

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 descriptors 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 was gathered of the occurrence of 3899 species from 29 phyla, taken from 93 marine sites located along the Italian coast in the period 2000–2012.

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3. In total, 61 AS belonging to 11 phyla have been recorded. Invertebrates were the most represented (63%). Alien species were found in all the habitats examined (EUNIS, level 2), although they showed highest abundance in benthic habitats. Most of the AS were associated with a single EUNIS habitat, while some of them were present in more than one habitat. Trans-habitat occurrence suggests the 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 of both 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 of performing large-scale studies, since adopting ecosystem approaches to marine invasion management seems especially fruitful.

6. The results, moreover, highlight the importance of AS monitoring of different habitats, from those subjected to anthropogenic pressure, historically considered to be hubs of introduction of AS, to the most biologically rich and diverse marine habitats. 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.

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KEY WORDS: marine alien species; Mediterranean EUNIS habitats; habitat vulnerability; invasive alien species; invasion

INTRODUCTION

The presence of alien species (AS) in areas where they have never been found previously is generating major concern in the international scientific community (Ricciardi and MacIsaac, 2008; Simberloff, 2014). The rate of aquatic AS introduction and the spread of invasive alien species (IAS) have increased rapidly in recent years, to the extent that these species are now considered to be one of the top five anthropogenic threats throughout the ocean (Nellemann *et al.*, 2008; Costello *et al.*, 2010; Coll *et al.*, 2012). Invasive alien species adversely 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). Discovering what makes 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 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, and biological invasions can alter the equilibrium among these components, thus affecting 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 human 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 to 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 depend mainly on the interaction between invasiveness (i.e. the biologically related property of species to become established, spread to, or 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 a habitat’s invasibility; (ii) the habitat lacks certain species which should be present under normal conditions; (iii) the habitat is disturbed by natural or human factors; and (iv) ecosystem properties are altered by 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 webs and life strategies (trophic niches). In

contrast, the ‘biodiversity increasing invasibility hypothesis’ describes highly diverse communities as being 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). The hypothesis emphasizes positive rather than antagonistic interactions among species (Ricciardi, 2001): AS–AS facilitation 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 thus be the effect 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 one of the most important marine AS hotspots in the world (Occhipinti-Ambrogi, 2000; Quignard and Tomasini, 2000) in terms both of the number of species (Costello *et al.*, 2010) and rate of introduction (Zenetos, 2010). To date 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 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). Among the most well-known marine biological invaders in the Mediterranean are the filamentous red alga *Womersleyella setacea* and the green alga *Caulerpa cylindracea*, two harmful invasive species (Athanasiadis, 1997; Boudouresque and Verlaque, 2002; Verlaque *et al.*, 2005; Streftaris and Zenetos, 2006) currently spreading along the Italian coasts as well (Piazzi *et al.*, 2005). These IAS can inhabit a wide range of subtidal hard and soft substrata 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 (Argyrou *et al.*, 1999; Gravez *et al.*, 2001; Zenetos *et al.*, 2005; Balzacconi and Corriero, 2009; de Caralt and Cebrian, 2013).

By combining the most complete dataset on the species inhabiting EUNIS (European Nature Information System, <http://eunis.eea.europa.eu/>) Mediterranean habitats, the aim of this work was 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 EUNIS habitat 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 classification: first, its use of widely accepted habitat types recognized by the scientific community, and second, it 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 along the Italian coast in marine ecosystem/habitat types considered in EUNIS, and thus it 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* (<http://www.lifewatch.eu/web/alien-species-showcase/virtual-lab>) created within the framework of LifeWatch, the 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, 12521 records (5067 planktonic, 7105 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 (two sites, EUNIS code level 2: A1), littoral sediment (three sites, EUNIS code level 2: A2), infralittoral rock and other hard substrata (eight sites, EUNIS code level 2: A3), circalittoral rock and other hard substrata (26 sites, EUNIS code level 2: A4), sublittoral sediment (eight sites, EUNIS code level 2: A5), deep-sea bed (two sites, EUNIS code level 2: A6), and pelagic water column (44 sites, EUNIS code level 2: A7). No lagoon or estuarial environments have been included in the present study. Each research unit provided lists of species generated from field research programmes on the biodiversity of specific habitats of reference. A nomenclatural revision of the dataset was carried out based on the taxonomic information provided by WoRMS (World Register of Marine Species, Boxshall *et al.*, 2014). All data were screened for

