Large-scale citizen science-based survey reveals impact of anthropogenic disturbances on gastropod communities of the North-East Atlantic rocky shores

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Graphical Abstract

Biological data

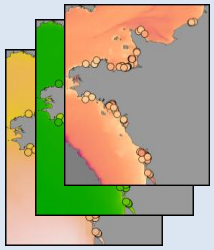
Citizen Science Program
BioLit – ABB



Sampling in intertidal seaweed canopies
5 shore levels investigated
Abundances of 14 gastropod taxa monitored
53 sites across 1000 km of NE Atlantic coast

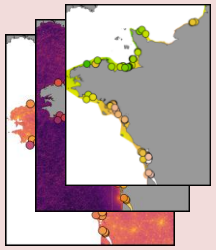
Environmental data

« natural environment » descriptors



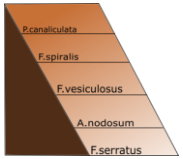
SST, Salinity, Chloa, Wave exposure …

Anthropogenic related processe descriptors



nutrients, suspended matter…

Large- scale



+



Seaweed belts - Shore levels

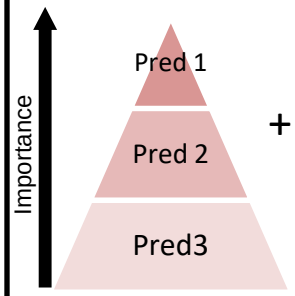
Canopy cover

Small-scale

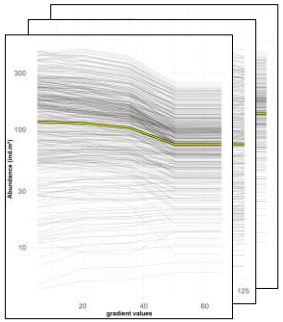
10 X 10 kfolds Crossvalidation

RF Models

Community and individual taxa responses



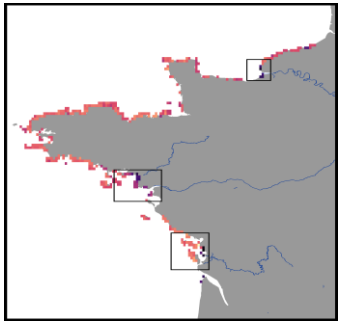
+



Variable importance

Response curves

Predicted mean spatial variability



NE Atlantic Rocky-shore community predictions

Main Results

- The Influence of small > large scale environmental descriptors
- Anthropogenic related processes highly Impact the intertidal gastropod community
- Responses to environmental perturbations are taxa-dependant
- Anthropogenic disturbances are carried by large river estuaries

Highlights:

- Rocky-shore are subjected to multiple stressors acting at different spatial scales
- Gastropod communities were investigated using a citizen-science scheme
- The relative importance of small/large-scale variables was evaluated with RF models
- Anthropogenic stressors alter the gastropod communities at large scale
- Citizen-science programs represent powerful tools in the context of bioindication

Manuscript (double-spaced and continuously LINE and PAGE numbered)
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Abstract

Rocky-shores are among the most threatened coastal habitats by human pressures. While rocky-shore communities have been increasingly used to evaluate local anthropogenic perturbations such as water eutrophication, large-scale variability in relation to both natural and anthropogenic stressors was poorly assessed. Here, using a Random Forest modelling approach applied on citizen science-based data, we assessed the relative impact of both small- and large-scale conditions (including natural and anthropogenic stressors) on intertidal gastropod communities as well as taxa-specific gastropod abundances over more than 1000 km of the North-East Atlantic coast. Our results demonstrate that small-scale conditions (*i.e.* within shore) dominate the shaping of gastropod communities. However, this community response is mainly driven by a taxa-specific affinity. Our work also highlights that inorganic nutrient concentrations and suspended matter related to large river inputs are the main drivers among large-scale predictors, impacting the gastropod communities by depleting both taxon abundances and richness. According to models, the expected decline in abundance of the yet most abundant taxa (*Steromphala umbilicalis*, *Patella* spp., *Steromphala pennanti* and *Phorcus lineatus*) is estimated to be between 65% and 85%, while the common periwinkle *Littorina littorea* was the only taxon being favoured by high anthropogenic activities. Such results provide relevant insights in the context of ever-increasing needs for bioindicators of coastal ecosystems. Finally, this work sheds light on the value of a citizen science program resulting from a consultation between professional and citizen volunteers as a useful and efficient tool to investigate large-scale processes.

Keywords: intertidal gastropod community, anthropogenic stressors, citizen science, scale-dependant processes, brown macroalgae canopy

Rocky-shores, located at the interface between land and sea, are particular habitats concentrating numerous environmental stressors on a very limited surface. As a result, they were considered for a long time as a “natural laboratory” to explore biological and ecological issues (Helmuth et al., 2006; Levin, 1992; Paine, 2010). Owing to the relative accessibility of rocky-shores, variability of the related intertidal communities were extensively documented since the late nineteenth century by marine biologists and naturalists (Benson, 2002; Mieszkowska, 2016). Former studies mainly focused on fine-scale patterns of variability (10s cm to 10s m) such as the vertical distribution pattern (the so-called “unidirectional zonation”) resulting from physical and biological stress gradients closely related to tide alternations, wave exposure and biotic interactions (see for instance Little et al. (2010)). While vertical zonation, and other fine-scale patterns (such as ‘patchiness’) represent major and ubiquitous sources of variability for rocky-shore communities (Barnes and Hughes, 1999; Little et al., 2010), other studies pointed out the needs to consider variability at larger spatial scales (from 100s m to 1000s km) as a response to different and entangled environmental processes (*e.g.* Benedetti-Cecchi (2001)). Over the years, there was a paradigmatic shift in the scale-dependant signals recognition from noise to a mean for assessing processes across scales (Cruz-Motta et al., 2010; Dal Bello et al., 2017). Exploring multi-scale variability of species distribution and abundance are important to identify and hierarchize the impact of very broad range of processes on structure assemblage (Levin, 1992; Dungan et al., 2002; Fraschetti et al., 2005).

In the context of increased anthropogenic pressures, of which impact on coastal systems are increasingly being recognised (Halpern et al., 2015, 2008), rocky-shores are described as one of the most threatened coastal habitat (Halpern et al., 2007). These concerns led to the development of various indicators to address water or environmental quality status as

50 required respectively by the Water Framework Directive (WFD; Directive 2000/60/EC) and
51 the Marine Strategy Framework Directive (MSFD; 2008/56 EC) for European marine waters
52 (Borja et al., 2008). Small-scale experimental investigations on the effects of anthropogenic
53 disturbances on rocky shore communities yielded mixed results depending on sites and taxa
54 (Crowe et al., 2000). On the whole, intertidal communities such as macroalgae (Neto et al.,
55 2012; Strain et al., 2014; Ar Gall et al., 2016) or, to a lesser extent, molluscan assemblages
56 (Espinosa et al., 2007; Wells et al., 2007; Atalah, 2012) were considered as cost-effective
57 tools to monitor anthropogenic impact on coastal zones (Vinagre, 2016a). Consequently,
58 numerous investigations have reported local intertidal community variations as a response
59 to additive and synergistic impacts from anthropogenic stressors such as nutrient
60 enrichment (Atalah, 2012), sediment deposition (Airoldi, 2007) and even trampling (Micheli
61 et al., 2016) through the comparison between pristine and impacted sites (Kraufvelin et al.,
62 2006; Atalah and Crowe, 2010). However, whether and to what extent human-related
63 stressors shape large-scale rocky-shore assemblages, where many processes are entangled,
64 is still poorly explored (Crowe et al., 2000).
65 Canopy-forming brown macroalgae (*e.g.* Fucal algae) represent a structuring and remarkable
66 element of these sheltered hard-substratum intertidal ecosystems of temperate regions (van
67 den Hoek, 1975). As bioengineer species, the high diversity of seaweed provides food but
68 also protection from desiccation, temperature, wave action and predation for numerous
69 species (Chapman, 1995; Mieszkowska et al., 2013; Watt and Scrosati, 2013a). Gastropods
70 represent a dominant and a key structuring group associated with these intertidal habitats.
71 For instance, some gastropods were shown to benefit from a shelter-effect provided by the
72 macroalgae canopy, in decreasing local temperature and evaporation as compared to
73 neighbour bare rock (Bertness et al., 1999), thus expanding their spatial distribution

