increases  
629 in turbidity on sandflat microphytobenthic productivity and nutrient fluxes. *J. Sea Res.* 92, 170-  
630 177. <https://doi.org/10.1016/j.seares.2013.07.009>

- 631 Qninba, A., Radi, M., Benhoussa, A., Bazairi, H., Menioui, M., 2003. Fiche descriptive sur les  
632 zones humides Ramsar (FDR). Catégories approuvées dans la Recommandation 4.7 modifiée par  
633 la résolution VIII.13 de la Conférence des Parties contractantes 2005, 9p.
- 634 Renaud, P.E., Webb, T.J., Bjørgesæter, A., Karakassis, I., Kędra, M., Kendall, M.A., Labruno, C.,  
635 Lampadariou, N., Somerfield, P.J., Włodarska-Kowalczyk, M., Vanden Berghe, E., Claus, S.,  
636 Aleffi, I.F., Amouroux, J.M., Bryne, K.H., Cochrane, S.J., Dahle, S., Degraer, S., Denisenko, G.,  
637 Deprez, T., Dounas, C., Fleischer, D., Gil J., Grémare, A., Janas, U., Mackie, A.S.Y., Palerud, R.,  
638 Rumohr, H., Sardá, R., Speybroeck, J., Taboada, S., Van Hoey, G., Węśławski, J.M., Whomersley,  
639 P., Zettler, M.L., 2009. Continental-scale patterns in benthic invertebrate diversity: insights from  
640 the MacroBen database. *Marine Ecology Progress Series*. 382, 239-252.  
641 <https://doi.org/10.3354/meps07963>
- 642 Rex, M.A., Stuart, C.T., Coyne, G., 2000. Latitudinal gradients of species richness in the deep-sea  
643 benthos of the North Atlantic. *Proceedings of the National Academy of Sciences of the USA*. 97,  
644 4082-4085. <https://doi.org/10.1073/pnas.050589497>
- 645 Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L., Wilson, G.D.F., 1993. Global-  
646 scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature*. 365, 636-639.  
647 <https://doi.org/10.1038/365636a0>
- 648 Rohde, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*.  
649 65, 514-527.
- 650 Roy, K., Jablonski, D., Valentine, J.W., 2000. Dissecting latitudinal diversity gradients: functional  
651 groups and clades of marine bivalves. *Proceedings of the Royal Society of London B. Biological*  
652 *Sciences*. 267, 293–299. <https://doi.org/10.1098/rspb.2000.0999>
- 653 Roy, K., Jablonski, D., Valentine, J.W., Rosenberg, G., 1998. Marine latitudinal diversity  
654 gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA*. 95,  
655 3699-3702. <https://doi.org/10.1073/pnas.95.7.3699>

- 656 Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am Nat.* 102, 243-282.  
657 <https://doi.org/10.1086/282541>
- 658 Semlali, A., Chafik, A., Talbi, M., Budzinski, H., 2012. Origin and Distribution of Polycyclic  
659 Aromatic Hydrocarbons in Lagoon Ecosystems of Morocco. *The Open Environmental Pollution  
660 & Toxicology Journal.* 3, 37-46. <https://doi.org/10.2174/1876397901203010037>
- 661 Snelgrove, P.V., 1998. The biodiversity of macrofaunal organisms in marine sediments.  
662 *Biodiversity and Conservation.* 7, 1123-1132. <https://doi.org/10.1023/A:1008867313340>
- 663 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern,  
664 B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia,  
665 C.A., Robertson, J., 2007. Marine ecoregions of the world: A bioregionalization of coastal and  
666 shelf areas. *Bioscience.* 57, 573-583. <https://doi.org/10.1641/B570707>
- 667 Thorson, G., 1957. Bottom communities. In *Treatise on Marine Ecology and Paleoecology.* Vol.  
668 1 Ecology (ed. G W Hedgpeth). *Memoir of the Geological Society of America.* 67, 461-534.  
669 <https://doi.org/10.1130/MEM67V1>
- 670 Touhami, F., 2018. Caractérisation des peuplements benthiques des habitats intertidaux de Merja  
671 Zerga et leur utilisation par les limicoles hivernants (Thèse Doctorat). Université Mohammed V  
672 de Rabat. 219pp.
- 673 Touhami, F., Bazairi, H., Badaoui, B., Morabbi, A., Benhoussa, A., 2019. Structure and spatial  
674 organization of macrobenthic fauna of intertidal habitats frequented by wintering shorebirds at  
675 Merja Zerga lagoon (Moroccan Ramsar Site). *Cah. Biol. Mar.* 60, 41-50. [https://  
676 doi.org/10.21411/CBM.A.26046E89](https://doi.org/10.21411/CBM.A.26046E89)
- 677 UN General Assembly, Convention of the Law of the Sea, 10 December., 1982. Available at:  
678 <https://www.refworld.org/docid/3dd8fd1b4.html> (accessed 9 April 2019).
- 679 Veiga, P., Torres, A.C., Aneiros, F., Sousa-Pinto, I., Troncoso, J.S., Rubal M., 2016. Consistent  
680 patterns of variation in macrobenthic assemblages and environmental variables over multiple

