



# Taxonomic relatedness does not reflect coherent ecological response of fish to protection



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## ABSTRACT

Marine Protected Areas (MPAs) are increasingly used for biodiversity conservation and the management of sustainable fisheries. The use of taxonomic surrogates in routine monitoring of the reserve effects on fish assemblages may represent a promising method due to its substantial technical and economic benefits. However, higher taxonomic ranks should be used as surrogates with caution, especially for fish, where the approach is still virtually undocumented. This study aims to shed light on relationships between taxonomic relatedness and ecological similarity, which is crucial to assess the relevance of species surrogacy to reflect species-level information and detect changes in fish related to protection regimes. By analyzing data from a Mediterranean MPA, we show that rather being related to taxonomic relationships, the ability of higher taxa to reflect species-level patterns was explained in terms of aggregation level and distribution of species within taxa. Null models using random aggregations of species were created to identify the best surrogates able to depict changes in responses of assemblages to protection observed at the species-level. Comparison of null model predictions with the more classical higher-taxon approach revealed that the latter was not reliable because, unlike null model outcomes, surrogates determined empirically were not relevant for other subsequent independent monitoring. The effectiveness of species surrogates to depict changes in responses of assemblages to protection observed at the species-level depended (1) on the numerical resolution of the aggregation and (2) the magnitude of differences between protected and unprotected locations. Such findings suggest that surrogacy approaches may be applied for routine monitoring of Mediterranean reef fish communities, although mere empirical determinations of sufficient taxonomy seems to be not reliable, legitimizing the use of alternative methods based on null models. Guidelines for the careful use of species surrogacy in the ecological evaluation of MPAs on fish assemblages are provided.

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## 1. Introduction

Overexploitation, habitat fragmentation, pollution and direct and indirect effects of climate change all concur to determine severe and possibly long-lasting alterations to marine ecosystems, particularly in coastal areas (Claudet and Fraschetti, 2010; Gray, 1997; Guidetti, 2006; Lotze et al., 2006). Especially at local scale (Micheli et al., 2012), Marine Protected Areas (MPAs) can represent effective tools in mitigating human impacts as they may help protecting or restoring biodiversity and ecosystem functioning by

reducing species mortality and habitat deterioration (Lester et al., 2009; Lubchenco et al., 2003), enhancing resilience and resistance of protected communities (Babcock et al., 2010; Bevilacqua et al., 2006; Fraschetti et al., 2013), and achieving sustainable fisheries by increasing catches outside their boundaries (Di Franco et al., 2012; Harmelin-Vivien et al., 2008; Roberts et al., 2001). The effective contribution of MPAs to conservation of marine ecosystems, however, strongly depends on the complex interplay among several factors, including the intensity of existing human pressures, spatial planning and networking, enforcement, social compliance, and economic issues (Abdulla et al., 2008; Claudet, 2011; Edgar et al., 2014). MPAs, therefore, require a constant evaluation of their effectiveness, which, in turn, is essential for an adaptive management in order to refine and achieve conservation goals (Gerber et al., 2005; Pomeroy et al., 2005).

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In most cases, evaluations aiming at quantifying the ecological effectiveness of MPAs consider the fish compartment, as it is directly affected by MPA regulations, rapidly respond to protection regimes (Halpern and Warner, 2002), include many commercial or attractive species, and can trigger, through trophic cascades, indirect effects on other ecological compartments (Guidetti, 2006). Whether at local (e.g. Guidetti, 2006; Williams et al., 2009), regional (e.g. McClanahan et al., 2007; Claudet et al., 2008, 2010; Guidetti et al., 2008, 2014), or global scale (e.g. Lester et al., 2009; Edgar et al., 2014), ecological assessment of MPAs often rely on single response variables, such as density, biomass, and diversity indices (Soykan and Lewison, 2015). Several works, however, highlighted the crucial role of considering structural and compositional changes in multivariate biological assemblages as indicators of ecological performances of MPAs (Ceccherelli et al., 2006; Claudet et al., 2011, 2006; Frascchetti et al., 2013, 2012; Micheli et al., 2005).

Such assessments are generally based on formal comparison of field data collected within and outside MPAs (Pelletier et al., 2008) through underwater visual census (Harmelin-Vivien et al., 1985), video recording (Cappo et al., 2003), experimental catches or landing data (Goñi et al., 2008). Irrespective of advantages and drawbacks of each sampling method, data collection implies the identification of fishes down to the species level. Fine taxonomic resolution may reveal problematic for inexperienced observers (Williams et al., 2006), particularly with some difficult taxa (e.g. Labridae), or when fish assemblages are very speciose. In most cases, the participation of expert taxonomists during and/or after sampling activities is advocated, although it is time-consuming and generates additional costs.

In such contexts, taxonomic sufficiency may represent a potential solution. The principle of this approach to species surrogacy is to detect changes in assemblages by identifying organisms at taxonomic levels higher than species (Ellis, 1985). The use of a coarse level of taxonomic resolution during sampling campaigns would be advantageous for the classification of organisms, which could be difficult even for expert taxonomists in certain conditions such as, for instance, during underwater visual censuses of fish assemblages. In the marine environment, taxonomic sufficiency has been mainly used to quantifying human impacts on benthic communities (see Terlizzi et al., 2003 for a review), showing that changes in assemblages observed at the species level might be often detected at coarse taxonomic resolution, and in most cases up to family level (Clarke and Warwick, 1998; Lampadariou et al., 2005; Terlizzi et al., 2009; Thompson et al., 2003). Many authors, however, argued that the use of a lower taxonomic resolution could obscure meaningful ecological information (e.g. Maurer, 2000; Terlizzi et al., 2003; Dethier and Schoch, 2006; Bevilacqua et al., 2009).

The taxonomic sufficiency approach relies on the implicit assumption that species within taxa of a given taxonomic rank (e.g. Family) would have close ecological niches, thus exhibiting similar responses to environmental conditions (Warwick and Clarke, 1993). However, taxa of the same taxonomic rank could denote separate categories without further equivalence (Bertrand et al., 2006) and functional similarity among species might not be related to close phylogenetic relationships (Carranza et al., 2011; Losos, 2008). Recent works on marine and freshwater invertebrates provided evidence that higher taxa might be considered as random groups of species not conveying coherent response to environmental changes (Bevilacqua et al., 2012; Siqueira et al., 2012). Therefore, the effectiveness of taxonomic surrogates in depicting species-level patterns might rely mostly on the numerical ratio between species and higher taxa rather than on taxonomic relatedness of species per se (i.e. the relative closeness of species in the Linnaean taxonomic hierarchy) (Bevilacqua et al., 2013). The

bulk of scientific literature on the use of taxonomic surrogates seems to suggest that such a condition might be common to different types of organisms (including plants, algae, and terrestrial invertebrates), habitats and environmental settings (Bevilacqua et al., 2012). Unfortunately, the limited number of case studies on the application of taxonomic sufficiency to fish assemblages (e.g. Saldivar-Lucio and Reyes-Bonilla, 2011; Hernandez et al., 2013; Mueller et al., 2013) strongly limits any generalization of such findings to this group of organisms. To date, some attempt has been done to explore the use of higher-taxon diversity as a proxy for species diversity in marine fish to set conservation priorities (Caro and O'Doherty, 1999; Vanderklift et al., 1998) although, to our knowledge, taxonomic sufficiency has never been applied to the assessment of the effectiveness of MPAs on fish assemblages.