taxonomic reliability, synonymy and for the definition of ‘alien’ by taxonomy experts in the LifeWatch-Italy network. The dataset included data referred to the period 2000–2012.

The definition of AS adopted in this study refers to the deliberate or inadvertent introduction of living organisms (species, subspecies or lower taxa, gametes or propagules) owing to human activities (IUCN, 2000; Hulme, 2009). According to Olenin *et al.* (2010), natural changes in areal distribution do not define AS per se.

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 this study, in accordance with Zenetos *et al.* (2010), the realization of the Suez Canal has been chosen as a benchmark for the Italian coasts. It represents a useful and convenient reference to indicate a period of great change in the Mediterranean, when the basin was put in communication with the Indo-Pacific flora and fauna, though it cannot be formally proved as the start of biological invasions.

Statistical analysis

To evaluate the richness of AS in relation to sampling efforts in different habitats, rarefaction curves for the whole dataset and for the two most represented EUNIS taxonomical groups in the LifeWatch dataset (algae and invertebrates) were obtained using the function *rare curve* 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 (GLMMs) were built by using three different potential predictor variables: native species richness (Rn), habitat (according to EUNIS level 2 classification) and geographical location (GMA). 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 were 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 zeros in the raw data (the norm in the presence

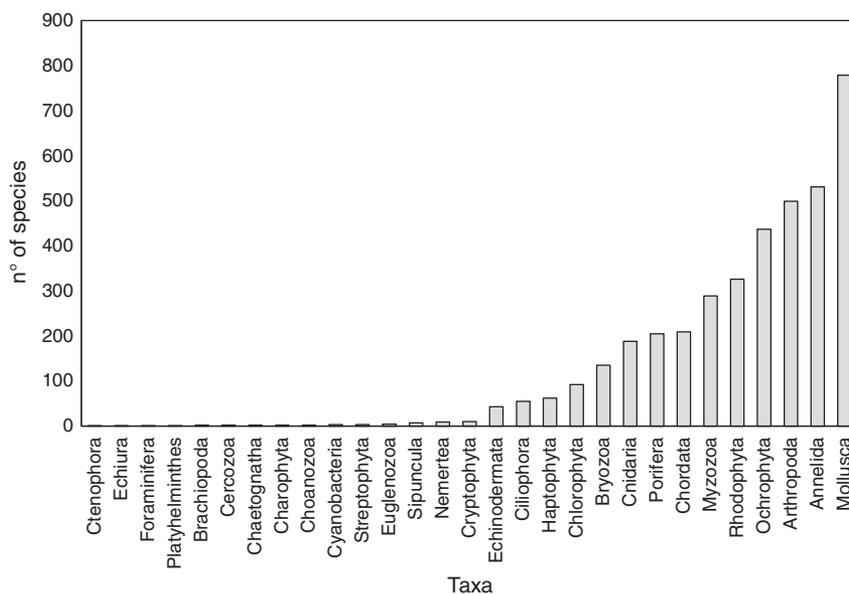


Figure 1. Distribution of total recorded species among taxonomic groups.

