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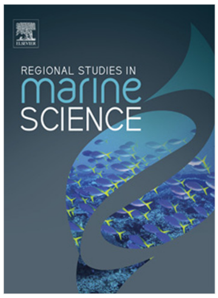
Journal Pre-proof



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PII: S2352-4855(21)00081-5
DOI: https://doi.org/10.1016/j.rsma.2021.101689
Reference: RSMA 101689

To appear in: *Regional Studies in Marine Science*

Received date : 6 August 2020
Revised date : 13 November 2020
Accepted date : 20 February 2021

Please cite this article as: S. Boutoumit, R. El Kamcha, O. Bououraour et al., Soft-bottom macrozoobenthos in semi-enclosed coastal systems of Morocco: A latitudinal and biogeographic analysis. *Regional Studies in Marine Science* (2021), doi: https://doi.org/10.1016/j.rsma.2021.101689.

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

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ABSTRACT

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

The best multivariate model, explaining 33% of the total variation observed in benthic assemblages' composition, included 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) as predictors of benthic macrofauna composition in the Moroccan SECS. In contrast to the general latitudinal diversity gradient (LDG) pattern, our results showed that species richness and taxonomic diversity showed no relationship with latitude. Such differences in benthic macrofaunal composition across a large scale could result from the fact that each ecosystem has its own specific characteristics, which implies an individualistic approach to ecosystem ecology.

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

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

1. Introduction

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

While the LDG is a well-recognized and long-established pattern in terrestrial ecology, the knowledge of global diversity patterns in marine ecosystems is limited to a small number of studies (Barboza & Defeo, 2015). For marine biota, the first suggestion of the latitudinal diversity cline was formulated in late 1950ies for hard bottom epifauna (Thorson, 1957) with pronounced decrease in the species richness of hard substratum epifauna towards arctic areas, whereas the number of soft-sediment infauna species was roughly the same in tropical, temperate and arctic areas. Latitudinal clines in benthic diversity of shallow waters have been also reported for gastropods (Roy et al. 1998), bivalve molluscs (Crame 2000; Roy, Jablonski & Valentine 2000), in shallow and deep-seas benthos (Sanders, 1968; Poore & Wilson 1993; Rex et al. 1993), and for pelagic taxa (Angel 1997; Pierrot-Bults 1997). Nevertheless, many studies have shown a deviation from the general LDG for the shallow-water marine fauna (Kendall & Aschan 1993; Boucher & Lambshead 1995). Furthermore, in the southern hemisphere the evidence of a latitudinal gradient of decreasing richness from the tropics to Antarctica is less convincing than in the northern hemisphere (Clarke 1992; Poore & Wilson 1993; Crame 2000). Recently, Kinlock et al. (2018) revisited the challenge of synthesizing individual LDGs and indicated that the phenomenon is not ubiquitous among habitats of the marine realm. More precisely, they indicated that the phenomenon is non-significant in the benthic habitat. However, Menegotto et al. (2019), in their comment on Kinlock et al. (2018), suggest that the marine habitat categories used by them (i.e., benthic, coral reefs, coastal, open ocean) are not independent and that reclassifying the studies significantly alters one of their main results. By assigning the studies into benthic and pelagic categories, and additionally into coastal or oceanic zones, they show that non-ambiguous, evolutionarily meaningful marine habitats display a significant latitudinal decline in species richness. Thus, there is no convincing evidence of a latitudinal cline across all taxa in the sea comparable to that seen on land (Clarke 1992; Clarke & Crame 1997).

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

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

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

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

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

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

2. Materials and methods *Study sites*

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

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

2.2. Data sources

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

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

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

2.3. Biological data

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

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

2.4. Data analysis

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

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

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

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

3. Results

3.1. Checklist

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

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

3.2. Species composition and taxonomic diversity

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

3). Sampling effort showed a wide variability among the studied sites, with the maximal value in Moulay Bousselham lagoon and the minimum in Loukkos estuary (Table 4). With the exception of average phylogenetic diversity (Φ+) and variation in taxonomic distinctness (Λ+), all the other indices showed significant dependence with the sampling effort ($p<0.05$). Moreover, all the taxonomic indices were significantly ($p<0.05$) related to species richness except the average taxonomic distinctness (Δ+). In the majority of the SECS, both average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (Λ+) were within the 95% confidence funnel ($p\geq0.05$). Only the Oum Rbia and the Sebou estuaries as well as the Khnifiss lagoon appeared out of the confidence funnels (Fig. 3).