Here, we use null models of taxonomic assembly to investigate mechanisms underlying the potential of taxonomic surrogates to retain species-level information when assessing changes in fish assemblages at varying regimes of protection. We based our work on density and biomass data collected at the Cerbère-Banyuls Marine Natural Reserve (France), one of the oldest and well-enforced MPAs of the Mediterranean Sea (Gabrié et al., 2012, <http://www.medpan.org>). More specifically, this study aims at (1) understanding whether the ability of higher taxa to mirror species-level patterns of change related to protection mostly depends on taxonomic relatedness or numerical relationships among taxa across the Linnaean taxonomic hierarchy, (2) exploring the putative links between taxonomic relatedness and functional similarity in fish assemblages, and (3) assessing the reliability of the classic taxonomic sufficiency approach compared with predictions from null models based on random taxonomic assembly. The potential application of taxonomic surrogates to fish assemblages is discussed, providing general guidelines for species surrogacy in monitoring the effectiveness of MPAs.

## 2. Methods

### 2.1. Study sites

The Cerbère-Banyuls Marine Natural Reserve is located on mainland and consists of a fully protected area (65 ha) surrounded by a partially protected area (585 ha). Fishing, diving and anchoring are banned in the fully protected area and regulated in the partially protected area. The MPA have been established for over 40 years (1974) and is well managed by local authorities. Positive effects of protection on fish has been demonstrated inside the MPA (Claudet et al., 2011; Lenfant et al., 2003) and outside its boundaries in term of spillover (Forcada et al., 2009; Harmelin-Vivien et al., 2008).

### 2.2. Sampling design and data collection

Sampling was undertaken at seven locations along the coast inside (one in the fully protected area, two in the partially protected area) and outside the MPA (two to the north and two to the south). Depending on the field characteristics, fish assemblages in each location were sampled in three or four randomly set sites hundreds of meters apart. At each site, six 25 × 5 m (125 m<sup>2</sup>) transects were positioned parallel to the coast on rocky bottoms between 8 and 10 m depth, corresponding to the depth range where the fish assemblage are the most sensitive to protection (Claudet et al., 2011). Fish were identified at species-level, counted and their size (total length) estimated by underwater visual censuses. Surveys were conducted during spring and autumn 2013 for a total of 264 transects.

Fish biomass was estimated by combining abundance with size estimates using existing length–weight relationships of each species (Crec'hriou et al., 2012, <http://www.fishbase.org>). Pelagic species (i.e. *Atherina* sp., *Boops boops*, *Sardina pilchardus*, *Sphyrna viridensis*, *Trachurus mediterraneus*), species with extremely heterogeneous distributions (i.e. *Chromis chromis*, *Oblada melanura*), and those individuals that were not identified down to species level (i.e. some *Mugilidae*, *Spicara* sp. and *Symphodus* sp.) were excluded from the analysis according to common practice in studies based on visual surveys (Claudet et al., 2006).

### 2.3. Grouping species into higher taxa

The ability of higher taxa (e.g. Genera, Families) to reflect species-level assemblage structure relies on the concept that taxonomically related species would share ecological features and coherent response to environmental variations. Thus, we assumed that grouping species into higher taxa would better reflect changes in fish assemblages related to protection regimes than if they were grouped regardless of the true taxonomic hierarchy. The assumption was tested by Spearman's rank correlation ( $\rho$ ) as a measure of the similarity of assemblage patterns between species and higher taxonomic levels (Somerfield and Clarke, 1995). We built a test based on random simulations in which  $\rho$  values between species and higher-taxon matrices were tested against  $\rho$  values between species and randomly aggregated matrices (see Bevilacqua et al., 2012, 2013 for further details). Firstly, for each of the four data sets (density and biomass during spring and autumn), we obtained matrices at different taxonomic levels (i.e. Genus, Family and Order) by summing for each sample (i.e. transect) the density or biomass of species belonging to the same taxa. Species-level and higher-taxon matrices were log-transformed and triangular matrices based on the Bray-Curtis among-sample dissimilarity were generated. Pair-wise Spearman correlations ( $\rho$ ) between the species-level and higher-taxon triangular matrices were then calculated (hereafter referred to as “observed”  $\rho$  values). Secondly, for each taxonomic level, we randomly aggregated species into higher taxa. Random assignments of species reflected their distribution among higher taxa in the true taxonomic hierarchy. Then, we also computed  $\rho$  values between species and randomly aggregated matrices (hereafter, referred to as “simulated”  $\rho$  values). Simulations were performed 1000 times for each taxonomic level. Finally, the observed  $\rho$  values (i.e. correlations  $\rho$  between species-level matrices and matrices at higher taxonomic levels) were tested against the mean ( $\pm 95\%$  CI,  $n = 1000$ ) of their corresponding simulated  $\rho$  values (i.e. correlations  $\rho$  between species-level matrices and randomly aggregated matrices).

### 2.4. Identifying suitable surrogates for species: taxonomic sufficiency vs. null models of species aggregation

The classical taxonomic sufficiency approach is based on separate analyses, which are performed at different taxonomic levels so to identify a suitable surrogate as the coarsest taxonomic level at which multivariate patterns of assemblages are consistent with those obtained at the level of species (Defeo and Lercari, 2004; Jones, 2008; Somerfield and Clarke, 1995). Such surrogates are assumed to give consistent results through time or in similar study contexts. Following the same rationale, we used spring data (density and biomass) as a pilot study to identify the sufficient taxonomic resolution able to depict species-level change in assemblages at varying protection levels following (1) the classical taxonomic sufficiency approach described above and (2) an alternative approach based on null models of species aggregation (see Bevilacqua et al., 2012, 2013). In contrast to the classical taxonomic sufficiency approach, which invokes putative ecological

similarities among species within taxa to explain the effectiveness of taxonomic surrogates, this alternative approach assumes that the ability of a given level of aggregation to depict species-level assemblage patterns depends on the aggregation ratio,  $\Phi$ , the ratio of the number of higher taxa to the total number of species in the assemblage (Bevilacqua et al., 2012). This procedure, therefore, aims at identifying the  $\Phi$  value below which changes in species-level assemblages cannot be detectable consistently. Autumn data (density and biomass) were employed to check whether surrogates derived from pilot data (spring) were suitable to detect the effect of protection as at species level in a subsequent independent survey.

