FEATURE ARTICLE

Geographic distance, water circulation and environmental conditions shape the biodiversity of Mediterranean rocky coasts

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ABSTRACT: Ecological connectivity is important for effective marine planning and biodiversity conservation. Our aim was to identify factors important in influencing variation in benthic community structure on shallow rocky reefs in 2 regions of the Mediterranean Sea with contrasting oceanographic regimes. We assessed beta (β) diversity at 146 sites in the littoral and shallow sublittoral from the Adriatic/Ionian Seas (eastern region) and Ligurian/Tyrrhenian Seas (western region) using a null modelling approach to account for variation in species richness. The distance decay relationship between species turnover within each region and geographic distance by sea was determined using generalised linear models. Mantel tests were used to examine correlations between β diversity and connectivity by ocean currents, estimated from Lagrangian dispersal simulations. Variation in β diversity between sites was partitioned according to environmental and spatial components using a distance-based redundancy approach. Species turnover along a gradient of geographic distance was greater by a factor of 3 to 5 in the western region than the eastern region, suggesting lower connectivity between sites. β diversity was correlated with connectivity by ocean currents at both depths in the eastern region but not in the western region. The influence of spatial and environmental predictors of β diversity varied considerably between regions, but was similar between depths. Our results highlight the interaction of oceanographic, spatial and environmental processes influencing benthic marine β diversity. Persistent currents in the eastern region may be responsible for lower observed β diversity compared to the western region, where patterns of water circulation are more variable.

Diverse benthic assemblages on a shallow Mediterranean reef.

Photo: Lisandro Benedetti-Cecchi

KEY WORDS: Beta diversity · Reefs · Spatial variation · MPA · Lagrangian modelling · Connectivity

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INTRODUCTION

Elucidating the mechanisms that control patterns of diversity is a central objective of community ecology (Hubbell 2001, Leibold et al. 2004), and has been the focus of considerable research across terrestrial (Tuomisto et al. 2003, De Cáceres et al. 2012), freshwater (Maloney & Munguia 2011, Angeler 2013) and marine systems (Watson et al. 2012, Moritz et al. 2013). A better understanding of these mechanisms is critically important for conservation planning, which has historically focussed on prioritizing protection of areas containing high species richness and threatened or endemic species, but often failed to incorporate underlying variation in regional species assembly driven by ecological connectivity, spatial processes and environmental heterogeneity (McKnight et al. 2007).

Beta (β) diversity is a fundamental concept that addresses the spatial organisation of biodiversity. Although there are a multitude of approaches to defining and measuring β diversity, it is generally recognised as the change in species composition among sites in a geographic area of interest (Koleff et al. 2003, Legendre et al. 2005, Anderson et al. 2011). It can act as a measure of the change in species identities between 2 or more local assemblages, or the relationship between the diversity of the species pool for a given geographic region (γ diversity) and community diversity at local scales (α diversity) (Whittaker 1960). In each case, it reflects the range of processes acting on regional metacommunities that create and maintain patterns of biodiversity within them (de Juan et al. 2013). Anderson et al. (2011) identified 2 broad approaches to distinguishing β diversity: (1) *turnover* in species identities among sites along predefined spatial, environmental or temporal gradients or (2) *variation* in species identities among sites without reference to any specific gradient, both of which are useful for conservation planning (Legendre et al. 2005, Smith & Lundholm 2010, Legendre & De Cáceres 2013). Additionally, patterns of β diversity provide a measure of ecological connectivity that can be related to broader environmental, spatial and temporal gradients and used to untangle drivers behind patterns of community assembly (Borcard et al. 1992, Thrush et al. 2010).

In the Mediterranean region, as elsewhere in the world, marine ecosystems are under mounting pressure from the combined effects of environmental stressors due to climate change and human impacts (Bianchi & Morri 2000, Lejeusne et al. 2010). Efforts to protect marine biodiversity through designation of Marine Protected Areas (MPAs) have been underway for decades, although designation of MPAs has often been based on opportunity rather than knowledge of ecosystem functioning (Fraschetti et al. 2002), leading to ad hoc systems rather than networks of MPAs (Guilhaumon et al. 2015). The importance of connected networks of reserves has been recognised as a critical requirement to protecting the Mediterranean marine ecosystem as a single interconnected entity (Andrello et al. 2013, 2015, Lagabrielle et al. 2014), leading to internationally coordinated efforts to plan for ecological connectivity between reserves (Lubchenco et al. 2003, Grorud-Colvert et al. 2014).