681 spatial scales using taxonomic and functional approaches. *Mar. Environ. Res.* 120, 191-201.  
682 <http://dx.doi.org/10.1016/j.marenvres.2016.08.011>

683 Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern,  
684 process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics.* 34, 273-309.  
685 <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>

686 WoRMS Editorial Board., 2020. World Register of Marine Species. Available from  
687 <http://marinespecies.org/> (consulted January 14, 2020).

688 Zidane, H., Mannan, M., Mouradi, A., Maanan, M., El Barjy, M., Zourarah, B., Blais, J.F., 2017.  
689 Environmental and ecological risk of heavy metals in the marine sediment from Dakhla Bay,  
690 Morocco. *Environmental Science and Pollution Research.* 24, 7970-7981.  
691 <https://doi.org/10.1007/s11356-017-8367-0>

692 Zine, N.E., 1989. Etude de la malacofaune de la lagune de Nador et dynamique de population de  
693 *Venerupis decussata* (Linné 1767) (Thèse Doctorat 3ème cycle). Université Mohammed V. Rabat,  
694 97 pp.

695 Zine, N.E., 2005. Etude éco-biologique et dynamique des populations de la palourde (*Ruditapes*  
696 *decussatus*) et analyse typologique de la faune benthique de milieux paraliques atlantico-  
697 méditerranéens du Maroc (Thèse Doctorat d'Etat). Université Moulay Ismail. Meknès, 200 pp.

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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.  
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	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

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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.

