Space invaders; biological invasions in marine conservation planning

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ABSTRACT

Aim Biological invasions are major contributors to global change and native biodiversity decline. However, they are overlooked in marine conservation plans. Here, we examine for the first time the extent to which marine conservation planning research has addressed (or ignored) biological invasions. Furthermore, we explore the change of spatial priorities in conservation plans when different approaches are used to incorporate the presence and impacts of invasive species.

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Location Global analysis with a focus on the Mediterranean Sea region.

Methods We conducted a systematic literature review consisting of three steps: (1) article selection using a search engine, (2) abstract screening and (3) review of pertinent articles, which were identified in the second step. The information extracted included the scale and geographical location of each case study as well as the approach followed regarding invasive species. We also applied the software MARXAN to produce and compare conservation plans for the Mediterranean Sea that either protect, or avoid areas impacted by invasives, or ignore the issue. One case study focused on the protection of critical habitats, and the other on endemic fish species.

Results We found that of 119 papers on marine spatial plans in specific biogeographic regions, only three (2.5%) explicitly took into account invasive species. When comparing the different conservation plans for each case study, we found that the majority of selected sites for protection (ca. 80%) changed in the critical habitat case study, while this proportion was lower but substantial (27%) in the endemic fish species case study.

Main conclusions Biological invasions are being widely disregarded when planning for conservation in the marine environment across local to global scales. More explicit consideration of biological invasions can significantly alter spatial conservation priorities. Future conservation plans should explicitly account for biological invasions to optimize the selection of marine protected areas.

Keywords

alien species, biological invasions, conservation planning, impacts, management actions, marine biogeographic regions, marine protected areas, Mediterranean Sea. 34203, France, ¹⁶Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA

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INTRODUCTION

Biological invasions are amongst the major components of current global change and drivers of native biodiversity loss in terrestrial, freshwater, and marine ecosystems (Pyšek & Richardson, 2010; Simberloff et al., 2013). Alien species (i.e. organisms introduced outside their natural range) can become invasive and substantially change species composition and the functioning of native ecosystems by a range of processes: competition, predation, overgrazing, release of toxins, hybridization, disease transmission, and habitat alteration (Levine, 2008; Vilà et al., 2011). In the marine environment, ecological impacts including the loss of native genotypes, degradation of habitats, changes in trophic interactions, and displacement of native species have been documented (Albins, 2012; Katsanevakis et al., 2014; Verges et al., 2014). Invasives can also impact the provision of ecosystem services with negative socio-economic consequences for coastal communities, for instance causing the decline of commercial fish and shellfish stocks or decreasing the potential for recreational activities (Bax et al., 2003; Katsanevakis et al., 2014). Moreover, some marine invasives are venomous or toxic and can have negative impacts on human health (Streftaris & Zenetos, 2006). The multidimensional consequences of invasives render their distribution and impact major topics of scientific interest with crucial conservation implications (Molnar et al., 2008; Katsanevakis et al., 2016).

Globally, there is an urgent need to adopt management strategies for the control of invasive populations and the mitigation of their impacts. The Aichi Target 9 of the Convention on Biological Diversity (CBD) states that by 2020, (1) invasive alien species and pathways are identified and prioritized, (2) priority species are controlled or eradicated and (3) measures are in place to manage pathways to prevent their introduction and establishment (Convention on Biological Diversity, 2015). Regional policies have also focused on the uptake of management actions for the mitigation of invasives' impacts. For instance, under the European Union Marine Strategy Framework Directive (EU, 2008), member states are committed to developing strategies to achieve Good Environmental Status (GES) by 2020. One of the GES descriptors dictates that alien species should be at density levels that do not adversely alter ecosystems. Nevertheless, comprehensive strategies to mitigate impacts of alien species on marine biodiversity and ecosystem services have not yet been developed in the EU.

Despite the increasing number of studies addressing the assessment of invasion pathways (e.g. Seebens et al., 2013; Essl et al., 2015) and impacts of biological invasions on marine ecosystems (e.g. Katsanevakis et al., 2014, 2016), there is still a gap in our understanding of how to use such information to guide conservation planning. Should conservation plans target areas that are highly invaded by alien species and invest resources in mitigating negative impacts of invasives? Alternatively, should plans avoid highly invaded areas and invest resources in non-invaded or less invaded areas? In marine conservation planning, the first hypothesis would favour an approach to protect areas highly impacted by invasives to restore them by taking additional management actions, for example eradication, within those areas. The second hypothesis would lead planners to avoid such areas and protect areas less vulnerable to invasions. In the absence of a good knowledge base on which hypothesis is valid under which conditions, the easy approach is to just ignore the issue.

Here, we examine whether marine conservation plans have directly addressed biological invasions by either protecting or avoiding impacted areas, or not (thus they have ignored the issue deliberately or not). Furthermore, we use two case studies (one habitat-based and one species-based) to explore how spatial priorities change when areas with high alien species density and impacts are protected, avoided or ignored (i.e. information about biological invasions was not considered). We base our case studies in the Mediterranean Sea, one of the major hotspots of marine biological invasions (Edelist et al., 2013). Approximately 1000 alien species have been reported in the Mediterranean Sea (Zenetos et al., 2012), and this number is expected to grow after the enlargement of the Suez Canal (Galil et al., 2014). Simultaneously, the identification of priority areas for conservation is ongoing in the region, as Mediterranean countries aim to achieve Aichi Target 11 of the CBD by protecting 10% of the sea under their jurisdiction. Invasive species may nullify or in some cases benefit (Schlaepfer et al., 2011) the effects of protection, such as ecosystem recovery. Thus, the presence of such species and their impacts should be explicitly considered when selecting marine protected areas (MPAs). Synthesizing our findings, we identify gaps in knowledge that need to be filled to optimize MPA site selection under global changes, specifically when accounting for invasive species, in the Mediterranean region and beyond.