74 (Burrows et al., 2020). In turn, gastropods grazers structured seaweed canopies, controlling
75 both cover and diversity of macroalgae assemblages (Bertness et al., 1999) as well as the
76 grazing pressure from other invertebrates (Pavia and Toth, 2000). Therefore, gastropod
77 species, as other sedentary macroinvertebrates, are considered as taxa of interest to explore
78 the impacts of environmental change on intertidal ecosystems in the context of increasing
79 anthropogenic stressors (Atalah, 2012) and climate change (Mieszkowska et al., 2007).
80 Regarding the global decline of canopy macroalgae species (Beck and Airoldi, 2007; Álvarez-
81 Losada et al., 2020), so far only few studies have attempted to investigate large-scale (*e.g.*
82 regional and global) spatial variations of intertidal gastropod communities (Schoch et al.,
83 2006; Dal Bello et al., 2017) and in relation with anthropogenic pressures (Cruz-Motta et al.,
84 2010; Miloslavich et al., 2013). Counterintuitively, the latter studies found a weak
85 relationship between gastropod diversity and anthropogenic variables at large-scales (*i.e.* at
86 Large Marine Ecosystems 'LME' and global scales). According to authors, this could be
87 explained, at least partially, by the monitoring process (Miloslavich et al., 2013). Indeed,
88 despite the recognized value of large-scale monitoring for reporting on the status and trends
89 of biodiversity, the inherent time and financial costs remain one of the main limitations of
90 such program implementation (Caughlan and Oakley, 2001; Pereira and David Cooper,
91 2006).

92 Recent studies have demonstrated how citizen science schemes can be used to address
93 ecological issues over large-scales (Chandler et al., 2017), for instance to improve
94 conservation biogeography (Devictor et al., 2010), test macroecological theories (Vye et al.,
95 2020) or for invasive species monitoring (Lehtiniemi et al., 2020). Although its definition
96 remains unclear in the literature, citizen science involves the contribution of non-scientist
97 volunteers to address scientific issues, often through data collection (Kullenberg and

98 Kasperowski, 2016). As a result, when associated with appropriate protocols and trainings,
99 citizen-science can provide valuable sources of data, whose quality may be equivalent to
100 professional scientific collection form (van der Velde et al., 2017), but whose quantity and at
101 spatial scales generally not affordable by the latest (Tulloch et al., 2013; Theobald et al.,
102 2015). Started in 2012 the " Algues-Brunes et Bigorneaux " sighting scheme (hereafter
103 "ABB") from the BioLit program from the French NGO Planète-Mer
104 (https://www.planetemer.org/actions/biolit-et-biolit-junior) focuses on gastropod
105 communities associated macroalgae canopy, by monitoring the co-occurrence of seaweeds
106 and their gastropod inhabitants. As such, the ABB protocol has the potential to account for
107 local habitat features (small-scale environment) while taking into account large-scale
108 variability. Here, we used this citizen science-based dataset to explore key drivers of
109 variability in gastropod communities associated with canopy-forming brown macroalgae
110 from North-Eastern (NE) Atlantic rocky-shores. More specifically, using an Ecological Niche
111 Modelling (ENM) method on abundance dataset, our aim was threefold: 1) to explore the
112 relative importance of local gradients linked to habitat-forming macroalgae and larger scale
113 processes, including anthropogenic processes, on gastropod communities, 2) to investigate
114 the large-scale and temporal variability on abundances and taxonomic richness of
115 gastropods across a transitional biogeographic area and 3) to evaluate species-specific
116 responses of key gastropod taxa to "natural" and anthropogenic stressors.

117

118

Material and Methods

Study area

From September 2012 to December 2020 (see details in Fig. SB), the AAB protocol was applied to 55 rocky-shore sites spread over more than 1000 km, including 500 km of latitude, along the French NE Atlantic coast (extending from 45° N to 50° N and from -4° E to 1° W). According to the 'Marine Ecoregion Of the World' (MEOW) biogeographic system (Spalding et al., 2007), the study sites covered 2 different provinces (Northern European Sea and Lusitanian), 3 ecoregions (North Sea, Celtic Sea and South European Atlantic Shelf) (Fig. 1) defining areas characterized by both specific physico-chemical features and biological communities (Dinter, 2001; Ramos et al., 2012). More particularly, the Brittany coast represented a biogeographical transition zone characterized by a gradual change in water temperature, tidal range and wave exposure (Ramos et al., 2012; Gallon et al., 2014).

Data Collection

The ABB protocol focused on 16 of the most common gastropod taxa in the NE Atlantic coast, associated with canopy-forming brown macroalgae and for whom the identification is relatively easy for a non-expert public (see details in Fig. SA). However, among these taxa, some species from the *Littorina* genus are known to exhibit significant morphological variations (as for *L. saxatilis* often confused with *L. compressa*) or a lack reliable morphological features to distinguish sister species (*i.e. L. fabalis* and *L. obtusata*). This represents an important source of bias in identification, even for experts. Consequently, we retrospectively decided to group abundances of these pairs into 2 species complexes, namely *L. saxatilis/L. compressa* and *L. fabalis/L. obtusata*. Prior to sampling sessions, each

141 volunteer received a minimum of 4 hours of formation in the use of the protocol and taxa
142 identification. In addition, during sampling session, beginner volunteers were assisted by
143 expert naturalists. Then, taxa abundances and distributions were obtained at low tide using
144 randomly placed 0.1 m^2 quadrats. When quadrats fell on complex rocky fields including
145 crevices of fissures or puddles, participants were asked to reiterate the throw to limit
146 influence of microhabitats. According to the protocol, sampling was only performed in the
147 presence of main temperate intertidal canopy-forming brown macroalgae species. These
148 seaweeds were known to exhibit a clear vertical zonation pattern (*i.e.* the sequence of
149 *Pelvetia canaliculata*, *Fucus spiralis*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Fucus*
150 *serratus*, from the top to the bottom of the mediolittoral level) (Schonbeck and Norton,
151 1978; Johnson et al., 1998). Therefore, in order to describe small-scale conditions, the
152 volunteers indicated for each sample the nature of the dominant brown macroalgae species
153 (hereafter 'seaweed belt') and provided a visual estimate of canopy cover using an ordinal
154 scale (0-5; 5-25; 25-50; 50-75; 75-100% of cover). Moreover, to avoid misidentification, the
155 entire sample and each different taxon identified within the sample were photographed.
156 Each sample and taxon identified was then visually validated by experimented naturalists.

157 Prior to analysis, we applied a percentile-based outlier removal method to improve reliability
158 of the data as detailed by Li et al. (2020). For each shore level (defined by the nature of the
159 dominant seaweed species), observations corresponding to the top 1% of total abundance
160 were then removed from the initial dataset (2337 samples). In addition, to reduce influence
161 of small-scale horizontal variability (such as patchiness), taxa abundances and canopy cover
162 estimates were averaged according to the site, date and the shore level. Only samples with a
163 minimum of 2 replicates were considered for further investigations (final dataset of 407
164 averaged samples).

165 **Environmental predictors**

166 Descriptors of small-scale conditions from field observations were coupled with large-scale
167 suited environmental variables to explore both local and larger scale controls on rocky-shore
168 communities (Table 1). Large-scale processes were investigated using mean annual and
169 range of Sea Surface Temperature (SST.M and SST.r), temperature of the coldest and
170 warmest month (SST.cold and SST.warm), mean and standard deviation of coastal Salinity
171 (Sal and Sal.sd), mean and standard deviation of chlorophyll a concentrations (Chloa and
172 chloa.sd), bathymetry, mean annual Kinetic Energy due to Waves (WKE) values and the
173 mean tide amplitude (TAmp) which was defined as the difference between high and low tide
174 during spring tide. We also added predictors related to anthropogenic activities such as
175 mean and standard deviation of inorganic nitrogen ($N\text{-}NO_2^-$ + $N\text{-}NO_3^-$) concentrations (Nit and
176 Nit.sd), mean and standard-deviation of total suspended matter (TSM.M and TSM.sd) and
177 coastal population density estimation (Pop) as proxies of eutrophication, sediment
178 deposition and direct anthropogenic pressure on coastal ecosystems, respectively.

