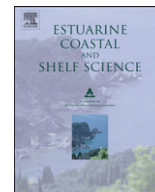




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Species–area relationships as a tool for the conservation of benthic invertebrates in Italian coastal lagoons

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ABSTRACT

Over the recent decades, the preservation of coastal and estuarine waters has been recognised as a priority at national and international levels. At the European scale, the Water Framework Directive (WFD) was established with the aim to achieve a good *ecological status* of all significant water bodies by the year 2015. Among the descriptors used to define the *ecological status* of water bodies, taxonomic diversity (usually species richness) is a widespread metric employed across taxa and habitats. However, species richness is known to increase with area at a decelerating rate, producing the species–area relationship (SAR). Thus, removing the effect of area (even in case of low magnitude), is mandatory before comparing species richness between sites. Here we tested recently developed multi-model SARs as a standardisation tool for comparing benthic species richness (annelids, arthropods, molluscs and total species richness) in 18 Italian coastal lagoons with a surface area ranging from 0.19 to 552 km², i.e. three orders of magnitude. However, the sampling effort was often incompletely described and certainly heterogeneous among the studies retrieved from the database. Therefore, we used the number of studies as a proxy for the sampling effort in each lagoon and estimated species richness from observed values using non-parametric occurrence-based estimators. We further corrected for bias that might be induced by sampling efforts being unrepresentative for the surface area of different lagoons. After applying these corrections, we estimated that *c.* 25–30% of species richness could be explained by surface area. We investigated the spatial congruence of species richness patterns across taxa and showed that molluscs could serve as a potential surrogate for total macro-invertebrate species richness. We further found that the intensity of conservation focus and the gradient of *ecological status* are decoupled in Italian coastal lagoons. More generally, our study paved the way for the use of flexible tools for the comparison of species richness across water bodies in the context of the WFD.

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1. Introduction

Estuarine and coastal ecosystems provide most of the goods and services upon which human welfare depends (Costanza et al., 1997). In the coastal landscape, transitional waters (hereafter TW) have been defined as “*bodies of surface water in the vicinity of river mouths which are partly saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows*” (EU Water Framework Directive, 2000

abbreviated as WFD). These TW comprise cornerstone habitat islands of various types: e.g. estuaries, fjords, deltas, lagoons, coastal lakes and ponds, brackish wetlands or salt-marshes (McLusky et al., 2007). Among TW, lagoons, which represent 13% of the world coastline length, are very productive ecosystems (300 g C m⁻² y⁻¹, Knoppers, 1994) holding a high gamma (large temporal or spatial scale) diversity of organisms resulting from strong abiotic variations within and among coastal lagoons that promote a high turnover of species (Sabetta et al., 2007; Sosa-Lopez et al., 2007; Vadrucchi et al., 2008).

In the past 40 years, TW conservation has been recognised as a priority on national and international levels through several acts (e.g. Federal Water Pollution Control Act, USA, 1972), conventions (e.g. Ramsar Convention, 1977), and initiatives (e.g. Mediterranean Wetland Initiative, 1991). In December 2000, the EU Water

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Framework Directive (2000) was established with the challenging goal to achieve good *ecological status* of all significant European water bodies by 2015. The WFD defines a classification scheme for water quality with five status classes: high, good, moderate, poor and bad. 'High status' is defined as the 'reference conditions' associated with no or very low human pressure; this is the best status achievable. These reference conditions are specific to each TW ecosystem type (see Basset et al., 2006; Lucena-Moya et al., 2009 or Galván et al., 2010 for examples of typologies) within the broad ecological regions in Europe (hereafter Geographical Intercalibration Group (GIG); WFD, 2000). Further quality assessments for particular water body types in an GIG are based on the deviations from these reference conditions: 'Good status' means 'slight' deviation, 'moderate status' means 'moderate' deviation, and so on.

The *ecological status* of a particular water body is a broad concept integrating both physico-chemical and biological measures. Biological elements are of particular importance in assessing such a status (Borja et al., 2008), and phytoplankton, macroalgae, angiosperms, benthos and fish have been proposed as Biological Quality Elements for water bodies (BQEs; WFD Annex V Section 1.1.3; 2000). The assessment of the different BQEs is based on diverse metrics (see Borja et al., 2008 for an overview of the different metrics). However, species richness is a common descriptor for all BQEs, and the definition of 'reference conditions' for a specific type of water body (e.g. lagoons) inside a particular ecoregion (e.g. the Mediterranean) with respect to species richness will ultimately lead to the comparison of species richness among water bodies of varying sizes (Basset et al., 2006).

Among the biogeographical tools available to conservationists, the species–area relationship (SAR) is one of the most valuable. Indeed, inference about the SAR is mandatory in the wide range of conservation applications that require the comparison of diversity patterns when regions differ in area (Smith, 2010), such as the comparison of species richness among lagoons of varying sizes. Indeed, larger coastal lagoons are more likely to hold more species because they are more likely to hold, at least, more diverse habitats and more individuals (Sabetta et al., 2007). Thus, biodiversity comparisons among coastal lagoons must take into account the effect of area. Furthermore, because it describes the scaling of species richness with lagoon surface, the SAR has already been suggested as a standardisation tool to characterise lagoon's *ecological status* with respect to species richness (Basset et al., 2006; Sabetta et al., 2007). This approach conceptually classifies good and poor status ecosystems with respect to their species richness taking lagoon surface into account. Accordingly, a good status is attributed to lagoons with species richness significantly above the value calculated according to the SAR model, while poor status is attributed to lagoons with species richness significantly below this value (Sabetta et al., 2007).

To mitigate the potential effects of human-induced threats on biodiversity some coastal lagoons and their watersheds have been protected by, for instance, implementing regulations of human density and controls on nutrient loadings (Livingston, 1991; Valiela and Bowen, 2002; Paerl, 2009). However, these regulations are more driven by local socio-political considerations than by a regional planning scheme implemented from macroecological view. For instance, the level of spatial congruence between species richness and lagoon protection effort is still unknown despite its crucial importance to assess the efficiency of environmental protection actions and to guide future WFD conservation actions.

