Ecosystem vulnerability to alien and invasive species: a case study on marine habitats along the Italian coast

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ABSTRACT

1. Spread of alien species (AS) is a serious threat to marine habitats and analysis of principal correlates of their occurrence is pivotal to set reliable conservation strategies.

2. In order to assess the susceptibility of marine habitats to biological invasions, a dataset of occurrence of 3,899 species from 29 phyla, taken from 93 marine sites located along the Italian coast in the period 2000-2012, was gathered.

3. A total of 61 AS belonging to 11 phyla has been recorded. Invertebrates were the most represented (63%). AS were found in all the examined habitats (EUNIS, level 2), although they showed highest abundance in the benthic ones. Most of the AS were associated with a single EUNIS habitat, whilst about 30% were present in more than one habitat. Trans-habitat occurrence suggests a potential invasiveness of AS.

4. According to statistical analysis, AS recorded could have been more numerous, since some of the marine habitats seemed to be still unsaturated. The model that best describes the spread of AS takes account both of native species richness (Rn) and EUNIS habitat type as explanatory variables. The number of observed AS was directly related to Rn and it was highest in rocky circalittoral and infralittoral habitats.

5. The results of this macro-ecological study focus on the importance to perform large scale studies, since adopting ecosystem approaches for marine invasion management seems especially fruitful.

6. The results moreover highlight the importance of AS monitoring on different habitats, from those subjected to anthropogenic pressure, historically considered as hubs of introduction of AS, to the most biologically rich and diverse marine ones. Indeed, it is necessary to set monitoring strategies to detect the introduction, the distribution and persistence of AS over time. These recommendations are especially significant in the light of the strategic plans currently under formulation in Mediterranean countries with regard to AS monitoring.

KEY WORDS: marine alien species, Mediterranean habitats, habitat vulnerability, invasive alien species, invasion.

RUNNING HEAD: Marine habitat vulnerability and alien species.

INTRODUCTION

The presence of Alien Species (AS) in areas where they never have been found previously is generating major concern in the international scientific community (Ricciardi and MacIsaac, 2008). The rate of aquatic AS introduction and the spread of Invasive Alien Species (IAS) have rapidly increased in recent years, to the extent that these species are now considered as one of the top five anthropogenic threats throughout the oceans (Nellemann *et al*., 2008). IAS negatively affect the stability of receiving ecosystems, leading to significant socio-economic costs and hazards for human health (Carlton, 1985; Lodge, 1993; IUCN, 2000; Mack *et al*., 2000; Streftaris and Zenetos, 2006; Galil, 2007; Kettunen *et al*., 2009). To discover what makes the ecosystems susceptible to biological invasion (Holdgate, 1986; Li *et al*., 2000) is one of the most important goals in invasion ecology. Thus, the ability to predict the habitat invasibility, as an expression of the ecosystem's vulnerability to invasions, and to interpret the responses to bioinvasions is crucial for the implementation of ecosystem conservation tools (Hayes and Barry, 2008).

Ecosystem functioning is related to the strict relationships between their biotic and abiotic components, while biological invasions can alter the equilibrium among these components, thus menacing the biodiversity and the integrity of natural environments worldwide (Hulme, 2007; Vilà *et al.,* 2010). Nilsson and Grelsson (1995) defined fragility as the inverse of stability, relating these two ecosystem characteristics to the degree of change in species abundance and composition following anthropogenic disturbance. Habitat fragility results from the multiple interactions of climatic, edaphic and biotic factors (Lonsdale, 1999; Davis *et al*., 2000) that shape the temporal and spatial heterogeneity of habitats and their biological communities. Climate variations, nutrient availability, and external disturbances, contribute influencing interspecific interactions (facilitation, competition, and predation), their strength, and niche availability (Elton, 1958; Herbold and Moyle, 1986; Moyle and Light, 1996; Mack *et al*., 2000; Rejmanek, 2000; With, 2004; Paavola *et al*., 2005; Romanuk and Kolasa, 2005).

However, successful invasions are relatively rare (Williamson and Fitter, 1996) and mainly depend on the interaction between invasiveness (i.e. the biologically-related property of species to become established, spread to, or become abundant in new communities) and invasibility (i.e. the susceptibility of habitats to the establishment or proliferation of invaders) (Colautti *et al*., 2006). Most AS do not find optimal environmental conditions for reproduction, persistence, or survival, and are kept under control by unfavourable physical and chemical variables or by biotic interactions within the native community. Habitat heterogeneity, community complexity, species-habitat interactions, biological traits (e.g. fecundity, propagule pressure, population growth rate), and the stochastic nature of environmental phenomena, are likely to play a key role in determining the invasion success of AS (Elton, 1958; Mack *et al*., 2000; Colautti *et al*., 2006; Hayes and Barry, 2008). According to Zaiko *et al.* (2007) the generalized model of an 'invader friendly' habitat could be defined by the following features; i) the habitat has favourable physical conditions for maintaining diverse communities, and thereafter high native species richness might be considered as an indicator of habitat's invasibility; ii) the habitat lacks certain species which should to be present under normal conditions; iii) the habitat is disturbed due to natural or anthropogenic factors; iv) ecosystem properties are altered due to previous introductions, creating unstable conditions (successfully established habitat engineering species should be considered as a powerful facilitative factor for further invasions).

While some communities are prone to bioinvasions, others are naturally resistant (Elton, 1958; Tilman, 1997; Stachowicz and Whitlatch, 1999; Levine, 2000). The "*biotic resistance hypothesis*" (Elton, 1958; Rejmanek, 1989, Chapin *et al*., 1998; Levine *et al*., 2004) is based on the consideration that more diverse communities are very competitive and have an inherent ability to resist invasions. Conversely, communities with a small number of species offer a greater opportunity to access resources using different food chains and different life strategies (trophic niches). Just the opposite the "*biodiversity increasing invasibility hypothesis*" describing diverse communities to be more subject to invasions because of the facilitative effect of both native richness and previously introduced species (Cohen and Carlton, 1998; Stohlgren *et al.,* 2003). It emphasizes positive (e.g. mutualism, commensalism, or habitat modification) rather than antagonistic interactions (e.g. competition, predation) among species (Ricciardi, 2001). Facilitation AS-AS has been widely recognized in terrestrial environments (Simberloff and von Holle, 1999, Richardson *et al*., 2000) and facilitation by natives could be equally common (Maron and Connors, 1996). These two hypotheses do not necessarily need to be mutually exclusive and certain invasive phenomena may be thus the effect (or at least one factor of) and not the cause of ecological changes (Boero, 2002; Galil, 2007).