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

3.3. Macrobenthic assemblages' affinity

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

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

Through the DistLM analysis, only the SECS-type set of predictor variables had a significant relationship (type-estuary and type-lagoon) with species-derived multivariate cloud ($p<0.01$), explaining 27% of the total variation. However, the best model obtained through the DistLM procedure included height variables (Type-estuary, Type-lagoon, Type-bay, Province-Atlantic Surface, m-Temp, m-Sal and M-Sal) as predictors of benthic macrofauna composition, explaining 33% of the total variation (Adjusted R^2=0.33). When transposed to the dbRDA plot, the first two axes captured nearly 62% of the variability in the fitted model and 47% of the total variation in the data cloud (Fig. 6). Axis 1 (representing 20% of total variation) was negatively correlated to Type-estuary (r = -0.58) and to M-Sal (r = -0.52). Axis 2 (representing 14% of total variation) was negatively correlated to Surface (r = -0.53). The axis 3 (representing 13% of total variation) was negatively correlated to Province-Atl (r = -0.52) and Type-bay (r = -0.55).

3.4. Gaps and knowledge gained

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

4. Discussion

Checklists of marine species at regional scale have multiple uses. In addition to offering comparative facts for biodiversity studies, they serve as a crucial device in spotting and delimiting regions in need of protection, inferring the capacity effect of anthropogenic interest, assessing the complexity of organic communities, and estimating the provision of dwelling resources (Hendrickx and Harvey, 1999).

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

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

Patterns in diversity are often related to latitude, a phenomenon known as the latitudinal diversity gradient (LDG), whereby a decrease with increasing latitude is found (Roy et al., 1998; Rex et al., 2000; Attrill et al., 2001; Willig et al., 2003; Hillebrand, 2004). Several hypotheses for the underlying causes for such pattern are suggested, yet none of them is solely sufficiently convincing (Willig et al., 2003; Hillebrand, 2004), although solar energy input (and for the marine territory, the sea surface temperature as its proxy) is most often mentioned as the main acting principle (Rohde, 1992; Roy et al., 1998). Species richness is the most elementary, easy to interpret and widely used measure of biodiversity (e.g. Dornelas et al., 2014). It has been shown to follow a – generally unimodal – large-scale (>45°) latitudinal gradient for marine benthic invertebrates with a peak in equatorial regions (Chaudhary et al., 2016). In contrast to the general LDG pattern, our results showed that species richness and taxonomic diversity indices showed no relationship with latitude. Deviations from the general LDG pattern have also been reported before for European marine benthos by Renaud et al. (2009) who found no or weakly positive relationships. The explanation for this kind of diverting trend is that the impact of local variation in environmental factors is stronger than that of latitude related factors (Gaston, 2000; Renaud et al., 2009). Marine diversity might not follow a strict latitudinal gradient as the drivers of marine diversity themselves are not usually correlated with latitude (Piacenza et al., 2015).

In terms of assemblages composition, the best multivariate model, explaining 33% of the total variation observed in benthic assemblages, included 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) as predictors of benthic macrofauna composition in the Moroccan SECS. Such differences in benthic macrofaunal composition across a scale could result from the fact that each ecosystem has its own specific characteristics, which implies an individualistic approach to ecosystem ecology. Indeed, all ecosystems are subject to climatic and environmental forces and it is assumed that their variations induce a response from communities (Möllmann and Diekmann, 2012). The diversity and distribution of organisms can be influenced by the stochastic, ecological and evolutionary processes at local and regional scales (Hubbell, 2001), the limits of dispersion and recruitment of macroinvertebrate taxa (Hurtt & Pacala, 1995), the structural heterogeneity of the transitional waters (Basset & Abbiati, 2004) and the consequent selection of macroinvertebrate taxa according to their functional traits and niche needs (MacArthur, 1970).

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

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

5. Conclusion

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

Acknowledgements

Data for the Tahaddart estuay were obtained in the framework of EU funded WADI Project. Those of the Dakhla bay and the Khnifiss lagoon were partially obtained in the framework of the

Saharian wetlands of Morocco. The authors are indebted to two anonymous reviewers for their kind and helpful contributions.