In the present study, connectivity can be defined as the exchange of individuals between populations (Almany et al. 2009). It is widely recognised that high connectivity increases resilience of individual MPAs within a network by enhancing exogenous sources of recruits, increasing genetic diversity and ultimately maximising adaptive potential in the case of local disturbance (Momigliano et al. 2015). Thus, connected networks of MPAs can improve the ability of ecosystems to face both natural and anthropogenic perturbations. There is evidence that the potential of connectivity generally decreases with geographic distance (Cowen et al. 2006), but pathways and barriers imposed by ocean currents, fronts and physicochemical conditions are also critical aspects to understanding the processes related to species' dispersal (Shanks 2009). Most benthic species show benthic–pelagic coupling of life cycles, where sedentary or sessile adult stages rely on current-mediated advection for dispersal of pelagic juvenile forms (i.e. larvae and propagules). Subsequent settlement success and survival is dependent on the suitability of the receiving environment to species' requirements.

Assessing the relative contribution of distance, ocean currents and suitability of environmental conditions to patterns of β diversity represents an important prerequisite for MPA network design (Watson et al. 2011b, Rassweiler et al. 2012). Planning connected networks of MPAs requires an understanding of how each of these factors contributes to network connectivity as a whole. While a number of studies have explored the interrelated influence of these factors at the population level, their role in community-level dynamics is less well understood. This is partly due to the difficulties of incorporating the wide variation in species life histories and dispersal traits into a single conceptual model (Moritz et al. 2013).

Recent refinement of ocean circulation models and improvements in computing power have allowed for a better understanding of the degree of hydrodynamic

connectivity between populations (Andrello et al. 2013, 2015) and communities (Watson et al. 2011a). Similarly, ocean color satellite imagery provides synoptic information on the distribution of biologically relevant environmental conditions across temporal and geographic scales not readily attainable by direct sampling alone. In this study, we combined this information to examine the influence of geographic distance, current connectivity potential and environmental variability on patterns of β diversity in 2 regions of the Mediterranean Sea with contrasting oceanographic regimes. Persistent oceanographic features in the southern Adriatic and Ionian Seas and more variable, seasonal patterns in the northern Tyrrhenian and Ligurian Seas provide a unique opportunity to assess the effects of connectivity potential on β diversity. We specifically addressed the following questions: (1) Do patterns of β diversity vary consistently between depths and regions of the Mediterranean Sea? (2) Which measure of connectivity, geographic or connection by ocean currents, best correlates with β diversity? (3) What environmental factors determine the variation in β diversity between depths and regions, and what are their relative contributions?

MATERIALS AND METHODS

Biological data

We analyzed β diversity in assemblages of algae and sessile invertebrates from rocky substrates at 2 depths on coastlines in the Ligurian, Tyrrhenian, Adriatic, Ionian and Central Mediterranean Seas (Fig. 1). Data for littoral areas (0 to −0.2 m relative to mean low water level) were obtained for 60 replicated sites (5100 quadrats) from surveys carried out between 2000 and 2008. A total of 86 sites (4150 quadrats) in the shallow sublittoral (5 to 7 m) were sampled between 1999 and 2011. At littoral sites, visual estimates of species cover were made directly in the field using 20×20 cm $(0.04 \ m^2)$ quadrats. For the sublittoral, an area of 16×25 cm $(0.04 \ m^2)$ was photographically sampled, and then species cover was visually estimated from slides under magnification. For comparative regional analyses, sites were assigned to 2 regions. The western region (35 littoral and 48 sublittoral sites) encompassed the eastern Ligurian and northern Tyrrhenian Seas including MPAs at Portofino, Cinque Terre, and the Tuscan
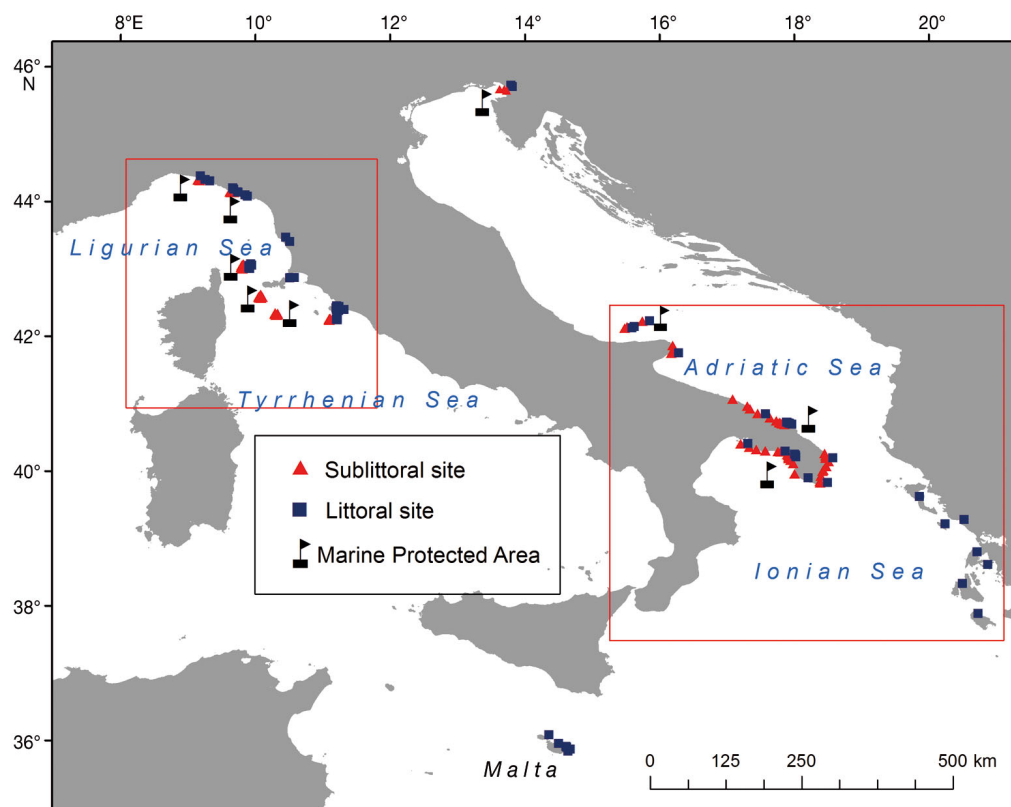