As a first step, Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001) was performed to test for differences in fish density and biomass at species level between protection regimes. Three separated analyses were done, one for each pair-wise comparison between protection regimes, i.e. contrasting FP vs. PP, FP vs. UP and PP vs. UP. The design for the first two analyses (i.e. FP vs. PP and FP vs. UP) is asymmetrical because of the presence of a single fully protected location for FP. Here, the designs for the analyses involved two factors: “Location” (L, 3–5 levels, random) and “Site” (Si(L), 3–4 levels, random, nested in L). In the analyses, the Location term was partitioned into 1-d.f. contrast of the single FP location against PP (or UP) locations, and the variability among location in PP (or UP) (see Terlizzi et al., 2005). The design for the analysis contrasting PP vs. UP, instead, involves three factors: Protection (PP vs. UP, 2 levels, fixed), Location (L(PP vs. UP), 2–4 levels, nested in PP vs. UP) and Site (Si(L(PP vs. UP)), 3 levels, nested in L). Analyses were done separately for the two times of sampling (i.e. Spring and Autumn).

A Similarity Percentage analysis (SIMPER, Clarke, 1993) was also conducted for pair-wise tests to identify species most contributing to differences between protection regimes.

As a second step, results of species-level analyses on spring and autumn data were used as reference to identify surrogates and to check for their effectiveness, respectively. As far as the classical taxonomic sufficiency approach, PERMANOVA (designs as above) was conducted at different taxonomic resolutions (i.e. from species to order) on both density and biomass data from spring survey in order to empirically identify the sufficient taxonomic level. The coarser taxonomic resolution able to depict species-level patterns was considered as suitable, following the logic of taxonomic sufficiency. For the alternative approach based on null models of species aggregation, three separated null models of decreasing  $\rho$  at decreasing  $\Phi$  (one for each comparison between paired protection regimes) for both density and biomass spring data were built. For each null model, species were aggregated at random into progressively decreasing number of groups, thus simulating decreasing aggregation ratios  $\Phi$ . For each  $\Phi$ , random aggregations were repeated 1000 times and  $\rho$  values between species and randomly aggregated matrices were calculated. A semi-log model of  $\rho$  against  $\ln(\Phi)$  was fitted. Finally, for each  $\Phi$ , PERMANOVAs (designs above) were carried out based on all randomly aggregated matrices. The lowest aggregation ratio  $\Phi$  at which more than 95% of PERMANOVA tests on randomly aggregated matrices provided results consistent (i.e. within the same level of significance) with those obtained analyzing the species-level data was noted as  $\Phi_{low}$ . This value corresponds to the minimum  $\Phi$  predicted by the null model to detect difference in assemblage structure between the two examined protection regimes. Among the  $\Phi_{low}$  values obtained from the three separated null models, we selected the  $\Phi_{low}$  value sufficient to detect the same pattern of difference between all paired protection regimes as at species level. Each taxonomic level with a corresponding aggregation ratio higher than this  $\Phi_{low}$  value was then considered as a suitable surrogate (see Bevilacqua et al., 2012, 2013 for further details on the whole

procedure). Finally, to examine the reliability of the two methods, data from the subsequent independent survey carried out in autumn were analyzed using surrogates identified following the two approaches and results compared with those obtained at species level.

All PERMANOVAs were based on Bray-Curtis dissimilarity of log-transformed data, and each term in the analysis was tested with 5000 random permutations.

### 2.5. Relationships between taxonomic distance and functional similarity

The taxonomic sufficiency approach is based on the idea that species within the same taxon, especially at intermediate taxonomic levels (i.e. Genus, Family), would exhibit similar responses to environmental conditions because they are likely to share similar ecological features. Thus, it is reasonable to assume that functional similarity between two species might be strictly dependent on their closeness in the taxonomic hierarchy. To explore such a relationship, nine functional traits related to habitat preference, diet and behavior were selected (Table A.1; Claudet et al., 2010) and trait modalities were assigned to each fish species identified during the sampling. Some traits (variables) being semi-qualitative (e.g. average maximal size or depth and home ranges), whereas others are categorical (e.g. trophic guild or territoriality), we used the Gower distance between each pair of species to express their functional similarity based on the derived functional trait matrix (functional traits  $\times$  species). For each pair of species, we then determined the taxonomic distance ( $\omega$ ) in the Linnaean taxonomic hierarchy as a measure of taxonomic relatedness ( $1 - \omega$ ) (Clarke and Warwick, 1998). Functional similarity between each pair of species was plotted against the corresponding taxonomic relatedness and a linear regression was fitted to check whether closely related species were also functionally similar.

All analyses were implemented in the R statistical software version 3.0.1 (R Core Team, 2014) using the “doMC” package (Revolution Analytics, 2013) to optimize loops for simulations. PERMANOVAs were performed by recoding the “adonis” function of package “vegan” (Oksanen et al., 2013).

## 3. Results

For each taxonomic level, the observed  $\rho$  values between the species-level and higher-taxon matrices always fell within the 95% confidence interval obtained from simulated  $\rho$  values (Fig. 1), suggesting that grouping species according to the Linnaean

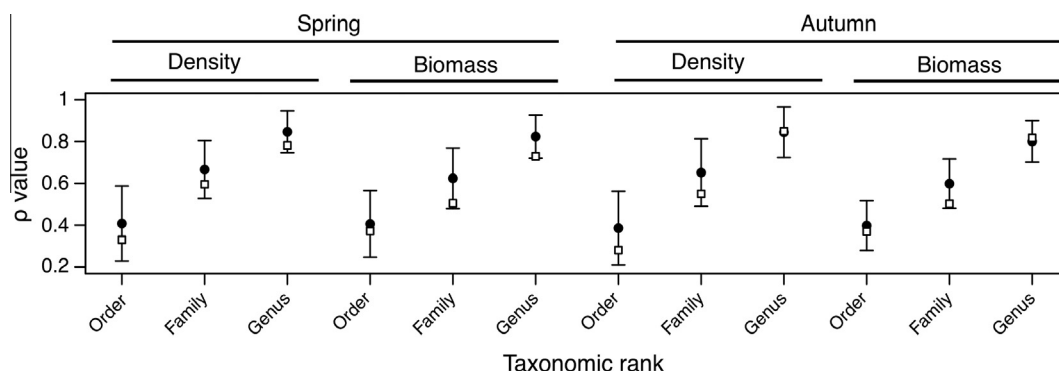
taxonomy does not allow retaining significantly greater information on species-level patterns than what expected by chance.

Results of PERMANOVA based on spring data showed that fish assemblages in the fully protected and partially protected areas did not differ, whereas both significantly differed from those in the unprotected area (Table 1). A significant effect of protection at the level of species was also detected for fish density in autumn, showing significant differences among all protection regimes (Table 1). The same patterns observed for fish density in spring and autumn, respectively emerged analyzing the corresponding biomass data (Table 1; see Tables B.1–3 for further details).

Results of PERMANOVA based on spring data at decreasing taxonomic resolution showed that species-level patterns in fish density were retained up to Family level (Table 2) indicating that, following a classical taxonomic sufficiency approach, genera and families should be considered as suitable surrogates for species in assessing protection effects. Results from spring data also showed that species-level patterns in fish biomass may be depicted consistently even up to order level (Table 2; see Table B.4 for further details).