179 For inorganic nitrogen, we produced an interpolated raster layer from monthly data
180 collected between 2012 and 2020 within the framework of the SOMLIT ("Service
181 d'Observation en Milieu LITtoral") program from the INSU/CNRS (http://somlit.fr) and from
182 the REPHY ("REseau de surveillance du PHYtoplancton et des phycotoxines") program from
183 Ifremer ("French Research Institute for the Sustainable Exploitation of the Sea"), which are
184 both national networks monitoring the hydrological parameters of French waters. Only non-
185 estuarine stations completing a minimum of 3 years of monitoring were considered in order
186 to reduce bias from sampling effort and seasonality effect. Prior to interpolations, time
187 series from each selected station were visually inspected to evaluate presence of abrupt

change in phenological signal and suspicious data. Finally, a 1 km resolution layer of coastal waters was interpolated from mean and standard-deviation concentration values using an inverse distance weighting kriging method.

All environmental variables were regridded to a 1 km pixel resolution from their native resolution. Then, extraction at each sampling point was performed by averaging values using a buffer of 2 km to deal with the heterogeneity in predictor resolutions and the potential inaccuracies in the spatial localisation of sampled shores. In addition to environmental variables, temporal changes in taxa abundances and taxonomic richness were investigated by considering the 'season' (winter: January to March ; spring: April to June ; summer: July to September ; fall: October to December) and 'year' of each sampling session. We also included the number of replicates as predictor in the modelling step to explicitly account for the impact of sampling effort on mean abundances.

Modelling framework

Abundance distribution of each taxon, as well as total gastropod abundance (Tot_ab), and taxonomic richness (S) (hereafter 'response variables') were investigated using the Random Forest (RF) method (Breiman, 2001). RF is a supervised tree-based approach relying on a bootstrap-aggregative (bagging) scheme which aggregates predictions from multiple independent decision trees (weak learners) using a subset of the dataset at each iteration (Biau and Scornet, 2016). The RF is considered as a highly suitable method to address ecological issues such as taxon spatial occurrence and abundance distribution (Cutler et al., 2007; Hengl et al., 2018), because it allows to identify complex relationship between the response variable and numerous predictors and is poorly sensitive to multicollinearity as well as outliers or missing value (Li and Wang, 2013). Moreover, the RF algorithm consistently outperforms other classical regression methods (Cutler et al., 2007; Li and Wang, 2013; Prasad et al., 2006), even for rare or occasional taxa (Mi et al., 2017).

In the RF approach, two main parameters can be tuned to improve predictions: 'mtry' and the 'ntrees', where 'mtry' characterizes the number of predictors selected at each tree split, and 'ntrees' is the number of trees produced. For each model, 500 trees were established as sufficient to stabilize the error rate in most of cases in a preliminary tests while the optimal 'mtry' parameter was assessed using a tuning grid as implemented in the 'caret' R package (Kuhn, 2008). The setting of the 'mtry' parameter was obtained using the overall performance of each model after 10 folds cross-validation repeated 10 times. This procedure randomly split the response variable into training (90%) and testing datasets (remaining 10%). Once the models were trained on the corresponding dataset, the performance was assessed using R^2 and the "Root Mean Square Error" (RMSE), which are two goodness-of-fit measures summarizing variations between observed and predicted values on the tested

dataset. Additionally, the performance was assessed by plotting predictions as a function of observations to identify model limitations (Fig. S4).

Finally, RF also allowed to quantify and rank the importance of each predictor (hereafter 'VarImp'), by computing the loss of performance associated with random permutations of predictors. Furthermore, the interpretability of VarImp was supplemented by performing Partial dependence Plot (PdP) and its Individual Conditional Expectations plot (ICE) produced with the 'ime' R package (Molnar et al., 2018). Both PdP and ICE aim to examine how a particular predictor impacts the response variable. While PdP provides an averaged model prediction, ICE allows the response variability to be explored by modulating values from other predictors. In the present case, predictions were performed for each particular shore level (seaweed belt).

Collinearity and spatial autocorrelation

To minimize collinearity (Dormann et al., 2013) while maintaining model performances, interpretability and comparison between taxa, predictor selection was performed following a methodology inspired by Georgian et al. (2019). Predictor variables were first clustered based on Pearson's correlation to identify highly correlated clusters (Fig. S3). Subsequently, we produced a RF model and assessed the variable importance for each predictor. Finally, among a cluster of correlated variables ($r > 0.8$), we retained the ones with the highest performance values for at least one taxon and with higher ecological relevance. Thus, despite their high correlation, both Total Suspended Matter and inorganic nitrogen concentrations were kept as they showed high variability in VarImp values according to the response variable (Fig. S3). We also computed the Variance Inflation Factor (VIF) to detect collinearity in selected predictors. Predictors were finally included in models if overall VIF values were lower than a tolerant threshold of 10. As a result, SSTwarm and SST.r were not included in the final models as they tended to hugely inflate the VIF value.

Spatial autocorrelation (Legendre, 1993) was evaluated in residuals of model predictions for each response variable using Moran's I test, which compares correlation measures between neighbouring error values with a null distribution using 999 permutations (Moran, 1948). Moran's I test was performed using the 'spdep' R package (Bivand and Wong, 2018). As predictions were made for different shore levels at the same station, the Moran'I test was only computed for the seaweed belt characterizing the more suitable shore level of each response variable.

Spatial variability of gastropod community at large scale

Response variables were predicted for the whole French Atlantic rocky shore (from 45 to 51° N; from 5°W to 2°E), but only for models considered as sufficiently robust (i.e. when R^2>0.35). To delineate rocky shores, high resolution coastline was first extracted from the Global Administration Areas (GADM) using the 'raster' R package (Hijmans, 2020). Then, the nature of the substrate was extracted from a 1:500 000 resolution composite raster layer from The Naval Hydrographic and Oceanographic Service (SHOM, 2020) for each coastline point and rasterized into a 1 km grid cell resolution. Pixels with a 'Rock' feature were selected to distinguish rocky from sandy and muddy shores. Large-scale predictor values were then extracted for selected each pixel. Small-scale predictor variables were fixed (*i.e.* seaweed belt and canopy cover class) for each response variable with the values characterizing the more suitable modality according to the models (Table 2). Spearman's correlation was then performed between predictions to compare the large-scale spatial variability of each response variable.

Results

Model performances

According to the cross-validation, the best models showed high performances (R^2>0.35) for dominant taxa as well as Tot_ab and S (Table 2). Among these response variables, the highest performance was found for the common and abundant taxon *Steromphala umbilicalis* (R^2=0.67±0.1; RMSE=1.11± 0.2) while *L. littorea* showed a lower relative accuracy of predictions (R^2=0.37 ± 0.1; RMSE= 1.05 ± 0.1). Abundance of rare taxa such as *Nucella lapillus* (R^2=0.29 ± 0.2; RMSE=0.92 ± 0.2), *Ocenebra erinaceus* (R^2=0.23 ± 0.2; RMSE=0.42 ± 0.1) and *Gibbula magus* (R^2=0.29 ± 0.1; RMSE=0.13 ± 0.1) were inadequately modelled, especially for *Ocenebra inornatus* or *Tritia reticulata* (R^2<0.1). Moran's I test applied on robust models did not identify any significant spatial autocorrelation (Table 2).

Variable importance and interpretation

For most of response variables, small-scale predictors showed higher variable importance than large-scale predictors (Table 3). The nature of the seaweed belt (shore level) was generally a good predictor for gastropod community. Indeed, it represents a critical predictor (rank 1) for *S. umbilicalis*, *Steromphala pennanti*, *L. fabalis/L. obtusata* and *L. saxatilis/L. compressa* abundances as well as for Tot_ab (rank2) and S (rank 1). Specifically, the higher bound of the shore (characterized by *P. canaliculata*) turned out to be highly discriminating to predict most of gastropod abundances. Only *S. pennanti* and *S. cineraria* abundances showed important affinity with lower bound (*F. serratus*) (Fig. 2). Moreover, the models captured the relative shore level preference for each taxon as illustrated by the PdP. *Steromphala umbilicalis*, *L. fabalis/L. obtusata*, *Patella* spp., *P. lineatus* and *L. littorea* showed a more generalist behaviour with abundances predicted for several intermediate seaweed belts, as compared to *S. pennanti* and *L. saxatilis/L. compressa*, which were mainly associated with an unique one (*F. serratus* and *P. canaliculata*, respectively).

The local estimated canopy cover also represented an important predictor for *P. lineatus, L. saxatilis/L. compressa, S. pennanti* (rank 2) and *Patella* spp., *L. fabalis/L. obtusata* (rank 3), and to another extent for *S. umbilicalis* (rank 4)*,* but PdP and ICE highlighted a taxa-specific response with the canopy cover (Fig. 2). The RF models predicted higher abundance in light cover (0-50%) for *P. lineatus* and *Patella* spp.*,* and in medium cover (25-75%) for *S. umbilicalis*, while *S. pennanti*, *L. fabalis/L. obtusata* and *L. saxatilis/L. compressa* were more abundant in dense seaweed canopies (50-100%).