Table 1. List of the recorded AS

Myzozoa

Alexandrium pacificum R.W. Litaker (syn. *A. catenella*)
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 coerulea (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, 1885

Ctenophora

Beroe ovata Bruguère, 1789

Mollusca

Anadara inaequalis (Bruguère, 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)
Ruditapes philippinarum (A. Adams, Reeve, 1850)

Annelida

Desdemona ornata Banse, 1957
Epidiopatra hupferiana monroi Day, 1957
Eunice floridana (Pourtales, 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 (Gravir, 1906)
Neanthes agulhana (Day, 1963)
Notomastus aberans Day, 1957
Pista unibranchia Day, 1963
Streblosoma comatus (Grube, 1859)
Syllis alosa San Martín, 1992

Arthropoda

Balanus trigonus Darwin, 1854
Caprella scaura Templeton, 1836
Dyspanopeus sayi (Smith, 1869)

(Continues)

Table 1. (Continued)

Myzozoa

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 harrisi (Gould, 1841)

Bryozoa

Bugula fulva Ryland, 1960

Chordata

Fistularia commersonii Rüppell, 1838

or absence of 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 sites and taxonomical groups were included as random effects in order to consider the spatial dependence of the data and potential bias introduced by 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 seven 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

In total, 3899 species belonging to five kingdoms (Bacteria, Chromista, Protozoa, Plantae, and Animalia) and 29 phyla are 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 (eight), and Mollusca (eight), together representing 75% of the observed AS. In the remaining seven groups (Myzozoa, Ochrophyta,



Figure 2. Distribution of marine 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.

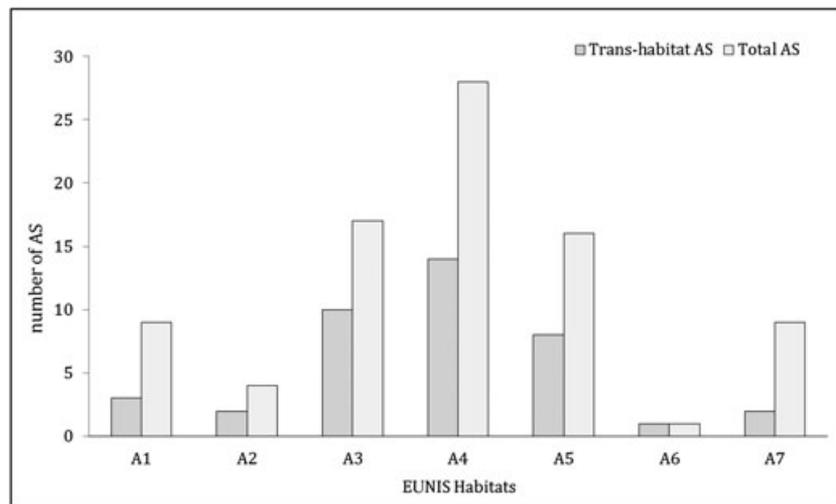


Figure 3. Distribution of total AS and trans-habitat AS in EUNIS Habitat level 2. A1, littoral rock and other hard substrata; A2, littoral sediment; A3, infralittoral rock and other hard substrata; A4 circalittoral rock and other hard substrata; A5, sublittoral sediment; A6, deep-sea bed; A7, pelagic water column.

Table 2. Model selection according to the Akaike 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.) are reported for each model.

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

Chlorophyta, Ctenophora, Cnidaria, Bryozoa, and Chordata), the number of AS ranged from one to four. No AS were detected in the remaining 18 phyla.

Figure 2 shows the distribution of AS in the investigated sites in the Italian seas, divided into Geographic Macro Areas (GMAs), according to Occhipinti-Ambrogi et al. (2011a). AS were found in all the GMAs except the southern Ionian Sea, with the highest percentage of AS over species richness detected in the northern Tyrrhenian Sea (4.4%), followed by the southern Tyrrhenian (2%), eastern central Tyrrhenian and northern Adriatic (1.4%).