Our study is focused on benthic macro-invertebrates, which have been demonstrated to constitute suitable bio-indicators for water ecosystem monitoring because they respond rapidly to anthropogenic and natural stress (Pearson and Rosenberg, 1978). In

this paper we studied the SARs of these benthic macro-invertebrates across Italian coastal lagoons with a threefold aim:

- (1) To propose the recently developed multi-model SAR approach (Guilhaumon et al., 2008) as a standardisation tool for comparing benthic species richness between Italian coastal lagoons, taking into account potential differences between the types of organisms (annelids, arthropods, molluscs and total species richness).
- (2) To use the results of the former analyses to determine the level of congruence among annelid, arthropod, mollusc and total macro-invertebrate species richness, which could reveal the potential of particular higher taxa to act as surrogates for the overall macro-invertebrate fauna.
- (3) To investigate the level of spatial congruence between *ecological status* (with respect to macro-invertebrate species richness) and protection effort of Italian coastal lagoons.

2. Materials and methods

2.1. Data collection

We obtained data about macro-invertebrate species richness in Italian lagoons from the Transitional Water Data Platform developed within the CIRCLEMED project ClimBioMedNet (www.circlemmednet.unisalento.it). Data were originally gathered from published sources, including international journals retrieved from electronic databases (i.e. ASFA, WebSpis, Biological Abstracts, Current Contents e Zoological Records), Italian journals covering the fields of ecology and zoology (i.e. Accademia Peloritana, Il naturalista siciliano, Oebalia, Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari, Thalassia Salentina) and proceedings of Italian scientific societies covering the field of aquatic ecology and zoology (i.e. Associazione Italiana di Oceanografia e Limnologia, Società Italiana di Biologia Marina, Società Italiana di Ecologia, Società Sarda di Scienze Naturali). The search was restricted to publications published in the last 40 years. The electronic search was performed through a three-way factorial combination of the following groups of keywords: (a) Italy, Italian; (b) lagoon, coastal lake, coastal pond, saltmarsh, saltern, brackish; (c) benthos, macrobenthos, macro-invertebrate, benthic invertebrates, benthic fauna. Publications retrieved were further screened according to three main criteria: (a) taxonomic resolution (most taxa classified down to the genus or species level); (b) taxonomic comprehensiveness (the taxonomic list of a lagoon, resulting from one or more publications, cannot be limited to a few selected phyla); (c) sampling design (samplings carried out at a seasonal or higher resolution). Finally, 194 publications were selected for the analysis, referring to 32 lagoon ecosystems (the references scrutinised for each lagoon are presented in [Appendix A – supplementary references](#)). For each lagoon, surface area (km²) was obtained from the published publications as well as from satellite images. The initial database considered for the present study constitutes a representative sample of Italian lagoons, accounting for 18.2% of lagoon numbers and ~71% of lagoon surface in Italy (Basset and Sabetta, 2005).

Additionally, a semi-quantitative level of protection was estimated for each lagoon using a list of all actions of environmental protection (hereafter, AEP). The 11 AEP considered here were: Ramsar Sites, National Reserves, Regional Reserves, Sites of Community Interest (SCI), Special Protection Areas (SPA), Regional Parks, National Parks, Marine Protected Areas, Marine Protected Reserves, Natural Oasis. For each of the 32 Italian coastal lagoons, we evaluated the level of cumulative protection as the number of

the 11 AEP applied. This procedure for estimating the protection efforts implicitly attributes equal weights to the different AEPs.

2.2. Measures of species richness

For this study, data were gathered from heterogeneous sources (publications) for which the sampling strategy and effort varied. This may lead to potential bias when performing SAR analyses and possible spurious interpretations and conclusions when comparing species richness among lagoons. Indeed, to make such a comparison without any bias, the data need be obtained using a standardised protocol across lagoons, taking into account their respective surface area (i.e. the sampling effort should be proportional to the lagoon area; Schoereder et al., 2004). However, even standardised protocols, when carried out in different areas or community types, may lead to different sampling success, leading to biased estimations of species richness inventoried at each site (Hortal et al., 2006). In the Transitional Water Data Platform information about sampling effort for each lagoon is not systematically available. Therefore, we used the number of publications as a proxy for the sampling effort in the different lagoons. We recognise that this approach is not completely satisfactory as the sampling effort may vary substantially among different published studies. However, for the given database, the number of publications was the only possible proxy for the sampling effort. In addition, in the Transitional Water Data Platform there is a substantial heterogeneity in the number of publications dealing with the different lagoons considering the range of lagoon surface areas. For example some of the largest lagoons are under-represented relatively to smallest ones and lagoons of similar area are represented by alternatively very high or low numbers of publications (Appendix A – Figure A.1). Towards the overcoming of these drawbacks (i.e. lack of information on sampling effort, bias in species richness inventories and sampling effort not being proportional to lagoon area) we employed a three-step correction procedure. We first restricted our analyses to the lagoons for which data about annelids, arthropods and molluscs were available and presented a minimum of 4 publications, leading to the inclusion of 18 lagoons out of 32. The final list of literature sources used is of 149 publications (Appendix A – supplementary references). This 4 publications threshold value is somewhat arbitrary; it was chosen based on the distribution of paper numbers as a compromise between the need to eliminate poorly-studied lagoons while retaining enough lagoons for subsequent SAR analyses. Second, to account for potential incompleteness of inventories across different sites and types of organisms, we estimated the species richness in the macro-invertebrate higher taxa for each lagoon from the observed values by using non-parametric occurrence-based estimators with the different publications considered as different samples. Because no particular estimator has been shown to be the best suitable for all particular situations or taxa (Walther and Moore, 2005) we used a variety of richness estimators, namely the Chao2 (Chao; Chao, 1984, 1987), the First-order Jackknife (Jack1; Burnham and Overton, 1979), the Second-order Jackknife (Jack2; Smith and van Belle, 1984) and the Bootstrap (Boot; Smith and van Belle, 1984) estimators. These richness estimators were calculated using the “vegan” package (Oksanen et al., 2011) running under the R statistical programming environment (R Development Core Team, 2011). Finally, because we observed that the sampling effort was in several cases not representative of the lagoon surface area, we applied a third correction (Appendix A – Figure A.1). We regressed the log-transformed estimated species richness against log-transformed sampling effort (number of publications available for each lagoon) for each combination of richness estimator and each macro-invertebrate higher taxa. We used the residual richness in our subsequent analyses that are, by construction, independent of

sampling effort. Log-transformations are justified given the expected saturation of richness with increasing sampling effort, and because this procedure yields residuals whose distribution is more suitable for model-fitting. However, when plotting richness against lagoon area, richness residuals include negative values that cannot be handled by the SAR model-fitting algorithms. They were therefore rescaled using the formula $Y_{new} = Y_{res} + \min(Y_{res}) + 0.1$ where Y_{res} are the residuals from the above regressions and Y_{new} are the values used for model-fitting. This resulted in a vertical translation of residual values along the y-axis, so that they are all positive. This has no effect on the structural parameters of the models (i.e. their shape) or on model-selection results (Poulin et al., 2011).