In Europe, all coastal waters are inhabited by AS: some habitats, such as lagoons and ports, act as "hubs" of introduction, and some regions have a larger array of AS (Paavola *et al*., 2005; Lotze *et al*., 2006; Zaiko *et al*., 2011). The Mediterranean Sea is considered as one of the most important marine AS hotspots in the world (Occhipinti-Ambrogi, 2000; Quignard and Tomasini, 2000) both in terms of the number of species (Costello *et al*., 2010) and rate of introduction (Zenetos, 2010). To date a total of 986 AS have been described (Zenetos *et al*., 2010, 2012) with an increasing trend due to shipping, aquaculture trade, and migration through the Suez Canal (Zenetos *et al*., 2010; Occhipinti-Ambrogi *et al*., 2011b; Katsanevakis *et al*., 2013). The Italian peninsula is like a biogeographical crossroads of the Mediterranean between the western and eastern basins, hosting 164 marine and brackish AS along its long coastline (Occhipinti-Ambrogi *et al*., 2011a, b), where physical and biological features vary considerably. The western side (Tyrrhenian Sea, Sicily and Sardinia) nearest to the north-western Mediterranean (Astraldi *et al*., 1995), whereas the Adriatic and Ionian Sea are more influenced by the eastern basin (Pinardi and Masetti, 2000). Among the most well-known marine biological invasions in the Mediterranean there are the filamentous Rhodophyta *Womersleyella setacea* and the Chlorophyta *Caulerpa cylindracea,* two harmful invasive species (Athanasiadis, 1997; Boudouresque and Verlaque, 2002; Piazzi *et al*., 2005; Verlaque *et al*., 2005; Streftaris and Zenetos, 2006) currently spreading along the Italian coasts as well. These IAS can inhabit a wide range of subtidal hard and soft substrata (sand, mud, rocks, and dead mattes of seagrasses) from 0 to 70 m depth, thus altering the structure of native assemblages. Such species are deemed to alter the structure of the communities of hard substratum leading to a change in the species composition of associated fauna, thus threatening the conservation status of several marine communities in the Mediterranean (e.g. Argyrou *et al*., 1999; Gravez *et al*., 2001; Zenetos *et al*., 2005; Baldacconi and Corriero, 2009; de Caralt and Cebrian, 2013).

By combining the most complete data set on the species inhabiting EUNIS Mediterranean habitats, the aim of this paper is to document the spread of AS in different marine habitats along the Italian coasts, showing the potential susceptibility of these habitats to biological invasions. Since the success of an invasion could be the result of a combination of different biological, ecological and environmental factors, the richness of AS was evaluated as a function of different predictors (native species richness, habitat differences and geography). Several models identifying the variables that best explain the observed pattern of AS were realized in order to assess the impact of different predictors on the presence-absence of AS. In addition, the pattern of presence-absence of AS in different habitats was explicitly explored in order to assess habitat preferences (i.e. single or multiple habitats) of different species.

The study focused on the ecosystem/habitat type of the European Nature Information System (EUNIS: http://eunis.eea.europa.eu/). The EUNIS habitat types classification is a comprehensive pan-European system to facilitate the harmonized description and collection of data across Europe through the use of criteria for habitat identification. Thus, there are two advantages of using the EUNIS habitat: first, the use of widely accepted habitat types recognized by the scientific community, and second, the EUNIS classification is a reference for the development of indicators and environmental reporting at both administrative and political levels.

The present paper represents the first comprehensive effort to analyse the distribution of AS across the Italian coast in marine ecosystem/habitat types considered in the European Nature Information System, and thus is an important step in setting conservation priorities, providing further insights of patterns of invasion across this area of the Mediterranean Sea.

MATERIAL AND METHODS

Data collection, geographical and temporal scales of the datasets

Taxonomic records were gathered from specific datasets belonging to several research institutions, both public and private. These data were shared within the context of the *Alien Species Showcase* created within the framework of the infrastructure LifeWatch (http://www.lifewatch.eu), the large European e-science infrastructure offering ecological informatics services and tools to scientists and other public and private institutions involved in biodiversity and ecosystem research (Basset and Los, 2012).

The resulting dataset gathers biological diversity records from marine sites along the Italian coastline, subsequently merged into Geographic Macro Areas (GMAs) as suggested by

Occhipinti-Ambrogi *et al*. (2011a). Some of the sites belong to the LTER-Italy network (Long Term Ecological Research Italian network, http://www.lteritalia.it).

Overall, 12,521 records (5,067 planktonic, 7,105 benthic, and 349 nektonic) from 93 marine sites have been gathered by the LifeWatch community in Italy. Marine sites included habitats classified as *littoral rock and other hard substrata* (2 sites, EUNIS code level 2: A1), *littoral sediment* (3 sites, EUNIS code level 2: A2), *infralittoral rock and other hard substrata* (8 sites, EUNIS code level 2: A3), *circalittoral rock and other hard substrata* (26 sites, EUNIS code level 2: A4), *sublittoral sediment* (8 sites, EUNIS code level 2: A5), *deep-sea bed* (2 sites, EUNIS code level 2: A6), and *pelagic water column* (44 sites, EUNIS code level 2: A7). No lagoon and estuarial environments have been analysed in the present study. Each research unit provided lists of species generated from field research programmes on the biodiversity of specific habitats of reference and listed according to EUNIS codes. A nomenclatural revision of the dataset was carried out based on the taxonomic information provided by WoRMS (World Register of Marine Species, Appeltans *et al*., 2012). All data were screened for taxonomic reliability, synonymy and for the definition of "alien" by taxonomy experts in the LifeWatch-Italy network. The data-set included data referred to the period 2000 - 2012.

The definition of an AS adopted in this study refers to the deliberately or inadvertently introduction of living organisms (species, subspecies or lower taxa, gametes or propagules) by human activities and found outside of their past and current distribution area with survival and reproduction success (IUCN, 2000; Hulme, 2009). According to Olenin *et al.* (2010), natural changes in areal distribution (e.g. due to climate change or because of occasional leakage due to marine currents) do not define AS *per se*. AS have been identified through literature searches and taxonomic experts belonging to the LifeWatch infrastructure.

In operational terms and taking into account the history of species introduction, it is also useful to establish temporal benchmarks beyond which records of new species should be considered as part of the native biota. These benchmarks conventionally refer to events that have broken down natural barriers or have created new connections.

In the Mediterranean, two major benchmarks are recognized: the realization of the Suez Canal (Zenetos *et al*., 2010); the end of the Second World War and the increasing traffic due to shipping, aquaculture and research (Occhipinti-Ambrogi *et al*., 2011a; GSA-SIBM, 2012). In this study, the realization of the Suez Canal has been chosen as benchmark for the Italian coast; this decision is tied to the need to establish a reference period that cannot be formally proved as the limit for biological invasions. It represents a time interval useful and convenient to indicate a period of great change in the Mediterranean, which was accompanied by climatic variation dependent on other factors.

Statistical analysis

To evaluate the richness of AS in relation to sampling efforts in different EUNIS habitats (Habitats), rarefaction curves for the whole dataset and for the two most represented EUNIS groups in the LifeWatch dataset (algae and invertebrates) were obtained using the function *rarecurve* implemented in the R (R Core Team, 2014) package Vegan (Oksanen *et al*., 2013).

In order to model the AS richness, different Generalized Linear Mixed Models (GLMM) were built by using three different potential predictor variables: native species richness (Rn), habitat (according to EUNIS level 2 classification) and geographical location (according to GMA defined in Figure 2). GLMMs offer a flexible approach to model the sources of variation and correlation that arise from grouped data by combining the properties of linear mixed models, which incorporate random effects, and generalized linear models, which handle non-normal data (Bolker *et al*., 2009).

In this work, models have been fitted using the AD Model Builder implemented in the glmmADMB package (Fournier *et al*., 2012) in the R statistical environment. The AD Model Builder fits models using a GLMM that takes into account an excess of zero in the raw data (the norm in presence-absence data). In addition, models were fitted with a negative binomial distribution to take into account the over-dispersed data (Bliss and Fisher, 1953). Both sampling site and EUNIS group were included as random effects in order to consider the spatial dependence of the data and potential bias introduced by the non-homogeneous sampling across taxa. All the possible combinations of the three variables were examined to evaluate the fit of different predictor variables. The best fit of the models obtained was evaluated using the Akaike Information Criteria (AIC).