Regression analyses based on spring data showed that reductions in  $\rho$  at decreasing  $\Phi$  followed a semi-log model for each pair-wise comparison between protection regimes for both fish density and biomass (Fig. 2), indicating that the information in aggregated matrices, and the potential ability of analyses to give same response as at species level, strongly depended on the aggregation ratio  $\Phi$ . For fish density, the lowest aggregation ratio allowing the 95% of tests to give same results as at species level ( $\Phi_{low}$ ) ranges between 0.29 and 0.20 and between 0.80 and 0.89 for fully protected vs. unprotected areas and partially protected vs. unprotected areas, respectively (Fig. 2). For fish biomass,  $\Phi_{low}$  was below 0.06 and between 0.09 and 0.06 for fully protected vs. unprotected areas and partially protected vs. unprotected areas respectively (Fig. 2). For both fish density and biomass,  $\Phi_{low}$  for fully protected vs. partially protected areas was not determined since fish assemblages did not differ between the two protection regimes. The overall aggregation ratios sufficient to obtain consistent response with species-level analyses for any comparison between protection regimes was  $\Phi_{low} = 0.89$  for density and  $\Phi_{low} = 0.09$  for biomass. Based on these thresholds, null models predicted that none of the investigated taxonomic levels might be suitable to detect the effect of protection on fish density as at species level, whereas all of them might be suitable analyzing fish biomass (Table 2).

Results of PERMANOVA on autumn data showed that, in contrast to predictions based on a classical taxonomic sufficiency approach, none of the higher taxonomic levels were able to depict consistently species-level patterns in fish density (Table 3; see Table B.4 for further details), suggesting that the empirical



**Fig. 1.** Observed and simulated Spearman's rank correlations ( $\rho$ ) between the species level matrix and taxonomically aggregated matrices (Genus, Family, Order) for each of the four data sets analyzed. □ = observed  $\rho$  values; ● = mean simulated  $\rho$  values ( $\pm 95\%$  CI,  $n = 1000$ ).

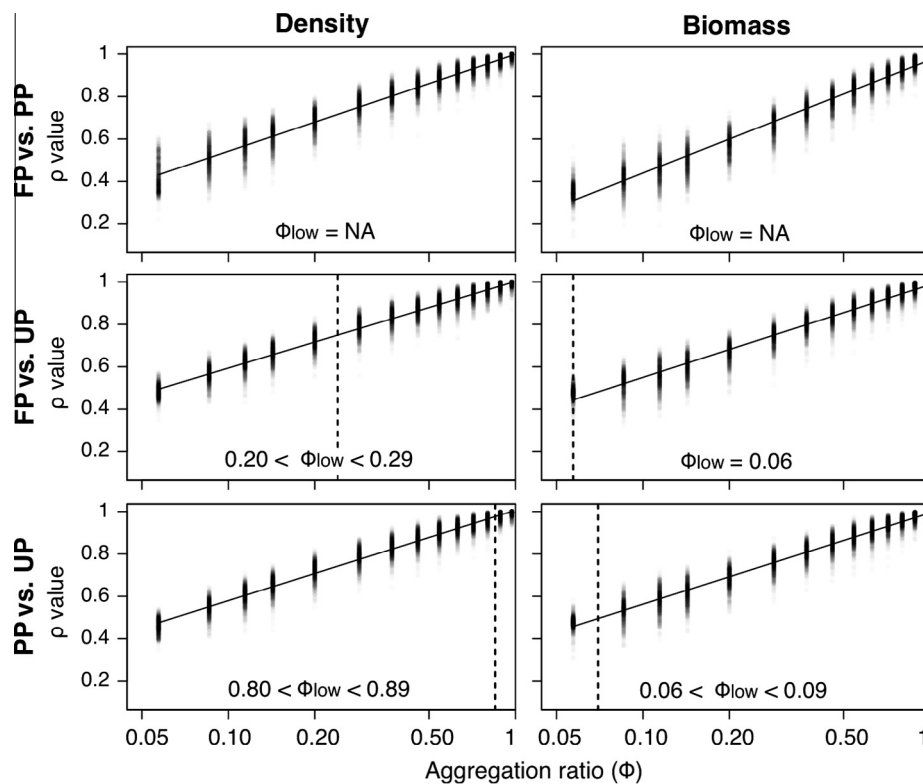


**Table 1**  
Summary of results of PERMANOVA tests for differences at species level between protection regimes in fish assemblage density and biomass for each time of sampling (spring and autumn). Analyses were based on Bray-Curtis dissimilarity of log-transformed data, with 5000 permutations (see Section 2).

Source of variation	SPRING						AUTUMN					
	Density			Biomass			Density			Biomass		
	MS	F	P	MS	F	P	MS	F	P	MS	F	P
FP vs. PP	876.4	0.71	0.724	762.5	0.63	0.771	1965.9	2.33	0.020	2278.4	2.07	0.037
FP vs. UP	2572.2	1.96	0.041	3209.3	2.4	0.030	3698.1	2.48	0.027	7518.7	5.49	0.001
PP vs. UP	2001.3	1.47	0.045	2167.1	1.75	0.027	1657.1	1.45	0.047	1826.7	1.77	0.013

**Table 2**  
Summary of PERMANOVA results based on spring data (density and biomass) at decreasing taxonomic resolution (see Table B.4 for further details). Congruence of results with those obtained using species-level data (see Table 1) is indicated and suitable taxonomic surrogates identified following the classical approach based on taxonomic sufficiency are given in bold. Aggregation ratios ( $\Phi$ ) for each taxonomic level are also showed along with null model predictions on surrogate effectiveness based on  $\Phi_{low}$ .  $\Phi$  values exceeding  $\Phi_{low}$  (see Fig. 2) are considered as indicative of surrogate effectiveness and are given in *italic*. \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; FP = fully protected area; PP = partially protected area; UP = unprotected area.

Data	Taxonomic level	Overall difference	Pair-wise comparisons	Congruence with species-level pattern	Aggregation ratio ( $\Phi$ )	Model prediction
Density	Genus	***	FP = PP $\neq$ UP	Yes	0.56	No
	Family	***	FP = PP $\neq$ UP	Yes	0.28	No
	Order	**	FP $\neq$ UP; FP = PP; PP = UP	No	0.11	No
Biomass	Genus	***	FP = PP $\neq$ UP	Yes	0.56	Yes
	Family	***	FP = PP $\neq$ UP	Yes	0.28	Yes
	Order	***	FP = PP $\neq$ UP	Yes	0.11	Yes



**Fig. 2.** Plot of Spearman's rank correlations ( $\rho$ ) values between the species level matrix and randomly aggregated matrices against the corresponding aggregation ratios ( $\Phi$ ) (spring data). The lowest aggregation ratio at which more than 95% of PERMANOVA tests on randomly aggregated matrices provided results consistent (i.e. within the same level of significance) with those obtained analyzing the species-level data ( $\Phi_{low}$ ) is indicated by the dotted line. FP = fully protected area; PP = partially protected area; UP = unprotected area. FP vs. PP:  $R^2 = 0.94$  and  $P$ -value  $< 0.001$  (density and biomass). FP vs. UP:  $R^2 = 0.95$  and  $P$ -value  $< 0.001$  (density);  $R^2 = 0.94$  and  $P$ -value  $< 0.001$  (biomass). PP vs. UP:  $R^2 = 0.95$  and  $P$ -value  $< 0.001$  (density);  $R^2 = 0.94$  and  $P$ -value  $< 0.001$  (biomass).