The mean of total suspended matter and inorganic nitrogen concentrations were among the most important large-scale predictors for Tot_ab (rank 1 and 4, respectively) and S (rank 4

and 2, respectively) as well as for taxon (Fig. 2). The models predicted a clear negative impact of suspended matter on *S. umbilicalis* (rank 2), *Patella* spp. (rank 1) and *P. lineatus*, while *S. pennanti* (rank 3) was negatively impacted by inorganic nitrogen, especially in the *F. serratus* belt. More specifically, the mean loss of abundance associated with these stressors was estimated to be 65% for *Patella* spp., 70% for *S. umbilicalis*, and 85% for *S. pennanti.* Conversely, *L. littorea* (rank 4) abundance was the only taxon positively affected, albeit slightly (+25%) by increased inorganic nitrogen concentrations.

WKE also appeared to be an important predictor of *Patella* spp. (rank 1) and *P. lineatus* (rank 2) with a positive impact on abundances. While the importance of sampling effort logically increased as the taxa became rare (Fig. S5), it nevertheless represents an important predictor for relatively abundant taxa such as the complexes *L. saxatilis/L. compressa* (rank 3) and *L. fabalis/L. obtusata* (rank 4). Regarding the PdP and ICE, it turned out that around 10 replicates were necessary in most cases to correctly predict the abundance of dominant taxa, albeit not for *S. cineraria*. By contrast, predictors defining temporal scales (*i.e.* 'season' and 'year') displayed a lower importance among predictors, indicating low temporal variability of all response variables (Fig. S5).

Spatial abundance distributions

For robust models (R^2>0.35), predictions of spatial abundance distributions were generated along the NE Atlantic rocky shores. Taxonomic richness and total gastropod abundance exhibited overall similar spatial variations of predicted values (r=0.7) (Fig. 3) in which the lowest values were associated with areas subjected to inputs from the estuaries of major rivers: The Seine, the Vilaine, the Loire and the Charente. Among the predicted taxa *S. umbilicalis* showed the highest predicted abundances (from 3.7 to >100 ind.m^2) and *S.*

cineraria represented the less abundant species (from 1 to 5 ind.m²) of the mediolittoral zone (Fig. S6). According to the Pearson's correlation applied on taxa-specific spatial predictions, the pattern showed by the total abundance and the taxonomic richness was logically shared by the abundant *S. umbilicalis* (Tot_ab: r=0.91, p<0.001, S: r=0.76, p<0.001), *Patella* spp. (Tot_ab: r=0.75, p<0.001, S: r=0.43, p<0.001), *S. pennanti* (Tot_ab: r=0.45, p<0.001, S: r=0.28, p<0.001) and to some extent by *S. cineraria* (Tot_ab: r=0.29, p<0.001, S: r=0.34, p<0.001) and *P. lineatus* (S: r=0.4, p<0.001) (Fig. 4). Conversely, *L. littorea* showed a significant opposite pattern (Tot_ab: r=-0.37, p<0.001, S: r=-0.17, p=0.002), with highest abundance values (~7 ind.m^{-2}) predicted in southern rocky-shores and particularly near the Vilaine, the Loire and the Charente estuaries (Fig. S6). Finally, weak but significant correlations in spatial predicted values were found for species complexes *L. fabalis/L. obtusata* (Tot_ab: r=0.17, p=0.002, S: r=0.25, p<0.001) and *L. saxatilis/L. compressa* (Tot_ab: r=-0.12, p=0.03).

Discussion

Small-scale vs large-scale

Based on a citizen science scheme, this study provides a quantification of the relative importance of both local and regional scale processes on NE Atlantic mediolittoral gastropod communities. Our results reveal that small-scale conditions (*i.e.* the shore scale) have a greater impact than large-scale gradients on total abundance and taxonomic richness for most of investigated taxa. Particularly, the seaweed belt proxy of vertical zonation is the most critical factor in determining taxa abundance and diversity. While it was previously considered as an universal pattern (Barnes and Hughes, 1999), the relative importance of horizontal and vertical variations of intertidal rocky-shore community at large-spatial scale is still debated in the scientific community. Indeed, some authors argue that vertical variations have an equivalent or greater impact than horizontal ones at the site level (10s to 100s meters), but not at the shore and regional levels (from 100s m to 1000s km), where horizontal variability is superior in both NW Mediterranean sea (Benedetti-Cecchi, 2001) and NE Atlantic rocky-shores (Valdivia et al., 2011). These former studies were recently challenged by results demonstrating that vertical zonation is determinant even at the regional level in shaping species composition and richness along the Catalonian shoreline (NW Mediterranean sea) (Chappuis et al., 2014; Cefalì et al., 2019) but also along the NW Altantic and SE Pacific (Catalán et al., 2020). Here, our results strengthen these results on a 500 km latitudinal gradient along the NE Atlantic coast with a specific focus on gastropods communities associated with canopy habitat. Differences in the definition of the intertidal zone as well as the nature of communities considered in former studies can explain differences of results obtained in NE Atlantic rocky-shores. Our results identify the *Pelvetia canaliculata* belt, located at the limit of the supralittoral zone, as the main source of vertical

variability in both gastropod total abundance and taxonomic richness. By contrast, in Valdivia et al. (2011), authors have characterized the intertidal range using the *F. spiralis* belt as the upper boundary, thus omitting the upper belts which in our study represent an important part of the observed vertical variability.

Additionally, canopy cover also highly shapes the gastropod assemblage driven by an idiosyncratic taxa response. Through experimental studies, brown macroalgae canopy cover was shown to structure the temperate (Watt and Scrosati, 2013a) and sub-artic (Ørberg et al., 2018) intertidal communities by mediating the temperature, light and desiccation stresses caused by prolonged emergence but only at medium and high shore levels. As a result of this facilitation effect, higher canopy cover was associated with an increase of biomass and diversity (Watt and Scrosati, 2013a, 2013b). Our results on taxonomic richness only partially support this trend, probably due to the limited number of taxa involved. However, following the so-called "space-time" substitution paradigm (Pickett, 1989; Blois et al., 2013), taxa-specific responses bring new insights into how intertidal gastropod communities can shift in the context of macroalgae canopy regression (Airoldi et al., 2008; Álvarez-Losada et al., 2020). According to our model responses, a decrease of macroalgae canopy cover may promote *P. lineatus* and *Patella spp.* as dominating the communities by thriving abundance collapse of more sensitive species such as *S. pennanti*, *L. fabalis/L. obtusata* and, to a lesser extent, the abundant *S. umbilicalis,* which are all associated with higher macroalgae canopy cover. These predictions are in accordance with results obtained in a recent canopy regression experiment where authors showed that abundances of *P. lineatus* are negatively impacted by the *A. nodosum* cover as opposed to *L. obtusata* and *S. umbilicalis* ones (Pocklington et al., 2018). The absence of significant response observed for *L. littorea* in the cover regression experiment also supports the weak importance of the

canopy cover exhibited by our results. Furthermore, the antagonistic relation between limpets and the canopy cover highlighted by our model is well recognized as an observed pattern of temperate rocky-shore (Johnson et al., 1997; Jenkins et al., 1999a,1999b; Jenkins et al., 2004; Davies et al., 2007).

Large spatial scale processes

At large-scale, our findings reveal the overall dominant influence of both inorganic nitrogen and total suspended matter concentrations on gastropod spatial abundance distribution. These results contrast with environmental gradients frequently mentioned as shaping the intertidal community structure at regional and larger scale such as sea water temperature (Chapman, 1995; Burrows et al., 2008; Ramos et al., 2012; Mieszkowska et al., 2013), wave exposure (Burrows et al., 2008) as well as upwelling or salinity (Schoch et al., 2006). More specifically, our results do not attribute the large-scale variations of gastropod community to a biogeographical gradient induced by changes in water temperature. Located at the intersection of 3 coastal ecoregions (Spalding et al., 2007), the same area was however identified as a transitional zone for macroalgae distribution defining a boundary between colder and warmer temperate waters (Dauvin, 1997; Ramos et al., 2014). In the present study, the studied taxa exhibit a broad spatial distribution, as most of them are found from the North of the British waters to the Lusitanian coast (Hayward et al., 2005) (for details, see Fig. S1). Thus, this macroalgae transitional zone could represent the core of the thermal niche of most of the gastropod taxa considered in this study, where density variations induced by temperature are expected to be small. Furthermore, this apparent difference in driver processes may also be partially explained by the scope of these former studies in which anthropogenic related predictors were generally neglected (Sagarin et al., 2006). Finally, and in a consistent way, Kinetic Energy from Waves was found to be an important

predictor positively affecting taxa abundance associated with low brown macroalgae cover, namely *Patella* spp. and *P. lineatus*. This result highlights the overall consistency of our models since high canopy cover is favoured by sheltered shores (van den Hoek, 1975) where the fetch is expected to be lower than in exposed shores.