METHODS

Literature review and synthesis

We performed a bibliographic search using the Elsevier's Scopus database (www.scopus.com). Eligibility criteria included any paper or review published between 1950 and the cut-off date 18 April 2015 with the terms 'conservation planning' and 'marine' or 'sea' in the title, keywords or abstract. Grey literature and non-English publications were not considered in this review.

The results summed up to 793 peer-reviewed papers. Our review started with a screening of these 793 paper abstracts. Articles were excluded if they: (1) were unrelated to conservation planning, (2) did not include a specific case study for which a conservation plan was developed, (3) took into account only terrestrial or freshwater species, habitats, or ecosystems and not marine or (4) mentioned the term 'conservation planning' only for justification or discussion of results but did not produce a conservation plan. As a result, 214 abstracts (27%) qualified for the next round of reviews. These were papers that presented conservation plans in marine environments, or included content that was potentially relevant after reading the abstract alone, and were thus retained for the second step of the analysis.

In the second selection process, the entire 214 articles were read, using the same exclusion criteria listed above. Finally, 119 studies were suitable for the qualitative and quantitative synthesis (see Appendix S1 in Supporting information for final list of articles).

The following information was extracted from each article (Table S1): (1) year of publication; (2) scale of case study (local < national < regional < global); (3) geographical location of the case study; (4) the relevant marine biogeographic region ('realm' according to Spalding *et al.* (2007); (5) the features (species, habitats, ecosystems) that were targeted for conservation; (6) the conservation planning method/tool that was used (e.g. MARXAN, ZONATION); (7) the approach the study followed regarding biological invasions, that is whether biological invasions were taken into account in the planning process by 'protecting' or 'avoiding' areas impacted by invasive species or the issue was 'ignored'; and (8) the method that was used if the 'avoid' or 'protect' approach was followed.

Conservation plans: applying the 'protect', 'avoid' or 'ignore' approaches in two Mediterranean case studies

In addition to the literature review exploring how biological invasions have been treated in past conservation plans, we examined whether and how spatial priorities change when biological invasions are explicitly accounted in conservation planning. Here, we used two case studies to compare systematic conservation plans that followed three different approaches for dealing with invasive species: protect, avoid or ignore areas impacted by invasives. One case study aimed to account for impacts of invasives on two critical marine habitats, the seagrass *Posidonia oceanica* meadows and coralligenous formations. The second case study aimed to assess changes in priority conservation areas for endemic fish species when accounting (or not) for invasives.

To identify conservation priority areas for our features of interest (habitats and species), we used the conservation planning software MARXAN (Ball et al., 2009). This software uses a simulated annealing algorithm to find a suite of good near-optimal systems of priority areas that meet conservation targets while minimizing socio-economic costs. In MARXAN, the user sets a target for every feature to be protected, which in our case was expressed as the percentage of the feature's overall distribution range (see below case studies 1 and 2). The study area was the entire Mediterranean Sea excluding areas deeper than 1000 m, where the habitats and species included in these analyses do not occur (Giakoumi et al., 2013; Guilhaumon et al., 2015). The study area was divided into a grid of 12,828 cells (hereafter planning units) each of 10×10 km. MARXAN was run 1000 times and consisted of 1,000,000 iterations per run. We defined areas of greater irreplaceability using the selection frequency of each planning unit, which is the proportion of runs in which a planning unit is selected amongst the 1000 runs. These areas were considered higher priority for protection. The boundary length modifier (measure of trade-off between cost and compactness of the solution) was set to 0, as our aim was to examine differences in the selection of priority areas among the scenarios and not to design an MPA network with a desirable level of compactness.

Case study 1: critical habitats

Data (presence/absence) on the distribution of seagrass P. oceanica meadows and coralligenous formations were obtained from Giakoumi et al. (2013). We set a 60% target of the current distribution of the P. oceanica meadows and 40% of the distribution of coralligenous formations as per Giakoumi et al. (2013) following guidelines by the EU (ETC/ BD, 2010). Although these targets are policy-based and are not supported by solid ecological evidence, they represent the current practice in EU and it is thus a pragmatic approach to follow. In the 'protect' scenario, we targeted the proportion of seagrass meadows and coralligenous formations impacted by alien species in each planning unit. The impacted habitat feature within each site was estimated based on the CIMPAL index (Cumulative IMPacts of invasive ALien species) developed by Katsanevakis et al. (2016). For the CIMPAL index, cumulative impact scores were estimated on the basis of the distributions of habitats and alien species, the reported magnitude of ecological impacts, and the strength of such evidence. Evidence for most of the reported impacts of marine aliens in the literature is weak, mostly based on expert judgement or dubious correlations (Katsanevakis et al., 2014). Hence, in the estimation of the CIMPAL index, the weights of impacts with low supporting evidence are downweighted, in comparison with impacts documented through manipulative or descriptive experiments (Katsanevakis *et al.*, 2016). The index was normalized as follows to obtain values between 0 and 1:

$$I_i = \frac{x_i - \min(\mathbf{x})}{\max(\mathbf{x}) - \min(\mathbf{x})},$$

where I_i is the normalized index value and x_i is the initial index value for the planning unit *i*.

Then, to estimate an index (E) of the magnitude of impacts on each planning unit *i* in which a specific feature is present, the presence or absence of the feature (F) was multiplied by the index value (I):

$$E_i = F_i * I_i$$

In the 'avoid' scenario, we only set targets for the features in good condition (i.e. not impacted by alien species). An index of the condition (H) of a specific feature in each planning unit *i* was estimated as:

$$H_i = F_i - E_i$$

In the 'ignore' scenario, we did not consider the information about impacts from invasives on the critical habitats as per Giakoumi *et al.* (2013).