In order to explore the pattern of AS distribution across different habitats, a Multiple Correspondence Analysis (MCA) was applied on the matrix of AS-habitat interactions (matrix of presence-absence with 61 species and 7 habitats). MCA analysis is the counterpart of principal component analysis for categorical data, which shows the underlying structure in the dataset. The MCA was performed using the R package FactoMineR (Husson *et al*., 2014).

RESULTS

The dataset

A total of 3,899 species belonging to 5 kingdoms (Bacteria, Chromista, Protozoa, Plantae, and Animalia) and 29 phyla were listed in the LifeWatch database (Figure 1). Of these, 61 AS belonging to 11 phyla were recorded (Table 1), representing nearly 1.6% of the total number. Annelida was the most represented taxon in terms of AS (16 species), followed by Rhodophyta (14), Arthropoda (8), and Mollusca (8), together representing the 75% of the observed AS. In the remaining seven groups (Myzozoa, Ochrophyta, Chlorophyta, Ctenophora, Cnidaria, Bryozoa, and Chordata), the number of AS ranged from 1 to 4. No AS was detected in the remaining 18 phyla.

Figure 2 shows the distribution of the considered AS along the Italian coast considering all the habitats investigated. The dataset included records from 11 GMAs (see Occhipinti-Ambrogi *et* *al*., 2011a) and AS were found in 10 of them, with the highest percentage values detected in the northern Tyrrhenian Sea (4.4%), followed by the southern Tyrrhenian (2%), central Tyrrhenian and northern Adriatic (1.4%). No AS was recorded in the dataset from the southern Ionian Sea.

Eighteen AS were detected in more than one GMA: in particular, the benthic seaweed species (*Acrothamnion preissii, Caulerpa cylindracea, Womersleyella setacea, Asparagopsis armata*) and the hydroid (*Clytia linearis*) were detected over three GMAs. The remaining 13 species were detected in two GMAs.

AS were recorded in all the considered habitats (Figure 3), with a maximum of 28 species in circalittoral hard substrata and a single AS in deep-sea bed. In terms of proportions to the native species, the maximum percentage of AS (3.7% of the present species richness) was found in littoral hard substrata, and the minimum (0.4%) in deep-sea bed. Fifty-four AS were found in the 49 sites of the benthic domain (EUNIS habitat A1, A2, A3, A4, A5, and A6) and 9 in the 44 pelagic sites (A7), with a prevalence of phytoplankton AS.

Generalized linear models

According to AIC, all the models performed better than the null model (Table 2). The best model describing AS richness took account of both native species richness (Rn) and EUNIS habitat type (Habitat) but not Geographic Macro Areas (GMAs) as explanatory variables.

The model that explicitly considers the difference in taxonomic coverage and spatial bias detected a significant ($p<0.001$) and positive trend in increase of AS with the increase in Rn (Figure 4). Concerning the effect of habitat, all EUNIS categories showed a significant relationship with AS richness (Ras) except for infralittoral rock substrata and deep-sea beds. According to regression coefficients (Figure 5) and the Tukey test, the differences observed are due to a lower number of AS found in the pelagic water column compared to littoral rock and other hard substrata, infralittoral rock and other hard substrata, circalittoral rock and other hard substrata, and sublittoral sediments (Tukey test: $p<0.05$ in all the pairwise comparisons). Conversely, the other habitats showed no significant differences between them.

Multivariate analysis of species-habitat interaction

The ordination plot obtained from MCA (the first two axes shown account for 44.7% of the total variance) shows how species are assembled according to their habitat of occurrence (pelagic waters, soft substrata, hard substrata, deep-sea beds) (Figure 6). MCA highlights three main groups of species, namely species found in a single EUNIS habitat, species shared across similar habitat categories (i.e. between sublittoral and littoral sediments or among rocky substrata) and also species that can be found across very different habitats (i.e. pelagic waters and sediments).

While 43 of the AS (70% of the total AS) can be found within a specific EUNIS habitat (level 2), the others are shared among different habitats (trans-habitat AS). Circalittoral rock and other hard substrata showed the largest number of AS and the largest amount of trans-habitat AS (50% of total).

Of the nine AS found in the pelagic water column, *Anadara inaequivalvis* and *Ruditapes philippinarum* were also detected in sublittoral sediments. Two Terebellidae polychaetes shared littoral and sublittoral sediments habitats while the polychaete *Notomastus aberans* was found both in sublittoral sediment and in circalittoral rock and other hard substrata. Littoral, sublittoral and infralittoral rocks shared the algae *Acrothamnion preissii*, *Asparagopsis armata*, and, together with sublittoral sediments, also *Caulerpa cylindracea*, and *Womersleyella setacea*. The hydrozoan *Clytia linearis,* the only AS found in deep-sea bed, was also found in littoral and infralittoral rocks.

Correlates of AS presence

Sample-based rarefaction curves (cumulative count of AS against the number of sites, for homogeneous subsets of data) are reported in Figure 7, considering all the AS (whole sample) and the two most represented groups: invertebrates and algae.

When AS are considered as a whole, all the habitats but one (littoral rock and other hard substrata) showed a logarithmic trend of rarefaction curves. Sublittoral sediment tended quickly towards a plateau while others habitats showed a continuous increase of number of AS (marked up to 20 sample sites for circalittoral rock and other hard substrata).

Looking at rarefaction curves for invertebrates AS only, circalittoral rock and other hard substrata still showed a constant increase of AS with the increase of the number of sampled sites. Conversely, pelagic water column and partially sublittoral sediments were close to a plateau. The situation changes when algae AS are considered: all habitats except littoral rock and other hard substrata began to show a tendency to decrease the slope of the curves. Infralittoral rock and other hard substrata also showed an evident decrease but it occurred at a higher number of sampled sites. Finally, for littoral rock and other hard substrata there was a marked and continuous increase of AS number with the number of sampled sites.

DISCUSSION

A picture of marine AS presence across EUNIS habitats along the Italian coast

Although the spread of AS is becoming an increasing problem, studies comparing the distribution of AS among habitats are surprisingly uncommon in marine environment (e.g. Zaiko *et al*., 2007). Literature referred to the marine biota mainly focuses on the distributional traits of single invasive species in a few habitats (e.g. Piazzi and Cinelli, 2001; Zaiko *et al*., 2007; Gollasch *et al*., 2008; Baldacconi and Corriero, 2009; Piazzi and Balata, 2009; Olenina *et al*., 2010; de Caralt and Cebrian, 2013). Thus, the present paper represents the first study on the occurrence and distribution of AS in a large number of marine habitats within the Mediterranean. Despite the dataset here processed did not include all known AS and the geographical coverage was piecewise, the paper provides a reasonably comprehensive overview of the distribution of AS in all the EUNIS habitats (second level) present along the Italian coast.