Fig. 1. Littoral and sublittoral study locations for analysis of biodiversity distribution. Western and eastern sites used in regional comparisons are defined by red bounding boxes. Sites in the northern Adriatic and central Mediterranean (Malta) were included in a global analysis of species turnover

Archipelago (Capraia, Montecristo, Giannutri and Elba Islands). The eastern region (25 littoral and 38 sublittoral sites) included the southern Adriatic and northern Ionian Seas including MPAs at Porto Cesareo, Torre Guaceto, and the Tremiti Islands. An additional 10 sites in Malta and the northern Adriatic (Miramare MPA) were not assigned to either of the regions but were included in a global analysis of β diversity combining sites from both regions.

β diversity as variation

Observed β diversity ($β_O$) was derived separately for all pairs of littoral and sublittoral sites in each region using Jaccard's coefficient of dissimilarity (d_J):

$$d_J = \frac{(b+c)}{(a+b+c)} \tag{1}$$

in which a is the number of species shared by 2 sites, b is the number of species in the other site, but not in the focal one, and c is the number of species unique to the focal site. Estimates of β diversity are concomitantly dependent on variation in local species richness (α diversity) (Chase et al. 2011, Kraft et al. 2011). To separate underlying assembly processes that create β diversity from the influence of α diversity, a null modelling approach was used. A 'null community' for each site was derived by randomly sampling from the full species pool within each depth category and region. Sample size was equal to the number of taxa observed at a given site, and the probability of each taxon being sampled was weighted proportionally to its relative cover. Jaccard dissimilarities were calculated and averaged between all possible pairs of sites over 9999 iterations of the resampling procedure to obtain a null estimate of between-site β diversity ($β_N$). Resulting differences ($β_{DEV}$) between observed and expected beta diversity under the null expectation ($β_O − β_N$) were used in all subsequent analyses.

Environmental covariates

A suite of satellite-derived oceanographic variables were selected as environmental predictors of β diversity. Level 3 Moderate Resolution Imaging Spectro-radiometer (MODIS) data with spatial resolution of ~4 km at the equator and with daily temporal resolution were acquired from NASA's Goddard Space Flight Centre (http://oceancolor.gsfc.nasa.gov/). Cumulative climatologies between the years 2000 (the earliest available MODIS data) and 2011 were

derived for night-time sea surface temperature (SST), sea surface salinity (Salinity), net primary productivity (NPP) (Behrenfeld & Falkowski 1997), diffuse light attenuation coefficient at 490 nm (k_d490), Chlorophyll a concentration (CHL) and concentration of colored dissolved organic matter (CDOM). For each of the satellite products the mean, standard deviation around the mean, mean annual range and highest monthly mean were calculated over the full time-series for each pixel corresponding to a single sampling site. A long-term averaging approach was taken in order to accommodate the differences in field sampling times. Sites beyond the extent of the satellite climatologies (n = 7) were assigned the value of the nearest adjacent pixel without interpolation. Prior to analysis, multi-collinearity and correlation of environmental predictor variables was assessed for each region using a step-wise procedure, where at each iteration the variable with the greatest variance inflation factor (VIF) was removed until remaining co-variates (SST_{August}, $SST_{Ann.Range}$, $CDOM_{Mean}$, $CDOM_{SD}$, k_d490_{SD}) displayed VIF values <5. Since sampling sites were located within and outside MPAs, we included protection status (fully protected vs. partially protected and unprotected) as an environmental covariate in the analyses to account for any effects of protection on β diversity.