The most commonly accounted for and significant cost in marine planning is opportunity cost, for example fishing profits that are forgone when an area is made a no-take zone (Ban & Klein, 2009). The socio-economic cost used herein represents the spatial distribution of the combined opportunity cost for three marine sectors: commercial (small and large-scale) fishing, non-commercial fishing (recreational and subsistence) and aquaculture. Data were obtained from Mazor *et al.* (2014).

Case study 2: endemic fish species

Data on the distribution of 80 endemic fish species were obtained from Guilhaumon et al. (2015). Among the 80 species, 54 were benthic, 18 demersal and 8 pelagic (Appendix S2). We used area-based species-specific representation targets following the methods in Guilhaumon et al. (2015). A representation target of 100% was set for endemic species with restricted ranges (geographical range of <1000 km²) and a target of 10% was used for widespread endemics (those endemic species with a geographical range $> 35,860 \text{ km}^2$, corresponding to one-third of the species). For endemics with intermediate range sizes, the target was interpolated as a linear function of log-transformed area of occupancy. Additionally, we modified the area-based targets according to the species level of threat as determined by the IUCN Red List categories (Abdul Malak et al., 2011). Following Kark et al. (2009), the representation target of critically endangered species (n = 1) was set to 100% irrespective of their geographical range; the targets for species that are vulnerable (n = 1) or endangered (n = 3)were defined as the maximum between the 30% of their

geographical range and their linearly interpolated target. Data-deficient species (n = 1) and species not evaluated by IUCN (n = 71) were attributed the 'least-concern' IUCN category (Appendix S2).

We accounted for impacts of alien species by combining the values of the relative Functional Nearest Neighbour index (FNNr; see Elleouet *et al.*, 2014) with the socio-economic cost (Mazor *et al.*, 2014). The FNNr index arises from a trait-based approach and expresses the magnitude of functional similarity (or niche overlap) between endemic and alien species as a proportion of the total number of endemic species per planning unit. The FNNr index assumes that co-occurring native and alien species are more likely to interact if they have greater similarity in their ecological (e.g. habitat use) and biological (e.g. diet) attributes, that is greater similarity in their ecological niches (sensu Violle & Jiang, 2009).

In the 'avoid' scenario, we summed the values of FNNr index (ranging from 0 to 1) and the socio-economic cost in each planning unit. To give the same weight to the two components, the FNNr index and the socio-economic cost were rescaled to range in the same magnitude. High FNNr index values increased the cost of planning units in the 'avoid' scenario, and thus, the optimization algorithm avoided the selection of these areas. This scheme was reversed in the 'protect' scenario, where FNNr values were added to the socio-economic cost. Planning units with high FNNr values contributed less to the cost of the planning units, and these areas were more likely to be selected for protection. In the 'ignore' scenario, we did not consider the information about potential ecological interactions between endemics and aliens and ran MARXAN considering only the socio-economic cost.

RESULTS

Biological invasions in past marine conservation plans

Since 2000, there has been a progressive increase in the number of publications on marine conservation plans, resulting in a total of 119 publications (Appendix S1; Fig. S1a). Most of these publications (57%) referred to local scales (Fig. S1b). The reviewed conservation plans covered all marine realms, with a higher concentration in the Temperate Northern Atlantic and the Central Indo-Pacific realms (Fig. 1). The majority of conservation plans (58%) included habitats or ecosystems as features to conserve (Fig. 2). A large percentage of studies also set fish species distributions as conservation features (33%). Charismatic marine animals, particularly mammals and birds, were also commonly targeted for protection (23% and 22%, respectively). For the identification of priority areas for conservation of these features, half the studies used conservation planning software. Of those, the vast majority (88%) used some version of the software MARXAN, whereas the rest of them used C-Plan (Pressey et al., 2009) and ZONATION (Moilanen et al., 2009). The other half of the studies used a variety of tools: geospatial analyses (e.g. ARCGIS), species distribution and

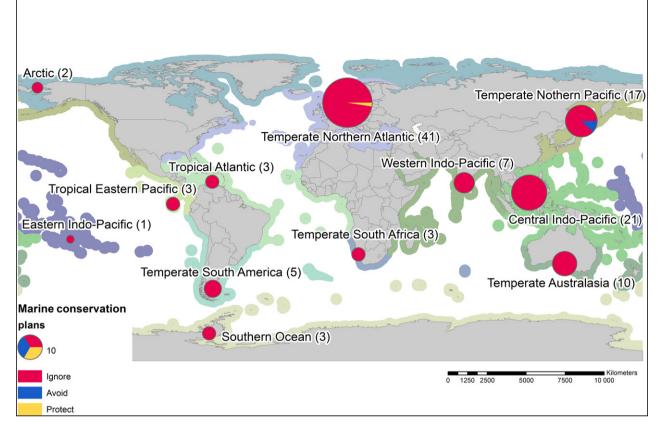


Figure 1 Distribution of marine conservation plans across realms. The different realms (biogeographic regions) are presented with different colours, whereas conservation plans following: the 'ignore' approach is presented in red, the 'protect' in yellow and the 'avoid' in blue. Realms are defined according to Spalding *et al.* (2007).

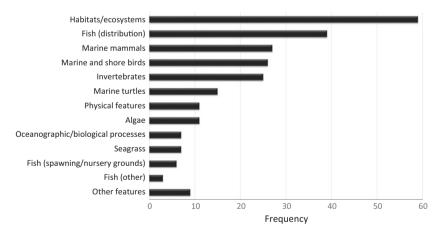


Figure 2 Conservation features accounted for in the conservation plans (frequency computed over a total of 119 publications).

habitat suitability models, complementarity analyses, hotspot analyses, food-web models, univariate and multivariate statistical methods, GLM models, tracking methods, scoring methods, vulnerability assessments and combinations of those.