To date, current literature on the Mediterranean does not allow to distinguish the pool of AS inhabiting natural marine environments from those exclusive to harbours, polluted sites and lagoon environments. In recent reviews, Occhipinti-Ambrogi *et al*. (2011a, b) computed 164 AS (both marine and brackish) for the Italian coasts, corresponding to about 20% of the non-native species totally reported for the Mediterranean Sea (GSA-SIBM, 2012). Most of them, however, were recorded from lagoons, coastal lakes, harbours and marine areas heavily exploited by human activities (e.g. Occhipinti-Ambrogi and Savini, 2003; Sfriso *et al*., 2009; Longo *et al*., 2012; Petrocelli *et al*., 2013; Cardone *et al*., 2014), which are hubs for biological invasions (e.g. Pérez-Ruzafa *et al*., 2011; Petrocelli *et al*., 2013), whereas the records of AS from natural environments are less common in literature. The list of 61 AS in the present paper, exclusively referred to natural marine habitats, seems to confirm that, to date, most of AS present along the Italian coast are closely associated to the introduction hot spot areas, and only a fraction of them spread across natural marine habitats.

The AS taxonomic analysis indicated invertebrates as the most represented group (about 62% of the total AS number). Such a result is in agreement with the current literature reviews for the Italian coasts, where this group includes about 80% of the known AS (Occhipinti-Ambrogi *et al*., 2011a, b). In the marine environment species extinctions caused by invertebrate AS are poorly documented (Gurevitch and Padilla, 2004; Pranovi *et al.,* 2006; Briggs, 2007), while most of the literature mainly refers to the effect on native community by non-native algal spread (Piazzi *et al.,* 2005; Baldacconi and Corriero, 2009; de Caralt and Cebrian, 2013). This lets imagine a scenario still waiting to be explored, since this animal component is dominant among AS also at Mediterranean scale (Zenetos *et al.,* 2010; 2012).

In the framework of this study, AS occur in all habitats and almost all geographic areas (GMAs), albeit with different distributions. Most of them were detected in benthic environments (54 species), and only 9 in the pelagic domain, in accordance with Occhipinti-Ambrogi *et al*. (2011a, b), reporting most of the AS within benthic habitats. This could be due to the different mechanisms of introduction, spreading and persistence of AS in the two environmental compartments. Many AS spread through pelagic propagules within ballast waters (e.g. Olenin *et al*., 2010; Gollasch *et al*., 2013), but they are very hard to find, because of their biological and ecological characteristics (e.g. ephemeral and patchy distribution, heteromorphic life cycles) and relative difficulties in their sampling.

According to the statistical analysis, AS recorded during the present study could have been more numerous, since some marine habitats seemed to be still unsaturated. There were clear differences in the number of species observed with respect to the number of sites sampled and no habitat really reached a plateau (Figure 7). This is particularly evident in littoral, infralittoral and circalittoral rocks, thus indicating that these marine habitats could host an even larger number of

AS. On the contrary, the sublittoral sediment showed an initial logarithmic increase in the number of AS, followed by a reduction in the curve slope very close to a plateau, thus suggesting that this habitat could not be prone to host a much greater number of AS. The pelagic habitat showed a little steep slope in the rarefaction curves, suggesting a possible lower (or slower) propensity to host AS compared to benthic habitats.

Within the benthic domain, the circalittoral rock and other hard substrata (in the LifeWatch database mostly represented by coralligenous assemblages) is the habitat with the greatest number of AS (8 algae, 1 ctenophore, 2 hydrozoan, 9 polychaetes, 5 molluscs, 2 crustaceans, and 1 bryozoan). It is indeed the habitat with the highest native species richness. According to Byers and Noonburg (2003) native and exotic species diversity are often positively related in large-scale observational studies, but negatively correlated in small-scale ones. In the present study, including large scale biodiversity data, a significant positive relationship between AS richness and native species richness was revealed by the GLMM analysis, thus suggesting a pattern that fits with the "*biodiversity increasing invasibility hypothesis*" (Cohen and Carlton, 1998; Stohlgren *et al.,* 2003) as well. Furthermore, observational studies carried out in terrestrial environments at regional scale, have found that exotic species richness in plants is associated with high native plant species richness (Lonsdale, 1999; Stohlgren *et al*., 2006). On broader spatial scales, the physical complexity of natural communities (i.e. environmental heterogeneity) appears to obscure the resistance to the spread of AS provided by high species richness (Levine, 2000; Shea and Chesson, 2002). Hence, according to these studies, the combination of ecological processes and factors that maintain high native species richness in plant communities also increases the spread of AS.

Along the Italian coasts, the coralligenous biogenic habitat characterizes circalittoral and, partially, infralittoral hard substrata. It is a highly biologically differentiated marine community (Hong, 1982; Laborel, 1987) with more than 1,500 species (Ballesteros, 2006), characterized by wide variations in invertebrate and algal composition in relation to increasing depth and varying ecological and edaphic conditions (Ferdeghini *et al*., 2000; Ballesteros, 2006; Bedini *et al*., 2014). The high number of AS found in circalittoral and infralittoral hard substrata could be related to the high biodiversity of coralligenous assemblages, enhanced by their environmental stability and habitat heterogeneity (Cocito, 2004; Ballesteros, 2006).

The importance of coralligenous outcrops is also due to the presence of numerous species of conservation interest. To date, more than 50 exclusive coralligenous invertebrate key-species has been reported in international biodiversity conventions and/or in European red lists (e.g. *Spongia officinalis*, *Cladocora caespitosa*, *Corallium rubrum*). Although pollution and increased sedimentation rates are recognized to be the main threats to coralligenous assemblages (Boudouresque *et al*., 1990), the spread of AS could represent an emerging threat, since it could lead to profound changes in the community by changing the pattern of distribution and abundance of native structuring species (Occhipinti-Ambrogi, 2000; Piazzi and Cinelli, 2000). As coralligenous outcrops represent one of the most important biodiversity hotspots in the Mediterranean, the loss of their unique characteristics leads to significant threats to the entire littoral system (Piazzi *et al*., 2012).

The scenario changes among soft bottom habitats.

Native communities associated to sublittoral sediment habitat strongly varies in presence of vegetal coverage, in particular seagrasses (mainly *Posidonia oceanica* and *Cymodocea nodosa*), that are very important for their structural complexity, ecological function, and high levels of associated species richness (Klumpp *et al.,* 1992, Mazzella *et al*., 1992). When vegetal coverage is lacking, native communities are much depleted in species, and mainly dominated by scavenger invertebrates. Although sublittoral sediment habitat appears to be close to reaching a balance in the number of AS (see rarefaction curves, Figures 7), the presence of 16 AS (2 algae and 14 invertebrates) should be emphasized. According to the literature, seagrasses represent the most suitable substrate for the spread of the invasive algae *Caulerpa cylindracea* and *Womersleyella setacea* (e.g. Piazzi and Cinelli, 2003; Piazzi and Balata, 2009). Present data, however, highlight the dominance of invertebrates among AS associated to sublittoral sediments, with 6 species of polychaetes, 5 molluscs, and 3 crustaceans. Among them, *Arcuatula senhousia* is considered locally invasive along the Italian coast (Mistri *et al*., 2004) and it is able to alter sedimentary properties of soft bottoms, through the construction of byssal mats on the surface of sediments. Although the other identified invertebrate AS are not considered invasive, their spread in the soft-bottom habitats may be considered as a potential threat, being their interactions with native fauna unexplored. Along the coast of the Italian peninsula, a well-known case refers to the North Adriatic, where repeated introductions of the commercial mollusc *Ruditapes philippinarum* allow to the depletion and locally the disappearance of the close native *R. decussatus* (Pranovi *et al.,* 2006). In extra Mediterranean environments, however, a positive interaction between alien and native species in sublittoral sediment is also reported. It regards the polychaete *Marenzelleria* sp., which has been described positively affects the keystone species *Zostera marina*, by burying the seeds of the phanerogam, so reducing seed predation and facilitating seed germination (Delefosse and Kristensen, 2012).