While both nutrient and suspended matter concentrations are related to the influence of large river plumes, they referred to two different anthropogenic stressor processes affecting the rocky shore community: the sedimentary reposition and eutrophication. As a consequence of anthropogenic activities and particularly through soil erosion, increase of sediment loads is pointed out as a major concern for hard substratum coastal communities (Airoldi, 2003), impacting both cover of brown algae such as *A. nodosum* (Airoldi, 2003) or *F. vesiculosus* (Eriksson and Johansson, 2005), as well as grazer gastropods (Airoldi, 2007; Atalah and Crowe, 2010). Similarly, impact of coastal eutrophication, defined as anthropogenic excessive nutrient enrichment, is increasingly documented since the mid 90s (Nixon, 1995) as one of the main anthropogenic process impacting coastal community (Cloern, 2001; Crowe et al., 2000; Thompson et al., 2002; Worm and Lotze, 2006). Numerous experimental studies, mainly focussing on small spatial scales, have reported negative impacts of high nutrient concentrations on perennial macroalgae abundance such as canopy-forming brown macroalgae species (Kraufvelin et al., 2006; Worm and Lotze, 2006) and sometimes in conjunction with other stressors such as sedimentation (Atalah and Crowe, 2010) or wave action (Kraufvelin et al., 2010). However, less attention was paid for grazer molluscs such as gastropods. For instance, Atalah & Crowe (2012) showed that contaminated sites were also characterized by a reduction of molluscan total abundance, while emphasising a species-specific response. Our results are in agreement with former results demonstrating a decrease of total abundance and taxonomic richness as a result of

447 both total suspended matter and nutrient concentration gradients. Interestingly, significant
448 impacts of these human related stressors are especially found in taxa associated with
449 medium and low mediolittoral levels and appear to be smaller for *L. saxatilis*/*L. compressa*,
450 located at higher shore levels. Such differences in responses across shore levels are
451 consistent with the hypothesis of water mediated disturbances as lower habitats are more
452 frequently immerged than upper ones. The taxon responses we observed in this study are
453 congruent with recent integration of these taxa as sensitive species to inorganic pollution
454 (Ecological Group I in the AZTI Marine Biotic Index (Borja et al., 2000)) (Vinagre, 2016a,
455 2016b), except for the grey top shell *S. cineraria*. This could be explained by inadequacy of
456 our sampling protocol as *S. cineraria* habitat extent further the subtidal level. Our results
457 also show that *L. littorea* is the only taxon positively affected by the gradient of nutrient
458 concentrations. *Littorina littorea* is widely reported as a species tolerant to contamination
459 since it was unaffected (Atalah, 2012) or even favoured by nutrient enrichment conditions
460 (Kraufvelin et al., 2002) or by microplastic concentrations (Doyle, 2020). Finally, this work
461 demonstrates the ability of a citizen-science program to detect local and regional changes in
462 communities and can therefore be considered as a powerful tool for monitoring intertidal
463 ecosystems, as previously discussed for instance in (Conrad and Hilchey, 2011).

464 **Caveats**

465 Notwithstanding the relevance of our results, it is important to delineate the limitations of
466 our approach in terms of data collection and methods used. One of the main caveats of this
467 study is that rare taxon abundance is zero-inflated in our dataset, and the methodology we
468 used is not sufficiently adapted to deal with it (see fig. S4). Indeed, this study provides robust

models for 8 taxa out of 14, therefore excluding taxa for which abundance is zero-inflated (6 taxa). Increasing sampling effort may allow overcoming this limitation.

To assess large-scale variability of the community, small-scale predictors were fixed, assuming that the key brown macroalgal species defining shore height were found in all shores. However, these canopy-forming brown macro-algae, have their own environmental niche specificity (Chapman, 1995) and may not to be evenly distributed along the NE Atlantic coast. Furthermore, grouping species with similar morphologies into species complexes may also have led to an incorrect assessment of stressor impacts since the species-specific responses were neglected. For instance, the lack of response to nutrient concentrations by the *L. obtusata/L. fabalis* complex group, can be related to proven ecological differences between the two merged species (Williams, 1992, 1990). Our results may also inadequately address the specific effect of each stressor related to large river plumes because of potential collinearity between some predictors (*e.g.* inorganic nitrogen and suspended matter concentrations). Moreover, the revealed pattern could encompass other anthropogenic stressors that were not considered in this study such as metallic contamination or microplastic pollution (Gutow et al., 2015; Doyle, 2020). Finally, we found a weak importance of temporal predictors ('season' and 'year'), describing a lesser impact on abundance and species richness than spatial predictors. This low temporal variability could also be due to irregularities in the time series of our dataset or the relative short time period of monitoring (8 years) as compared to the time needed to observe responses to climate change (Hawkins et al., 2008). As such, our findings should be interpreted with caution.

Conclusion

On top of their inherent fundamental interests, our results provide strong supports that citizen science databases can provide robust scientific information to assess and understand responses of biodiversity to environmental variability. Indeed, our modelling study reveals that anthropogenic processes are the main source of variability of gastropod coastal communities at the large-scale along more than 1000 km of coast within a biogeographic transitional zone. Although this spatial scale is one of the most investigated one by citizen science projects, only a small proportion of the provided data ends in peer-reviewed publications, probably highlighting the absence of acknowledgements of citizen science data in publications, which seems particularly true for marine ecosystems (Theobald et al., 2015). Combined efforts of both professional and citizen scientists may achieve relevant outcomes for biodiversity research as well as for the management of marine ecosystems. Finally, rocky-shores community responses to anthropogenic pressures observed in this study, could be used as a bioindicator of coastal water quality at the local scale as previously demonstrated (Borja et al., 2000; Vinagre, 2016a) but also at regional ones where larger anthropogenic processes take place.

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	Variable		Abb	Units	Native Spatial résolution	Temporal coverage	Source
Selected in final models	*Large-scale*						
X		Bathymetry	Bath	m	1 km	-	MARSPEC (Sbrocco and Barber, 2013)
X		Mean of annual SST	SST.M	°C	1 km	Mean (2002-2010)	MARSPEC (Sbrocco and Barber, 2013)
X		SST of the coldest month	SST.cold	°C	1 km	Mean (2002-2010)	MARSPEC (Sbrocco and Barber, 2013)
		Annual range of SST	SST.r	°C	1 km		MARSPEC (Sbrocco and Barber, 2013)
		SST of the warmest month	SST.warm	°C	1 km		MARSPEC (Sbrocco and Barber, 2013)
X		Mean Salinity	Sal	-	~3 km x ~2 km	Average value of 2020 daily mean	(Tonani et al., 2019)
		Salinity Standard deviation	Sal.sd	-	~3 km x ~2 km	Average value of 2020 daily mean	(Tonani et al., 2019)
X		Mean Chloa concentrations	Chloa	$mg.m^{-3}$	1 km	Average value of daily mean (2013-2015)	(Gohin et al., 2010; Hu et al., 2012)
		Chloa concentrations Standard déviation	Chloa.sd	$mg.m^{-3}$	1 km	Average value of daily mean (2013-2015)	(Gohin et al., 2010; Hu et al., 2012)
X		Kinetic Energy due to Waves	WKE	$N.m^{-2}.s^{-1}$	300 m	Mean of 90^{th} percentile (2010-2015)	(Boudière et al., 2013)
X		Tide amplitude	Tamp	m			(SHOM, 2020)
X		Wave Exposure index	WE	-	90 m		(Burrows et al., 2008)
X		$N\text{-}NO_2^-$ + $N\text{-}NO_3^-$ concentrations	Nit	$\mu mol.l^{-1}$	-	Mean (2012-2020)	(Belin et al., 2019)
		$N\text{-}NO_2^-$ + $N\text{-}NO_3^-$ concentrations Standard deviation	Nit.sd	$\mu mol.l^{-1}$	-	Mean (2012-2020)	(Belin et al., 2019)
X		Mean of Total Suspended Matter	TSM.M	$mg.l^{-1}$	300 m	Average value of daily mean (2008-2012)	(Nechad et al., 2015)
		Total Suspended Matter Standard deviation	TSM.sd	$mg.l^{-1}$	300 m	Average value of daily mean (2008-2012)	(Nechad et al., 2015)
X		Coastal population density	Pop			2015	(WorldPop, 2020)
	Small-scale						
X		Nature of seaweed belt (shore level)	SW	-	-	-	BioLit program
X		Sampling effort (N° of replicates)	Rep	-	-	-	BioLit program

X		Canopy cover class	Cover	% class	-	-	BioLit program

Table 1 Environmental predictors considered during the modeling process, with abbreviation used, units, native résolution and temporal coverage. Predictors were grouped according to their scale of influence (Small- vs. Large-scale). Predictors included in the final set are identified by X.