2.3. Statistical analyses

2.3.1. SAR modelling

Various shapes of SARs have been described in the literature and no real consensus has emerged about an “ubiquitous” model across taxa and environmental conditions (Tjørve, 2003, 2009; Guilhaumon et al., 2008). Consequently, for each higher taxa under study (annelids, arthropods and molluscs) and for total macro-invertebrates, we compared the fit of eight SAR models including five convex functions (power, exponential, negative exponential, rational function, and Monod) and three sigmoid functions (logistic, Lomolino and cumulative Weibull) (see Table 1 for model formulas and characteristics). Power and exponential models also represent non-asymptotic functions, whereas the other functional forms are asymptotic. We discriminated between different models in an information-theoretic framework. The information-theoretic framework for model selection is based on the evaluation of multiple working hypotheses (Burnham and Anderson, 2002). This evaluation of competing hypotheses, each represented by a different model, is achieved through the estimation, for each model, of the probability to be the best to explain the data. Model-selection uncertainty may arise when several different models are equally supported by the data and such situations invalidate the use of only the best model for analyses. To take into account model-selection uncertainty, a multi-model inference is recommended (Burnham and Anderson, 2002).

Here, our approach follows that proposed by Guilhaumon et al. (2008) to cope with uncertainty in SAR modelling. Each of the eight SAR models was fitted by minimising the residual sum of squares in non-linear regressions using the unconstrained Nelder–Mead optimisation algorithm. We used R^2 values that compare the fit of non-linear regression models with that of a linear intercept-only model (Kvålseth, 1985) as indicators of the proportion of the total variation in species richness among lagoons that is explained by lagoon surface area. In contrast, R^2 values are not recommended to compare the fit of different non-linear regression models that use a different number of parameters (Ratkowsky, 1983; Gitay et al., 1991). Therefore, we compared the fit of the different SAR models using the small-sample corrected Akaike’s Information Criterion (AICc). AICc is given by the following equation (Johnson and Omland, 2004):

$$AICc = n \log \left(\frac{RSS}{n} \right) + 2p \left(\frac{n}{n-p-1} \right) \quad (1)$$

where RSS is the residual sum of squares, p is the number of fitted parameters in the model (plus one for the estimated variance) and n the sample size. With a lower AICc, the model is considered better in explaining the data. We used Akaike weights derived from the AICc (AICc-W) to evaluate the relative likelihood of each model given the data and the set of models. Akaike weights can be interpreted directly in terms of a models’ probability of best explaining the data, and they provide the basis for the construction

of robust multi-model inference. For a fitted model i , its weight w_i is given by

$$w_i = \frac{e^{-1/2\Delta_i}}{\sum_{r=1}^M e^{-1/2\Delta_r}} \quad (2)$$

where M is the number of models in the set and Δ_i is defined as $\Delta_i = AICc_i - AICc_{min}$ with $AICc_{min}$ the $AICc$ value for the best model.

As advocated for differently parameterised models, we implemented model averaging and considered the weighted average of model predictions with respect to model weights to construct multi-model SARs

$$\bar{S} = \sum_{i=1}^M \hat{S}_i w_i \quad (3)$$

where \bar{S} is the multi-model averaged species richness and \hat{S}_i is the species richness inferred from model i . Prior to averaging, regressions were evaluated by examining the normality and homoscedasticity of residuals. A model was considered as not providing an adequate fit and excluded from final averaging if the Lilliefors extension of the Kolmogorov normality test or the Pearson's product moment correlation coefficient with areas was significant at the 5% level.

2.3.2. Species richness comparisons between taxa across lagoons

The SAR, because it describes the scaling of species number with area, has recently been suggested as a standardisation tool to classify a lagoon's *ecological status* with respect to species richness (Sabetta et al., 2007). This approach conceptually distinguishes good and poor status ecosystems with respect to species richness as those with observed species richness higher and lower respectively than predicted by their surface area using the SAR (Sabetta et al., 2007). However this approach does not provide a strict criterion to define the distance to the SAR above or below which water body can be classified in different classes of *ecological status*. Here we extend this approach and exemplify it for macro-invertebrates in Italian lagoons, building on recent methodological advances in richness hotspot detection (Guilhaumon et al., 2008).

In conservation biology, hotspots of species richness are identified using SARs, based on departures from the regression predictions. Residuals have been used repeatedly (Veech, 2000; Hobohm, 2003; Fattorini, 2006) but cannot distinguish between true hotspots and other areas of high species richness (Ulrich and Buszko, 2005), which may lead to the unsettling conclusion that functions with the poorest fit to the data are the best at identifying hotspots (Veech, 2000). As a robust alternative, the use of the position of regions relative to the confidence interval of multi-model SARs has been advocated (Guilhaumon et al., 2008). In the multi-model SAR framework, confidence intervals are devised to take into account model-selection and parameter estimation uncertainty by using a non-parametric bootstrapping procedure (see Guilhaumon et al., 2008).