In the framework of the habitat examined in present study, littoral sediment may be considered among the less rich in native species. The pool of data in the LifeWatch database refers to a considerable number of observations on a few sites, which if on the one hand it does not allow to highlight trends on the relationship species/area (rarefaction curves), on the other hand provides a glimpse indication on the occurrence of AS in this habitat. The AS here recorded are all invertebrates, 3 polychaetes and 1 arthropod, reflecting the attitude of this environment to host more than anything else animals. The low number of AS recorded may be explained by the great temporal variability that characterizes the littoral communities, due to the action of waves and to the seasonal hydrological (e.g. temperature, salinity) variations.

Even the deep-sea habitats have AS, despite being generally imagined as the best preserved and by far the most distant from the hubs of introductions. In the present paper a single hydroid AS has been identified (*Clytia linearis*) with large ecological plasticity and trans-habitat distribution. The species is one of the most common Mediterranean hydroids on shallow hard bottom (Bouillon *et al*., 2004), and thereafter may be considered as invasive. To date however, no data are available about its possible influence within native communities.

As expected, the MCA showed how most of the AS occupies the same position on the factorial map, because they are associated with one EUNIS habitat. However, a large fraction of the benthic AS reported in the present work (about 30% of the total AS recorded) showed a trans-habitat distribution (Figure 6), since these species are able to indifferently colonize pelagic and benthic compartments (both hard and soft bottoms) within a wide bathymetric range. The ability to colonize habitats characterized by wide variations in edaphic and bathymetric conditions could reflect the intrinsic characteristics of the species in their native range, but it could also be considered as a measure of the potential invasiveness of the AS. The circalittoral habitat presented the highest number of trans-habitat AS (14) in addition to a greater AS species richness, providing a further indication of its vulnerability to biological invasions.

From a geographical point of view, a higher concentration of AS could have been expected in GMAs including marine sites close to centres characterised by intense maritime traffic (e.g. harbours and lagoons). However, although a high number of AS were recorded in some GMAs, the GLMM does not support a geographical effect on their localization, probably because the present analysis included only natural marine environments. The lack of differences from a geographical point of view could be explained in terms of differences between introduction and persistence of AS (most invasions fail; Williamson and Fitter, 1996). While the introduction of AS in marine environments could be mainly due to the presence of point entry vectors, their spread and persistence could be related to biotic and ecological factors regulating the AS success.

Conclusive remarks

Data gathered from the present study allow to get a view of AS, widely distributed along the Italian coast, from shallowest to deepest and from stressed to pristine habitats, getting a glimpse on the proneness of marine habitats to host AS.

The results of this macro-ecological study enable to focus on important points in order to highlight aspects not easily detectable by researches carried out on a single species or habitat.

The most relevant feature regards the importance to perform large scale studies, in order to develop effective management strategies and to move forward the discipline of invasion ecology, since the impacts of AS need to be seen in an ecosystem perspective.

Another feature concerns the occurrence of a positive relationship between alien and native species richness in marine environments. Whereas it has varied explanations, from the intrinsic characteristics of the system, allowing to sustain a demographically successful AS population, to the presence of external factors acting on the community (Davis *et al*., 2000; Zaiko *et* *al*., 2007), this evidence confirms to focus the interest of monitoring programs on the most pristine marine habitat as well (Otero *et al*., 2013).

Even though the introduction of AS locally increases specific richness (Gurevitch and Padilla, 2004; Briggs, 2007), in most cases the invasion has not a positive value, since the receiving systems become ecologically off-balance. According to several authors (Dick *et al*., 2002; Gurevitch and Padilla 2004; Piscart *et al*., 2009; Hänfling *et al*., 2011), the most serious consequences may be changes in native species composition and some instances of extirpation of local native populations. However, what invaded ecosystems really lose is not biodiversity, but biological uniqueness, integrity, and ecological functions (Rilov, 2009). On the other hand, studies on positive effects of AS are receiving increasing attention (Thieltges *et al*., 2006; Schlaepfer *et al*., 2011; McLaughlan *et al*., 2013; Thomsen *et al*., 2014) and some authors (Katsanevakis *et al*., 2014) suggest that positive impacts of AS may be underestimated.

The occurrence in habitats not traditionally considered hubs for biological invasions, suggests that the patterns of introduction and persistence of AS probably follow different models. It must be assumed that the AS present in marine communities are not so much the result of point introductions, but rather the effect of expansions of species previously introduced in different environments (e.g. lagoons, ports, mussel plants). Consequently, from a conservation point of view, two different monitoring models should be distinguished, a first one aimed to get an early warning of the arrival of AS in the hot spots of introduction and a second one aimed to evaluate the success of these species in marine environments. Thus, the present study highlights the importance to design monitoring strategies suitable for different habitats (all those hosting a great number of AS) such as those historically considered AS hubs (mainly transitional waters), and the biologically rich and diverse benthic ones (infra and circalittoral rocky substrata). The importance of AS monitoring programs on benthic habitats is also supported by the need to assess the potential impact of AS on key species, among which the pool of bioconstructors (mainly algae) able to sustain specific assemblages. Besides having an indisputable ecological and conservation value, diverse benthic communities also have an economical value since their spectacular landscape value attracts divers.

Monitoring programs should lead to conservation strategies that allow the possibility of mitigating biological invasions, but studies in marine habitats are still in their infancy. While researches on the vulnerability of freshwater and lagoon environments bring to the conclusion that biological invasions can potentially be controlled and limited by mitigating human activities in the environment (Pyšek *et al.,* 2010; Boggero *et al*., 2014), it is still difficult to determine in marine habitats the most significant correlates to set conservation priorities. According to Ekebom (2013), the process of incorporating the ecosystem approach into marine and environment policies is "a long and winding road" and to date, considering the unpredictability of the invasion process, what can be done is to improve methods to detect impacts and implement experimental and mensurative studies at different spatial scale.

Still more particularly, it should be emphasized that the literature on invertebrate AS and their impact is still quite poor. According to Occhipinti-Ambrogi *et al*. (2011a, b), invertebrates dominate the scenario of AS along the Italian coast (including the transitional environments) and they are the main component in the sea as well. Working up the studies on the interaction between invertebrate AS and native communities is necessary, since sometimes they escape to immediate observations (such as worms and molluscs in sediments), but can lead to local species replacement, such as for example the case of *Ruditapes Philippinarum* (Pranovi *et al*., 2006).

In the present paper, EUNIS habitats (Level 2: 8 habitats of the Mediterranean) have been used, but the level of detail should be much higher. Moving forward in this direction seems fruitful, allowing to describe the relationship between AS and habitats at a higher level of detail, and to investigate more thoroughly what makes marine habitats able to accommodate AS.

To date, the only realizable recommendations are on one hand to stimulate the ability of ecosystems to intrinsically resist biological invasions, by improving environmental quality, and, on the other hand, to prevent further invasions. These recommendations are more significant in the light of the strategic plans that Mediterranean countries are currently preparing, all of which consider AS monitoring as an important issue.