Geographic distance

Pair-wise distances were calculated between sites for each region. Distances by sea between each site were calculated using a least-cost paths approach (hereafter least-cost distance). Land areas were masked using the European Environment Agency coastline polygon (1:100 000) (www.eea.europa.eu/legal/copyright) and defined as a barrier in distance calculations. Given the complex geometry of coastlines in the study regions this was considered a more realistic estimate of effective spatial separation than the more commonly used Great Circle or Euclidean distances.

Connectivity by ocean currents

A current connectivity matrix was derived using Lagrangian particle simulations in order to estimate potential connectivity by ocean currents. Three-dimensional sea current velocities and directions were obtained from the 1/12th degree (6 to 8 km resolution) NEMOMED12 model (https://hal-ensta.archives-

ouvertes.fr/hal-01138958/). Due to the inherent difficulties in developing a model representing the multitude of species' dispersal strategies, no weighting or biotic parameterization was applied to the model. Simulation of Lagrangian particle transit times therefore represents the movement of particles of water between sites. In this vein, current connectivity was defined as the minimum particle transit time between pairs of sites. A detailed description of the hydrodynamic simulations can be found in Andrello et al. (2013).

Spatial analysis

Spatial predictors were generated as Moran's eigenvector maps (MEMs) (Dray et al. 2006) by a principal coordinate analysis (PCoA) on the truncated spatial distance matrix. Eigenvectors represent spatial relationships among sampling sites across a range of spatial scales. Primary eigenvectors define relationships between sampling sites over broad spatial scales, and subsequent eigenvectors provide information at progressively finer scales. Additionally, the decomposition of the spatial relationships between sampling locations was weighted using the current connectivity matrix (days) described above. The spatial predictors are therefore representative of site connectivity by currents across multiple scales.

β diversity as turnover

Distance decay of similarity is a measure describing the contribution of geographic distance to changes in community similarity. Based on the distance decay relationship, measures of initial similarity (S_0) and halving distance (D_h) can be calculated. S_0 reflects β diversity at small spatial extents, whereby higher values of S_0 indicate lower β diversity at small scales. D_h indicates the distance at which S_0 halves, and provides relevant information regarding the spatial scale of species turnover. Pair-wise Jaccard similarities ($S_{ij} = 1 - d_{ij}$) (Anderson et al. 2013) were plotted against least-cost distance with distance decay relationships estimated by generalised linear models (GLMs) with binomial observation error and a log-link function (Millar et al. 2011), taking the form:

$$\log(E[S]) = \alpha - \beta D \qquad (2)$$

where $\log(E[s])$ denotes the expected similarity, D is least-cost distance (km), and α and model slope, β, are the parameters of the log-linear model. As pair-wise similarities are not independent, parameter esti-

mates and their standard errors for α, β and D_h were obtained by a leave-one-out jackknife procedure using 9999 permutations (Millar et al. 2011). Because species turnover was positively related to protection status (Table 2), we performed a sensitivity analysis to evaluate the potential confounding effect due to having a larger number of sites within MPAs in the western than in the eastern region. Parameters α, β and D_h were estimated for residuals of a regression of Jaccard similarity against level of protection for depths within regions. Since the results and their interpretation were not substantially different from the results obtained using the approach outlined above, they have not been included in the main text (See Table S1 in the Supplement at www.int-res.com/articles/suppl/m553p001_supp.pdf). Distance decay relationships were similarly derived between pair-wise Jaccard similarity and travel time (minimum and mean) estimated from Lagrangian particle simulations and are presented in Fig. S1 in the Supplement.

Correlation of species turnover with current connectivity and least-cost distance

To assess the relative influence of connectivity by ocean currents and geographic distance on variation in β diversity, Mantel tests were used to test the significance of the Pearson product-moment coefficient (r) between pair-wise Jaccard dissimilarity (d_J) and matrices of environmental distance, least-cost distance and current connectivity with significance assessed using 9999 random permutations. The Euclidean environmental distance matrix was calculated between sites using non-collinear (VIF < 5) environmental covariates (SST_{August}, $SST_{Ann.Range}$, $CDOM_{Mean}$, $CDOM_{SD}$, k_d490_{SD}). Complementary partial Mantel tests were then done to determine correlations between β diversity, least-cost and current distance whilst controlling for the effect of environmental distance.

Partitioning the contribution of environmental and spatial predictors

A variation partitioning approach (Borcard et al. 1992, Legendre et al. 2005) was used to determine the relative contribution of each set of environmental and spatial predictors (i.e. MEMs) to β diversity. This was carried out by means of 3 distance-based redundancy analyses (dbRDA) considering both spatial and environmental predictors together or separately.