determination of the sufficient taxonomic resolution might be not reliable. Such results, instead, were completely aligned with predictions from null models of aggregation ratios (Table 3). Analyses on biomass data in autumn showed that all taxonomic

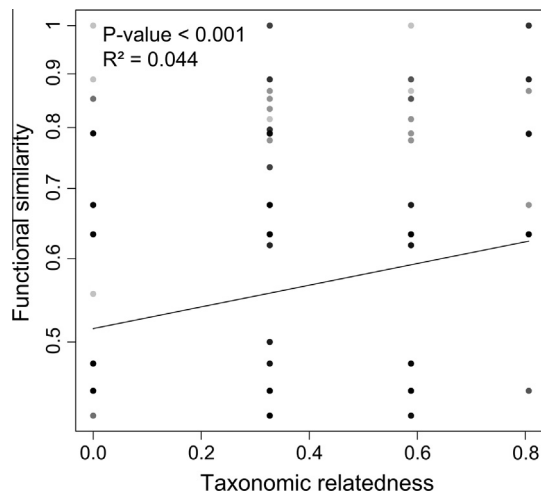
levels were suitable as surrogates, confirming predictions from both the taxonomic sufficiency approach and null models (Table 3).

Regression analysis on the fish sampled during this study showed that functional similarity and taxonomic relatedness were

**Table 3**

Summary of PERMANOVA results based on autumn data (density and biomass) at decreasing taxonomic resolution (see Table B.4 for further details). Congruence of results with those obtained using species-level data (see Table 1) is indicated. Congruence with predictions from the classical taxonomic sufficiency approach and from null models of taxonomic assembly based on spring data (see Table 2) are also showed. \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; FP = fully protected area; PP = partially protected area; UP = unprotected area.

Data	Taxonomic level	Overall difference	Pair-wise comparisons	Congruence with species-level pattern	Congruence with the TS predictions	Congruence with model predictions
Density	Genus	***	FP = PP ≠ UP	No	No	Yes
	Family	**	FP = PP ≠ UP	No	No	Yes
	Order	*	FP ≠ UP; FP = PP; PP = UP	No	No	Yes
Biomass	Genus	***	FP ≠ PP ≠ UP	Yes	Yes	Yes
	Family	***	FP ≠ PP ≠ UP	Yes	Yes	Yes
	Order	***	FP ≠ PP ≠ UP	Yes	Yes	Yes



**Fig. 3.** Plot of functional similarity against taxonomic relatedness calculated on each of the 630 pairs of the 36 species identified in the study. Results of the regression analysis are also reported.

significantly, but very weakly, correlated (Fig. 3), with variations in taxonomic relatedness between species explaining less than 5% of variability in their functional similarity ( $R^2 = 0.044$ ).

#### 4. Discussion

Difficulties in identifying fish to species level can lead to the use of higher taxa as surrogates for estimating species diversity when selecting and monitoring areas for conservation purposes. Our results showed that the aggregation of species into higher taxa (Genera, Families and Order) did not outperform random groups of species with the same aggregation ratio ( $\Phi$ ), in terms of reflecting species-level assemblage structure. As a corollary, random aggregation of species at a decreasing aggregation ratio ( $\Phi$ ) showed that the ability of taxonomic surrogates to mirror species-level changes in the multivariate patterns of fish assemblages depended on the numerical ratio between surrogates and species ( $\Phi$ ) rather than on the presumed ecological information they convey. This confirms results obtained in other organisms, from plants to invertebrates (Bevilacqua et al., 2012), and strengthens the generality of this pattern. In addition, the lack of a strong correlation between the functional similarity and taxonomic relatedness of fish species found in this study (see also Somerfield et al., 2008) reinforces the idea that higher taxa could not be considered as ecologically coherent groups of species. These outcomes combine in casting doubts on the ecological meaning of taxonomic surrogates and on the reliability of empirical determination of the sufficient taxonomic level.

In this study, we used two independent sampling occasions, i.e. spring and autumn, on fish assemblages to investigate the response of two approaches to species surrogacy: a more classical one based on taxonomic sufficiency and a new approach based on null models. At species level, the structure of fish assemblages, in terms of either density or biomass, differed between fully protected (FP) or partially protected (PP) and unprotected (UP) locations in spring and autumn, whereas assemblages between FP and PP locations only differed in autumn. The lack of significant differences between FP and PP locations in spring could be attributed to the low use of the partially protected area during winter (i.e. decrease in recreational fishing, anchoring and diving) that allowed the fish community to reach the state comparable to that of the fully protected area before summer (Claudet et al., 2011). For both approaches, spring samples were used as pilot data to identify taxonomic surrogates, whereas autumn data were used to check their effectiveness. It could be argued that pilot data might be too limited to appropriately identifying the sufficient taxonomic level, since any approach to species surrogacy requires representative pilot data in order to select surrogates in a particular context, especially in highly variable systems (e.g. Bevilacqua et al., 2015). Then, it is assumed that the surrogates would remain consistent and effective in similar ecological contexts (e.g. akin data variability, species composition, experimental settings and sample size; Bevilacqua et al., 2009). It is worth noting, however, that here the interest lies on comparing the performance of empirical determination and null models in identifying the sufficient taxonomic resolution, and that both approaches were constrained by the same restriction on pilot data. In spite of this common limit, the sufficient taxonomic level empirically determined based on spring data failed in detecting the pattern of differences among protection regimes as at species level, whether using density or biomass data, unlike null model predictions.

Results from multiple comparisons among protection levels at different taxonomic aggregations should be interpreted with caution due to the possibility of increasing type I error probability. This eventuality, however, further calls into question the empirical determination of taxonomic surrogates. Indeed, empirical determination of the sufficient taxonomic level can hide high probability of type I error (i.e. the probability of rejecting the null hypothesis that a given taxonomic resolution is not sufficient, whereas it is actually true) when accepting a given taxonomic resolution as suitable, resulting in overestimating the effectiveness of coarser taxonomic resolutions to detect differences in assemblage structure (Narayanaswamy et al., 2003; Pagola-Carte et al., 2002; Quijón and Snelgrove, 2006; Somerfield and Clarke, 1995; Vanderklift et al., 1996). This could occur, for instance, when the sufficient taxonomic level is set on its ability to detect the significant effect of a fixed factor, assuming that it is sufficient to discern differences among its different levels (Bevilacqua et al., 2012, 2009). In our case, for example, the order level was sufficient to detect the

overall effect of protection on fish density for both spring and autumn data, although it was actually unable to discriminate among protection regimes as at species level. Such findings stress the importance of taking into account not only the main effect of a fixed factor to determine the sufficient taxonomic resolution for analyses, especially when interest lies in quantifying patterns of change in assemblages structure at varying levels of the factor (e.g. increasing distance from sources of impact, natural gradients).