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Table 1. List of the recorded AS.

Myzozoa
Alexandrium catenella (Whedon, Kofoid) Balech, 1985
Ostreopsis cf. *ovata* Fukuyo, 1981
Ochrophyta
Chaetoceros bacteriastroides G.H.H.Karsten
Halothrix lumbricalis (Kützing) Reinke, 1888
Pseudo-nitzschia multistriata (Takano) Takano, 1995
Skeletonema tropicum Cleve, 1900
Chlorophyta
Caulerpa cylindracea Sonder 1845
Caulerpa taxifolia (M. Vahl) C. Agardh, 1817
Rhodophyta
Acrothamnion preissii (Sonder) E.M.Wollaston, 1968
Aglaothamnion feldmanniae Halos, 1965
Antithamnion hubbsii E.Y.Dawson, 1962
Apoglossum gregarium (E.Y. Dawson) M.J. Wynne, 1985
Asparagopsis armata Harvey, 1885
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon, 1845
Botryocladia madagascariensis G. Feldmann
Ceramium bisporum D.L. Ballantine
Chondria coerulescens (J. Agardh) Falkenberg
Hypnea cornuta (Kützing) J. Agardh

Lophocladia lallemandii (Montagne) F. Schmitz
Neosiphonia harveyi (Bailey) M.S. Kim, H.G. Choi, Guiry, G.W. Saunders
Polysiphonia atlantica Kapraun, J.N. Norris
Womersleyella setacea (Hollenberg) R.E. Norris
Cnidaria
Clytia hummelincki (Leloup, 1935)
Clytia linearis (Thorneley, 1900)
Coryne eximia Allman, 1859
Eudendrium merulum Watson, 1985
Ctenophora
Beroe ovate Bruguière, 1789
Mollusca
Anadara inaequivalvis (Bruguière, 1789)
Anadara transversa (Say, 1822)
Aplysia parvula Mörch, 1863
Arcuatula senhousia (Benson in Cantor, 1842)
Crassostrea gigas (Thunberg, 1793)
Crepidula fornicata (Linnaeus, 1758)
Fulvia (Fulvia) fragilis (Forsskål in Niebuhr, 1775)
Venerupis philippinarum (A. Adams, Reeve, 1850)
Annelida
Desdemona ornata Banse, 1957
Epidiopatra hupferiana monroi Day, 1957
Eunice floridana (Pourtalès, 1867)
Ficopomatus enigmaticus (Fauvel, 1923)
Hyboscolex longiseta Schmarda, 1861
Hydroides dianthus (Verrill, 1873)
Hydroides elegans (Haswell, 1883)
Leiochrides australis Augener, 1914
Lysidice collaris Grube, 1870
Mediomastus capensis Day, 1961
Megalomma claparedei(Gravier, 1906)
Neanthes agulhana (Day, 1963)
Notomastus aberans Day, 1957
Pista unibranchia Day, 1963
Streblosoma hesslei Day, 1955
Syllis alosa San Martín, 1992
Arthropoda
Balanus trigonus Darwin, 1854
Caprella scaura Templeton, 1836
Dyspanopeus sayi (Smith, 1869)
Paracartia grani Sars G.O., 1904
Penaeus semisulcatus De Haan, 1844 [in De Haan, 1833-1850]
Percnon gibbesi (H. Milne Edwards, 1853)
Pseudodiaptomus marinus Sato (1913)
Rhithropanopeus harrisii (Gould, 1841)
Bryozoa
Bugula fulva Ryland, 1960
Chordata
Fistularia commersonii Rüppell, 1838

Table 2. Model selection according to Akaike's Information Criterion (AIC). The AIC was compared with different fitted models in order to identify the best explanatory model. The fixed term and degrees of freedom (d.f.) were reported for each model. A1, littoral rock and other hard substrata; A2, littoral sediment; A3, infralittoral rock and other hard substrata; A4 circalittoral rock and other hard substrata; A5, sublittoral sediment; A6, deep-sea bed; A7, pelagic water column.

Fixed effect	df	AIC
Habitat+Rn	**12**	**361.418**
Habitat+Rn+GMA	22	370.852
Rn+GMA	16	383.342
Rn	6	386.846
Habitat	11	400.77
Habitat+GMA	21	403.62
GMA	15	412.032
Null model	5	434.566

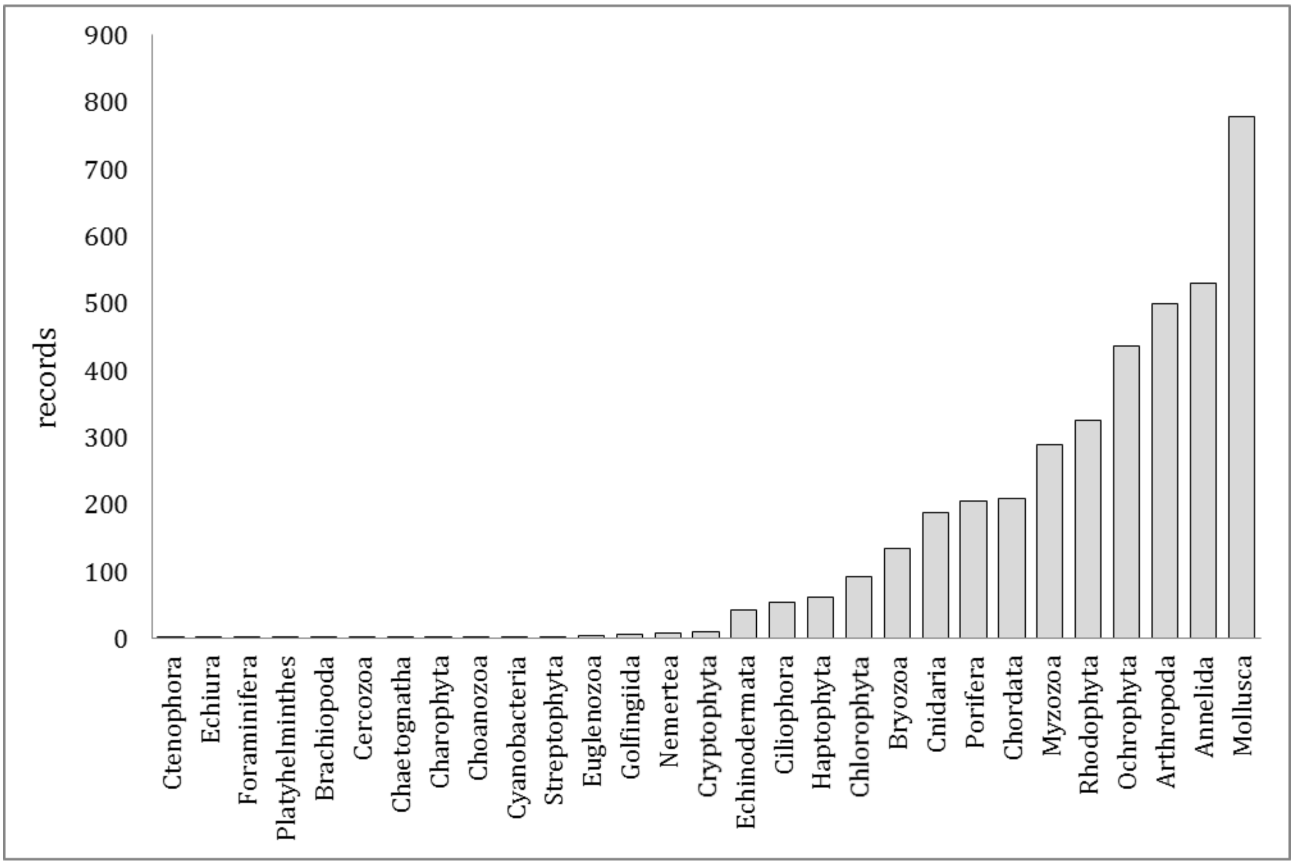

Figure 1. Distribution of total recorded species among taxonomic groups.