Authors' Contributions

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 Benhousssa:** 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.

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Table 1

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

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

Table 2

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

Sites	**Sampling effort**	**S**	**Δ^+**	**$S\Delta^+$**	**Λ^+**	**Φ^+**	**$S\Phi^+$**
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

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

Source	*df*	MS	Pseudo-F	P (perm)	*df*	MS	Pseudo-F	P (perm)
		Species richness (S)				***Taxonomic distinctness (Δ+)***		
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			
		Total taxonomic distinctness (SΔ+)				***Variation in taxonomic distinctness (Λ^+)***		
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			
		Average phylogenetic diversity (Φ+)				***Total phylogenetic diversity ($S\Phi^+$)***		
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			

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

	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

Figure Captions:

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

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

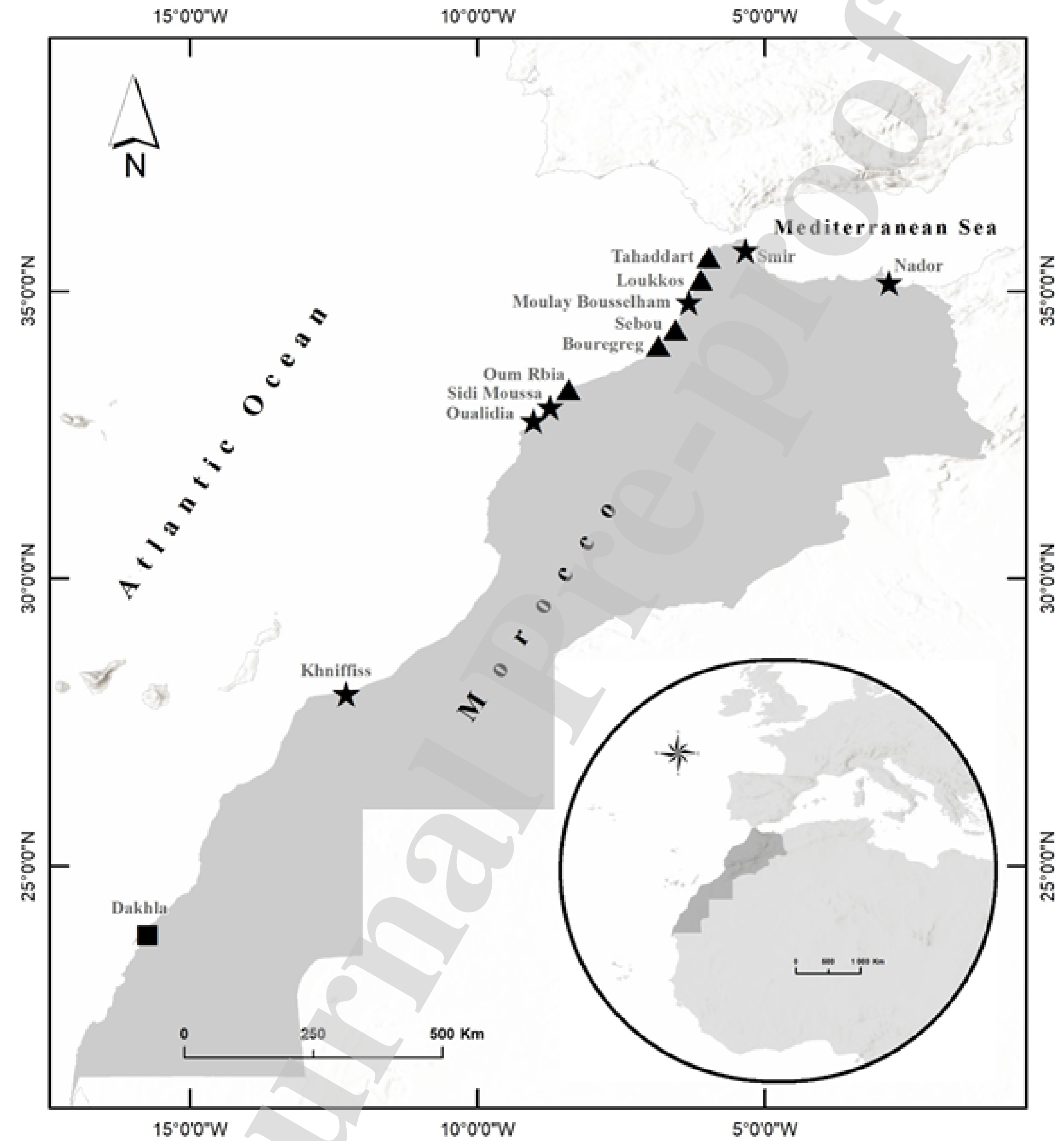
Figure 3. Confidence funnel (mean and 95% confidence interval) of the variation in taxonomic distinctness (A) and taxonomic distinctness (B) in the Moroccan Semi-enclosed coastal systems. NA: Nador. SM: Smir. TA: Tahaddart. LO: Loukkos. MB: Moulay Bousselham. SE: Sebou. BR: Bouregreg. OR: Oum Rbia. SI: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