The identification of the sufficient taxonomic rank in the classic higher-taxon approach relies on single tests at decreasing taxonomic resolution in the absence of any control of uncertainty. Therefore, the experimenter should assume such surrogates as suitable without any information on whether such results might be strictly contingent or exportable to subsequent studies despite of natural variability or changes in the effects of the investigated factor. The weakness of this procedure stems from the fact that, since higher taxa behave as random groups of species and do not mirror functional similarity, they only represent a single random scenario of aggregation. Null models, instead, allow performing a number of simulations for each  $\Phi$ , providing a wide range of potential scenarios. As a result, their predictions are likely to be more sensitive to variations in species-level patterns and allow controlling for uncertainty, thus representing a more reliable method to species surrogacy in routine monitoring.

The outcomes of the null model procedure may vary according to several factors. In our study, for instance, the aggregation level ( $\Phi_{low}$ ) beyond which differences between the partially protected area and unprotected area were no longer detectable strongly differed depending on the type of response variable considered. For fish density, the null model built on spring data predicted that differences between partially protected and unprotected assemblages can be detected only by a small range of  $\Phi$  whereas, using biomass, differences could be detected at even the lowest possible aggregation ratio (corresponding to all species collapsed in single group or, in other words, to total biomass). This could be due to a greater magnitude of the response to protection (i.e. effect size; [Osenberg et al., 1999](#); [Soykan and Lewison, 2015](#)) on fish biomass. In fact, since biomass combines abundance and size, and increased size of individuals is the first response to a decrease in fishing mortality ([Lester et al., 2009](#)), the effect size may be greater with respect to considering fish density only ([Soykan and Lewison, 2015](#)). Also, differences in  $\Phi_{low}$  between the inside and the outside of the MPA are larger when comparing the unprotected area with the fully protected area rather than with the partially protected area. The protection regime in the fully protected area is more restrictive than in the partially protected area, which is likely more effective in mitigating human pressures and thus strengthen the ensuing effect on fish assemblages. In this view, the loss of information due to the use of coarser taxonomic resolution could prevent tests to detect subtle effects of protection on fish (i.e. when effect size is low), as could have been the case for differences between the fully protected area and the partially protected area in autumn. In this last case, for example, species most contributing to differences belonged to the Family of Sparidae (i.e. *Diplodus vulgaris*, *Diplodus sargus*, *Sarpa salpa*) ([Table C.1](#)). However, while density of species belonging to the Genus *Diplodus* were higher in fully protected vs. partially protected areas, density of *S. salpa* showed an opposite pattern smoothing differences between this two protection regimes at coarser taxonomic resolution (e.g. at Family level).

## 5. Guidelines on the use of species surrogacy for evaluating the ecological performance of MPAs

Null models seem to represent more sensitive and robust tools for species surrogacy with respect to the mainstream approach of

taxonomic sufficiency. We advance that the use of null models for species surrogacy could be extended to assessing the effectiveness of protection on fish assemblage in any other MPA. The underlying assumption of neutral relationships between taxonomic relatedness and the ecological response of fish species or their functional similarity relates to species that are commonly found in other coastal areas of the Mediterranean ([Guidetti et al., 2014](#)). Moreover, several studies found evidence of the weak correlation between taxonomic and functional diversity in fish assemblages from other basins (e.g. [Somerfield et al., 2008](#)), suggesting the potential application of this approach in different geographical regions. Although further investigations are desirable, our case study on fish assemblages allows tracking some general guidelines on the use of species surrogacy for evaluating the ecological performance of MPAs:

- (i) The use of surrogates for species only represents a practical framework to overcome taxonomic, methodological, and/or context-dependent impediments. Analyses at the level of species, or at the highest taxonomic resolution as possible, are required especially when interest lies not only in quantifying patterns but also in understanding underlying processes and, more importantly, the functioning of the community. Neither the taxonomic relatedness might represent a reliable proxy of functional redundancy, nor taxonomic distinctness might inform about functional diversity of fish assemblages. Therefore, methods for assessing the effectiveness of protection regimes in preserving the functional properties of fish communities are likely to be more reliable when focusing primarily on trait-based frameworks ([Brind'Amour et al., 2011](#); [Claudet et al., 2010](#); [Stuart-Smith et al., 2013](#)).
- (ii) Surrogates for species should be applied preferentially to implement cost-effective procedures for routine monitoring. In such cases, mere empirical determinations of the sufficient taxonomic level appear not reliable, and alternative methods based on null models could be more appropriate (e.g. [Bevilacqua et al., 2013](#)). Such procedures are based on the  $\Phi$  (i.e. the aggregation ratio) at which the probability to fail in obtaining consistent results with species level is below a threshold set a priori by the experimenter (e.g. 5% as in our case), irrespective of taxonomic relatedness or similarity in ecological responses among aggregated species. This allows controlling for uncertainty when using a given set of surrogates and, therefore, may help experimenters and managers to optimizing trade-offs between the reliable information on the status of protected communities and objective constraints related to accessible taxonomic and scientific expertise, funding, and quality of available data.
- (iii) The identification of surrogates to use during routine monitoring should rely on sound pilot assessments at species level. It is advised to project the appropriate sampling design and sample size for the study prior the pilot assessment, which should be carried out under the same experimental settings. Pilot assessments should provide an exhaustive characterization of the structure of assemblages under study. Although the use of null models appear more robust to limited pilot assessments with respect to the empirical determination of taxonomic surrogates ([Bevilacqua et al., 2015](#)), pilot data collection should be as representative as possible of the spatial and temporal variability of the system being investigated, irrespective of the surrogacy approach employed. Periodical reassessments at species level are also recommended ([Musco et al., 2011](#)).
- (iv) Surrogates should not be based necessarily on taxonomic relationships. The use of null models leads to identifying the sufficient number of surrogates, irrespective of their

type. Any type of surrogates (e.g. taxonomic, phylogenetic, functional) could be employed. This allow the selection of ecologically meaningful operational units, in contrast to taxonomic surrogates that are based on taxonomic relatedness, regardless of whether higher taxa could actually represent ecologically meaningful units (Bevilacqua et al., 2013). The use of null models for species surrogacy, and subsequent selection of surrogates aligned to functional traits of species, therefore, could be used to maximize the ecological information conveyed in surrogate data.

- (v) Surrogates could not be applied to experimental contexts other than those on which they are based on. Whether obtained through the use of null models or by empirical determination, surrogates are strictly study-specific, because depending on the investigated source of variability (e.g. its effect size), experimental settings (e.g. experimental design, sample size), and the aim of the study. They could be only carefully applied to very similar case studies (e.g. same objective, same geographic area, same assemblages, same habitat) or in subsequent reiteration of the same study (e.g. monitoring programs) (Bevilacqua et al., 2015).

The identification of suitable surrogates for species requires a comprehensive understanding of the system of interest to better serve forthcoming monitoring initiatives. Further efforts aiming at extending their application to a wide range of environmental contexts are nevertheless needed to ensure the reliability and the accuracy of surrogacy methods applied to fish assemblages. The empirical selection of the sufficient taxonomic level could be misleading and alternative approaches based on null models might represent more formal and reliable procedures to species surrogacy.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.06.002>.