Of the 119 papers included in our analyses, we found only three papers (Tallis *et al.*, 2008; Giakoumi *et al.*, 2011; Klein *et al.*, 2013) that explicitly took into account invasive species in their conservation plans (Table S1). All other papers ignored invasives' presence and/or impacts (Table S1; Fig. S1a). All three studies used MARXAN software. Tallis *et al.* (2008) incorporated threats in a site-prioritization exercise for the Pacific Northwest coast ecoregion (USA), including invasive species, into MARX-AN's cost function. Areas with higher threat had higher cost; thus, highly invaded areas were avoided. Similarly, Klein *et al.* (2013) in a conservation plan for California incorporated threats, including invasives, into MARXAN by adding an additional constraint: minimize the chance that the reserved features are in poor condition. The algorithm, therefore, favoured the selection of priority conservation areas less impacted by threats, one of which was vulnerability to invasives. In contrast, Giakoumi *et al.* (2011) set conservation targets for all fish species of the shallow sublittoral of the Cyclades Archipelago (Greece), including the invasive herbivore species *Siganus luridus*, following, thus, the 'protect' approach.

Comparing the consequences of 'protect', 'avoid' or 'ignore' strategies for conservation plans

Critical habitats case study

We found that the selection frequency of the great majority of planning units changed depending on the approach that was followed (protect, avoid or ignore). Only ~13% of the planning units containing a conservation feature had maximum irreplaceability (i.e. a selection frequency of 1,000) across all three scenarios (green-bordered planning units in Fig. 3). In all pairwise scenario comparisons ('protect' versus 'ignore', 'avoid' versus 'ignore' and 'protect' versus 'avoid'), the selection of ~80% of planning units differed (Table 1; Fig. 3). Areas highly impacted by invasive species, such as the Balearic Islands (eastern Spain), Sicily (south Italy) and the Greek Ionian coastal waters (western Greece), presented higher selection frequency in the 'protect' rather than the 'ignore' scenario. These same areas presented higher selection

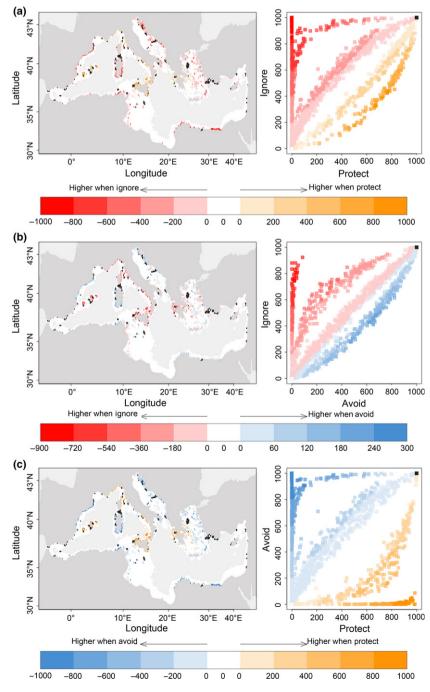


Figure 3 Critical habitats case study (data from Giakoumi et al., 2013). Difference in planning unit (12,828 cells, 10×10 km) selection frequency, from MARXAN outputs, when following the different approaches: (a) 'ignore' versus 'protect', (b) 'ignore' versus 'avoid' and (c) 'avoid' versus 'protect'. Planning units in red are those presenting higher selection frequency in the 'ignore' scenario, in orange those with higher selection in the 'protect' scenario and in blue those with higher selection in the 'avoid' scenario. Planning units are black if they had maximum selection frequency (1000) in all three scenarios. Scatter plots show the selection frequency for the planning units under the different scenarios. For the maps, we used ETRS89 Lambert Azimuthal Equal-Area projection.

 Table 1 Percentage of planning units presenting higher

 selection frequency in the 'ignore', 'protect' or 'avoid' scenario

 in each pairwise scenario comparison.

	Scenarios		
	Ignore (%)	Protect (%)	Avoid (%)
Comparisons for critical l	habitat case stu	dy	
Protect versus Ignore	59	21	
Avoid versus Ignore	49		32
Protect versus Avoid		22	61
Comparisons for endemic	c fishes case stu	dy	
Protect versus Ignore	11	16	
Avoid versus Ignore	12		14
Protect versus Avoid		16.5	10.5

in the 'ignore' scenario than in the 'avoid'. When comparing the 'protect' and 'avoid' scenarios, the highly impacted areas presented higher selection in the 'protect' than in the 'avoid' scenario.

Endemic fish species case study

In all pairwise scenario comparisons, the selection of nearly one-third (27%) of planning units differed (Table 1; Fig. 4). Only ~3% of planning units presented maximum irreplaceability across all three scenarios (green-bordered planning units in Fig. 4). When comparing the 'protect' and 'ignore' scenarios, no clear geographical pattern arose. Planning units showing greater irreplaceability in the 'protect' approach were spread across the Mediterranean Sea. However, some patches of markedly higher irreplaceability could be identified in the Gulf of Lions (France) and in the Adriatic Sea (eastern Italian coast). These areas presented higher irreplaceability in the 'avoid' scenario compared to the 'ignore' scenario. Finally, in the pairwise comparison 'protect' versus 'avoid' scenario, irreplaceability substantially increased in the 'avoid' scenario along the coastal waters of Italy in the Adriatic Sea and moderately increased in patchy locations along all Mediterranean coasts. Planning units exhibiting higher irreplaceability in the 'protect' scenario were mainly located along the Greek coast and remaining Adriatic Sea.

DISCUSSION

Our literature review demonstrates that the role of biological invasions has been widely overlooked when planning for conservation in the marine environment, at all spatial scales. Yet, the explicit consideration of biological invasions can significantly change spatial conservation priorities. This is clearly shown by the comparison we made of conservation plans following three different approaches: 'avoid', 'protect' or 'ignore' areas with high presence and/or impacts of invasives. Our findings have important implications on the placement of new MPAs in order for countries to achieve the 10% goal set by Aichi Target 11 of the Convention on Biological Diversity (2015).