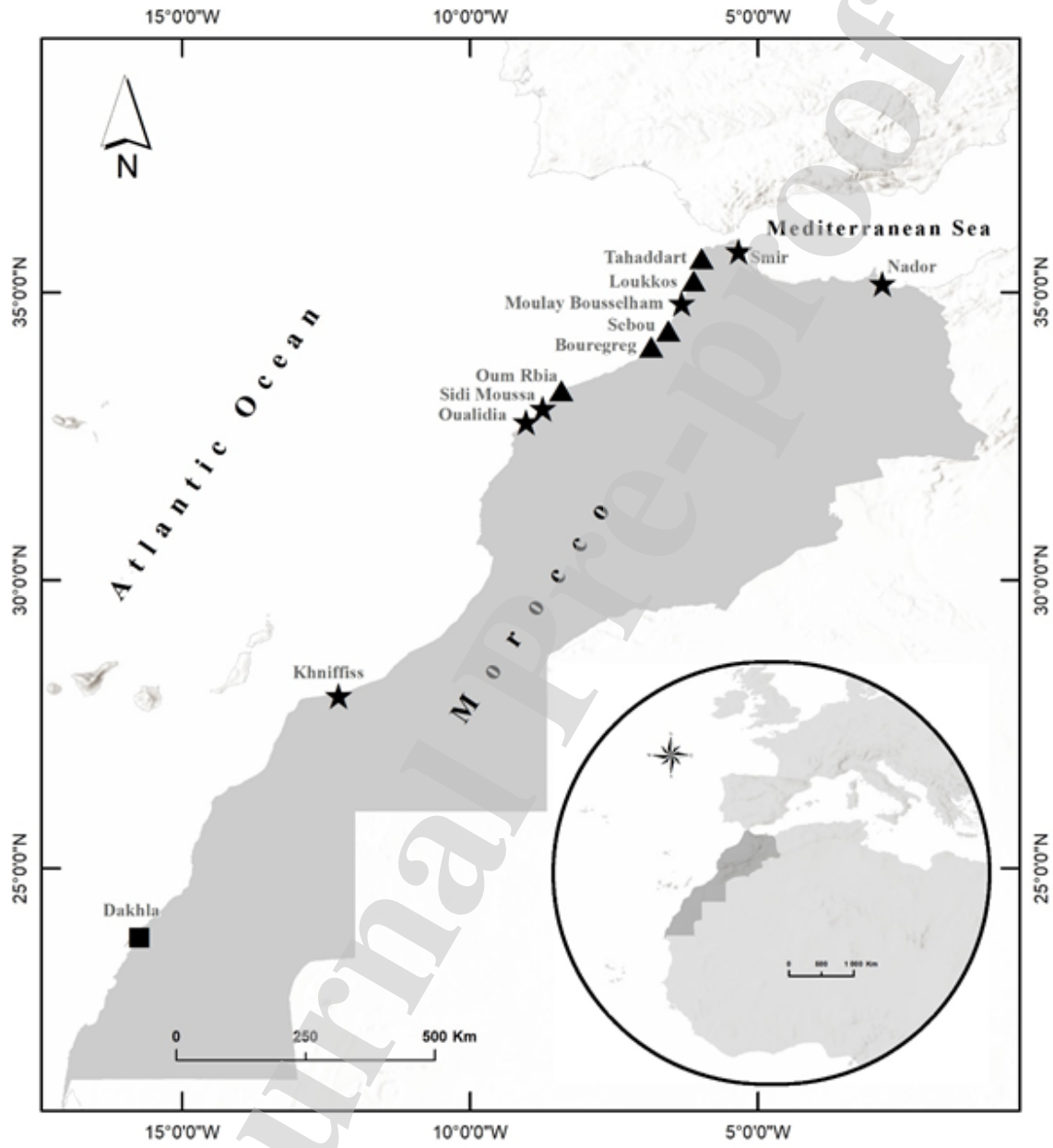
754 **Figure 4.** Dendrogram of cluster analysis using group-average linkage of Bray-Curtis similarities  
755 based on benthic macrofauna composition in the semi-enclosed coastal systems of Morocco. NA:  
756 Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bouselham. SE: Sebou. BR:  
757 Bouregreg.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