## References

- Abdulla, A., Gomei, M., Maison, E., Piante, C., 2008. Status of Marine Protected Areas in the Mediterranean Sea. France.
- Anderson, M., 2001. A new method for non-parametric multivariate analysis of variance. *Aust. Ecol.* 26, 32–46.
- Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci. USA* 107, 18256–18261.
- Bertrand, Y., Pleijel, F., Rouse, G.W., 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Syst. Biodivers.*
- Bevilacqua, S., Terlizzi, A., Fraschetti, S., Russo, G.F., Boero, F., 2006. Mitigating human disturbance: can protection influence trajectories of recovery in benthic assemblages? *J. Anim. Ecol.* 75, 908–920.
- Bevilacqua, S., Fraschetti, S., Musco, L., Terlizzi, A., 2009. Taxonomic sufficiency in the detection of natural and human-induced changes in marine assemblages: a comparison of habitats and taxonomic groups. *Mar. Pollut. Bull.* 58, 1850–1859.
- Bevilacqua, S., Terlizzi, A., Claudet, J., Fraschetti, S., Boero, F., 2012. Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *J. Appl. Ecol.* 49, 357–366.
- Bevilacqua, S., Claudet, J., Terlizzi, A., 2013. Best practicable aggregation of species: a step forward for species surrogacy in environmental assessment and monitoring. *Ecol. Evol.* 3, 3780–3793.
- Bevilacqua, S., Terlizzi, A., Mistri, M., Munari, C., 2015. New frameworks for species surrogacy in monitoring highly variable coastal ecosystems: applying the BestAgg approach to Mediterranean coastal lagoons. *Ecol. Indic.* 52, 207–218.
- Brind'Amour, A., Boisclair, D., Dray, S., Legendre, P., 2011. Relationships between species feeding traits and environmental conditions in fish communities: a three-matrix approach. *Ecol. Appl.* 21, 363–377.
- Cappo, M., Harvey, E., Malcolm, H., Speare, P., 2003. Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. *Aquat. Prot. Areas – what Work. Best how do we know?* World Congr. Aquat. Prot. Areas. Cairns, Aust. August 2002, pp. 455–464.
- Caro, T.M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. *Conserv. Biol.* 13, 805–814.
- Carranza, A., Defeo, O., Arim, M., 2011. Taxonomic relatedness and spatial structure of a shelf benthic gastropod assemblage. *Divers. Distrib.* 17, 25–34.
- Ceccherelli, G., Casu, D., Pala, D., Pinna, S., Sechi, N., 2006. Evaluating the effects of protection on two benthic habitats at Tavolara-Punta Coda Cavallo MPA (North-East Sardinia, Italy). *Mar. Environ. Res.* 61, 171–185.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531.
- Claudet, J., 2011. *Marine Protected Areas: A Multidisciplinary Approach*. Cambridge University Press – Ecology, Biodiversity and Conservation Series, Cambridge, UK.
- Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: a regional meta-analysis in the Mediterranean Sea. *Biol. Conserv.* 143, 2195–2206.
- Claudet, J., Pelletier, D., Jouvenel, J.-Y., Bachet, F., Galzin, R., 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: identifying community-based indicators. *Biol. Conserv.* 130, 349–369.
- Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruza, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-M., Dimech, M., Falcón, J.M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P.J., Stobart, B., Vandepierre, F., Valle, C., Planes, S., 2008. Marine reserves: size and age do matter. *Ecol. Lett.* 11, 481–489.
- Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.-A., Goñi, R., Borg, J.A., Forcada, A., de Lucia, G.A., Pérez-Ruza, A., Afonso, P., Brito, A., Guala, I., Diréach, L., Le, Sanchez-Jerez, P., Somerfield, P.J., Planes, S., 2010. Marine reserves: fish life history and ecological traits matter. *Ecol. Appl.* 20, 830–839.
- Claudet, J., García-Charton, J.A., Lenfant, P., 2011. Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. *Conserv. Biol.* 25, 105–114.
- Crec'hriou, R., Neveu, R., Lenfant, P., 2012. Length-weight relationship of main commercial fishes from the French Catalan coast. *J. Appl. Ichthyol.* 28, 861–862.
- Defeo, O., Lercari, D., 2004. Testing taxonomic resolution levels for ecological monitoring in sandy beach macrobenthic communities. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 14, 65–74.
- Dethier, M., Schoch, G., 2006. Taxonomic sufficiency in distinguishing natural spatial patterns on an estuarine shoreline. *Mar. Ecol. Prog. Ser.* 306, 41–49.
- Di Franco, A., Coppini, G., Pujolar, J.M., De Leo, G.A., Gatto, M., Lyubartsev, V., Melià, P., Zane, L., Guidetti, P., 2012. Assessing dispersal patterns of fish propagules from an effective mediterranean marine protected area. *PLoS ONE* 7, e52108.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–220.
- Ellis, D., 1985. Taxonomic sufficiency in pollution assessment. *Mar. Pollut. Bull.* 16, 459–459.
- Forcada, A., Valle, C., Bonhomme, P., Criquet, G., Cadiou, G., Lenfant, P., Sánchez-Lizaso, J., 2009. Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar. Ecol. Prog. Ser.* 379, 197–211.
- Fraschetti, S., Bevilacqua, S., Guarnieri, G., Terlizzi, A., 2012. Idiosyncratic effects of protection in a remote marine reserve. *Mar. Ecol. Prog. Ser.* 466, 21–34.
- Fraschetti, S., Guarnieri, G., Bevilacqua, S., Terlizzi, A., Boero, F., 2013. Protection enhances community and habitat stability: evidence from a mediterranean marine protected area. *PLoS ONE* 8, e81838.
- Gabriel, C., Lagabriele, E., Bissery, C., Crochelet, E., Meola, B., Webster, C., Claudet, J., Chassanite, A., Marínique, S., Robert, P., Goutx, M., Quod, C., 2012. The Status of Marine Protected Areas in the Mediterranean Sea. In: *MedPAN, RAC/SPA, MedPAN & R. (Eds.)*
- Gerber, L.R., Beger, M., McCarthy, M.A., Possingham, H.P., 2005. A theory for optimal monitoring of marine reserves. *Ecol. Lett.* 8, 829–837.
- Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., Polti, S., Cadiou, G., Valle, C., Lenfant, P., Bonhomme, P., Pérez-Ruza, A., Sánchez-Lizaso, J., García-Charton, J., Bernard, G., Stelzenmüller, V., Planes, S., 2008. Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. *Mar. Ecol. Prog. Ser.* 366, 159–174.
- Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodivers. Conserv.* 6, 153–175.
- Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecol. Appl.* 16, 963–976.