In the Mediterranean Sea, invasive species are considered one of the most severe threats to species and ecosystems (Coll *et al.*, 2012; Micheli *et al.*, 2013a). When making decisions about the establishment of new MPAs, this threat should be explicitly taken into account for an effective allocation of conservation funds. Particular attention should be given to areas where changes in the priority selection among scenarios are more pronounced: the Balearic Islands in Spain, the Gulf of Lions in France, Sicily in Italy, the Adriatic Sea and the Greek coasts (especially in the west). The importance of biological invasions in these areas differed depending on which features were targeted for protection (habitats or fish species). To make informed decisions about the placement of new MPAs, a holistic approach targeting numerous species and habitats would be desirable.

We propose that to effectively incorporate biological invasions into marine conservation planning in the future, the scientific community should urgently fill information gaps regarding: (1) the spatial distribution of invasive species both at present and in the future; (2) the ecological and socioeconomic impacts of biological invasions; and (3) the role of MPAs in controlling invasive populations and mitigating their impacts.

Extensive mapping efforts of invasive species distributions should urgently be applied. Whether the planning approach is 'avoid' or 'protect', accurate information about the distribution of alien species is a prerequisite for effective planning as we demonstrated in our case studies. Several governmental and intergovernmental bodies have already invested important resources in the creation of georeferenced databases of the current distribution of alien species (e.g. Katsanevakis et al., 2015). Nevertheless, biological invasions are a dynamic threat (Strayer et al., 2006), and predictions of their future distributions are crucial for effective management plans and selection of new MPA sites. Areas that are currently unaffected by biological invasions may be severely affected in the future; therefore, a dynamic conservation approach is required. At present, accurate projections of future distributions of marine alien species are limited. Species distribution models forecasting the spread of aliens are currently based on climate predictions and may underestimate the potential spread of aliens (Parravicini et al., 2015), and interactions with other sources of disturbance (Bulleri et al., 2011). Studies comparing source and front populations across a species new range could prove useful for better understanding and predicting population dynamics of marine aliens and thus providing guidance for potential mitigation actions and for new MPA siting.

Further research is required to better understand the ecosystem changes biological invasions may cause to native ecosystems and their impacts on socio-economic activities. To date, evidence shows that most alien species have negative impacts on native biodiversity and human well-being (e.g. Katsanevakis *et al.*, 2014). However, in some cases, alien

-1000 -800 -600 (b) 43°N 40°N Latitude 35°N 30°N Figure 4 Fish species case study (data 0 from Guilhaumon et al., 2015). Difference in planning unit (12,828 cells, 10×10 km) selection frequency, from MARXAN outputs, when following the -1000 -800 -600 different approaches: (a) 'ignore' versus (c) 'protect', (b) 'ignore' versus 'avoid' and 43°N (c) 'avoid' versus 'protect'. Planning units in red are those with a higher selection frequency in the 'ignore' 40°N scenario, in orange those with higher Latitude selection in the 'protect' scenario and in blue those with higher selection in the 35°N 'avoid' scenario. Planning units are black if they had maximum selection frequency 30°N (1000) in all three scenarios. Scatter plots show the selection frequency for the 0° planning units under the different scenarios. For the maps, we used ETRS89 Lambert Azimuthal Equal-Area projection. -1000-800 -600 -400

(a)

species can provide conservation benefits and contribute to conservation objectives; for instance, they can provide habitat or food resources to rare species, serve as functional substitutes for extinct taxa and facilitate the recovery of degraded ecosystems (Schlaepfer *et al.*, 2011). For example, in New England, USA, the invasion of green crabs, *Carcinus maenas*, into heavily burrowed salt marshes partially promoted cordgrass recovery by reversing trophic cascades that were triggered by overfishing of salt marsh predators (Bertness & Coverdale, 2013). Invasives can also provide new economic opportunities. For instance, Mollo *et al.* (2014) showed how targeted exploitation of invasives can lead to new biotechnological and pharmacological applications. In the Levantine Sea, the world's most invaded sea, a large percentage of fisheries is now composed of invasive fish species (Edelist *et al.*, 2013). The commercial exploitation of such species has created new opportunities for local fisheries. Schlaepfer *et al.* (2011) speculate that alien species might contribute to achieving conservation goals in the future because they may be more likely than native species to persist and provide ecosystem services in areas where climate and land use are changing rapidly. Nevertheless, the contribution of alien species to achieving conservation and economic goals is likely species specific, as is their response to the alternative

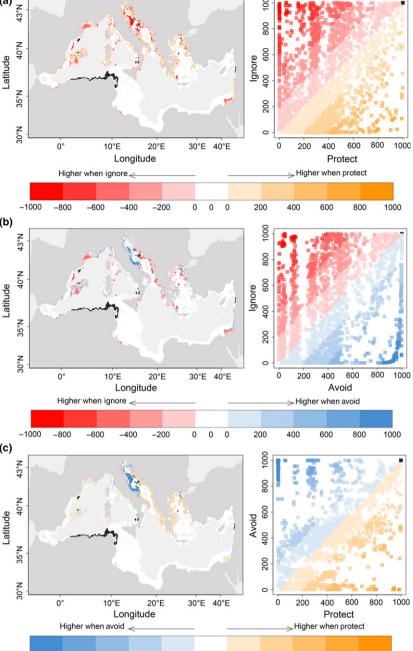
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planning strategies ('protect' or 'avoid'). Therefore, additional information on the impacts (negative or positive) alien species have on ecosystems and human activities is crucial for the formulation of conservation targets for specific species or habitats during the planning process.