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 in three

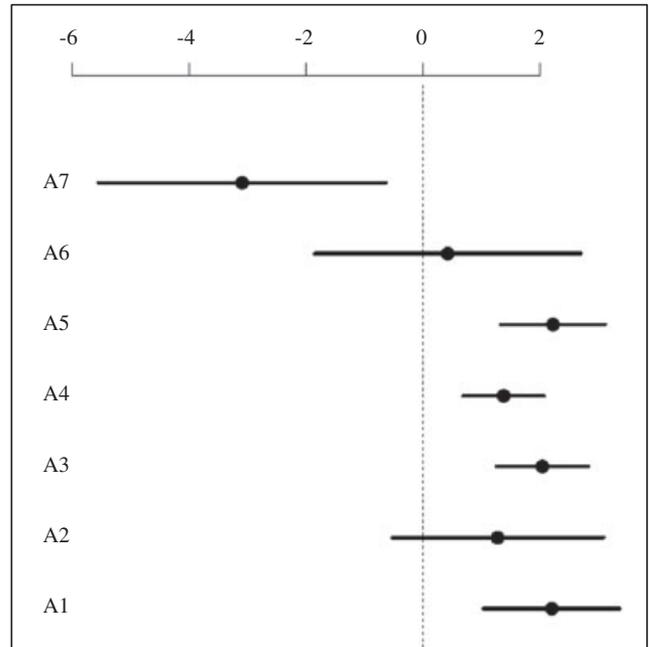


Figure 5. Regression coefficients obtained from GLMM for the seven EUNIS habitats included as factors. Circles represent estimated coefficients, while lines represent 95% confidence interval. A1, littoral rock and other hard substrata; A2, littoral sediment; A3, infralittoral rock and other hard substrata; A4, circalittoral rock and other hard substrata; A5, sublittoral sediment; A6, deep-sea bed; A7, pelagic water column.

GMAs. The remaining 13 species were detected in two GMAs.

AS were recorded in all habitats considered (Figure 3), with a maximum of 28 species on circalittoral hard substrata and a single AS on the deep-sea bed. Fifty-four AS were found in the 49

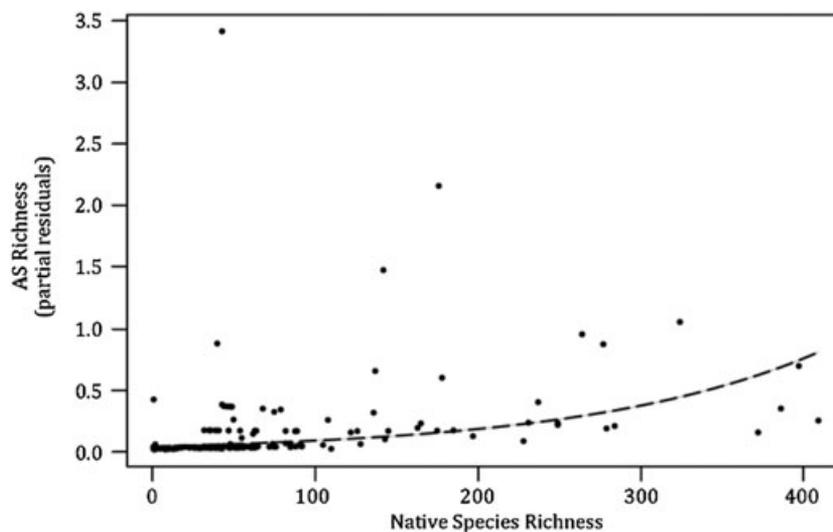


Figure 4. Relationships between native species richness and AS richness at site level for each taxonomic group and habitat EUNIS according to the results of GLMM.