The total percentage of variation explained by the model (adjusted R^2) was partitioned into unique and common contributions of each of the sets of environmental and spatial predictors. Fractions of variation describing the independent effects of spatial and environmental processes (along with their non-separable fractions and unexplained variation) were then obtained by subtraction (e.g. Borcard et al. 1992, Peres-Neto et al. 2006).

Environmental drivers of β diversity

Finally, we used multiple regression to determine the contribution of individual environmental covariates to predicting β diversity for combined littoral sites from both regions (including those in the northern Adriatic and Malta), and combined sublittoral sites (including those in the northern Adriatic). In order to reduce pairwise dissimilarities to a single measure of β diversity for each site, the average Jaccard dissimilarity was calculated among all pairs of sites (Anderson et al. 2013, de Juan et al. 2013). That is, the β diversity for a given focal site was computed as the mean of all the pair-wise dissimilarities between the focal site and each of the other sites. As

significant positive spatial autocorrelation ($\alpha < 0.05$) was present in the residuals of the ordinary least squares (OLS) regression, a spatial generalised least squares (GLS) regression was used. The GLS is derived from standard regression, but differs in the incorporation of the spatial structure directly into the residuals, assuming in this study an exponential relationship between the error term and geographic distance (Diniz Filho & Bini 2005).

All statistical analyses were done using R version 3.1.2 (R Development Core Team 2014) (packages 'vegan', 'nlme', 'spacemakeR', 'simba', 'spam') with code obtained from Millar et al. (2011) and Chase et al. (2011).

RESULTS

β diversity as turnover

Initial similarities were relatively high between littoral sites in both the eastern (0.239) and western (0.293) regions, and low between sublittoral sites (0.161 and 0.120 in the eastern and western regions respectively). This pattern of lower β diversity at small spatial extents in littoral habitats was reflected
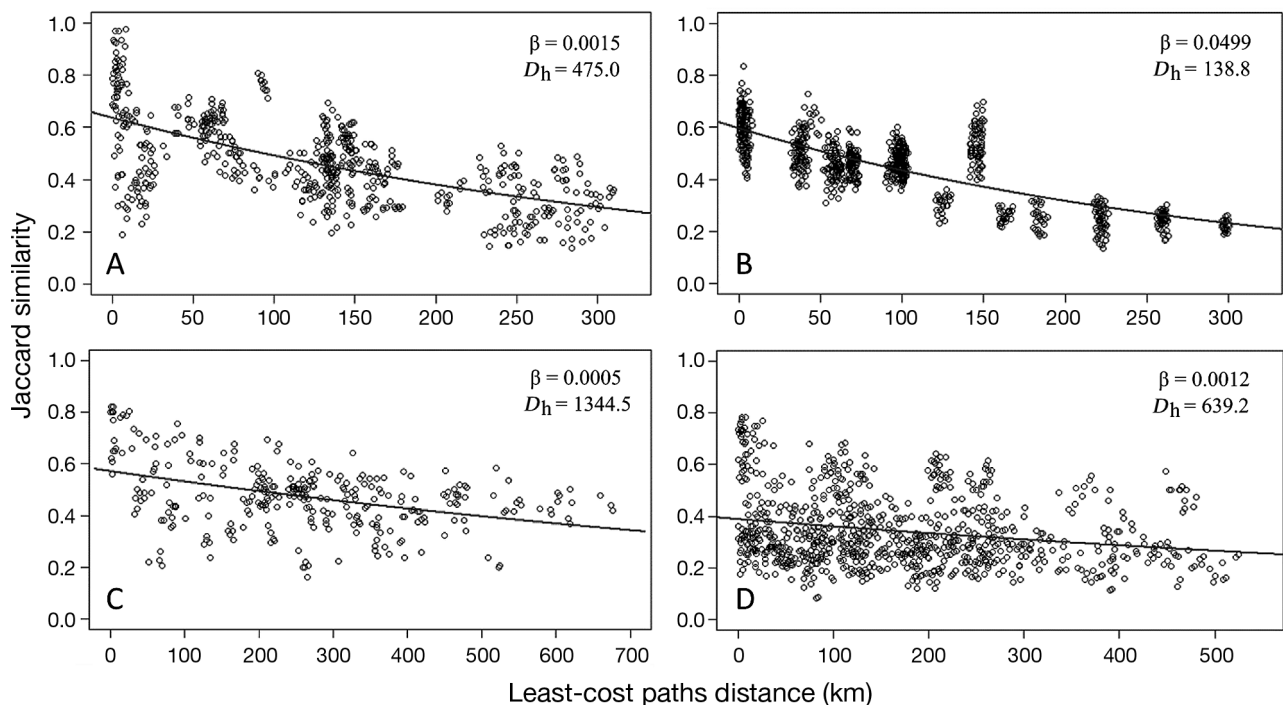