Lastly, more information is required on whether MPAs are a useful conservation strategy for the management of alien populations. The 'biotic resistance hypothesis' states that ecosystems with high species richness are more resistant to invaders than those with low biodiversity (Levine & D'Antonio, 1999; Jeschke, 2014). Hence, the expected recovery of native species richness within MPAs could prevent the penetration and settlement of alien species. Furthermore, the restoration of top-down regulation processes (e.g. restoration of top predators' populations) in MPAs could help control the spreading of some alien species inside MPAs (Mumby et al., 2011). Nonetheless, numerous studies have reported the opposite pattern, that is positive relationships between the numbers of native and alien species (McKinney, 2002). These observations led to the 'biotic acceptance hypothesis' which supports the notion that ecosystems can accommodate the establishment of aliens and their coexistence with native species - and to a rich-get-richer pattern where areas with high native species richness support high numbers of alien species (Stohlgren et al., 2006). Moreover, the populations of some alien species could be enhanced in MPAs mainly because they would benefit from non-harvesting (Burfeind et al., 2013). Therefore, further empirical studies are necessary to assess the potential role of MPAs in controlling alien species and mitigating their impacts. If MPAs prove to have no effect or even favour invasive species, then their establishment in impacted areas should be either avoided (Boudouresque & Verlague, 2005) or complemented with other management measures for successful invasion control and mitigation of invasives' impacts (Thresher & Kuris, 2004).

Based on current evidence and until the effects of MPAs on alien and particularly invasive species are clearly demonstrated the 'protect' or 'avoid' planning approaches should be selected. This selection will depend on the specificities of the study area, the expected response of invasive populations to protection and their negative or positive impacts on ecosystem functioning and services. A 'protect' approach could be followed for the restoration of some habitats and the protection of specific populations impacted by invasives, or for the protection of alien species that have proven to be beneficial for ecosystems or human well-being. Conversely, an 'avoid' approach may be developed for harmful alien species that cannot be controlled at a reasonable cost as well as for habitats on which no substantial effect of protection is anticipated. An alternative would be to prioritize for conservation areas that are always selected as priorities regardless of the approach, and are thus less susceptible to biological invasions. In our case studies, these areas are those highlighted in green in Figs 3 and 4, and interestingly most of them coincide with 'consensus areas' proposed by Micheli et al. (2013b).

Despite the potential effectiveness of MPAs in mitigating the impacts of invasive species locally, MPAs alone are unlikely to be sufficient for managing the impact of invasives. Additional management actions aimed at prevention as well as mitigation of invasives' impacts are required both inside and outside MPAs. For instance, eradication of recent alien introductions (Myers et al., 2000; Anderson, 2005) and actions to control well-established invasive populations, such as harvesting by divers (Green et al., 2014), the use of selective fishing gear (Archdale et al., 2010) and the controlled development of targeted fisheries may be examined as management actions to assist the recovery of highly impacted areas under a 'protect' approach. Suppressing invasives below population densities that cause environmental harm can have a similar effect to complete eradication, in terms of protecting the native biodiversity on a local scale (Green et al., 2014). Such management actions should be incorporated into spatial plans and be prioritized on the basis of their cost-effectiveness, accounting for the cost of actions and their expected benefits on ecosystems (Giakoumi et al., 2015).

CONCLUSION

Our review reveals that explicit consideration of biological invasions is lacking in marine conservation plans. At the same time, our case studies highlight that the approach taken to include this issue (protect or avoid invasive species) or not (ignore the relevant information) can lead to different recommendations regarding conservation priorities. The lack of explicit consideration of biological invasion in conservation planning might be partly driven by the large remaining uncertainty regarding how invasive species respond to conservation actions and how they may influence the outcomes of such actions. Other reasons might be the limited data availability and scientific understanding of biological invasions; the limited awareness and concern by policy makers; and consequently, the limited funding directed to the control of alien populations and mitigation of their impacts. More research is clearly needed to determine the more effective strategy for incorporating biological invasions in marine conservation planning. Research priorities should involve multidisciplinary approaches and include (1) extensive mapping efforts of invasive species distributions and development of accurate models for the prediction of their future distributions; (2) assessment of invasive species ecological and socioeconomic impacts in host ecosystems; and (3) assessment of the role MPAs have in controlling invasive populations and mitigating their impacts. Ultimately, the management of invasives and their potential integration into conservation plans depend on how conservation goals are set in the future. A shift from a species-based towards a function-based approach, focusing on invasives' functional role and their interactions with native communities (see Brown & Mumby 2014), would provide better guidance on the appropriate strategies for managing invasive species.

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REFERENCES

- Abdul Malak, D., Livingstone, S.R., Pollard, D., Polidoro, B.A., Cuttelod, A., Bariche, M., Bilecenoglu, M., Carpenter, K.E., Collette, B.B., Francour, P., Goren, M., Kara, M.H., Massutí, E., Papaconstantinou, C. & Tunesi, L. (2011) Overview of the Conservation Status of the Marine Fishes of the Mediterranean Sea. 61 pp. IUCN, Gland, Switzerland and Malaga, Spain.
- Albins, M.A. (2012) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. *Biological Invasions*, **15**, 29–43.
- Anderson, L.W.J. (2005) California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response*. *Biological Invasions*, **7**, 1003–1016.
- Archdale, M.V., Anasco, C.P. & Nakagawa, A. (2010) Liftnets compare favorably with pots as harvesting fishing gear for invasive swimming crabs. *Journal of Fisheries and Aquatic Science*, 5, 510–516.
- Ball, I.R., Possingham, H.P. & Watts, M. (2009) Marxan and relatives: software for spatial conservation prioritisation. *Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools* (ed. by A. Moilanen, K.A. Wilson and H.P. Possingham), pp. 185–195. Oxford University Press, Oxford, UK.
- Ban, N.C. & Klein, C.J. (2009) Spatial socioeconomic data as a cost in systematic marine conservation planning. *Conservation Letters*, **2**, 206–215.
- Bax, N., Williamson, A., Aguero, M., Gonzalez, E. & Geeves,
 W. (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy*, 27, 313–323.
- Bertness, M.D. & Coverdale, T.C. (2013) An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. *Ecology*, **94**, 1937–1943.
- Boudouresque, C.F. & Verlaque, M. (2005) Nature conservation, marine protected areas, sustainable development and the flow of invasive species to the Mediterranean Sea.