Response variables	mtry	RMSE	R^2	Moran's I	Fixed predictors SW / Cover class
S	15	0.87±0.1	0.51±0.1	-0.11 NS	Fvesi/ 0-5%
Tot_ab	15	0.75 ±0.1	0.57±0.1	-0.1 NS	Fvesi/ 0-5%
S.umbi	15	1.11 ±0.2	0.67±0.1	-0.11 NS	Fvesi/ 25-50%
L.fab/obt	15	1.07 ±0.1	0.44±0.1	-0.07 NS	Fvesi / 75-100%
Patella.spp	15	1.16 ±0.1	0.45±0.1	-0.02 NS	Fvesi/ 0-5%
S.penn	15	1.22 ±0.1	0.48±0.1	-0.1 NS	Fser/ 75-100%
P.line	15	1.08 ±0.1	0.55±0.1	-0.09 NS	Fspir/ 0-5%
L.litto	2	1.05 ±0.1	0.37±0.1	-0.07 NS	Fvesi/ 0-5%
L.saxa/comp	15	0.87 ±0.1	0.46±0.2	0.01 NS	Pel/ 0-5%
N.lapi	28	0.92 ±0.2	0.29±0.2	-	-
S.cine	25	0.50 ±0.2	0.37±0.2	-0.15 NS	F.ser/ 75-100%
T.reti	28	0.65 ±0.2	0.08±0.1	-	-
O.erin	2	0.42 ±0.1	0.20±0.2	-	-
C.zyzi	2	0.29 ±0.2	0.29±0.2	-	-
O.inor	28	0.15 ±0.1	0.01±0.0	-	-
G.magu	28	0.13 ±0.1	0.29±0.1	-	-

Table 2. Performance metrics of the best RF models (RMSE and R^2) according to the 'mtry' parameter from cross-validation procedure for taxonomic richness (**S**), total abundance (**Tot_ab**) and for each taxon. *Steromphala umbilicalis* (**S.umbi**), the complex *Littorina fabalis/L. obtusata* (**L.fab/obt**), *Patella spp* (**Patella.spp**), *Steromphala pennanti* (**S.penn**), *Phorcus lineatus* (**P.line**), *Littorina littorea* (**L.litto**), complex *Littorina saxatilis/L. compressa* (**L.saxa/comp**), *Nucella lapillus* (**N.lapi**), *Steromphala cineraria* (**S.cine**), *Tritia reticulata* (**T.reti**), *Ocenebra erinaceus* (**O.erin**), *Calliostoma zyziphynum* (**C.zyzi**), *Ocinebrellus inornatus* (**O.inor**) and *Gibbula magus* (**G.magu**). Small-scale fixed predictors (*i.e.* seaweed belt (**SW**) and canopy cover class (**Cover class**)) used for model predictions and spatial

autocorrelation index (Moran's I) were indicated for robust models (R^2>0.35). SW abbreviations: *Pelvetia canaliculata* (**Pel**), *Fucus spiralis* (**Fspir**), *F. vesiculosus* (**F.vesi**),*F. serratus* (**Fser**). Non significant (NS) low values of Moran'I index indicate an absence of spatial autocorrelation in model residuals.

	Rank 1	Rank 2	Rank 3	Rank 4	Rank 5	Rank 6
S	SW.Pel (100)	Nit (79.8)	Cover (76.9)	TSM.M (72.8)	WKE (70.9)	Pop (62.3)
Tot_ab	TSM.M (100)	SW.Pel (87.3)	WKE (62)	Nit (53.4)	Cover (50.3)	SST.cold (48.7)
S.umbi	SW.Pel (100)	TSM.M (38.4)	Nit (27.8)	Cover (23.1)	WKE (18)	SST.cold (10)
Patella.spp	WKE (100)	TSM.M (96)	Cover (78.5)	SST.cold (49.6)	Rep (38.03)	SW.Pel (37.1)
S.penn	SW.Fser (100)	Cover (30.5)	Nit (30)	TSM.M (21.5)	Pop (20.1)	Rep (19.2)
P.line	Cover (100)	WKE (48.6)	SW.Fser (33)	TSM.M (25.9)	Nit (20.2)	Rep (20.1)
L.fab.obt	SW.Pel (100)	Pop (60.4)	Cover (51.5)	Rep (36.6)	Sal (31.5)	Nit (24.2)
L.litto	Nit (100)	Chloa (97.3)	Sal (94.2)	WKE (92.1)	Pop (87.9.2)	SSTcold(80.3)
L.saxa.comp	SW.Pel (100)	Cover (48.5)	Rep (38.2)	SW.Fspir (35.5)	Nit (30.4)	Bath (25.3)
S.cine	SW.Fser (100)	Rep (97.7)	WKE (72.5)	Cover (46.7)	Pop (39.8)	Sal (39.4)

Table 3. Ranking of the 6 most important predictors according to standardized values of variable importance (in brackets) of each robust model (R^2>0.35). Standardized values represent the relative importance scaled to 100, identifying the most important predictor. Abbreviations: Mean total suspended matter **(TSM.M)**, Canopy cover class (**Cover)**, inorganic nitrogen concentrations **(Nit)**, Kinetic Energy due to Waves **(WKE)**, Sampling effort **(Rep)**, Chlorophyll a concentration **(Chloa)**, Mean salinity **(Sal)**, Coastal population density **(Pop)**, Sea Surface Temperature of the coldest month **(SST.cold)**, and the nature of seaweed belt **(SW)**, namely *Pelvetia canaliculata* **(SW.Pel)**, *Fucus spiralis* **(SW.Fspir)**, *Fucus serratus* **(SW.Fser)**.