In the same vein, as for richness hotspot detections, coastal lagoons can be classified according to their *ecological status* with respect to species richness by ranking them based on their position with respect to the confidence interval of a multi-model SAR. The WFD classification scheme for water quality includes five status classes: high, good, moderate, poor and bad. 'High status' being defined as the 'reference conditions' associated with no or very low human pressure. The quantitative transposition of such a qualitative classification scheme can be formalised in the context of species richness by imposing "bounds" in the confidence interval of a multi-model SAR. For example we defined here 'High status' lagoons – equivalently richness hotspots – as those above the 99%

confidence interval of the multi-model SAR for Italian coastal lagoons, these lagoons would thus represent the best status achievable. The present framework will provide effective standardisation tools only if the multi-model SAR is built using a representative set of TW ecosystem type in a given GIG, i.e. encompassing all the possible *ecological statuses* (from 'High' to 'Bad') and, ideally, across the whole range of lagoons areas. The present study was established at a national scale and although the data set was certainly representative for the Italian Peninsula region, we do not have sufficient lagoons available to propose a complete classification including all the different thresholds for the distinction among the 5 status categories. We illustrate our conceptual approach by simply proposing working definitions for 'High status' (true species richness hotspots) and respectively 'Bad status' (or true species richness coldspots) as the lagoons respectively above and below the 99% confidence interval of the multi-model SAR among the 18 lagoons under study. We additionally used the position of lagoons in multi-model SAR confidence interval to rank the 18 Italian lagoons under study with respect to their annelid, arthropod, mollusc and total species richness, and used these rankings as proxies for the relative *ecological status* at the Italian country scale.

We investigated the concordance of spatial patterns of *ecological status* with respect to annelid, arthropod, mollusc and total macro-invertebrate species richness. To this aim we tested pair-wise correlations between taxa using Kendall rank correlation tests (the ranking with respect to area was such that the largest lagoon ranked first). We additionally used Kendall rank correlation tests to investigate whether the current levels of protection in Italian lagoons reflect their *ecological status* with respect to annelid, arthropod, mollusc and total macro-invertebrate species richness (the ranking with respect to protection level was such that the lagoon accumulating the most protection measures ranked first) or simply reflect their area (with small or conversely large lagoons better protected).

All analyses described below were implemented within the R statistical programming environment (R Development Core Team, 2011). SAR analyses were conducted using the "mmSAR" R-package (Guilhaumon et al., 2010).

3. Results

3.1. Species richness observations and estimations

Observed total macro-invertebrate species richness per lagoon ranged from 34 to 487 species with a mean of 130.44 (Appendix A, Table A.1). The relative contribution of arthropods to the total macro-invertebrate diversity in coastal lagoons was higher than that of annelids and molluscs for observed species richness and all the estimators considered (Appendix A, Table A.2). However, the arthropod contribution was generally only significantly higher than mollusc contribution, except for the Jackknife2 estimator (Appendix A, Table A.3; Multiple comparison test between treatments after Kruskal–Wallis test; Siegel and Castellan, 1988).

The estimated richness values were significantly higher than the observed ones for all the estimators considered (one-sided paired two-sample Wilcoxon tests, $n = 18$, all significant at the 0.001 level; Appendix A, Table A.4). Depending on the estimator and the higher taxon considered, observed species richness represented between about 11% and 100% of the estimated species richness (Appendix A, Table A.1). All estimators yielded species richness estimations which were not significantly different for the majority of macro-invertebrate higher taxa and total species richness (Kruskal–Wallis rank sum test, $n = 18$, p -values: Annelids (0.72), Molluscs (0.84), Total (0.06)). Arthropods were an exception

(p -value: <0.01), but only the Chao2 and Bootstrap estimators yielded significantly different richness estimations at the 5% level (Multiple comparison test between treatments after Kruskal–Wallis test).

3.2. SAR modelling

The results of SAR analyses are presented in Table 2. The best R^2 values for non-linear regressions across data sets ranged from 0.015 (Arthropods/Chao) to 0.335 (Molluscs/observed richness). None of the eight SAR models considered in this study provided an adequate fit for the “total macro-invertebrates/Chao” data set. Model-selection results were homogeneous both across macro-invertebrate higher taxa and across species richness estimators for the same higher taxa, with substantial support for the simplest models (i.e. models with 2 parameters, Table 2). Summing $AICc-W$ across model shapes revealed that convex models were given the strongest support for all data sets. The exponential model provided generally the best fit for the total number of macro-invertebrates, annelids and molluscs, whereas the Monod model provided the best fit for arthropods (Table 2). Simple asymptotic and non-asymptotic models generally obtained equivalent support for all the data sets ($D-AICc < 2$, Table 2).

The hotspot analysis revealed a consistent pattern across the data sets in that the number of lagoons identified as coldspots (or ‘Bad’ ecological status with respect to species richness) always surpassed the number of hotspots (or ‘Good’ ecological status with respect to species richness), regardless of the species richness estimator considered (Fig. 1; Appendix A, Table A.5).

3.3. Correlation analyses

The results of Kendall ranking correlation analyses are presented in Tables 3 and 4. Pair-wise correlation coefficients between rankings based on the different species richness estimators considered were generally positive, strong and highly significant regardless of the macro-invertebrate higher taxon considered (Table 3). Arthropod is the only higher taxon for which the Chao2 estimator yielded moderate ranking correlations with observed species richness and the Bootstrap estimator (respective Kendall's taus 0.386 and 0.373, p -values 0.003 and 0.032, Table 3).

The different estimators of species richness yielded comparable pair-wise correlation coefficients between rankings based on the species richness of the four higher taxa considered, and total macro-invertebrate species richness (Table 4): although all rankings of lagoons based on macro-invertebrate higher taxa were significantly correlated with the ranking based on total macro-invertebrate species richness, the ranking based on mollusc richness consistently showed the highest correlation (mean Kendall's taus $0.595 \pm SD 0.026$). Correlations between rankings based on

molluscs and annelids or arthropods were generally low and non-significant (Table 4).

The correlations between the rankings based on species richness and the ranking based on the level of protection of Italian lagoons were consistently low and non-significant across taxa, regardless of the species richness estimator considered (range of Kendall's tau $[-0.249, 0.178]$, range of p -values $[0.174; 0.969]$). Correlations between the ranking based on lagoon area and all other rankings were marginal and non-significant (range of Kendall's tau $[-0.15, 0.268]$, range of p -values $[0.131; 1]$).