Travaux Scientifiques du Parc National de Port-Cros, 21, 29–54.

- Brown, C.J. & Mumby, P.J. (2014) Trade-offs between fisheries and the conservation of ecosystem function are defined by management strategy. *Frontiers in Ecology and the Environment*, **12**, 324–329.
- Bulleri, F., Alestra, T., Ceccherelli, G., Tamburello, L., Pinna, S., Sechi, N. & Benedetti-Cecchi, L. (2011) Determinants of *Caulerpa racemosa* distribution in the north-western Mediterranean. *Marine Ecology Progress Series*, 431, 55–67.
- Burfeind, D.D., Pitt, K.A., Connolly, R.M. & Byers, J.E. (2013) Performance of non-native species within marine reserves. *Biological Invasions*, 15, 17–28.
- Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W.W.L., Christensen, V., Karpouzi, V.S., Guilhaumon, F., Mouillot, D., Paleczny, M., Palomares, M.L., Steenbeek, J., Trujillo, P., Watson, R. & Pauly, D. (2012) The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecology and Biogeography*, **21**, 465–480.
- Convention on Biological Diversity (2015) *Aichi biodiversity targets*. Available at: https://www.cbd.int/sp/targets/ (accessed 6 November 2015).
- Edelist, D., Rilov, G., Golani, D., Carlton, J.T. & Spanier, E. (2013) Restructuring the Sea: profound shifts in the world's most invaded marine ecosystem. *Diversity and Distributions*, **19**, 69–77.
- Elleouet, J., Albouy, C., Ben Rais Lasram, F., Mouillot, D. & Leprieur, F. (2014) A trait-based approach for assessing and mapping niche overlap between native and exotic species: the Mediterranean coastal fish fauna as a case study. *Diversity and Distributions*, **20**, 1333–1344.
- Essl, F., Bacher, S., Blackburn, T.M. *et al.* (2015) Crossing frontiers in tackling pathways of biological invasions. *BioScience*, **65**, 769–782.
- ETC/BD (European Topic Centre on Biological Diversity) (2010) http://bd.eionet.europa.eu/activities/Natura_2000/pdfs/Additional_marine_guidelines.pdf (accessed 14 May 2013).
- EU (2008) Directive of the European Parliament and the Council Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive), European Commission Directive 2008/56/EC, OJ L 164.
- Galil, B.S., Boero, F., Campbell, M.L., Carlton, J.T., Cook, E., Fraschetti, S., Gollasch, S., Hewitt, C.L., Jelmert, A., Macpherson, E., Marchini, A., McKenzie, C., Minchin, D., Occhipinti-Ambrogi, A., Ojaveer, H., Olenin, S., Piraino, S. & Ruiz, G.M. (2014) 'Double trouble': the expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biological Invasions*, 17, 973–976.
- Giakoumi, S., Grantham, H.S., Kokkoris, G.D. & Possingham, H.P. (2011) Designing a network of marine reserves in the Mediterranean Sea with limited socio-economic data. *Biological Conservation*, **144**, 753–763.

- Giakoumi, S., Sini, M., Gerovasileiou, V., Mazor, T., Beher, J., Possingham, H.P., Abdulla, A., Çinar, M.E., Dendrinos, P., Gucu, A.C., Karamanlidis, A.A., Rodic, P., Panayotidis, P., Taskin, E., Jaklin, A., Voultsiadou, E., Webster, C., Zenetos, A. & Katsanevakis, S. (2013) Ecoregion-based conservation planning in the Mediterranean: dealing with large-scale heterogeneity. *PLoS One*, 8, e76449.
- Giakoumi, S., Brown, C.J., Katsanevakis, S., Saunders, M.I. & Possingham, H.P. (2015) Using threat maps for cost-effective prioritization of actions to conserve coastal habitats. *Marine Policy*, **61**, 95–102.
- Green, S.J., Dulvy, N.K., Brooks, A.M.L., Akins, J.L., Cooper, A.B., Miller, S. & Côté, I.M. (2014) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications*, 24, 1311–1322.
- Guilhaumon, F., Albouy, C., Claudet, J., Velez, L., Ben Rais Lasram, F., Tomasini, J.-A., Douzery, E.J.P., Meynard, C.N., Mouquet, N., Troussellier, M., Araújo, M.B. & Mouillot, D. (2015) Representing taxonomic, phylogenetic and functional diversity: new challenges for Mediterranean marine-protected areas. *Diversity and Distributions*, 21, 175–187.
- Jeschke, J.M. (2014) General hypotheses in invasion ecology. *Diversity and Distributions*, **20**, 1229–1234.
- Kark, S., Levin, N., Grantham, H.S. & Possingham, H.P. (2009) Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. *Proceedings of the National Academy* of Sciences USA, **106**, 15368–15373.
- Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E., Oztürk, B., Grabowski, M., Golani, D. & Cardoso, A.C. (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, 9, 391–423.
- Katsanevakis, S., Deriu, I., D'Amico, F. et al. (2015) European Alien Species Information Network (EASIN): supporting European policies and scientific research. *Management of Biological Invasions*, 6, 147–157.
- Katsanevakis, S., Tempera, F. & Teixeira, H. (2016) Mapping the impact of alien species on marine ecosystems: the Mediterranean Sea case study. *Diversity and Distributions*, 22, 694–707.
- Klein, C.J., Tulloch, V.J., Halpern, B.S., Selkoe, K.A., Watts, M.E., Steinback, C., Scholz, A. & Possingham, H.P. (2013) Tradeoffs in marine reserve design: habitat condition, representation, and socioeconomic costs. *Conservation Letters*, 6, 324–332.
- Levine, J.M. (2008) Biological invasions. *Current Biology*, 18, R57–R60.
- Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.
- Mazor, T., Giakoumi, S., Kark, S. & Possingham, H.P. (2014) Large-scale conservation planning in a multinational marine environment: cost matters. *Ecological Applications*, **24**, 1115–1130.