Fig. 2. Decay in site similarities (Jaccard) of benthic communities with increasing distance in (A) littoral and (B) sublittoral sampling sites in the western region; and (C) littoral and (D) sublittoral sampling sites in the eastern region. The fitted models from the binomial generalised linear models (GLMs) with log-link are shown with corresponding parameter estimates (β) and halving distances (D_h)

in broader-scale species turnover, although there was more variation between regions (Fig. 2). The rate of species turnover (i.e. slope ß) with distance was greater for the western region by a factor of ~3 between littoral sites and by a factor of ~5 for sublittoral sites. Corresponding D_h (the mean distance by sea at which community similarity halves) varied between depths and regions. These were estimated at 475 ± 168.9 and 1344.5 ± 592.8 km for littoral sites, and 138.8 ± 10.5 and 639.2 ± 157.1 km for sublittoral sites in the western and eastern study regions respectively.

Correlation of species turnover with current connectivity and least-cost distance

Pair-wise β diversity between littoral sites in the western region was strongly positively correlated with least-cost distance ($r = 0.670$, $p < 0.001$) and shared weaker, but significant correlations with current distance ($r = 0.185$, $p < 0.001$) and environmental distance ($r = 0.226$, $p < 0.01$) (Table 1). Least-cost distance was likewise strongly correlated with β diversity between sublittoral sites in this region ($r = 0.675$, $p < 0.001$), as was environmental distance ($r = 0.675$, $p < 0.001$). In the eastern region, β diversity was weakly but significantly correlated with current distance ($r = 0.248$, $p < 0.001$), but not with either distance by sea or environmental distance.

Partitioning the contribution of environmental and spatial predictors

The relative influence of spatial and environmental processes in describing community structure varied substantially between study regions, but was remarkably similar between littoral and sublittoral sites within each region (Fig. 3). In the western region, spatial and environmental predictors accounted for approximately equal portions of variation in community structure (7 to 10%) with large overlap between the two (51 to 53%). In contrast, spatial gradients mediated by current connectivity were significantly more important than environmental predictors in describing community variation in the eastern region for both littoral and sublittoral sites (19% in both cases). Environmental covariates alone explained only 5% of variation in β diversity between littoral sites and none of the variation between sublittoral sites.

Environmental drivers of β diversity

Multiple regression was conducted to test whether satellite-derived environmental covariates predicted species turnover for all littoral (including those in the northern Adriatic and Malta), and all sublittoral sites (including those in the northern Adriatic). Based on Akaike's information criterion (AIC), multivariate models based on spatial GLS regression showed a better description of environmental variables on species turnover than equivalent OLS models, which do not take spatial autocorrelation into account (Table 2). For littoral sites, SST variables ($SST_{Ann.Range}$, SST_{Mean}) and protection status were significant predictors of species turnover ($F_{6,60} = 7.19$, $p < 0.001$, $R^2_{adj} = 0.36$). In the sublittoral sites, long-term variation of CDOM ($CDOM_{SD}$) and mean annual range of SST ($SST_{Ann.Range}$) were the best environmental correlates of species turnover ($F_{6,78} = 7.45$, $p < 0.0001$, $R^2_{adj} = 0.33$).

Table 1. Correlations between β diversity (i.e. community variation), ocean distance, environmental distance and current connectivity between pairs of sampling sites and partial correlations after controlling for the effects of environmental distance. The statistical significance of comparisons was assessed using Mantel and partial Mantel tests based on Pearson's product-moment correlation using 9999 permutations; *p < 0.05, **p < 0.01

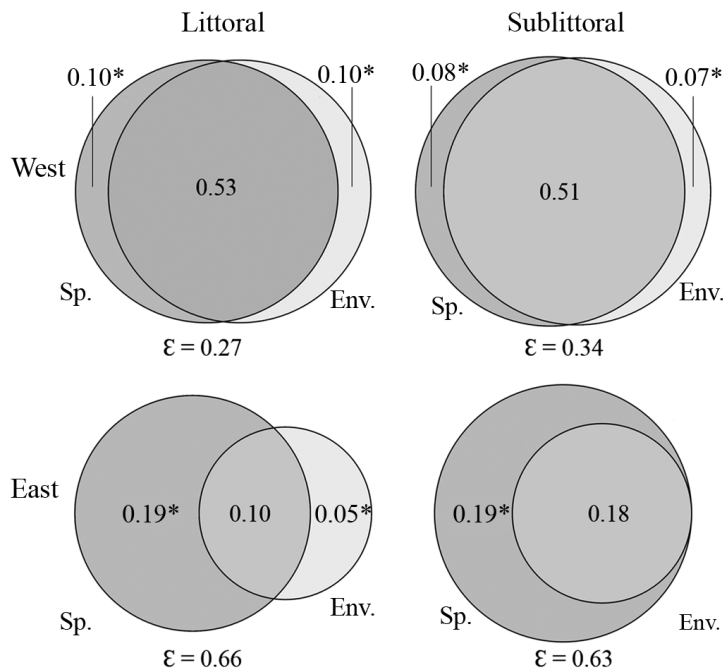|	N pairs	Least-cost distance (km)	Current distance (days)	Environmental distance
Correlations				
Littoral				
West	612	0.670**	0.185*	0.226**
East	312	0.161	0.248**	0.122
Sublittoral				
West	968	0.675**	0.097	0.567*
East	882	0.135	0.142**	0.1232*
Partial correlations, corrected for environmental distance				
Littoral				
West	612	0.661**	0.168*	–
East	312	0.109	0.217**	–
Sublittoral				
West	968	0.455**	−0.048	–
East	882	0.083	0.112*	–