Figure 2. Distribution of marine sampling sites and AS along the Italian coast. Circles: percentage of AS over species richness (R) for each sampling site; numbers: percentage of AS over R in each GMA; number between brackets: total number of AS recorded in each GMA.

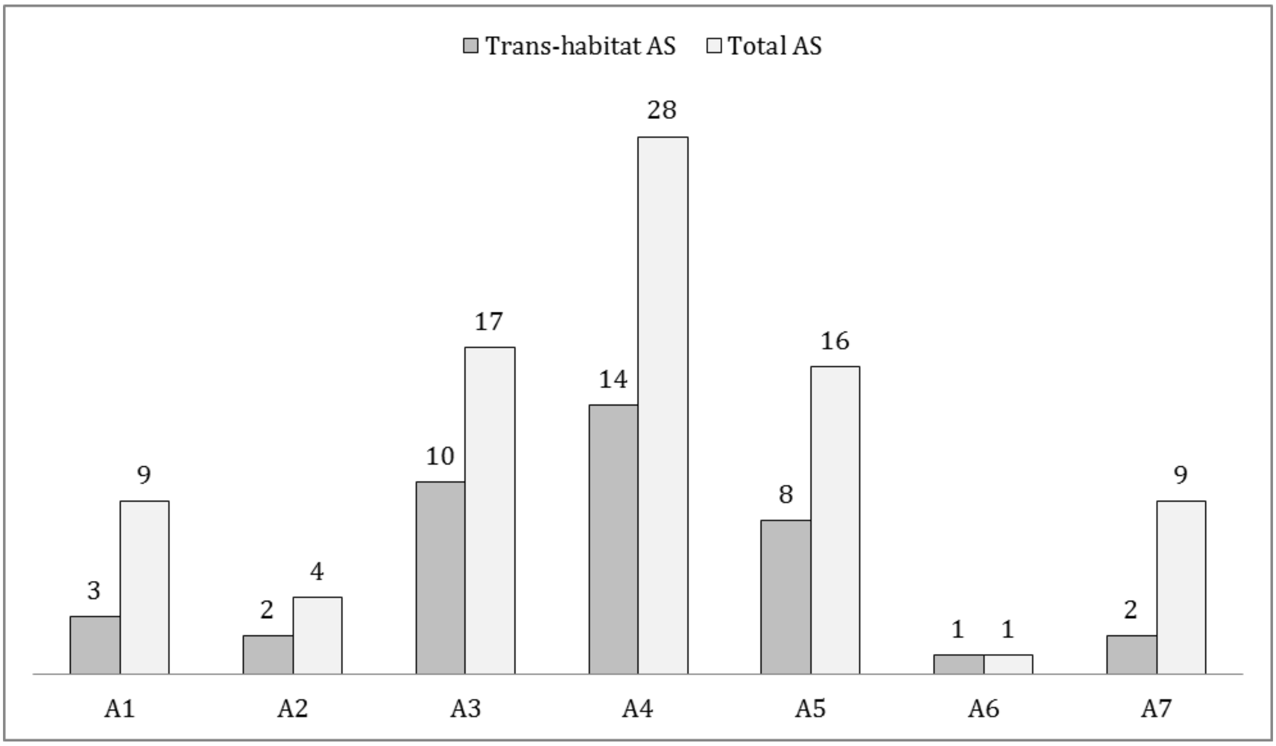

Figure 3. Distribution of AS and trans-habitat AS in EUNIS Habitat level 2.

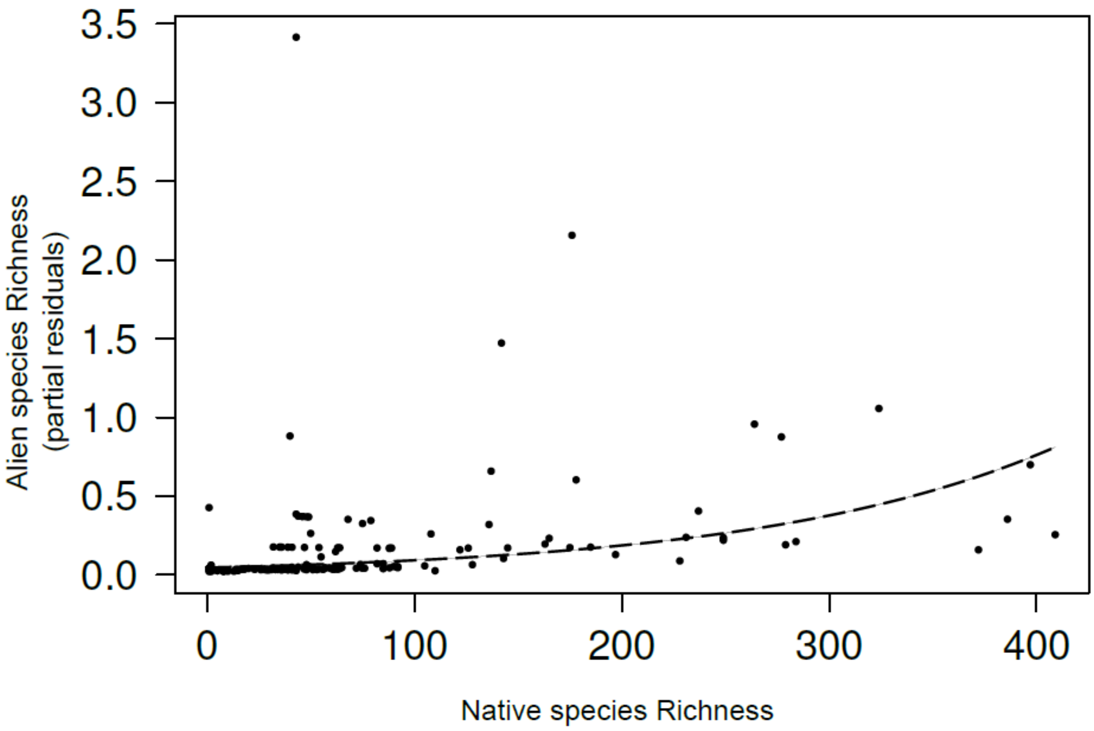

Figure 4 Relationships between native species richness and AS richness at a site level for each taxonomic group and habitat EUNIS according to the results of GLMM.