- Guidetti, P., Milazzo, M., Bussotti, S., Molinari, A., Murenu, M., Pais, A., Spanò, N., Balzano, R., Agardy, T., Boero, F., Carrada, G., Cattaneo-Vietti, R., Cau, A., Chemello, R., Greco, S., Manganaro, A., Notarbartolo di Sciarra, G., Russo, G.F., Tunesi, L., 2008. Italian marine reserve effectiveness: does enforcement matter? *Biol. Conserv.* 141, 699–709.
- Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M., Sala, E., 2014. Large-scale assessment of mediterranean marine protected areas effects on fish assemblages. *PLoS ONE* 9, e91841.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366.
- Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J., Lassere, G., 1985. Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Rev. d'écologie* 40, 467–539.
- Harmelin-Vivien, M., Diréach, L. Le, Bayle-Sempere, J., Eric Charbonnel, D., García-Charton, J.A., Ody, D., Pérez-Ruzafa, A., Reñones, O., Sánchez-Jerez, P., Valle, C., 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol. Conserv.* 141, 1829–1839.
- Hernandez, F., Carassou, L., Graham, W., Powers, S., 2013. Evaluation of the taxonomic sufficiency approach for ichthyoplankton community analysis. *Mar. Ecol. Prog. Ser.* 491, 77–90.
- Jones, F.C., 2008. Taxonomic sufficiency: the influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates. *Environ. Rev.* 16, 45–69.
- Lampadariou, N., Karakassis, I., Pearson, T.H., 2005. Cost/benefit analysis of a benthic monitoring programme of organic benthic enrichment using different sampling and analysis methods. *Mar. Pollut. Bull.* 50, 1606–1618.
- Lenfant, P., Louisy, P., Licari, M., 2003. Recensement des mérous bruns (*Epinephelus marginatus*) de la réserve naturelle de Cerbère-Banyuls (France, Méditerranée Nord Occidentale). *Cybium* 27, 27–36.
- Lester, S., Halpern, B., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B., Gaines, S., Airamé, S., Warner, R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11, 995–1003.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312, 1806–1809.
- Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol. Appl.* 13, S3–S7.
- Maurer, D., 2000. The dark side of Taxonomic Sufficiency (TS). *Mar. Pollut. Bull.* 40, 98–101.
- McClanahan, T.R., Graham, N.A.J., Calnan, J.M., MacNeil, M.A., 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.* 17, 1055–1067.
- Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano, F., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. *Ecol. Monogr.* 75, 81–102.
- Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., Rossetto, M., De Leo, G.A., 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS ONE* 7, e40832.
- Mueller, M., Pander, J., Geist, J., 2013. Taxonomic sufficiency in freshwater ecosystems: effects of taxonomic resolution, functional traits, and data transformation. *Freshw. Sci.* 32, 762–778.
- Musco, L., Mikac, B., Tataranni, M., Giangrande, A., Terlizzi, A., 2011. The use of coarser taxonomy in the detection of long-term changes in polychaete assemblages. *Mar. Environ. Res.* 71, 131–138.
- Narayanaswamy, B.E., Nickell, T.D., Gage, J.D., 2003. Appropriate levels of taxonomic discrimination in deep-sea studies: species vs family. *Mar. Ecol. Prog. Ser.* 257, 59–68.
- Oksanen, J., Balnch, G.F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H., Wagner, H., 2013. *Vegan: Community Ecology Package*.
- Osenberg, C.W., Sarnelle, O., Cooper, S.D., Holt, R.D., 1999. Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology* 80, 1105–1117.
- Pagola-Carte, S., Urkiaga-Alberdi, J., Bustamante, M., Saiz-Salinas, J.I., 2002. Concordance degrees in macrozoobenthic monitoring programmes using different sampling methods and taxonomic resolution levels. *Mar. Pollut. Bull.* 44, 63–70.
- Pelletier, D., Claudet, J., Ferraris, J., Benedetti-Cecchi, L., García-Charton, J.A., 2008. Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. *Can. J. Fish. Aquat. Sci.* 65, 765–779.
- Pomeroy, R.S., Watson, L.M., Parks, J.E., Cid, G.A., 2005. How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. *Ocean Coast. Manag.* 48, 485–502.
- Quijón, P.A., Snelgrove, P.V.R., 2006. The use of coarser taxonomic resolution in studies of predation on marine sedimentary fauna. *J. Exp. Mar. Biol. Ecol.* 159–168.
- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Found. Stat. Comput.
- Revolution Analytics, 2013. *doMC: Foreach Parallel Adaptor for the Multicore Package*.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. *Science* 294, 1920–1923.
- Saldivar-Lucio, R., Reyes-Bonilla, H., 2011. Ichthyofauna monitoring using higher taxa in Cabo Pulmo National Park, México. *Rev. Biol. Trop.* 59, 871–885.
- Siqueira, T., Bini, L.M., Roque, F.O., Cottenie, K., 2012. A metacommunity framework for enhancing the effectiveness of biological monitoring strategies. *PLoS ONE* 7, e43626.
- Somerfield, P., Clarke, K., 1995. Taxonomic levels, in marine community studies, revisited. *Mar. Ecol. Prog. Ser.* 127, 113–119.
- Somerfield, P.J., Clarke, K.R., Warwick, R.M., Duly, N.K., 2008. Average functional distinctness as a measure of the composition of assemblages. *ICES J. Mar. Sci.* 65, 1462–1468.
- Soykan, C.U., Lewison, R.L., 2015. Using Community-Level Metrics to Monitor the Effects of Marine Protected Areas on Biodiversity 00, pp. 1–9.
- Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airolidi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J., Edgar, G.J., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539–542.
- Terlizzi, A., Bevilacqua, S., Fraschetti, S., Boero, F., 2003. Taxonomic sufficiency and the increasing insufficiency of taxonomic expertise. *Mar. Pollut. Bull.* 46, 556–561.
- Terlizzi, A., Benedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guldetti, P., Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. *Mar. Ecol. Prog. Ser.* 289, 27–42.
- Terlizzi, A., Anderson, M.J., Bevilacqua, S., Fraschetti, S., Włodarska-Kowalczyk, M., Ellingsen, K.E., 2009. Beta diversity and taxonomic sufficiency: do higher-level taxa reflect heterogeneity in species composition? *Divers. Distrib.* 15, 450–458.
- Thompson, B.W., Riddle, M.J., Stark, J.S., 2003. Cost-efficient methods for marine pollution monitoring at Casey Station, East Antarctica: the choice of sieve mesh-size and taxonomic resolution. *Mar. Pollut. Bull.* 46, 232–243.
- Vanderklift, M.A., Ward, T.J., Jacoby, C.A., 1996. Effect of reducing taxonomic resolution on ordinations to detect pollution-induced gradients in macrobenthic infaunal assemblages. *Mar. Ecol. Prog. Ser.* 136, 137–145.
- Vanderklift, M.A., Ward, T.J., Phillips, J.C., 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. *Biol. Conserv.* 86, 307–315.
- Warwick, R., Clarke, K., 1993. Comparing the severity of disturbance: a metaanalysis of marine macrobenthic community data. *Mar. Ecol. Prog. Ser.* 92, 221–232.
- Williams, I.D., Walsh, W.J., Tissot, B.N., Hallacher, L.E., 2006. Impact of observers' experience level on counts of fishes in underwater visual surveys. *Mar. Ecol. Prog. Ser.* 310, 185–191.
- Williams, I.D., Walsh, W.J., Claisse, J.T., Tissot, B.N., Stamoulis, K.A., 2009. Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. *Biol. Conserv.* 142, 1066–1073.