4. Discussion

4.1. SAR modelling

Our SAR analyses for macro-invertebrates of Italian lagoons follow that from a similar study performed by Sabetta et al. (2007). Although these authors used a slightly different set of lagoons and modelled the SAR using only log-linear Power relationships, the two studies provide complementary results.

First, our analyses revealed substantial variation in the strength of the effect of area on macro-invertebrate species richness. The percentage of variation in species richness explained by area never exceeds 33.5% (Molluscs/Sobs) and has a lower bound of 0% for Arthropods/Chao2 (note that for this data set the Negative Exponential model yielded a negative R^2 , indicating a complete lack of fit of the model; Kvålseth, 1985). These results are in accordance with Sabetta et al. (2007) who reported low R^2 for macro-invertebrates log-linear power SARs. This suggests that variation in surface area, even if of more than 3 orders of magnitude, may explain only a small part of the variation in species richness and that other factors are particularly important in shaping biodiversity in coastal lagoon ecosystems like in other macroecological studies (e.g. Guilhaumon et al., in press). For example, physical factors such as the width of seaward outlet and water salinity have been demonstrated to increase the proportion of explained variation in species richness (Sabetta et al., 2007). Similarly, different degrees of human pressures for the studied lagoons that should be translated into different ecological statuses according to the WFD would lead to additional variability and high scattering around the SAR regression line. The low values of R^2 obtained with the Chao2 estimator as well as the general lack of fit of SAR models for total species richness using this estimator suggest that other estimators should be preferred when analysing SARs for macro-invertebrates in Italian lagoons.

Second, based on $AICc$ weights ($AICc-W$ in Table 2), there is generally substantial uncertainty surrounding the best-fitting model (no $AICc-W > 0.9$). Although the non-asymptotic exponential model was the most successful in explaining the SAR for all data sets but arthropods, asymptotic models obtained the best support depending on the species richness estimator considered (i.e. the Monod model for Annelids/Chao2 and Molluscs/(observed species richness, Chao2) and the negative exponential model for total species richness/Jackknife2). For arthropods, the two convex and asymptotic negative exponential and Monod models obtained the greatest support, depending on the species richness estimator considered. A consistent pattern across the data sets was that complex models always obtained low support compared to more simple ones (i.e. 3-parameters models always exhibited $D-AICc > 2$).

These results, taken together, support the view that SARs for macro-invertebrates in Italian lagoons may take different convex shapes according to the taxon under study and that various simple models should be examined in SAR analyses (Fig. 1, Connor and McCoy, 1979; Stiles and Scheiner, 2007; Guilhaumon et al., 2008,

Table 1

The SAR models used in our analyses, their analytical formula and their shape. S = species richness, A = Area, and c, d, f, z = fitted parameters.

Model	Code	Number of parameters	Formula	Shape type
Power	power	2	$S = cA^z$	Convex
Exponential	expo	2	$S = c + z \log A$	Convex
Negative exponential	negexpo	2	$S = d[1 - \exp(-zA)]$	Convex
Monod	monod	2	$S = d/(1 + cA^{-1})$	Convex
Rational function	ratio	3	$S = (c + zA)/(1 + dA)$	Convex
Logistic	logist	3	$S = c/(f + A^{-z})$	Sigmoid
Lomolino	lomolino	3	$S = d/1 + (z \log(f/A))$	Sigmoid
Weibull	weibull	3	$S = d[1 - \exp(-cA^z)]$	Sigmoid

Table 2
Results of model-selection procedures. $D-AICc$ are differences in $AICc$, $AICc-W$ values correspond to model weights that are equivalent to model probabilities in being the best to fit the data set, R^2 – coefficients of determination. Dashed cells correspond to models that failed to respect the regression hypotheses for the given data set. Results are given for each combination of macro-invertebrate higher taxon (annelids (a); arthropods (b); and molluscs (c); and total species richness (d)) and richness estimator (Chao2 (Chao), Jackknife1 (Jack1), Jackknife2 (Jack2) and Bootstrap (Boot)). Model codes as in Table 1.