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

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

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

768 **Figure 1**



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773 **Figure 2**

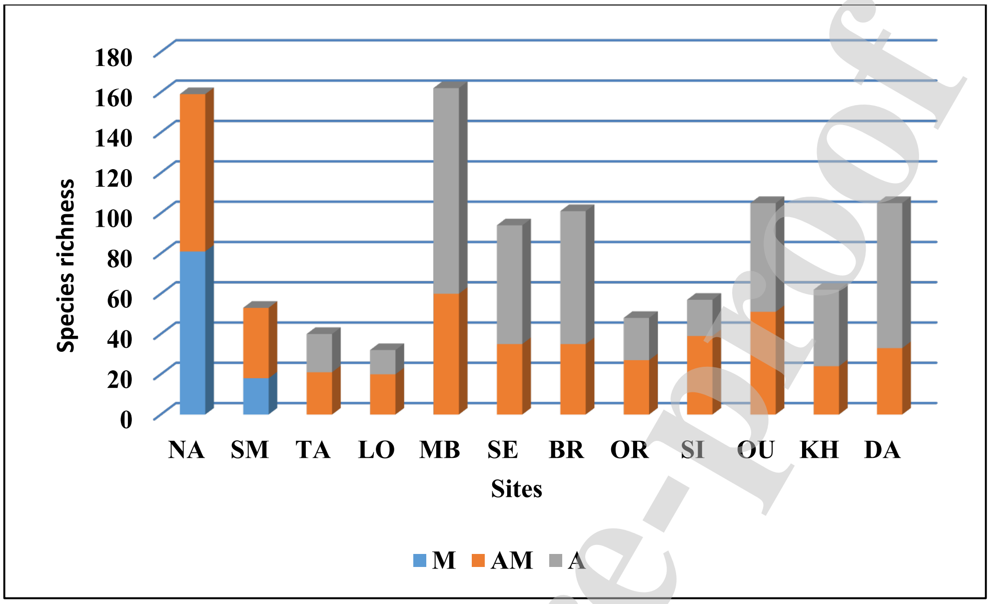
774 

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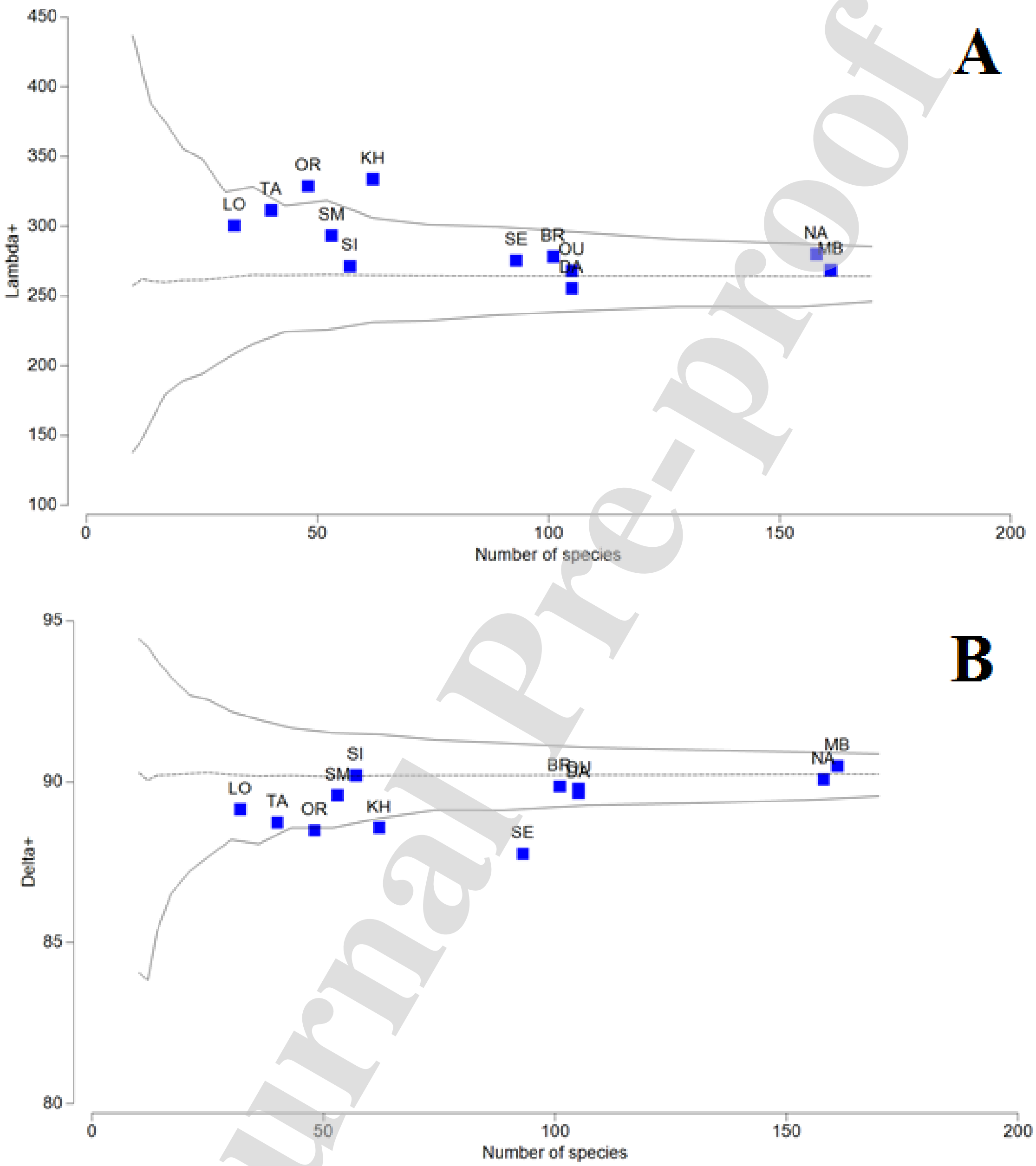
Figure 3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Lambda+
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300
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200
150
100
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50
100
150
200
Number of species
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TA
OR
KH
SM
SI
SE
BR
OU
DA
NA
MB
B
Delta+
95
90
85
80
0
50
100
150
200
Number of species
LO
TA
OR
SM
SI
KH
SE
BR
OU
DA
NA
MB