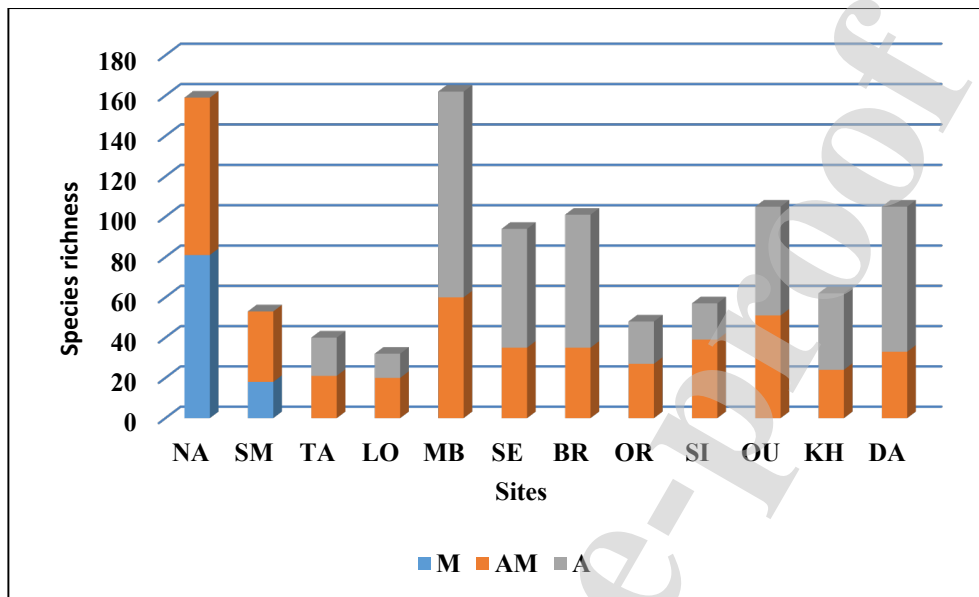


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773 **Figure 2**

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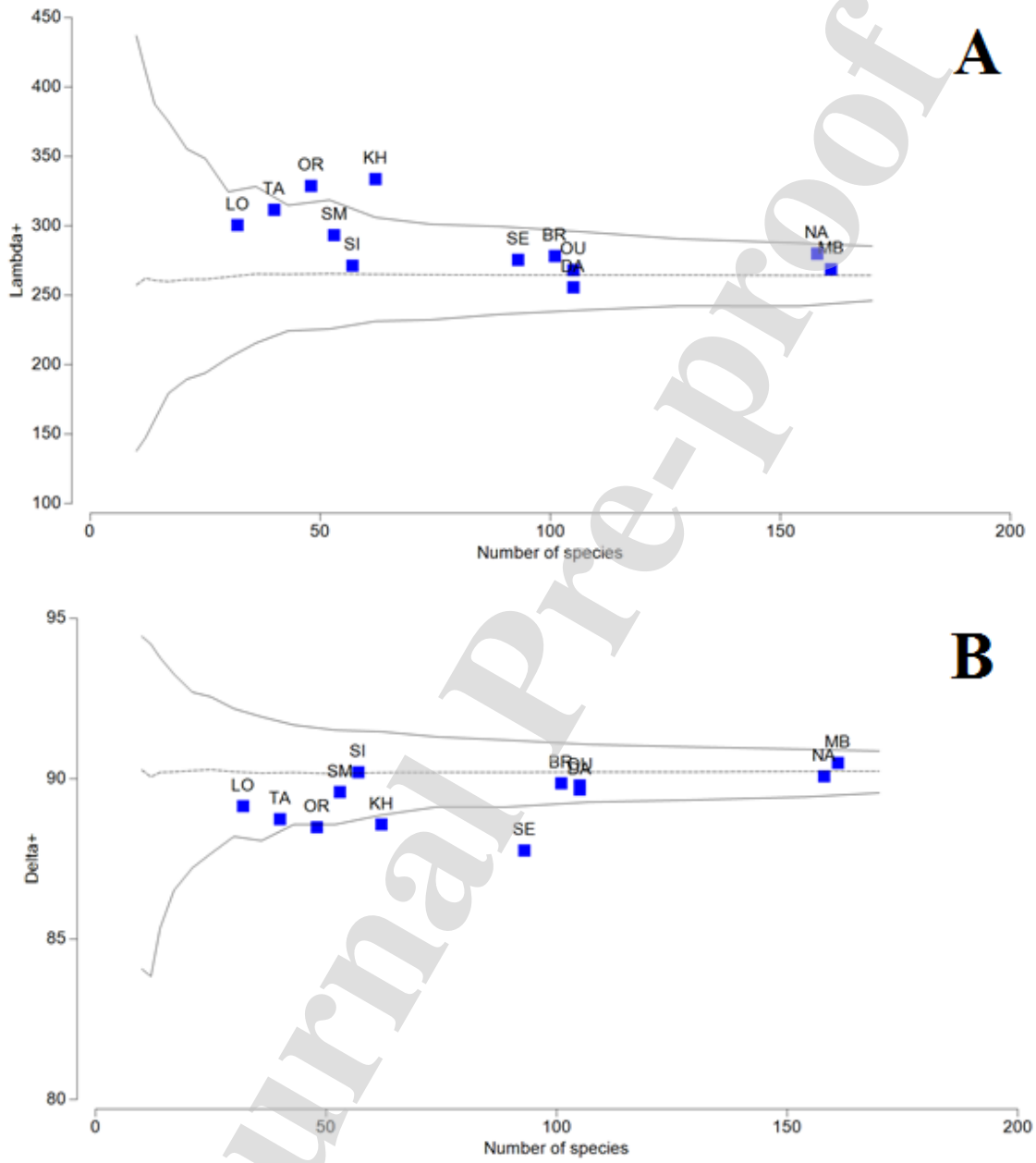
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785 **Figure 3**