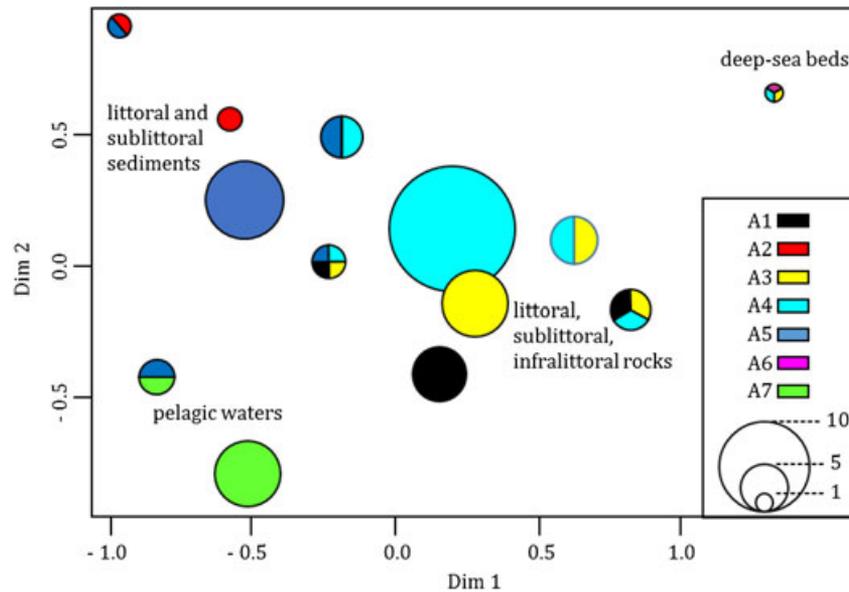


Figure 6. Multiple correspondence analysis (MCA) based on presence-absence matrix of AS. Colours represent different EUNIS Habitat (A1, littoral rock and other hard substrata; A2, littoral sediment; A3, infralittoral rock and other hard substrata; A4 circalittoral rock and other hard substrata; A5, sublittoral sediment; A6, deep-sea bed; A7, pelagic water column), where the species was found, while circle size is proportional to the number of species. The species are clustered according to habitat similarity.

sites of the benthic domain and nine in the 44 pelagic sites, with a prevalence of phytoplankton AS. In terms of proportions of the native species, the maximum percentage of AS (3.7% of the present species richness) was found on littoral hard substrata, and the minimum (0.4%) on the deep-sea bed.

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 habitat but not GMAs as explanatory variables.

The model explicitly considering the difference in taxonomic coverage and spatial bias detected a significant ($P < 0.001$) and positive trend in increase of AS with increase in Rn (Figure 4). All habitats showed a significant relationship with AS richness (Wald z test $P < 0.05$), 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 with littoral rock and other hard substrata, infralittoral rock and other hard substrata, circalittoral rock and other hard substrata, and

sublittoral sediment (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) showed how species were assembled according to their habitat of occurrence (pelagic waters, soft substrata, hard substrata, deep-sea beds) (Figure 6). MCA highlighted three main groups of species, namely species found in a single habitat, species shared across similar habitat categories (i.e. between sublittoral and littoral sediments or among rocky substrata) and also species found across different habitats.

While 43 of the AS (70% of the total AS) were found within a specific habitat (EUNIS level 2), the others were shared between 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 the total).

Of the nine AS found in the pelagic water column, *Anadara inaequalis* and *Ruditapes philippinarum* were also detected in sublittoral