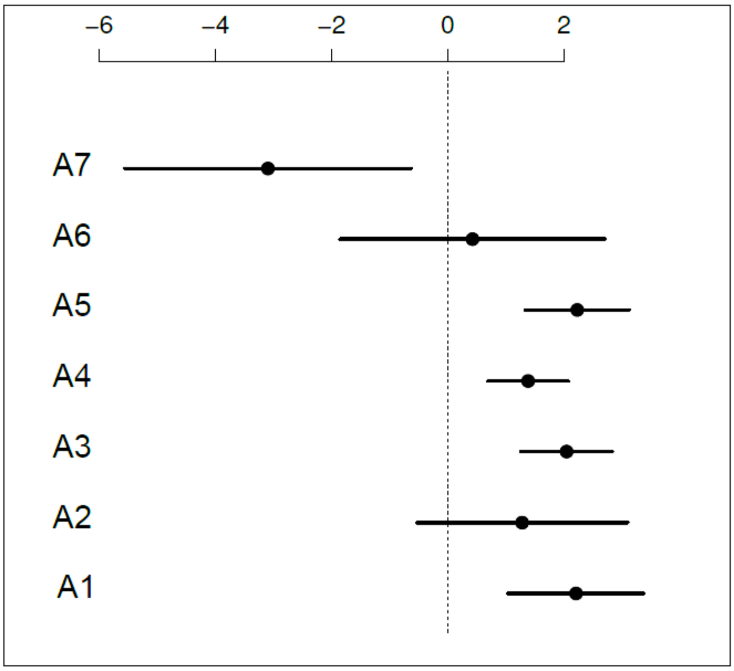

Figure 5. Regression coefficients obtained from GLMM for the seven EUNIS habitats included as factors. Circles represent estimated coefficients, while lines represent 95% confidence interval.

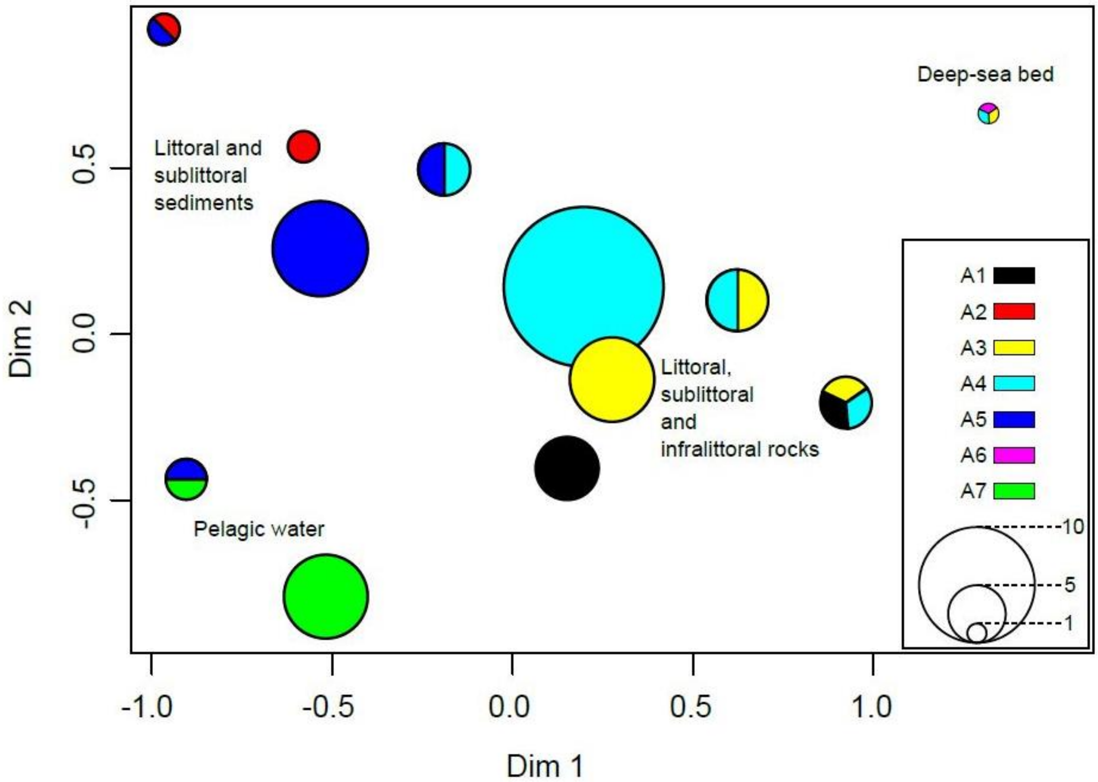

Figure 6. Multiple correspondence analysis (MCA) based on presence-absence matrix of AS. Colours represent different EUNIS Habitat where the species was found, while circle size is proportional to the number of species. The species are clustered according to habitat similarity.

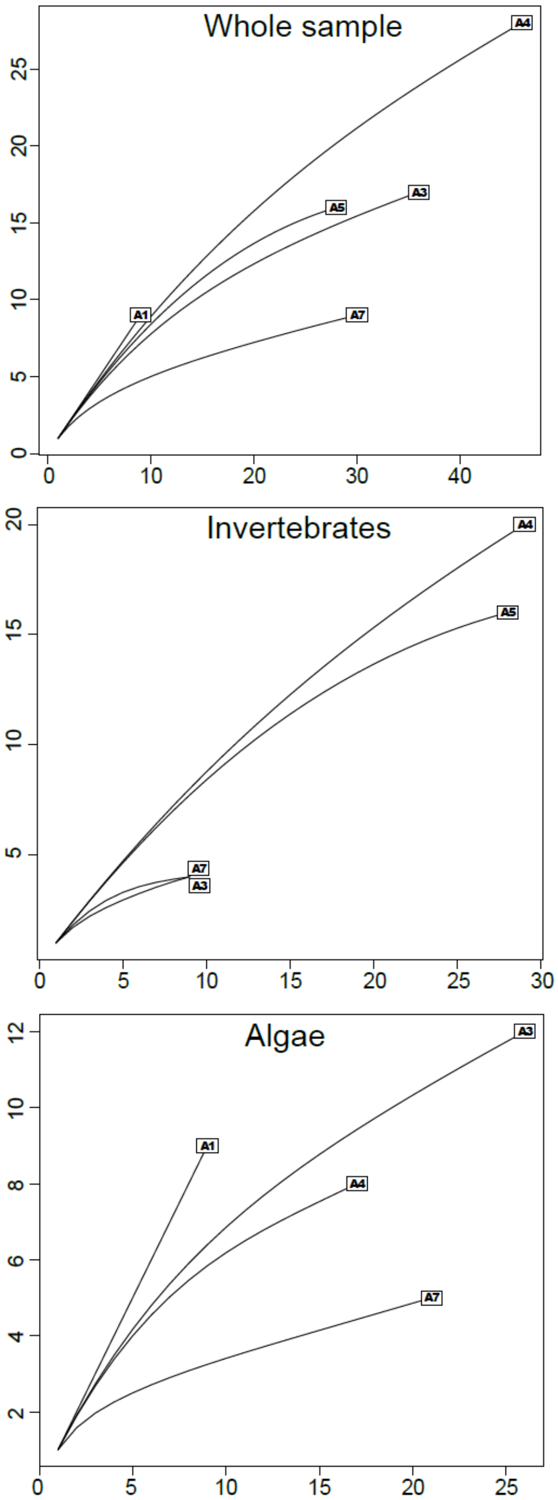

Figure 7. Rarefaction curves obtained as a count of AS against the sample size (number of sites) for the observed AS richness in the whole dataset, invertebrates and algae samples sub-datasets. On the "y" axis the number of observed species and on the "x" axis the sample size are reported. For Invertebrates EUNIS habitats A2 and A6 were excluded from the analysis due to the low sample size (4 and 1 respectively).

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