- McKinney, M.L. (2002) Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. *Diversity and Distributions*, **8**, 311–318.
- Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R., Nykjaer, L. & Rosenberg, A.A. (2013a) Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PLoS One*, 8, e79889.
- Micheli, F., Levin, N., Giakoumi, S., Katsanevakis, S., Abdulla, A., Coll, M., Fraschetti, S., Kark, S., Koutsoubas, D., Mackelworth, P., Maiorano, L. & Possingham, H.P. (2013b) Setting priorities for regional conservation planning in the Mediterranean Sea. *PLoS One*, 8, e59038.
- Moilanen, A., Kujala, H. & Leathwick, J.R. (2009) The Zonation framework and software for conservation prioritization. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools (ed. by A. Moilanen, K.A. Wilson and H.P. Possingham), pp. 196–210. Oxford University Press, Oxford, UK.
- Mollo, E., Cimino, G. & Ghiselin, M.T. (2014) Alien biomolecules: a new challenge for natural product chemists. *Biological Invasions*, 17, 941–950.
- Molnar, J.L., Gamboa, R.L., Revenga, C. & Spalding, M.D. (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6, 485–492.
- Mumby, P.J., Harborne, A.R. & Brumbaugh, D.R. (2011) Grouper as a natural biocontrol of invasive lionfish. *PLoS One*, **6**, e21510.
- Myers, J.H., Simberloff, D., Kuris, A.M. & Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, **15**, 316–320.
- Parravicini, V., Mangialajo, L., Mousseau, L., Peirano, A., Morri, C., Montefalcone, M., Francour, P., Kulbicki, M. & Bianchi, C.N. (2015) Climate change and warm-water species at the north-western boundary of the Mediterranean Sea. *Marine Ecology*, **36**, 897–909.
- Pressey, R.L., Watts, M.E., Barrett, T.W. & Ridges, M.J. (2009) The C-plan conservation planning system: origins, applications, and possible futures. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools* (ed. by A. Moilanen, K.A. Wilson and H.P. Possingham), pp. 211–234. Oxford University Press, Oxford, UK.
- Pyšek, P. & Richardson, D. (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, **35**, 25–55.
- Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011) The potential conservation value of non-native species. *Conservation Biology*, **25**, 428–437.
- Seebens, H., Gastner, M.T. & Blasius, B. (2013) The risk of marine bioinvasion caused by global shipping. *Ecology Letters*, **16**, 782–790.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pysek, P., Sousa, R., Tabacchi, E. &

Vila, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, **28**, 58–66.

- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, 57, 573–583.
- Stohlgren, T.J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. & Master, L.L. (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions*, 8, 427–447.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, **21**, 645–651.
- Streftaris, N. & Zenetos, A. (2006) Alien marine species in the Mediterranean – the 100 'worst invasives' and their impact. *Mediterranean Marine Science*, **7**, 87–118.
- Tallis, H., Ferdana, Z. & Gray, E. (2008) Linking terrestrial and marine conservation planning and threats analysis. *Conservation Biology*, **22**, 120–130.
- Thresher, R.E. & Kuris, A.M. (2004) Options for managing invasive marine species. *Biological Invasions*, **6**, 295–300.
- Verges, A., Steinberg, P.D., Hay, M.E. et al. (2014) The tropicalization of temperate marine ecosystems: climatemediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140846.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a metaanalysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708.
- Violle, C. & Jiang, L. (2009) Towards a trait-based quantification of species niche. *Journal of Plant Ecology*, 2, 87–93.
- Zenetos, A., Gofas, S., Morri, C. *et al.* (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, **13**, 328–352.

DATA ACCESSIBILITY

Critical habitats GIS layers (distribution of seagrass meadows *Posidonia oceanica* and coralligenous formations) used in this

article are available on MedOBIS database: http://lifewww-00. her.hcmr.gr:8080/medobis/resource.do?r=posidonia, http://life www-00.her.hcmr.gr:8080/medobis/resource.do?r=coralligenous. Endemic fish GIS layers are available on Ecological Archives: http://www.esapubs.org/archive/ecol/E096/203/#data.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Time trend in marine conservation plans and their scale.

Table S1 Articles' attributes included in the analyses.

Appendix S1 List of 119 articles included in the synthesis.

Appendix S2 List of endemic fish included in the case study with their functional traits and IUCN category.

BIOSKETCH

The authors belong to a larger group of scientists focusing on Advancing Marine Conservation Planning in the Mediterranean Sea. This group was formed in 2012 (http://link.spr inger.com/article/10.1007/s11160-012-9272-8#/page-1focusing), and its research interests include marine conservation planning, integrated conservation planning across realms (land– freshwater–sea), impact assessment on food webs and implications for conservation planning, transboundary conservation, governance of marine protected areas, cost-effective action prioritization accounting for climate change and biological invasions.

Author contributions: S.G., S.K., S. Kark, F.G., J.C., and A.T. conceived the ideas; S.G. led the writing and all aspects of the project; all authors conducted the literature review and revised the text; S.G. and F.G. analysed the data; S.G., F.G., S.K. and S.F. produced the figures.