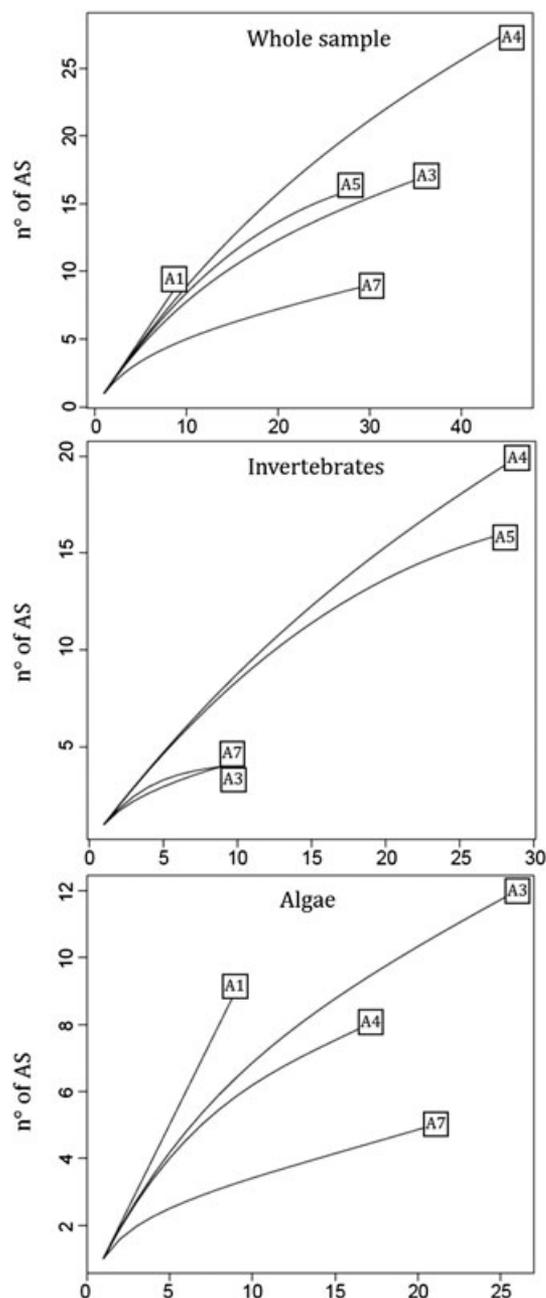


Figure 7. Rarefaction curves obtained as a count of AS against the sample size (number of sites) for the observed AS richness in the whole dataset, invertebrates and algae samples sub-datasets. On the “y” axis the number of observed species and on the “x” axis the sample size are reported. For Invertebrates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

sediments. Two polychaetes shared littoral and sublittoral sediment habitats while the polychaete *Notomastus aberans* was found both in sublittoral sediment and on circalittoral rock and other hard

substrata. Littoral, sublittoral and infralittoral rocks shared the algae *Acrothamnion preissii* and *Asparagopsis armata* as well as, together with sublittoral sediments, *Caulerpa cylindracea*, and *Womersleyella setacea*. The hydrozoan *Clytia linearis*, the only AS found on the deep-sea bed, was also found on 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 towards a plateau while other habitats showed a continuous increase in the number of AS (marked up to 20 sample sites for circalittoral rock and other hard substrata).

Looking at rarefaction curves for invertebrate AS only, circa-littoral rock and other hard substrata still showed a constant increase in 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 algal AS are considered and 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 in 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 between habitats are surprisingly uncommon in the marine environment (Zaiko *et al.*, 2007). Literature referring to the marine biota mainly focuses on the distributional traits of single invasive species in a few habitats

(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 analytical study on the occurrence and distribution of AS in a large number of marine habitats (EUNIS habitats) within the Mediterranean. Despite the dataset used here not presumably including all known AS and the geographical coverage being piecemeal, 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 any distinction between the pool of AS inhabiting natural marine environments and those exclusive to harbours, polluted sites and lagoon environments. In recent reviews, Occhipinti-Ambrogi *et al.* (2011a, b) compute 164 AS (both marine and brackish) for the Italian coasts, corresponding to about 20% of the non-native species reported in total 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 (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 (Pérez-Ruzafa *et al.*, 2011; Petrocelli *et al.*, 2013), whereas the records of AS from natural environments are less common in the literature. The list of 61 AS in the present paper, exclusively referred to natural marine habitats, seems to indicate that, to date, most of the AS present along the Italian coast are closely associated to the hot spot areas of introduction, and only a small 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 refers to the effect on native community of non-native algal spread (Piazzi and Cinelli, 2000, 2001; Piazzi *et al.*, 2005, 2012; Baldacconi and Corriero, 2009; de Caralt and Cebrian, 2013). Since the AS animal component is dominant within the whole Mediterranean Sea (Zenetos *et al.*, 2010; 2012), the current scenario regarding the influence of invertebrate AS is particularly worthy of further study. Increasing the studies on the interactions between invertebrate AS and native communities is necessary, since sometimes the former are not immediately detected (such as worms and molluscs in sediments), but can lead to local replacement of species, for example in the case of the Manila clam *Ruditapes philippinarum* in the Venice lagoon (Pranovi *et al.*, 2006).