	Sobs			Chao			Jack1			Jack2			Boot		
	$D-AICc$	$AICc-W$	R^2	$D-AICc$	$AICc-W$	R^2	$D-AICc$	$AICc-W$	R^2	$D-AICc$	$AICc-W$	R^2	$D-AICc$	$AICc-W$	R^2
a) Annelids															
power	0.061	0.276	0.227	1.114	0.177	0.118	0.148	0.270	0.24	0.265	0.247	0.24	0.087	0.277	0.235
expo	0.000	0.285	0.23	–	–	–	0.000	0.291	0.247	0.000	0.282	0.251	0.000	0.289	0.239
negexpo	2.374	0.087	0.121	0.405	0.253	0.152	2.633	0.078	0.128	2.403	0.085	0.144	2.569	0.080	0.122
monod	1.398	0.142	0.168	0.000	0.309	0.171	1.404	0.144	0.186	1.099	0.163	0.204	1.462	0.139	0.175
ratio	3.368	0.053	0.23	3.195	0.063	0.179	3.251	0.057	0.251	3.173	0.058	0.259	3.312	0.055	0.241
logist	3.508	0.049	0.224	2.833	0.075	0.195	3.563	0.049	0.238	3.298	0.054	0.254	3.533	0.049	0.232
lomolino	3.338	0.054	0.231	3.307	0.059	0.174	3.319	0.055	0.248	3.266	0.055	0.255	3.343	0.054	0.24
weibull	3.327	0.054	0.232	3.145	0.064	0.181	3.290	0.056	0.25	3.215	0.057	0.257	3.315	0.055	0.241
b) Arthropods															
power	1.186	0.151	0.168	0.095	0.233	0	0.906	0.161	0.137	0.805	0.163	0.116	1.053	0.157	0.155
expo	0.851	0.179	0.183	0.095	0.233	0	0.691	0.179	0.147	0.648	0.177	0.124	0.775	0.181	0.168
negexpo	0.598	0.203	0.195	1.620	0.109	–0.088	0.220	0.226	0.169	0.000	0.244	0.155	0.438	0.214	0.184
monod	0.000	0.274	0.221	0.000	0.244	0.005	0.000	0.253	0.18	0.036	0.240	0.153	0.000	0.266	0.203
ratio	3.361	0.051	0.221	3.336	0.046	0.007	3.295	0.049	0.183	3.214	0.049	0.162	3.345	0.050	0.204
logist	3.823	0.041	0.201	3.181	0.050	0.015	4.168	0.031	0.142	5.179	0.018	0.065	3.986	0.036	0.175
lomolino	3.347	0.051	0.222	3.458	0.043	0	3.306	0.048	0.182	3.131	0.051	0.166	3.363	0.050	0.203
weibull	3.427	0.049	0.218	3.458	0.043	0	3.145	0.052	0.189	2.905	0.057	0.176	3.495	0.046	0.197
c) Molluscs															
power	–	–	–	0.975	0.144	0.186	0.623	0.212	0.254	0.303	0.241	0.220	–	–	–
expo	–	–	–	0.327	0.199	0.215	0.000	0.289	0.279	0.000	0.280	0.232	0.000	0.336	0.300
negexpo	1.345	0.208	0.237	0.628	0.172	0.201	2.392	0.087	0.177	3.122	0.059	0.087	1.508	0.158	0.239
monod	0.000	0.407	0.292	0.000	0.235	0.229	0.679	0.206	0.252	1.136	0.159	0.183	0.461	0.267	0.282
ratio	2.251	0.132	0.335	2.811	0.058	0.252	2.758	0.073	0.303	3.758	0.043	0.215	2.810	0.082	0.321
logist	–	–	–	2.096	0.082	0.281	–	–	–	2.105	0.098	0.284	–	–	–
lomolino	2.433	0.121	0.244	3.015	0.052	0.244	3.028	0.064	0.293	3.137	0.058	0.242	3.009	0.075	0.314
weibull	2.250	0.132	0.253	2.797	0.058	0.252	2.866	0.069	0.299	3.011	0.062	0.247	2.826	0.082	0.320
d) Total															
power	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
expo	0.000	0.387	0.311	–	–	–	0.000	0.548	0.277	–	–	–	0.000	0.385	0.296
negexpo	2.050	0.139	0.228	–	–	–	1.745	0.229	0.203	0.000	0.706	0.192	1.957	0.145	0.216
monod	0.421	0.314	0.295	–	–	–	–	–	–	–	–	–	0.412	0.313	0.279
ratio	3.259	0.076	0.315	–	–	–	3.273	0.107	0.280	–	–	–	3.263	0.075	0.300
logist	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
lomolino	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
weibull	3.053	0.084	0.323	–	–	–	3.106	0.116	0.287	1.747	0.294	0.261	3.084	0.082	0.307

in press). For example, our findings of a substantial support for asymptotic SARs for arthropods (Table 2) would not be taken into account in classical analyses assuming (convex and non-asymptotic) power SARs. In turn, this could have affected the outcome of the present ecological status analysis. In our study the SAR for annelids was adequately fitted by the power model but not in Sabetta et al. (2007), this illustrates the fact that when compared with its non-linear counterpart, the log-linear power SAR model can provide fits at odds with real patterns (Fattorini, 2007). Furthermore, when regressions are tested for satisfaction of residual distributional properties (i.e. normality and homoscedasticity), having at hand a wide range of functional forms may allow one to make inferences about the SAR in situations where the power SAR model is not appropriate (Smith, 2010). Nevertheless, despite the uncertainties about the model used, the general picture that emerges is that a low albeit significant proportion, i.e. c. 25–30%, of species richness can be explained by surface area alone. Thus, it is critical to take area effects into account when comparing the biodiversity of the macrozoobenthos in Italian lagoons ranging in surface area from 0.19 to 552 km².

4.2. Species richness comparisons between taxa across lagoons

Our analyses are merely an exemplification of how multi-model SARs could be used for conservation applications by identifying areas of exceptionally high (or low) biodiversity in the specific context of the WFD. The data we used were compiled over 25 years

and represent the total species inventories rather than results of standardised sampling campaigns (which are generally not available at regional scales). In doing so, the differences in the SAR between taxa are likely related to differences in the species life history and ecological requirements. However, although we controlled for sampling incompleteness and uneven sampling effort, our data may not take into account potential local extinction and dispersion events since the time of study. Furthermore, because sampling effort was not available for each lagoon, the present analysis is certainly still imprinted by a bias resulting from different sampling efforts or sampling strategies (a work done in one paper could lead to a more exhaustive and adequate sampling than gathering several publications). Consequently caution is needed when using the results of our study to evaluate the protection of Italian lagoons.

From a methodological perspective, multi-model SARs appear as a simple and robust tool for definition and monitoring of ecological status of water bodies within the WFD context. Conditional on the proper parameterisation of a multi-model SAR (see Section 2.2) for each combination of GIG, BQE and types of water bodies (e.g. lagoons, coastal lakes or ponds), one can define a gradient of ecological conditions with respect to species richness that take into account model-based uncertainties in the scaling of species richness with area. The classification of water bodies into the five status classes of the WFD (high, good, moderate, poor and bad) for their species richness corrected for surface area effects can be based on the distribution of species richness levels around the multi-model

Table 3

Kendall rank correlations between ranks of lagoons based on observed species richness (Sobs), the Jackknife1 (Jack1), the Jackknife2 (Jack2) and the Bootstrap (Bootstrap) estimators of species richness. Kendall τ are presented in the lower part of the table and associated p -values are in the upper part. Results are given for (a) annelid; (b) arthropod; (c) mollusc species richness; and (d) total macro-invertebrates.