Figure 4

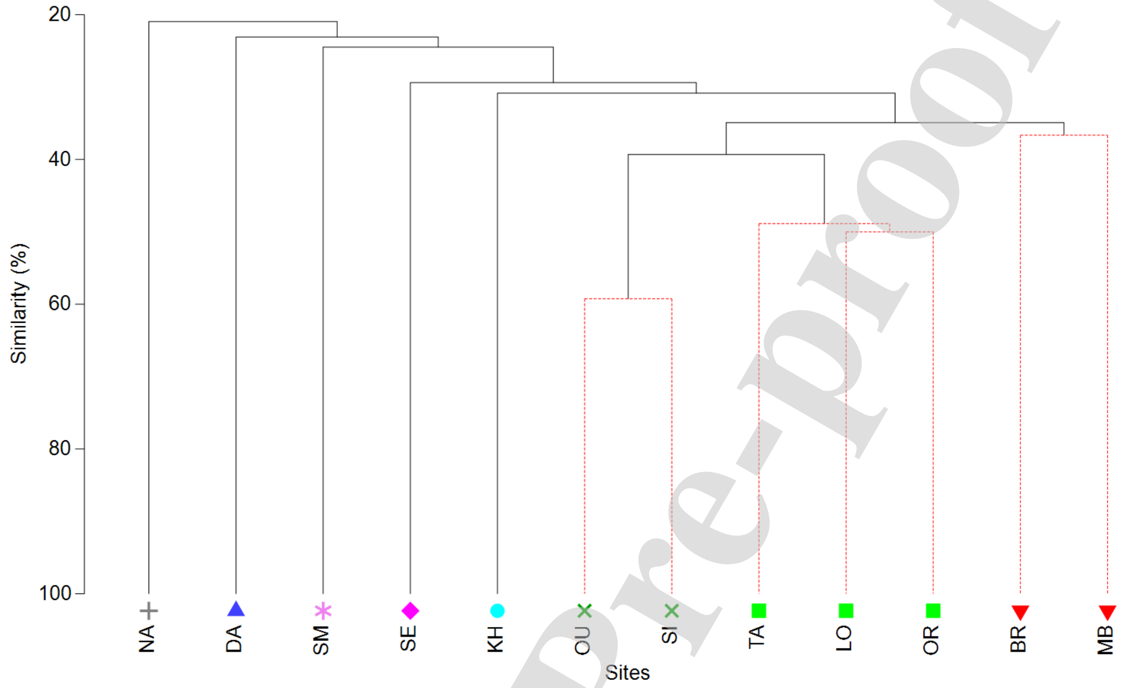

Similarity (%)
20
40
60
80
100
NA
DA
SM
SE
KH
OU
SI
TA
LO
OR
BR
MB
Sites

Figure 5

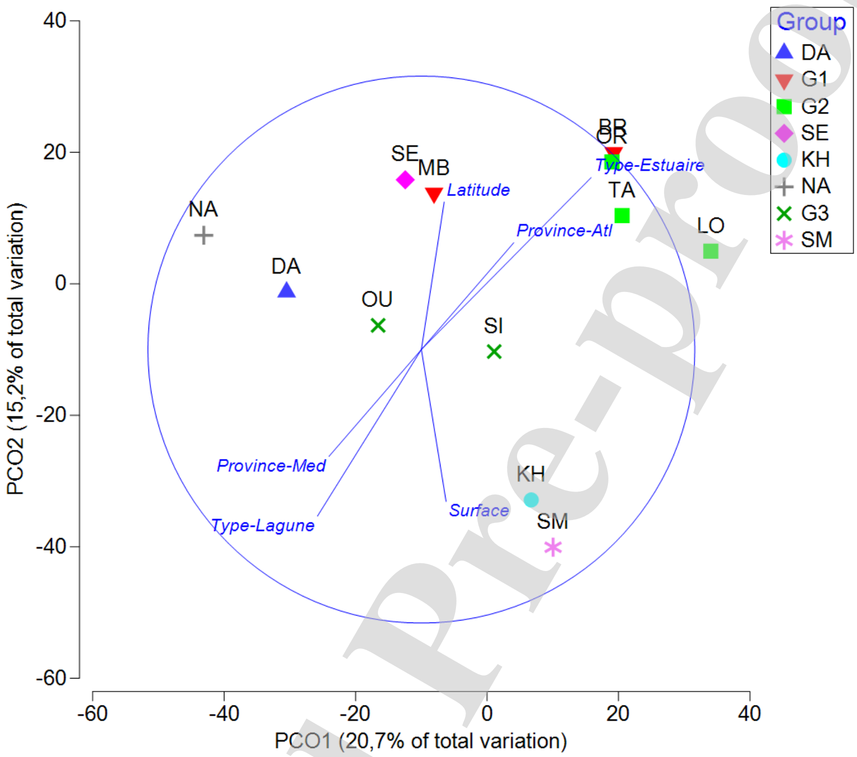
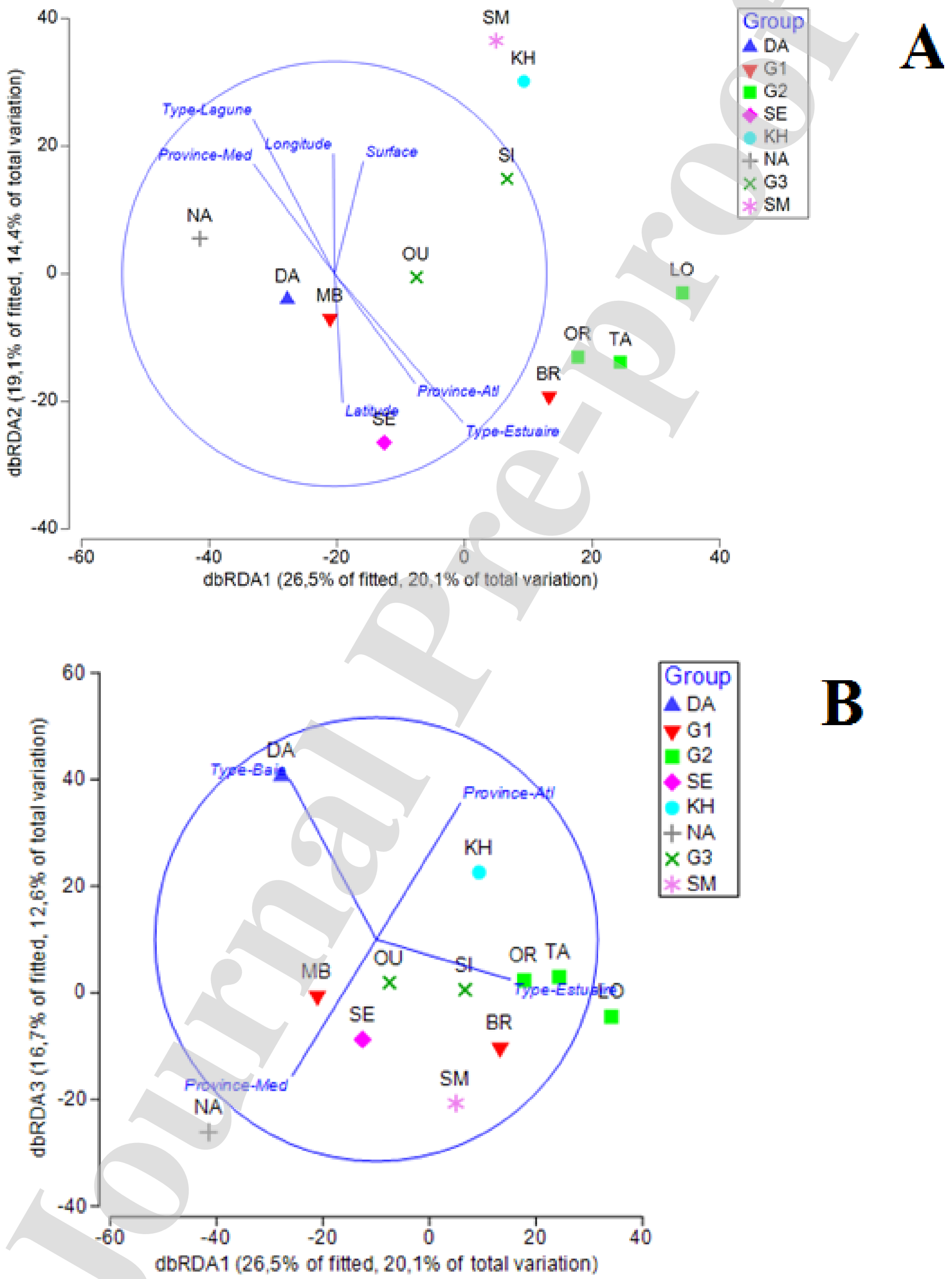

Group
DA
G1
G2
SE
KH
NA
G3
SM
NA
DA
OU
SE
MB
SI
BR
OR
TA
LO
KH
SM
Latitude
Type-Estuaire
Province-Atl
Province-Med
Type-Lagune
Surface
PCO2 (15,2% of total variation)
PCO1 (20,7% of total variation)
40
20
0
-20
-40
-60
-60
-40
-20
0
20
40

Figure 6


A
Group
DA
G1
G2
SE
KH
NA
G3
SM
Type-Lagune
Province-Med
Longitude
Surface
Province-Atl
Latitude
Type-Estuaire
dbRDA1 (26,5% of fitted, 20,1% of total variation)
dbRDA2 (19,1% of fitted, 14,4% of total variation)
B
Type-Baie
Province-Atl
Province-Med
Type-Estuaire
dbRDA1 (26,5% of fitted, 20,1% of total variation)
dbRDA3 (16,7% of fitted, 12,6% of total variation)

- 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 Benhousssa:** 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