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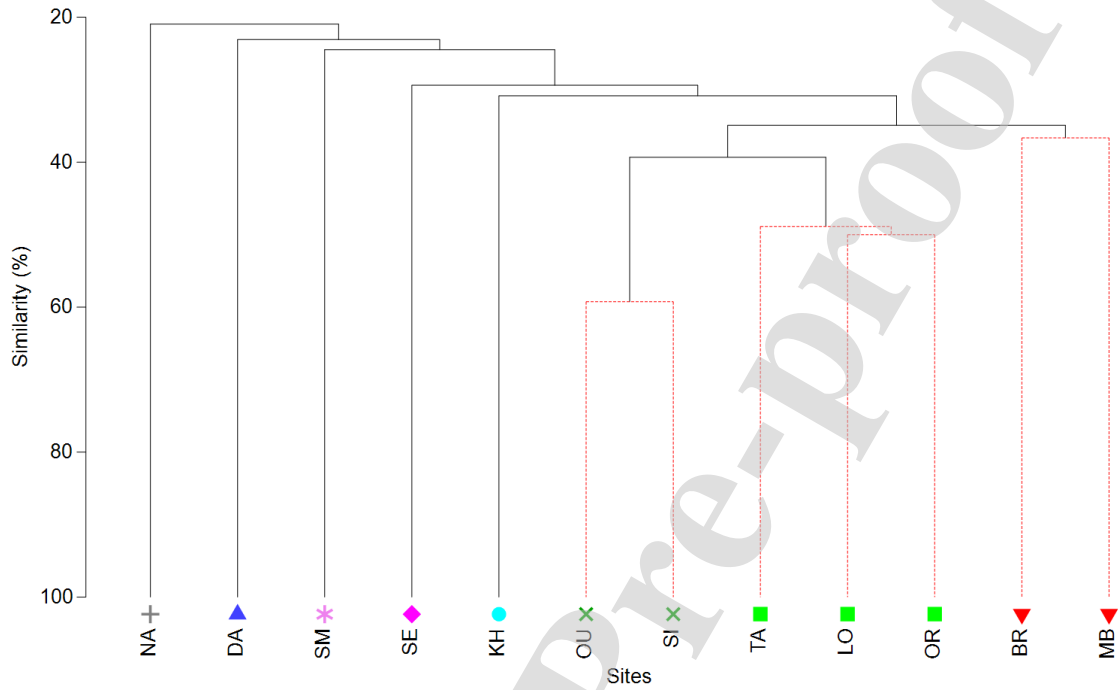
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790 **Figure 4**

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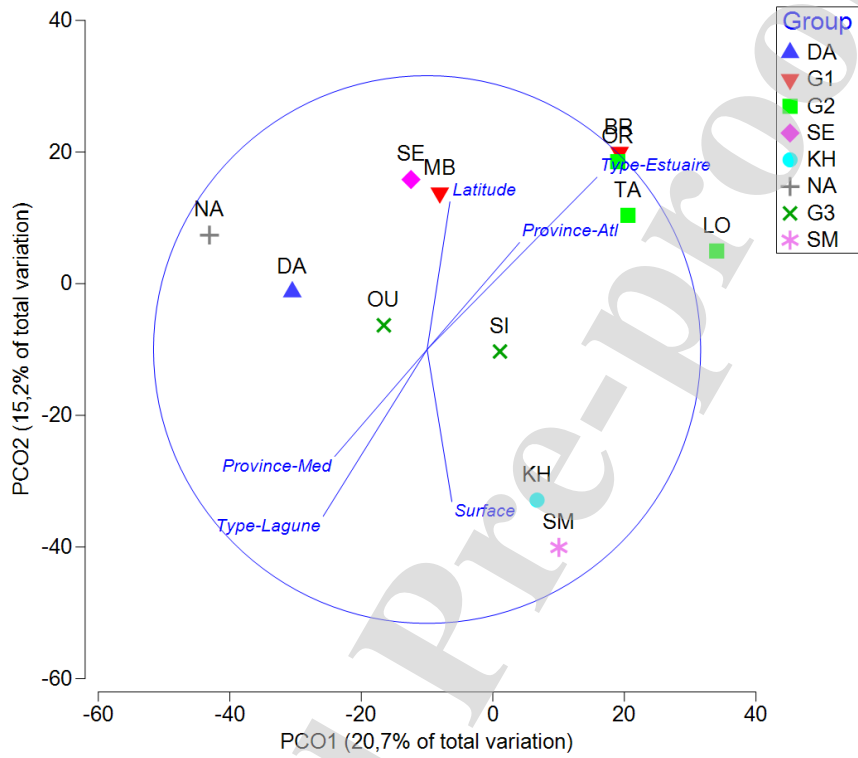
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801 **Figure 5**