	Species	Chao	Jack1	Jack2	Boot
a) Annelids					
Species	–	0	0	0	0
Chao	0.791	–	0	0	0
Jack1	0.791	0.817	–	0	0
Jack2	0.699	0.804	0.908	–	0
Boot	0.882	0.83	0.908	0.817	–
b) Arthropods					
Species	–	0.026	<0.001	<0.001	<0.001
Chao	0.386	–	0.003	<0.001	0.032
Jack1	0.804	0.503	–	<0.001	<0.001
Jack2	0.725	0.608	0.895	–	<0.001
Boot	0.935	0.373	0.843	0.765	–
c) Molluscs					
Species	–	<0.001	<0.001	<0.001	<0.001
Chao	0.699	–	<0.001	<0.001	<0.001
Jack1	0.908	0.739	–	<0.001	<0.001
Jack2	0.752	0.817	0.843	–	<0.001
Boot	0.987	0.712	0.922	0.765	–
d) Total					
Species	–	–	<0.001	<0.001	<0.001
Chao	–	–	–	–	–
Jack1	0.856	–	–	<0.001	<0.001
Jack2	0.83	–	0.922	–	<0.001
Boot	0.961	–	0.895	0.869	–

SAR fit. This will require the definition of appropriate quantiles in the distribution patterns around the multi-model SAR. Here we have only distinguished 'High' and 'Bad' status for water bodies as respectively hotspots and coldspots of species richness (for example here hotspots and coldspots were defined as the lagoons outside the 99% confidence interval of the multi-model SAR). Alternatively, another strategy would be to calibrate a multi-model SAR using only water bodies representative of the "reference status", resulting in a "reference status" SAR against which the other water bodies of the GIG can be compared. However it is unlikely that such "reference status" water bodies still exist currently along a wide range of areas.

The results of the present analyses revealed complementary insights about the use of species richness estimators, the spatial patterns of macro-invertebrates species richness and their congruence with the level of protection of Italian coastal lagoons.

First, for all taxa, estimated richness values were different (and higher) than the observed ones, although the magnitude of these differences varied widely among estimators, taxa and lagoons (Appendix A, Table A.1). However, regardless of the species richness estimator considered, model-selection patterns and R^2 values were similar (Table 2), suggesting a comparable SAR shape for all the estimators considered. These results suggest that little is gained when using these estimators which is in accordance with a recent study investigating the effect of species richness estimators on the shape of the SAR (Borges et al., 2009). Indeed, the authors found that although the intercept of log-linear power SAR was significantly higher when richness estimators were used instead of raw richness, the slope and goodness of fit of such SARs were not affected.

Second, the hotspot analysis revealed a consistent high relative number of coldspots (or 'Bad' ecological status lagoons with respect to species richness) (Fig. 1) ranging from 16.67% for Molluscs/Jackknife2 to 44.44% for Molluscs/Sobs, Annelids/Chao2, Arthropods/Chao2 and Molluscs/Bootstrap. These results may alternatively reflect a poor global ecological status across Italian lagoons or

Table 4

Kendall rank correlations between ranks of lagoons based on total macro-invertebrates, annelids, arthropods and molluscs species richness, the level of protection and surface area of Italian coastal lagoons. Kendall τ are presented in the lower part of the table and associated p -values are in the upper part. Results are given for: (a) observed species richness (Sobs); and (b) the Chao2 (Chao); (c) the Jackknife1 (Jack1); (d) the Jackknife2 (Jack2); and (e) the Bootstrap (Bootstrap) estimators of species richness. Dashed cells correspond to models that failed to respect the regression hypotheses for the given data set.

	Total	Annelids	Arthropods	Molluscs	Protection	Area
a) Sobs						
Total	–	0.014	<0.001	<0.001	0.969	0.201
Annelids	0.425	–	0.096	0.369	0.332	0.823
Arthropods	0.608	0.294	–	0.048	0.907	1
Molluscs	0.608	0.163	0.346	–	0.727	0.41
Protection	–0.007	0.178	–0.021	–0.064	–	0.174
Area	0.229	0.046	–0.007	0.15	0.249	–
b) Chao						
Total	–	–	–	–	–	–
Annelids	–	–	0.112	0.41	0.461	0.881
Arthropods	–	0.281	–	0.654	0.907	0.41
Molluscs	–	0.15	0.085	–	0.174	0.765
Protection	–	0.135	0.021	–0.249	–	0.174
Area	–	–0.033	–0.15	0.059	0.249	–
c) Jack1						
Total	0	0.004	<0.001	<0.001	0.727	0.131
Annelids	0.49	0	0.017	0.152	0.461	0.941
Arthropods	0.582	0.412	0	0.068	0.907	0.765
Molluscs	0.608	0.255	0.32	0	0.415	0.654
Protection	–0.064	0.135	–0.021	–0.149	0	0.174
Area	0.268	0.02	0.059	0.085	0.249	0
d) Jack2						
Total	–	0.002	0.009	0.001	0.786	0.175
Annelids	0.529	–	0.048	0.048	0.669	0.941
Arthropods	0.451	0.346	–	0.175	0.727	1
Molluscs	0.556	0.346	0.242	–	0.2	0.881
Protection	–0.05	0.078	–0.064	–0.235	–	0.174
Area	0.242	–0.02	0.007	0.033	0.249	–
e) Boot						
Total	–	0.009	0.001	<0.001	0.907	0.229
Annelids	0.451	–	0.021	0.369	0.415	1
Arthropods	0.556	0.399	–	0.048	0.846	1
Molluscs	0.608	0.163	0.346	–	0.669	0.369
Protection	–0.021	0.149	–0.036	–0.078	–	0.174
Area	0.216	0.007	0.007	0.163	0.249	–

a strong intra-type variability in the present set of water bodies (Sabetta et al., 2007).

Third, the high and significant ranking correlation for molluscs and total macro-invertebrate species richness suggest the potential use of molluscs as a surrogate for total macro-invertebrates diversity in Italian coastal lagoons. These results are consolidated by the fact that molluscs are not over-represented in the calculation of total macro-invertebrates diversity. Indeed, the relative contribution of molluscs to the total macro-invertebrates diversity was consistently significantly lower than the one of arthropods and equivalent to the contribution of annelids. These results illustrate also the relevance of surrogacy analyses: a specific taxon that is representative of total macro-invertebrate diversity and which is not over-represented should confidently serve as surrogate for total macro-invertebrates in the context of analyses relevant to the WFD.