Fig. 3. Variation partitioning (Venn diagrams) of unique contribution of spatial (Sp.) and environmental (Env.) components to benthic β diversity distribution, for the littoral and sublittoral in the western and eastern regions. Overlapping fractions represent the shared variation between the environmental and spatial components and the residual variation unexplained by the multivariate model. p-values showing the significance of each fraction of variation were estimated with 199 permutations under the full model (*p < 0.05)

DISCUSSION

The present study provides an example of how decoupling the influence of ocean currents, spatial and environmental drivers can provide important insights into the factors affecting regional patterns of β diversity. We found that regional scale (100s of km) patterns in species turnover of rocky reef benthos in the Mediterranean differ between regions and depths, the relationship between species turnover and connectivity by ocean currents was regionally variable, and finally, the relative influence of spatial and environmental processes in describing community structure varied substantially between study regions, but was remarkably similar between littoral and sublittoral sites within each region.

Mechanisms controlling the decay of community similarity with distance have been broadly, but not exclusively, attributed to 3 key factors (Nekola & White 1999, Soininen et al. 2007): niche-based processes, spatial configuration of the environment and stochastic processes posited by neutral theory (e.g. dispersal limitation) (Hubbell 2001). In agreement with previous studies (Watson et al. 2011a, Moritz et al. 2013), our findings provide support for each of these factors, varying in degree by region and across depths. We found that decay of community similarity with distance was comparatively lower for the southern Adriatic and Ionian Seas, suggesting greater regional community homogeneity than in the Tyr-

Table 2. Partial regression coefficients of the multiple regression models (*b*), standard errors of the estimates (SE), *t*-statistics and associated p-values for Mediterranean benthic β diversity at 2 depths regressed against satellite-derived environmental variables. An exponential model was assumed in generalised least squares (GLS) regression to describe spatial patterns in model residuals. Akaike's information criteria (AIC) values are reported from spatial GLS models (AIC_{GLS}) and non-spatial ordinary least squares (OLS) models (AIC_{OLS}) containing the same variables; adjusted R^2 (R^2_{adj}) are reported from non-spatial OLS models. For the littoral zone: $AIC_{OLS} = -212.2$, $AIC_{GLS} = -244.6$; $R^2 = 0.42$, $R^2_{adj} = 0.36$. For the sublittoral zone: $AIC_{OLS} = -322.1$, $AIC_{GLS} = -352.7$; $R^2 = 0.36$, $R^2_{adj} = 0.33$. SST: sea surface temperature; CDOM: colored dissolved organic matter; k_d490: diffuse attenuation coefficient for downwelling irradiance at 490 nm; 'other' protection status: partially protected and unprotected. *p < 0.05; **p < 0.01

Variable	Littoral (0–0.2 m)				Sublittoral (5–7 m)			
	b	SE	*t*	p	*b*	SE	*t*	p
Intercept	−1.06	0.373	−2.86	0.006**	0.159	0.274	0.58	0.563
SST								
Mean	0.047	0.016	2.85	0.006**	−0.009	0.015	−0.59	0.556
Annual range	0.024	0.009	2.74	0.008**	0.011	0.005	2.43	0.017*
CDOM								
Mean	0.013	0.008	1.59	0.117	0.001	0.007	0.16	0.873
SD	0.006	0.014	−0.42	0.675	−0.029	0.012	−2.42	0.019*
k_d490								
SD	0.297	0.525	0.56	0.573	0.621	0.381	1.63	0.108
Protection status								
Fully protected vs. other	0.028	0.009	2.84	0.006**	−0.009	0.007	−1.19	0.239

rhenian/Ligurian region. Halving distances in the eastern region were also large relative to the spatial scale of the study, suggesting a homogeneous and potentially well-connected system. The shallower rates of decay observed in the eastern region may be attributable to lower environmental variability, conforming to the concept of species sorting by environmental niche processes. This contention was further supported by regional differences in the contribution of environmental variables to partitioned variation in community similarity.