In the framework of this study, AS occurred in all habitats and almost all geographic areas, albeit with different distributions. Most of them were detected in benthic environments (54 species), and only nine 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 these two different environments.

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 on littoral, infralittoral and circalittoral rocks, thus indicating that these marine habitats could host an even larger number of AS. In contrast, 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 was unlikely to be able to host a much greater number of AS. The pelagic habitat showed a short steep slope in the rarefaction curves, suggesting a possible lower (or slower) propensity to host AS compared with benthic habitats. Many AS spread through pelagic propagules within ballast waters

(Olenin *et al.*, 2010; Gollasch *et al.*, 2013), but they are very hard to find. In addition, Zenetos *et al.* (2010) highlighted the difficulty in documenting phytoplankton AS in the Mediterranean Sea, especially because of the scarce background knowledge on diversity of marine microalgae owing to their biological and ecological characteristics (e.g. ephemeral and patchy distribution, short-time occurrence) and relative difficulties in their sampling (e.g. resolution of sampling programmes, difficulty in preservation). The presence of heteromorphic life cycles in several microalgae (e.g. dinoflagellates, diatoms and raphidophytes), with alternating phases of vegetative planktonic and benthic life stages, highlights the continuum among habitats (pelagic and benthic) and the necessity of an integrated water/sediment approach in their study (Satta *et al.*, 2010).

Within the benthic domain, the circalittoral rock and other hard substrata (in the LifeWatch database mostly represented by coralligenous assemblages) constitute the habitats with the greatest number of AS (eight algae, one ctenophore, two hydrozoans, nine polychaetes, five molluscs, two crustaceans, and one bryozoan) and with the highest native species richness as well. According to Byers and Noonburg (2003) the biodiversity of native and exotic species are often positively related at large-scale, but negatively correlated at small-scale. 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). Furthermore, studies carried out in terrestrial environments at a regional scale have found that exotic species richness in plants is associated with high native plant species richness (Lonsdale, 1999; Stohlgren *et al.*, 2006). At broader spatial scales, the physical complexity of natural community environments appears to reduce 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 1500 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 have been reported in international biodiversity conventions and/or on 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; Piazzini and Cinelli, 2000). As coralligenous outcrops represent one of the most important biodiversity hotspots in the Mediterranean, the loss of their unique characteristics would lead to significant threats to the entire littoral system (Piazzini *et al.*, 2012).

The scenario changes among soft bottom habitats.

Native communities associated with sublittoral sediment habitat varies greatly in the presence of plant coverage, in particular seagrass (mainly *Posidonia oceanica* and *Cymodocea nodosa*), which is very important for their structural complexity, ecological function, and high levels of associated

species richness (Klumpp *et al.*, 1992; Mazzella *et al.*, 1992). When plant coverage is lacking, native communities are much depleted in number of species, and mainly dominated by scavenger invertebrates. Although the sublittoral sediment habitat appeared to be close to reaching a balance in the number of AS (see rarefaction curves, Figure 7), the presence of 16 AS (two algae and 14 invertebrates) should be emphasized. According to the literature, seagrass represents the most suitable substrate for the spread of the invasive algae *Caulerpa cylindracea* and *Womersleyella setacea* (Piazzi and Cinelli, 2000, 2001; Piazzi and Balata, 2009). Present data, however, highlighted the dominance of invertebrates among AS associated with sublittoral sediments, with six species of polychaetes, five molluscs, and three 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 soft-bottom habitats may be considered as a potential threat, their interactions with native fauna still being 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* has led to the depletion and local disappearance of the closely related native *R. decussatus* (Pranovi *et al.*, 2006). In extra Mediterranean environments, however, a positive interaction between alien and native species in sublittoral sediment has also been reported. It regards the polychaete *Marenzelleria* sp., which has been described to positively affect 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 present study, littoral sediment may be considered among the less rich in native species. The pool of data in the LifeWatch database referred to a considerable number of observations on a few sites, which if, on the one hand, did not allow the highlighting of trends on