Finally, the correlations between the ranking based on the level of protection of Italian coastal lagoons and taxonomic diversities and the ranking based on surface areas were low (or marginal) and not significant. The low correlation between ranking based on lagoon surface areas and ranking based on taxonomic diversities simply illustrates the relevance of the use of SARs to compare species richness of regions of varying area and this even when variations in area contribute only moderately to variations in taxonomic richness. The marginal correlation between lagoon surface areas and levels of protection revealed no bias towards the

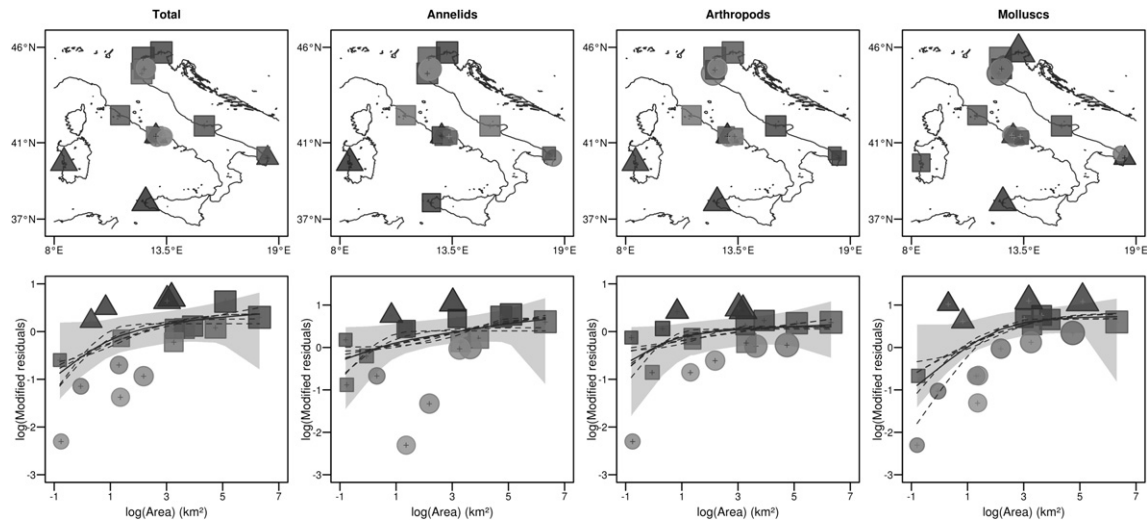


Fig. 1. Maps and species–area relationships (SARs) of Italian coastal lagoons. On maps and plots, a symbol represents a lagoon (triangle: richness hotspots, circles: richness coldspots, squares: none of the former). The size of the symbol is proportional to the lagoon surface area and the grey intensity is proportional to its ranking with respect to the diversity of the focus taxon. On plots the broken lines are regression lines of valid SAR models (see Table 1), the continuous line is the multi-model SAR and the grey shading is the 99% confidence interval around the multi-model SAR. Note that SARs are presented on a bi-logarithmic scale for clarity although SAR models were fitted in an arithmetic space (see Section 2.3.1). Species richness is shown as the modified ('positivised') residual of log richness regressed against log sampling effort (see Section 2.2).

better protection of small or large lagoons. The absence of a significant correlation between the ranking based on taxonomic diversities of macrozoobenthos and the ranking based on the level of protection highlights a decoupling between conservation measures and the gradient of *ecological status* with respect to macro-invertebrates species richness in Italian coastal lagoons. Using multi-model SAR may be very helpful to identify lagoons of exceptional biodiversity that merit particular conservation attention. In addition, the identification of coldspots may highlight lagoons with a bad ecological status that requires particular efforts to improve the current situation according to the WFD.

The methodological framework presented in this paper would also apply in the case of investigations beyond the taxonomic signal. One step further than relying on species richness to assess biodiversity hotspots and to detect 'Good' *ecological status*, we may include other biodiversity facets more related to human-mediated environmental pressures (e.g. Mouillot et al., 2006). For example, the level of functional diversity, defined as the diversity of traits held by organisms within a community, may show a more pronounced response to environmental stress than species richness (Flynn et al., 2009) with some functional groups or some particular combinations of traits being more sensible than others to such stress. Since the estimators of the level of functional diversity (functional richness), the number of functional groups or the range of functional traits (Villéger et al., 2008), monotonically increases with species richness (more species support more functions on average), multi-model SARs represent a valuable tool to estimate the expected level of functional diversity for a given area. Allowing to differentiate areas holding a higher diversity of functional traits than what is expected from their area, meaning that different functional strategies may co-occur in these systems or that many different resources or habitats are present, contributing to a 'Good' *ecological status*.

5. Conclusion

In conclusion, the present analysis of SARs for benthic invertebrates in Italian coastal lagoons highlights several points. From a methodological perspective, multi-model SARs seems simple and robust tools for the definition and the monitoring of *ecological*

status of water bodies within the WFD context. Although we focused here on macro-invertebrate species richness and coastal lagoons in the Italian country, the approach may be generalised to all BQEs (phytoplankton, macroalgae, angiosperms, benthos or fishes) and aspects of diversity that scale with area, water bodies types (e.g. rivers, lakes or coastal/transitional ecosystems) and GIGs (e.g. Atlantic Ocean, Baltic, Mediterranean, North Sea or Guyana). The flexibility of multi-model SARs provides a way to handle recurrent non-power function behaviour of the SAR which may happen for particular combinations of BQEs and GIGs (Smith, 2010).

In the particular context of benthic invertebrates in Italian coastal lagoons, despite our efforts to find meaningful corrections for bias, our analyses are still imprinted by a remaining bias resulting from varying sampling efforts among the different published studies we used as data sources. This said, our results clearly suggest that the strength of conservation management is decoupled from the gradient of *ecological status* with respect to macro-invertebrates species richness in Italian lagoons. Hence, a high level of macro-invertebrate biodiversity appears to be overlooked as a criterion for the prioritisation of conservation efforts. Indeed most of the current conservation efforts regarding Italian lagoons are focused on vascular plants and vertebrates. However, according to the WFD, the overall *ecological status* of water bodies may take into account phytoplankton and benthic macro-invertebrates communities (EU WFD Annex V Section 1.1.3; 2000) and calls for improving the status of lagoons with an *ecological status* below good. Our results suggest that the management plans of Italian protected areas should focus more strongly on the WFD requirements.

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Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.ecss.2011.12.001.

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