Spatial processes explained the greatest fraction of variation of β diversity in the eastern region. While it is difficult to relate spatial structures to the ecological processes that create them (Hubbell 2001, Smith & Lundholm 2010), significant correlations were also found between pair-wise measures of β diversity along a gradient of connectivity by currents. This may indicate that dispersal potential is an important factor determining community organisation in the region. The opposite is true for variation among sites in the western region. Here, we observed a strong and significant effect of geographic distance on decreasing similarity between communities, but only a relatively minor effect of current connectivity in littoral communities and no significant effect in sublittoral communities. While this may result from unmeasured anthropic disturbances such as localised extractive activities (Fraschetti et al. 2001) and urbanisation effects (Benedetti-Cecchi et al. 2001), at least some of these discrepancies between regions may be explained by differences in oceanographic regimes. The southern Adriatic (eastern region) is characterised by a generally stable cyclonic cell, largely controlled by the topography of the South Adriatic Pit, between the western and eastern Adriatic boundary currents (Poulain 2001). In contrast, current patterns along the Tyrrhenian and Ligurian coasts (western region) display a generally weak and variable northward trend as the Eastern Corsican Current moves through the Corsican channel into the Liguro-Provençal Basin (Astraldi et al. 1990). Several authors have noted an anti-cyclonic eddy persistently forming in the summer months at the latitude of the island of Capraia, which may seasonally limit or even reverse transport through the Corsican Channel (Astraldi et al. 1990, Iacono et al. 2013). Andrello et al. (2013) reported only north–south directional connectivity between the 2 basins in Lagrangian simulations between MPAs. The weaker and more variable current regime connecting the northern Tyrrhenian and southern Ligurian seas, coupled with complex seasonal wind-driven dynamics, may therefore consti-

tute a barrier to dispersal between northern and southern sites in the region. An important caveat to these findings is that our biophysical model was not calibrated according to the specific life histories of any single species or group of species. Species found within MPAs display a multitude of dispersal strategies which are dependent on many factors, including propagule morphology, movement characteristics, pelagic duration and timing of release (Shanks 2009), that may relate to habitat features on a different scale (Thrush et al. 2011). A number of theories have been proposed to explain dynamics and scales of metacommunity structure (Leibold et al. 2004). Deterministic and stochastic processes responsible for metacommunity assembly may interact over a range of spatial and temporal scales. In generally homogeneous environments, dispersal may be the more important organisational mechanism, while characteristics of the receiving environment may predominate where conditions show small-scale variability. The available evidence suggests that this is the case in the present study. Despite their similar latitudinal extents, environmental variation was lower in the eastern region than in the western region and was largely unrelated to patterns of species turnover, but significantly correlated with patterns in ocean currents.

Environmental variation as estimated from long-term satellite imagery indicated that sublittoral species turnover was best predicted by a negative relationship with CDOM variability and a positive relationship with annual variation in SST. Similarly, SST (mean and annual range) shared a significant positive relationship with species turnover at littoral sites, when considered against all other variables. Temperature is a well-documented correlate of broad-scale marine diversity gradients, although its effects may vary over finer scales according to local variation in primary productivity and community trophodynamics (Roy et al. 1998). Concentrations of CDOM in coastal waters vary according to *in situ* creation of fulvic acids (Hulatt et al. 2009), or to presence of humic acids in terrigenous effluent. Higher concentrations of CDOM dominate the absorption of both visible and blue spectrum UV light in the water column, potentially limiting photosynthetically available radiation to the sublittoral benthos. Modification of the underwater light regime can impact biomass and species richness of macroalgae (Desmond et al. 2015), which act as foundation species, providing habitat and hosting complex ecosystem processes to a suite of associated species.

A better understanding of the processes underlying patterns of regional biodiversity is highly relevant to

marine spatial planning, especially when assessing candidate sites for protection and inclusion in networks of MPAs. A significant finding of this study is that differences in patterns of community similarity do not appear to be driven uniformly by the same processes. Instead, the measured drivers behind variation in community structure were found to differ between regions, and to a lesser extent between depths. Current connectivity, geographic distance and environmental variability were all linked to patterns in β diversity at varying degrees of importance across regions and depths. This implies that strategies accounting for this wide range of connectivity drivers need to be considered when planning a network of MPAs aimed at ensuring connectivity between units. In the example of benthic communities in the study systems considered here, higher priority would need to be given to more heterogeneous regions, where species turnover is greater over smaller spatial scales. That is, units in the western region would need to be closer together to capture a similar gradient of change in diversity relative to those in the eastern region. Additionally, connectivity potential of candidate habitats for protection is an important consideration in network spatial arrangement. Our results suggest that sublittoral community structure changes more rapidly over distance than it does in the littoral. Therefore, evaluation of unit connectivity should be predicated on habitats that display the greatest community heterogeneity through space.

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