the species/area relationship (rarefaction curves), on the other hand provided an indication of the occurrence of AS in this habitat. The AS recorded were all invertebrates, three polychaetes and one arthropod, reflecting the capacity of this environment to hosting animals more than anything else. The low number of AS recorded may be explained by the great temporal variability that characterizes littoral communities, owing to the action of waves and to the seasonal hydrological variations.

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

As expected, the MCA showed how most of the AS occupied the same position on the factorial map, because they were associated with one 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 were able to 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 areas characterized by intense maritime traffic (e.g. harbours and lagoons). However, although a high number of AS were recorded in some GMAs, the GLMM did not support a geographical effect on

their localization, probably because the present analysis included only natural marine environments and not all the GMA were uniformly represented. Indeed, 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.

The results of this macro-ecological study have highlighted some large-scale features not detectable by studies carried out on a single species or habitat, and contributed towards the development of effective management strategies that approach the impacts of AS from an ecosystem perspective.

Furthermore, it revealed the occurrence of a positive relationship between alien and native species richness in marine environments. This has various possible explanations, from the intrinsic characteristics of the system allowing it 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).

Even though the introduction of AS locally increases species richness (Gurevitch and Padilla, 2004; Briggs, 2007), in most cases invasions have a negative effect, since the receiving systems become ecologically unbalanced. According to several authors (Dick *et al.*, 2002; Gurevitch and Padilla 2004; Piscart *et al.*, 2009; Hänfling *et al.*, 2011), the most serious consequences are changes in native species composition due to 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 the positive impacts of AS may be underestimated.

The occurrence of AS 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 into different environments (e.g. lagoons, ports, mussel plants). Consequently, from a conservation point of view, two different monitoring models should be distinguished, the first aimed at providing an early warning of the arrival of AS in the hot spots of introduction and a second aimed at evaluating the success of these species in marine environments. Thus, the present study highlighted the importance of designing monitoring strategies suitable for different habitats, from those historically considered AS hubs (mainly transitional waters), to the biologically pristine, rich, and diverse benthic ones (Otero *et al.*, 2013). The importance of AS monitoring programmes on benthic habitats is also supported by the need to assess the potential impact of AS on key species, among which is the pool of bioconstructors (mainly algae) able to sustain specific assemblages. Besides having an indisputable ecological and conservation value, diverse benthic communities provide economic benefits such as providing popular dive experiences.

Monitoring programmes should lead to conservation strategies that allow the possibility of mitigating biological invasions, but studies in marine habitats are still in their infancy. While research into the vulnerability of freshwater and lagoon environments leads 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 the most significant correlates in marine habitats so as to set conservation priorities. Furthermore pollution due to increased nutrients plays a crucial role, since the growth of invasive alien seaweed on marine hard bottom is enhanced by nutrient enrichment, leading to strong impacts on native macroalgal assemblages (Piazzi *et al.*, 2012).

Ekebom (2013) suggested that the process of incorporating the ecosystem approach into marine and environmental 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 and temporal scales.

In the present paper, the EUNIS habitat code (eight Mediterranean marine habitats) has been used, but the level of detail should be much higher (e.g. by choosing other habitat codes or more specific levels of the EUNIS code). Moving forward in this direction seems fruitful, allowing description of the relationship between AS and habitats at a higher level, and investigating 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, 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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