Figure Click here to access/download;Figure;Biolit_Figures_ok.docx

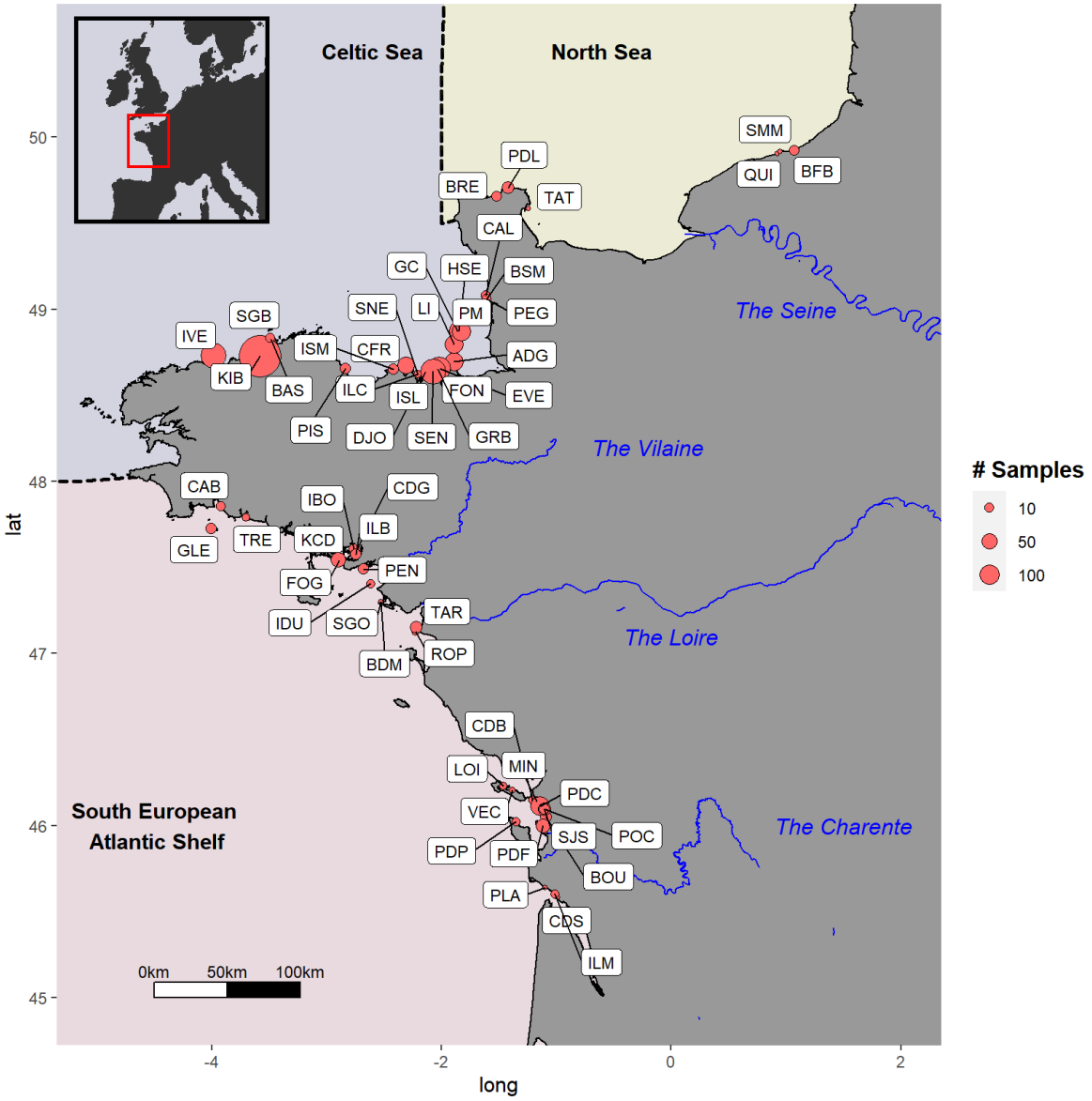


Figure 1. Locations of sampled rocky-shores. The study area crossed 3 ecoregions (the North Sea, the Celtic Sea and the South European Atlantic Shelf) according to the 'Marine Ecoregion Of the World' biogeographic system (Spalding et al., 2007). For each point, labels refer to the vernacular shore name: ADG: "Anse Du Gesclin", AUD: "Audresselles", AYT: "Aytre", BAS: "La Bastille", BDM: "Baie des Marsoins", BFB: "Bas Fort Blanc". BOU: "Les Boucholeurs", BRE: "Bretteville", BSM: "Blainville-sur-mer", CAB: "Cabellou", CAL: "Cale", CDB: "Chef de Baie", CDG: "Cale de Gornevez", CDS: "Concheau de Suzac", CFR: "Cap Fréhel", DEL: "Dellec", DJO: "Dame jouanne", EVE: "L'Eventail", FOG: "Fogeo", FON: "Fort National", GC: "Grande Corbière – Chausey »" , GLE: "Glénan (Saint-Nicolas)", GRB: "Grand Bé", HSE: "Houston SE – Chausey**",** IBO: "Ile de Boed", IDB: "Iles des Ebihens", IDU: "Ile Dumet", ILB: "Ile de Bailleron", ILC: "Ilot de la Colombière",ILM: "Iles aux Mouettes", ISL: "L'Islet", ISM: "Ilot Saint-Michel", IVE: "Ile Verte", KCD: "Kercouedo", KER:

“Kermorvan”, KIB: “KignerBell”, LI: “Longue Ile – Chausey”, LOI: “Loix”, MIN: “Les Minimes”, PAG: “Pors-Ar-Goret”, PDA: “Pointe de l’Arcouest”, PDC: “Pointe du Chay”, PDF: “Pointe de la Fumée”, PDL: “Pointe de la Loge”, PDP: “Pointe des Prouards”, PEA: “Petit Ailly”, PEG: “Père Gus”, PEN: “Penvins”, PIE: “Piegu”, PIS: “La Piscine”, PLA: “Platin”, PM: “Port Marie –Chausey” , PNA: “Port Navalo”, POC: “Pont de la Chaume”, PPL: “Pointe du Plomb”, QUI: “Quiberville”, ROP: “Roche Percée”, ROV: “Roche Vilaine”, SEN: “Saint-Enogat”, SGB: “Saint Guirec/Bastille”, SGO: “Saint Goustan”, SJS: “Saint Jean-des-Sables”, SMM: “Sainte Marguerite-sur-mer”, SNE: “Sud Nellière”, TAR: “La Tara”, TAT: “Tatihou”, TRE: “Trenez”, VEC: “Vert-clos”.

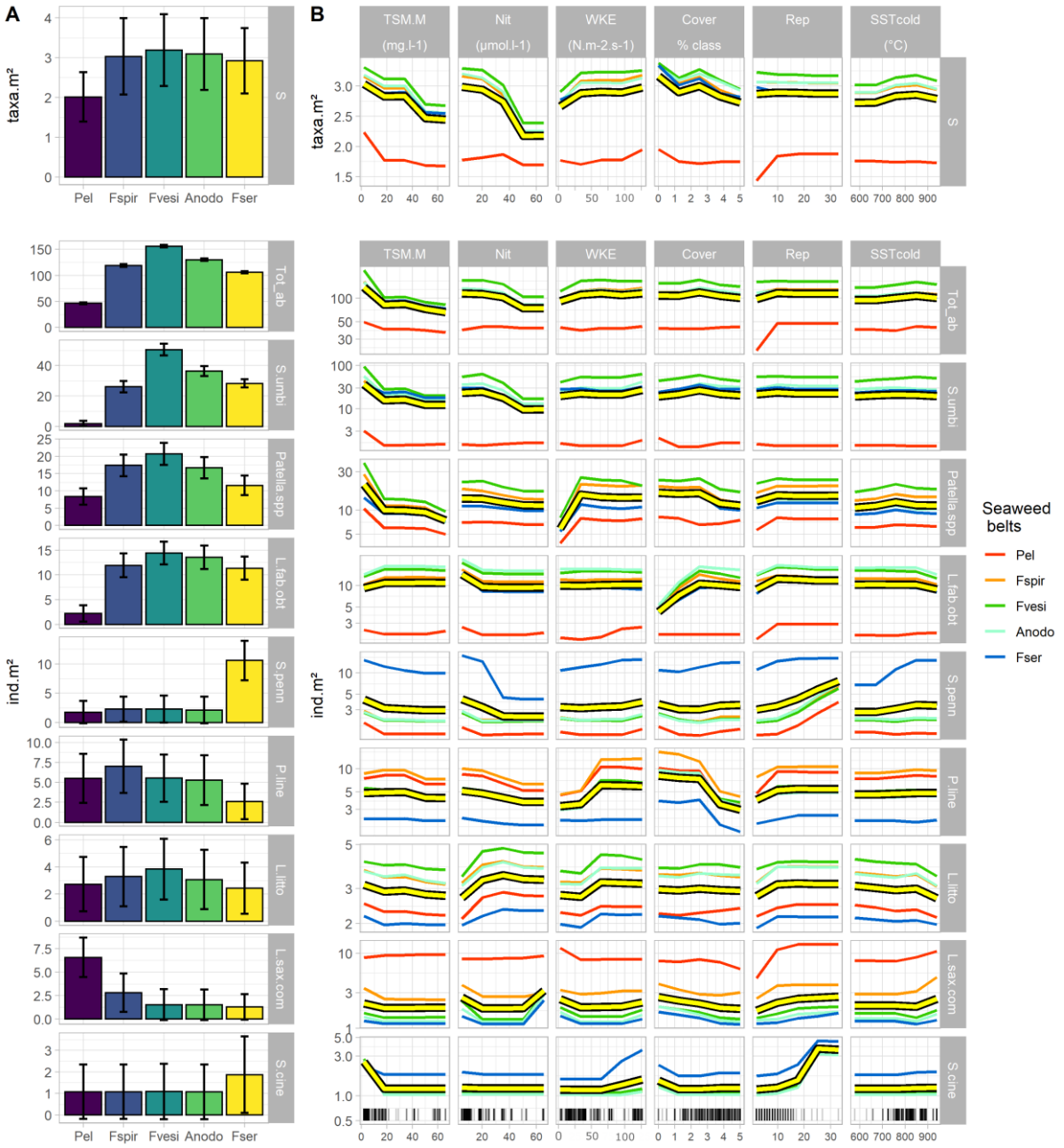


Figure 2. Partial dependance Plot (PdP) representing responses with the seaweed belts (**A**; barplot) and PdP in association with Individual Conditional Expectation (ICE) (**B**; yellow curve + coloured curves, respectively) representing relation with other most relevant predictors: Mean total suspended matter **(TSM.M)**, inorganic nitrogen concentrations **(Nit)**, Kinetic Energy due to Waves **(WKE)**, Sampling effort **(Rep)** and Canopy cover class (**Cover)** of each robust models ($R^2 > 0.35$): taxonomic richness (**S**), total gastropod abundance (**Tot_ab**), *Steromphala umbilicalis* (**S.umbi**), *Patella spp* (**Patella.spp**), the complex *Littorina fabalis/L. obtusata* (**L.fab.obt**), *Steromphala pennanti* (**S.penn**), *Phorcus lineatus* (**P.line**), *Littorina littorea* (**L.litto**), complex *Littorina saxatilis/L. compressa*