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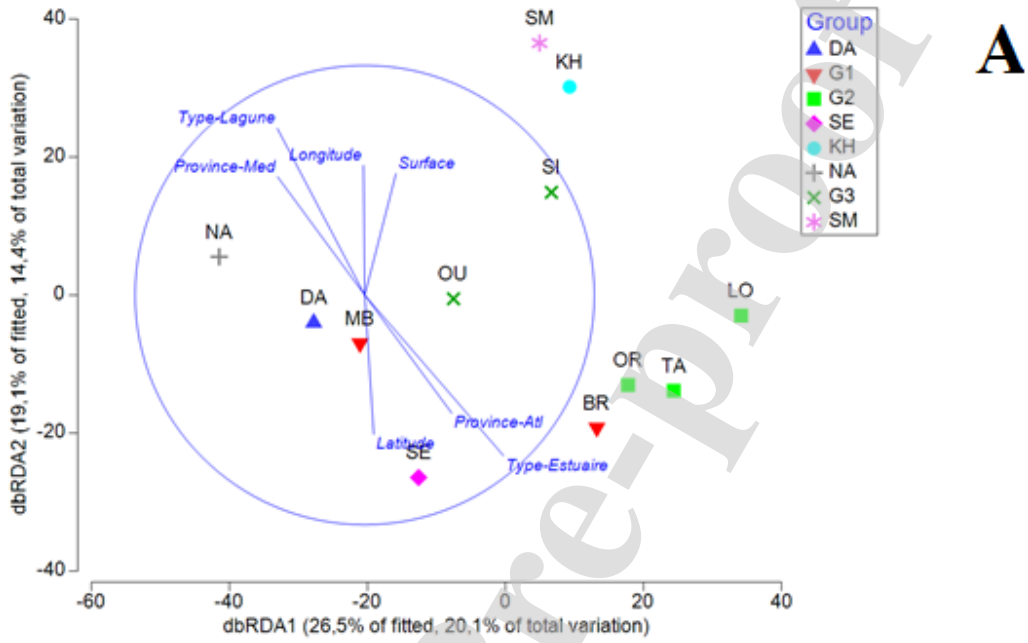
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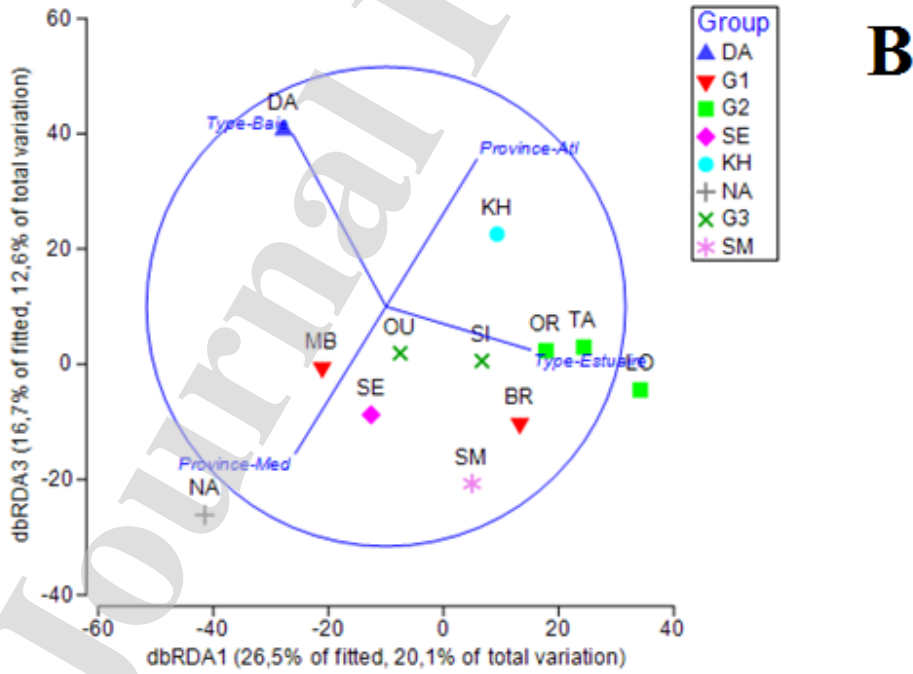
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814 **Figure 6**

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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



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A handwritten signature in blue ink that reads "Hocein".

Pr Hocein Bazairi