(**L.saxa.comp**) and *Steromphala cineraria* (**S.cine**); Cover class refers to the ordinal cover scale (**1**: 0-5%; **2**:5-25%; **3**:25-50%; **4**:50-75; **5**:75-100%). ICE describes the response for each seaweed belt, while PdP shows the overall average response. At the bottom of the subplot panel, black ticks provide the distribution of each predictor.

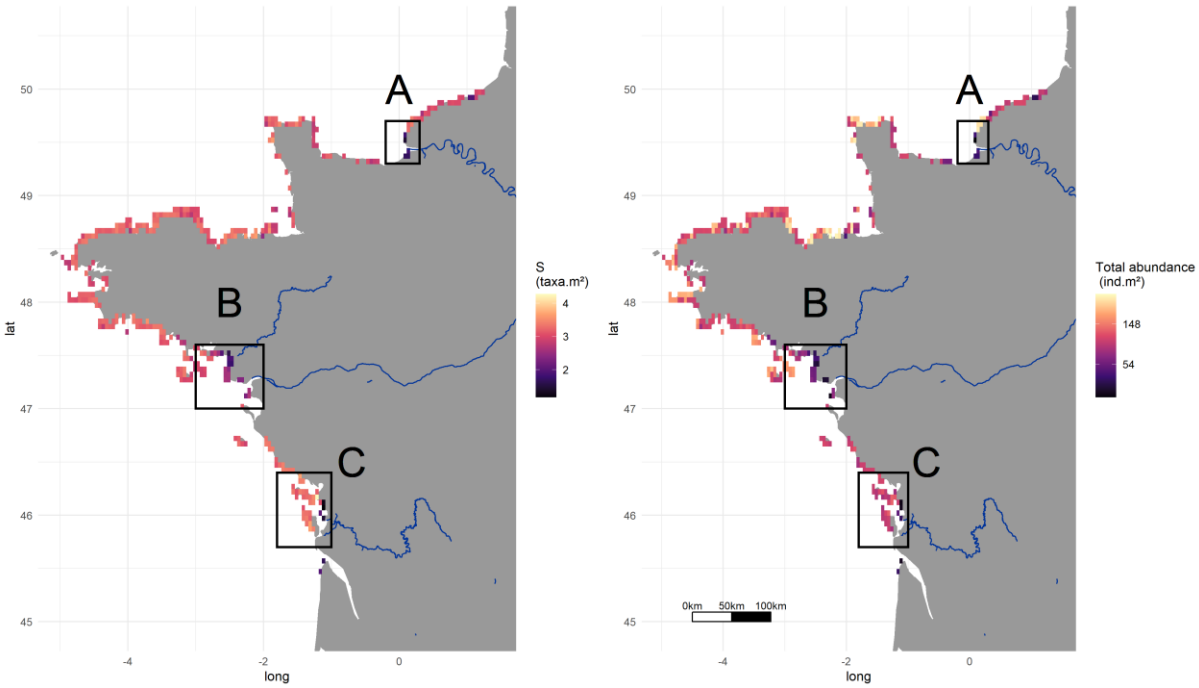


Figure 3. Predicted spatial variability of mean taxonomic richness (S, left panel) and mean total abundance (right panel) of gastropods along the rocky shores of the French Atlantic coast. Total abundance colour scale was log-transformed. Squares highlight lowest predicted values retrieved for the estuaries (A) The Seine (49°26’02’’N; 0°12’24’’E), (B) the Loire (47°30’00’’N; 2°28’52’’W) and the Vilaine (47°17’23‘’N; 2°07’28’’W) and (C) the Charente (45°57’19’’N; 1°04’41’’W).

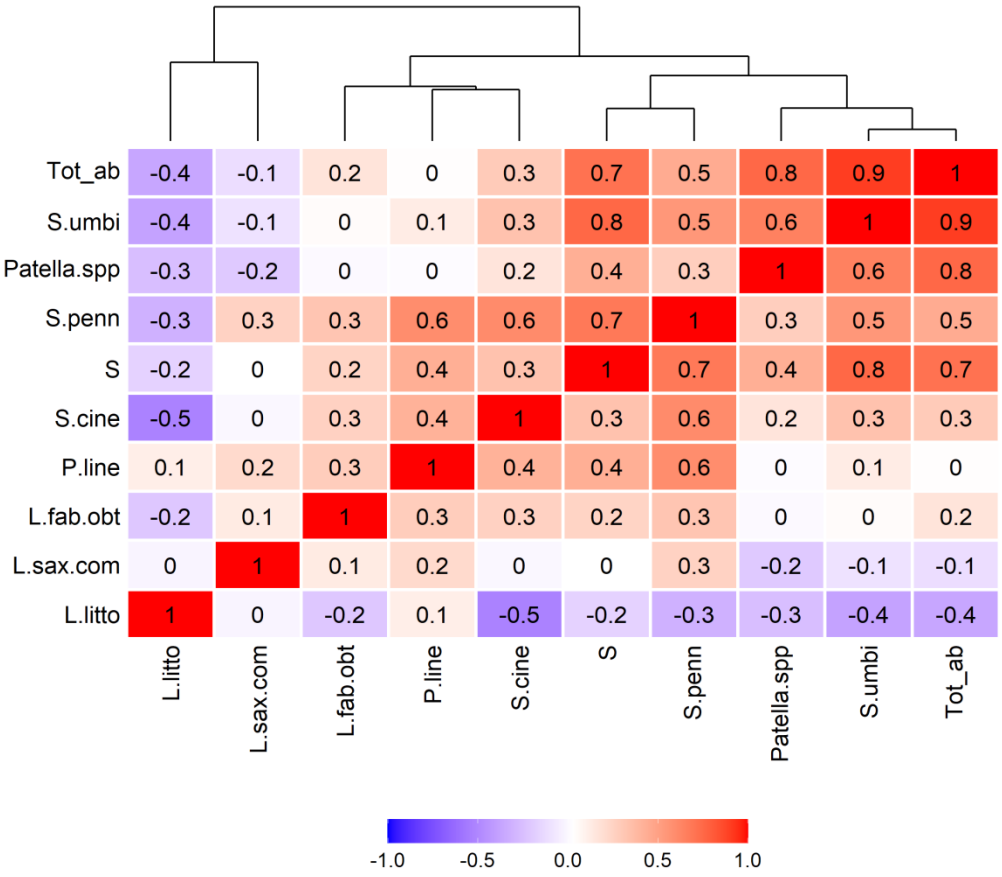


Figure 4. Pearson's correlation matrix of spatial abundance predictions for each response variable. Positive correlations (from orange to red) identify similarity in spatial abundance pattern, while negative ones (from violet to blue) highlight opposition.

CRediT authorship contribution statement

Bruno Serranito: Conceptualization, Methodology, Software, Data curation, Investigations, Visualization, Writing – Original Draft

Tristan Dimeglio: Conceptualization, Funding acquisition, Data curation, Ressource, Investigations, Writing – Review and Editing,

Fred Ysnel: Conceptualization, Supervision, Methodology, Investigations, Writing – Review and Editing

Anne Lizé: Supervision, Writing – Review and Editing

Eric Feunteun: Conceptualization, Supervision, Funding acquisition, Methodology, Investigations, Writing – Review and Editing**,** Project administration

Declaration of interests

- The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:
