

# Identifying where vulnerable species occur in a data-poor context: combining satellite imaging and underwater occupancy surveys

Stelios Katsanevakis<sup>1,\*</sup>, Maria Sini<sup>1</sup>, Thanos Dailianis<sup>1,2</sup>, Vasilis Gerovasileiou<sup>1,2</sup>,  
Nikoletta Koukouroufli<sup>1</sup>, Kostantinos Topouzelis<sup>1</sup>, Michalis Ragkousis<sup>1</sup>

<sup>1</sup>University of the Aegean, Department of Marine Sciences, University Hill, 81100 Mytilene, Greece

<sup>2</sup>Hellenic Centre for Marine Research, Institute of Marine Biology, Biotechnology, and Aquaculture, 71500 Heraklion Crete, Greece

**ABSTRACT:** For the effective conservation of vulnerable marine populations, knowledge of their distributions and spatially explicit management actions are essential. The use of physical features or coarse habitat types as surrogates of species distribution often does not provide an accurate enough (and hence useful) mapping of where species occur. This is further exacerbated in data-poor regions, where habitat maps in the marine environment are often patchy. A combination of satellite imaging analysis (for a rough classification of the main habitat types in shallow waters) and occupancy modelling based on data collected through dedicated underwater surveys is proposed as a relatively inexpensive and timely way to identify priority areas for the conservation of selected benthic species. The occupancy surveys provide estimates of the probability of presence, which can be used as weights of the importance of the available suitable habitat types in a potential habitat index (PHI). This approach was applied in the Aegean Sea (eastern Mediterranean) for 6 benthic hard-bottom species of conservation importance. Repetitive SCUBA diving surveys were conducted at six 5 m depth zones between 0 and 30 m at 47 locations in the Aegean Sea to detect the presence of the target species. Occupancy was modelled using several environmental spatial covariates. The applied method explicitly incorporated imperfect detectability in the modelling process. Predictive distributional maps of PHI were produced for each species, identifying areas that could be prioritized for conservation measures. Despite some limitations, this approach can provide a baseline for the protection of vulnerable species, in the framework of adaptive management for marine conservation planning.

**KEY WORDS:** Occupancy · Species distribution · Biodiversity mapping · Underwater visual survey · Detectability · Marine conservation

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Marine biodiversity is under threat due to the historical and current cumulative impacts of human activities (Halpern et al. 2008). In an effort to halt the loss of biodiversity and the related ecosystem services it provides, the international community has agreed on biodiversity-related targets to be reached through global, regional, and national conventions

and legislative instruments, e.g. the Convention on Biological Diversity.

Systematic conservation planning for the creation of networks of Marine Protected Areas (MPAs) is an important tool for the effective protection of marine biodiversity. Furthermore, one of the main aims of maritime spatial planning, besides resolving conflicts among users of marine space, is the protection of biodiversity and the marine environment (see e.g.

the European Directive 2014/89/EU [<http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A32014L0089>] establishing a framework for maritime spatial planning). The application of such tools requires sound knowledge of the distribution of species, habitats, and processes at the planning, legislation, and enforcement stages (Lourie & Vincent 2004, Moilanen et al. 2009). Such knowledge remains scarce, as well as time consuming and costly to obtain. To overcome this challenge, the distribution of physical features or habitats has often been used in spatial prioritization as a surrogate for species distribution (Ward et al. 1999, McArthur et al. 2010, Dalleau et al. 2010). In data-poor regions, acquiring high-quality information on species distribution is practically impossible due to limited resources, and even habitat mapping in the marine environment is often patchy. Furthermore, biophysical and habitat surrogates have often been criticized as being inadequate in terms of properly representing species biodiversity in space and time, as they often fail to predict trends over time, and provide limited information about species-specific and location-specific responses. In addition, spatial prioritization based on such surrogates may correlate poorly with prioritization based on species biodiversity. The need for the development of new methodological approaches has been stressed (Pierson et al. 2015, Jackson & Lundquist 2016).

We propose an approach, based on satellite imaging, to easily acquire large-scale habitat distribution information, and then a method of refining habitat surrogates based on species occupancy modelling. Species occupancy is defined as the proportion of area, patches, or sampling units occupied, or as the probability of a species' presence in a sampling unit (MacKenzie et al. 2006). It is chosen as an appropriate population state variable in many cases, e.g. in studies of distribution and range (Scott et al. 2002), alien invasions (Katsanevakis et al. 2011a), metapopulation studies (Moilanen 2002), community studies (Weber et al. 2004), and large-scale monitoring (Manley et al. 2004). The costs and effort involved in obtaining species occupancy data are much lower than those of retrieving the necessary data to estimate more informative state variables, such as population density and abundance (Pollock et al. 2002, MacKenzie et al. 2006).

The estimation of a population state variable is often confounded by 'imperfect detectability', i.e. the inability of investigators to detect all individuals or all species in a surveyed area (Yoccoz et al. 2001, Thompson 2004). Although much effort has been put

into developing methods that account for imperfect detectability when monitoring marine populations and communities, the application of such methods in the marine environment is not as common or apparent as it is in other systems (Katsanevakis et al. 2012). In occupancy surveys, non-detection of a species does not imply the species is genuinely absent from a sampling location. Frequently, a species can be present at an area but go undetected (Issaris et al. 2012). Such 'false absences' lead to occupancy underestimations if the imperfect detection of the species is not accounted for. Accordingly, methods to account for imperfect detectability, based on repetitive surveys of the same sites, have been developed (MacKenzie et al. 2006, Issaris et al. 2012).

Here, we used the Aegean ecoregion (eastern Mediterranean) as a case study to demonstrate the applicability of the method. Our aim was to provide large-scale distribution maps of priority areas for the conservation of hard-bottom, protected benthic species. To achieve this, shallow, hard-bottom substrates of the Aegean coastline were mapped by analyzing satellite images in order to define the availability of potential habitat for the target species. Then, a field survey by SCUBA diving, designed to account for imperfect detectability, was conducted to provide presence/absence data of a number of protected, hard-bottom benthic species in the study area. These data were used to model the occupancy of the target species, refine their potential habitat, and produce potential distribution maps that may be used for conservation planning purposes.

## MATERIALS AND METHODS

### Study area

The study area consisted of all shallow (depths <30 m) Greek territorial waters of the Aegean ecoregion (eastern Mediterranean) (Fig. 1, see also Fig. S1 in Supplement 1; all supplementary material for this article can be found at [www.int-res.com/articles/suppl/m577p017\\_supp.pdf](http://www.int-res.com/articles/suppl/m577p017_supp.pdf)). The Aegean Archipelago has a complex geomorphology, reflecting past geological and geodynamic processes (Sakellariou & Alexandri 2007). It is characterized by a lengthy coastline (approx. 16 000 km) with variable bathymetry, and more than 2000 islands. We subdivided the ecoregion into 4 sub-areas (i.e. North Aegean, South Aegean, Evoikos and Pagasitikos Gulfs, and Crete Island; Fig. 1), based on their distinctive geomorphology and oceanographic characteristics.

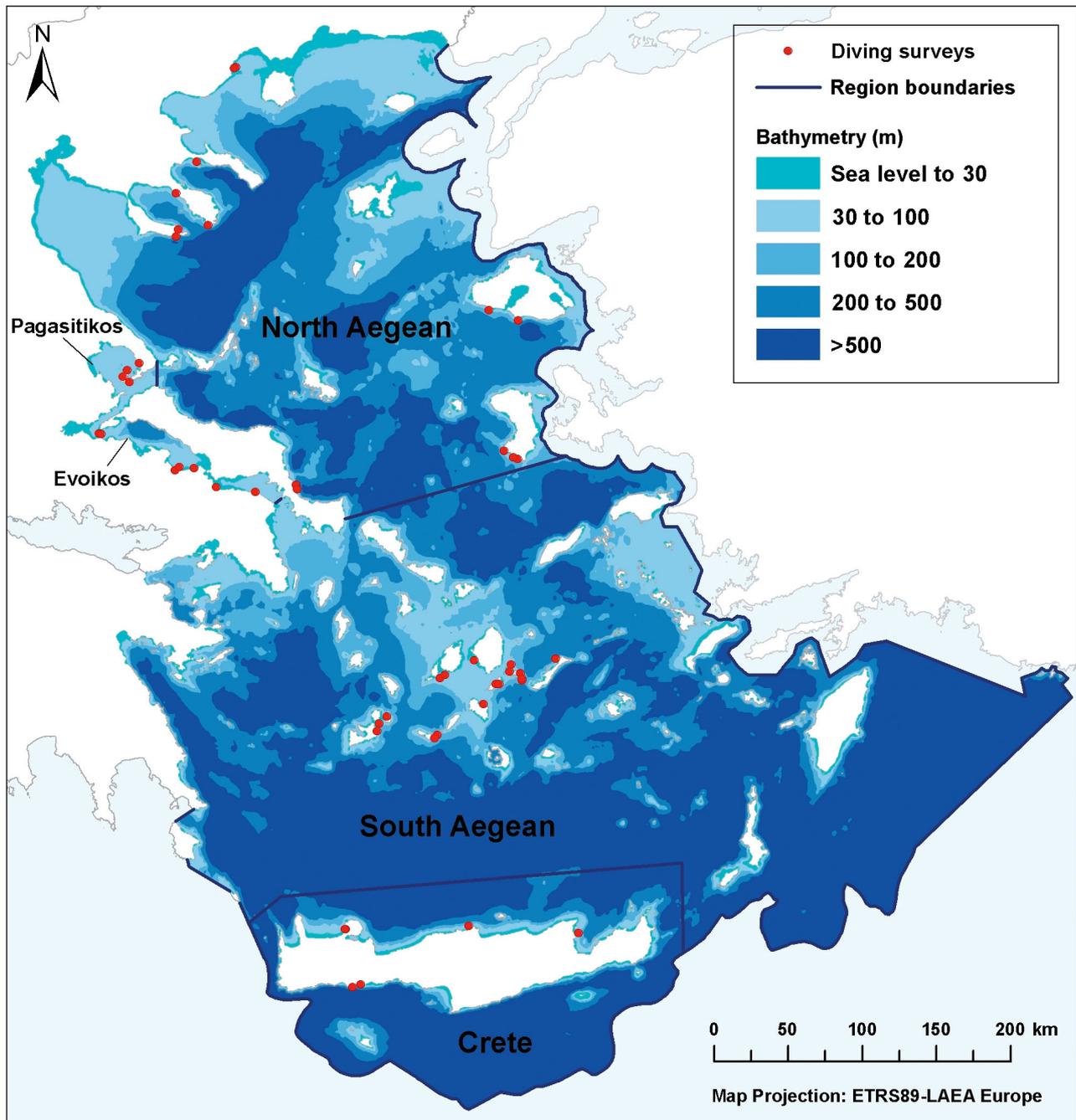


Fig. 1. Study area and division into 4 sub-areas (North Aegean, South Aegean, Crete, and Evoikos-Pagositikos Gulfs) based on each area's distinct geomorphological and oceanographic characteristics. Sampling stations are indicated by red dots. Each marine sub-area is depicted at a higher scale in Fig. S1 in Supplement 1

The North Aegean Sea has a wide continental shelf composed of shallow platforms, and represents the offshore continuation of the alluvial planes of northern Greece, which are drained by large rivers that feed the shelf with terrigenous clastic material (Sakellariou et al. 2005). This marine sub-area acts as a dilution basin due to the contribution of the light

brackish waters of the Black Sea through the Dardanelles Strait (Zervakis et al. 2005). In contrast, the South Aegean Sea is classified as a concentration basin, where evaporation exceeds freshwater input. It includes the Cyclades plateau, which is essentially a shallow platform with a mean depth of approximately 200 m, and numerous small islands. Crete is

located in the southernmost part of the Aegean Sea. The 1800 m deep Heraklion Basin, running along the northern part of the island, separates Crete from the south Aegean sub-area, while the Hellenic Trench that stretches along the south coasts of Crete, separates the island from the rest of the Levantine Sea (Sakellariou et al. 2005).

These distinctive characteristics result in lower mean and seasonal temperature and salinity values of the superficial water masses in the north Aegean basin compared to the south (Velaoras et al. 2013). The trophic state of the North Aegean sub-area (including the Evoikos and Pagasitikos Gulfs) is characterized as lower or higher mesotrophic, Crete as lower mesotrophic (northern part) or oligotrophic (southern part), whereas the southern Aegean is considered an oligotrophic area (Gotsis-Skretas & Ignatiades, 2005). However, due to the highly variable and complex morphodynamics of the Aegean coastline, local parameters can strongly influence the coastal hydrologic characteristics at a small spatial scale. The above environmental features have been associated with the variable biotic trends characterizing the distinct Aegean sub-areas, as shown for invertebrate taxa (e.g. Arvanitidis et al. 2002, Voultsiadou 2005, Gerovasileiou & Voultsiadou 2012), and motile fish fauna (e.g. Katsanevakis et al. 2010a,b).

### Target species

An initial list was created comprising 15 protected benthic animal taxa belonging to 5 phyla. The list included 5 Porifera, 1 Cnidaria, 5 Mollusca, 2 Echinodermata, and 2 Chordata (see Table 1, Fig. S2 in Supplement 1). Selection of target species was based on their occurrence in the shallow waters (<30 m depth) of the Aegean Sea, their preference for rocky substrates as a primary habitat, and their protection status. Only organisms with a strict protection status were considered, specifically those that are found in Annex II of the 'Protocol for Specially Protected Areas and Biological Diversity in the Mediterranean' of the Barcelona Convention, Annex IV of the EU Habitats Directive (92/43/EC), and Annex II of the Bern Convention; these Annexes prohibit the collection and deliberate capture or killing of the species included therein. According to the regulations, these species require protection as they are either rare or their populations are vulnerable to cumulative stressors such as fishing activities, habitat degradation, biological invasions, and climate change.

### Field work: modelling occupancy and detectability

The field survey in the Aegean aimed to collect presence/absence data of the target species in order to model their occupancy. The single-species, single-season occupancy models developed by MacKenzie et al. (2006) and the field protocol for marine underwater surveys proposed by Issaris et al. (2012) were applied. The goal of this method is to estimate the proportion of sites that are occupied, without assuming that a species will always be detected.

The general scheme of the Issaris et al. (2012) protocol involves  $K$  observers who simultaneously but independently search for the target species at each of  $N$  sampling sites. Occupancy,  $\psi$ , is jointly modelled with probability of detection,  $p$ , under a model-based approach. There are 2 stochastic processes affecting the detection of the target species at a site (MacKenzie et al. 2006). A site might be either occupied (with probability  $\psi$ ) or unoccupied (with probability  $1 - \psi$ ) by the target species. If the site is unoccupied, the target species will not be detected. If the site is occupied, each observer,  $j$ , will either detect the target species (with probability  $p_j$ ) or not (with probability  $q_j = 1 - p_j$ ). The probability of each detection history can be expressed as a function of  $\psi$  and  $p_j$ . For example, the probability of the detection history  $H_i = 10$  (denoting that site  $i$  was surveyed by 2 observers, with the species being detected by the first but not by the second) would be  $\Pr(H_i = 10) = \psi p_1 q_2 = \psi p_1 (1 - p_2)$ . For sites where the species is not detected by any of the observers, there are 2 possibilities—either the species is present but never detected (a 'false absent') or the species is genuinely absent. Thus,  $\Pr(H_i = 00) = \psi q_1 q_2 + (1 - \psi)$ . By deriving such expressions for each of the  $N$  observed detection histories, the likelihood (L) of the data will be

$$L(\psi, \mathbf{p} \mid H_1, H_2, \dots, H_N) = \prod_{i=1}^N \Pr(H_i) \quad (1)$$

where  $\mathbf{p}$  is the vector of detection probabilities;  $\psi$  and  $p_j$  can be estimated with standard maximum likelihood techniques (MacKenzie et al. 2006).

In the present study, rocky habitats were surveyed in 47 locations by means of SCUBA diving along 6 pre-defined depth zones (0 to 5, 5 to 10, 10 to 15, 15 to 20, 20 to 25, and 25 to 30 m), corresponding to distinct 'sampling stations'. Although the target was to distribute the sampling locations evenly across the study area, final selection was dictated by logistical constraints and the availability of continuous rocky habitats throughout the 0 to 30 m depth range. In some locations rocky habitats were unavailable

at certain depth zones, and thus the total number of sampling stations (257) was lower than the expected ( $6 \times 47 = 282$ ). At consecutive sampling stations (i.e. location  $\times$  depth zone), the presence/absence of the target species was recorded independently by 2 observers (from a pool of 3 diving researchers) who conducted visual surveys at fixed 5 min time intervals.

For each target species, the potential relationships between the model parameters (occupancy and detection probabilities) and environmental/spatial variables were investigated. Covariates were incorporated by using the logistic model  $\theta_i = \exp(\mathbf{Y}_i\boldsymbol{\beta}) \times [1 + \exp(\mathbf{Y}_i\boldsymbol{\beta})]^{-1}$ , where  $\theta_i$  is the probability of interest (occupancy or detection probability),  $\mathbf{Y}_i$  are the covariates to be modelled, and  $\boldsymbol{\beta}$  denotes the vector of the covariate coefficients to be estimated. Standard maximum likelihood techniques were applied to obtain estimates of the model parameters (MacKenzie et al. 2006).

The candidate models were selected in order to test the following 7 hypotheses for the occupancy of the target species in the study area: (O1) occupancy was constant; (O2) occupancy depended on the annual average sea surface temperature ( $T_m$ ); (O3) occupancy depended on the annual minimum sea surface temperature ( $T_{\min}$ ); (O4) occupancy depended on the annual maximum sea surface temperature ( $T_{\max}$ ); (O5) occupancy varied with the annual average chlorophyll *a* concentration (Chl); (O6) occupancy differed among marine sub-areas (MAreas); and (O7) occupancy varied with depth. Two hypotheses for detectability were investigated: (D1) detectability was constant across sampling stations and observer-independent; (D2) detectability was constant across sampling stations and observer-dependent.

Depth was included as a predictor variable as it is the main gradient along which faunal changes occur in shelf assemblages, mainly because of its correlation with crucial environmental variables such as light intensity, temperature, nutrient concentration, and primary and secondary productivity (Katsanevakis et al. 2009). Temperature and chlorophyll (as a proxy of productivity and nutrient supply) are also important in predicting species distributions (Tyberghein et al. 2012). Daily values of sea surface temperature (for the period 1 Jan 2012 to 31 Dec 2016) and chlorophyll concentration (for the period 14 Apr 2014 to 28 Feb 2017) were obtained from Copernicus Marine Service Products (<http://marine.copernicus.eu/>) at a  $1 \times 1$  km resolution. At this scale, average annual values of temperature and chlorophyll were estimated, along with average annual minimum and

maximum temperature values for each cell (see Figs. S3–S6 in Supplement 2).

A total of 36 occupancy models were fitted for each target species by combining the 7 hypotheses for occupancy with the 2 hypotheses for detectability. Due to collinearity (and thus to avoid spurious results) only one of the temperature variables was used in each model. MAreas was not combined with any other environmental covariate (except for depth) as it was considered a general surrogate of all environmental characteristics of each sub-area. Standardized values of temperature, chlorophyll, and depth were used as covariates, i.e. (value – mean) / SD, where for depth the central value of each depth zone was considered. For each candidate model, the average occupancy across sites was estimated as the mean of the estimated occupancies. The standard errors of the average occupancies were estimated by bootstrapping (1000 resamples). The software PRESENCE v.10.7 was used to fit the candidate models (Hines 2006).

Akaike's information criterion (AIC; Akaike 1973) and AIC differences ( $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$ ) were computed over all candidate models. To quantify the plausibility of each model, given the data and set of 36 models, the Akaike weight ( $w_i$ ) of each model was calculated, where  $w_i = \exp(-0.5\Delta_i) / \sum_k \exp(-0.5\Delta_k)$ . The Akaike weight is considered as the weight of evidence in favor of model *i* being the best model of the available set of models (Akaike 1983, Burnham & Anderson 2002). To assess absolute goodness of fit, a Pearson's chi-squared statistic was used, estimated by the parametric bootstrap procedure described by MacKenzie & Bailey (2004) based on 1000 bootstrap resamples. Estimates of the relative importance of each hypothesis (*k*) were made by summing the Akaike weights across all the models in the set where the corresponding variable occurs [ $w_+(k)$ ]: the larger the sum of Akaike weights, the more important that hypothesis is relative to the other hypotheses (Burnham & Anderson 2002).

A multi-model inference approach was followed for inference, i.e. rather than estimating occupancy from only the 'best' model, it was estimated from all the models considered. This was accomplished by estimating weighted averages of occupancy using Akaike weights for all the candidate models (Burnham & Anderson 2002). Hence, the model-averaged occupancy was estimated as  $\bar{\psi} = \sum_i w_i \hat{\psi}_i$ . The unconditional standard error of  $\bar{\psi}$  was estimated as (Burnham & Anderson 2002):  $\text{SE}(\bar{\psi}) = \sum_i w_i (\text{var}(\hat{\psi}_i | g_i) + (\hat{\psi}_i - \bar{\psi})^2)^{1/2}$ , where  $\text{var}(\hat{\psi}_i | g_i)$  is the variance of the estimated occupancy according to model  $g_i$ , conditional on the

model. The simultaneous use of all candidate occupancy models under a multi-model inference (MMI) approach is a more robust way for occupancy estimations that properly deals with model selection uncertainty (Burnham & Anderson 2002, Katsanevakis 2006).

### Habitat mapping with satellite imaging

Satellite-based remote sensing has been widely used for habitat mapping in the terrestrial realm but also in many cases in the marine realm, since satellite images cover wide areas and relevant classes can be derived with adequate accuracy (Torres-Pulliza et al. 2013, Hossain et al. 2015). In the present study, satellite images were used for the detection in the marine environment of 4 generic classes: (1) soft bottom, containing mainly sandy or muddy sediments and small pebbles; (2) hard bottom, including reefs and large rocks; (3) seagrass meadows, mainly of *Posidonia oceanica* and *Cymodocea nodosa*; and (4) deeper waters, where it was impossible to obtain any information through satellite imaging.

Data from the Landsat-8 satellite and its operational land imager (OLI) sensor were used. Landsat-8 is the latest satellite of the Landsat series from NASA and USGS, launched in February 2013 with a 16 d repeat cycle and swath size of 183 km. The OLI sensor operates in 7 bands, from coastal blue to short-wave infrared, with a spatial resolution of 30 m and 16-bit radiometric resolution. The coastal blue band (0.43 to 0.45  $\mu\text{m}$ ) was included in the Landsat series for the first time, and among others is dedicated to imaging shallow waters. Greek coastal or marine areas are covered in 25 Landsat-8 frames (row/path). In total, 50 cloud-free Landsat-8 images were downloaded for further processing (2 frame<sup>-1</sup>). During the image-selection phase, a strong preference was given for the months of August and December (or months close to them) due to better visibility. The first image of each frame was processed for habitat mapping; however, in locations with insufficient water clarity the second image was processed instead. This was due to the large swath of Landsat-8 images and the complexity of the Aegean Sea. The satellite images were acquired between June 2013 and July 2015. *In situ* sampling for ground-truthing was conducted in summer 2016. This time difference is not considered important, mainly because the 3 classification categories (seagrass, reef, sand) remain practically unchanged during such small time frames.

The developed methodology had 3 pillars. First, relevant data were acquired after identification of

the dedicated Landsat's frames and images of high water clarity. Images were selected to have low cloud coverage, calm sea state, and absence of large-scale oceanographic phenomena (e.g. fronts, eddies). Following acquisition of the data, a pre-processing phase was conducted, which included radiometric calibration, atmospheric correction, land mask, and image cropping. Radiometric calibration was required for transporting the images' digital numbers (DNs) to the top of atmosphere (TOA) radiance and preparing the image format for the next stage of atmospheric correction. The influence of the atmosphere on the satellite images was corrected by using the ENVI<sup>®</sup> 5.2 Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH<sup>®</sup>) toolbox software (Matthew et al. 2002).

The third pillar was image classification, where appropriate parts of the images were classified into the above-mentioned classes. Image classification relied on object-based image analysis, where images were segmented into objects, and then classified according to their spectral and spatial characteristics (Lyons et al. 2012). When necessary, objects were manually edited for better classification results. We used the eCognition Developer v.9.2 (Trimble) software for object-based image analysis. Using the classification methodology we had developed, we first identified coastal areas, secondly classified large segments of the image, and thirdly classified smaller detailed parts of the image. The coastal area selection was based on the operator's selection of large, predefined areas. These areas resulted from a large segmentation, representing coastal areas. The second step of broad classification divided the area of interest into 3 basic classes: shallow areas, deep sea, and possible seagrass. In the detailed classification step, reefs and seagrass areas were detected using a multiresolution segmentation and fuzzy logic rules. The rules used the 4 available visible Landsat-8 bands and differed for each category. For example, seagrass and coastal areas contained 7 and 5 fuzzy rules, respectively.

Rocky beds and seagrass meadows present very different spectral values in shallow waters when observed in satellite images, and therefore are clearly distinguishable. The largest problem with rocky beds is their size relative to the spatial resolution of the satellite images. The problem becomes more complicated when the rocky habitat exists at different depths, where its spectral values also differ. The accuracy of the method was estimated by comparing the habitat maps that were created by satellite imaging with ground-truthing measure-

ments. The level of accuracy was assessed using 6 orthophoto maps created by the use of unmanned aerial vehicles (UAVs) and snorkeling transects, conducted during summer 2016. The spatial accuracy of the orthophoto maps was 3 cm; however, this was transformed to 30 cm to require less computational power. For both datasets (orthophoto maps and satellite images), the coverage of the 3 desired categories in the assessed area (with availability of UAV orthophoto maps) was calculated and compared.

### Identifying priority areas for the target species

To identify priority areas for the target species, the study area was divided into 7178 cells ( $1 \times 1$  km), covering a depth range of 0 to 30 m. For each cell and depth zone, the total area covered by hard substrate was estimated using the analysis toolbox of ArcGIS v.10.2.2 (ESRI) software combined with SQL queries in MS Access 2007 (Microsoft).

The following potential habitat index (PHI) is herein proposed as an index of the importance of each cell for the population of each target species. It was estimated for each cell by the formula:

$$PHI_i = \sum_{z=1}^6 H_{iz} \bar{\psi}_{iz} \quad (2)$$

where  $H_{iz}$  is the hard substrate area of the bathymetric zone  $z$  at cell  $i$ , and  $\bar{\psi}_{iz}$  is the model-averaged predicted occupancy at each bathymetric zone  $z$  of the cell  $i$ .

PHI has a number of desirable properties: (1) it is linearly related to the area of the suitable habitat at each cell; (2) it is linearly related to the estimated occupancy of the species at each cell; (3) it is zero when the estimated occupancy of the species is zero; and (4) its maximum value corresponds to the total area of suitable habitat at each cell, when the estimated occupancy is 1. As the idea of the proposed index is to provide a metric that improves the use of habitat area as a surrogate of species distribution, using occupancy to weigh the importance of available habitat at each cell is totally reasonable.

In order to examine how the priority areas for the target species, as identified by the PHI index, relate to existing spatial measures in the study area, we estimated the overlap of these areas with the Natura 2000 network, which is the European network of protected areas. Specifically, for each species we calculated the percentage of the sum of the PHI within the Natura 2000 areas over the total sum of the PHI.

## RESULTS

### Habitat mapping

The 3 habitat type classifications (soft bottom, hard bottom, seagrass) did not present any specific large-scale pattern and were patchily distributed along the coastlines of the mainland and the islands (Fig. 2, see also Fig. S7 in Supplement 2). Among the 3 habitat types, soft bottom had the highest coverage (2750 km<sup>2</sup>), followed by seagrass meadows (1590 km<sup>2</sup>) and hard bottom (164 km<sup>2</sup>). Seagrass meadows are widely distributed throughout the Aegean ecoregion; however, they develop extensive continuous coverage mostly in northeast continental or insular locations. The largest single hard-bottom patch was identified in Gaidouronisi (southern part of study area), covering 3.5 km<sup>2</sup> (Fig. 2).

The comparison of remote sensing classified results and the 6 orthophoto maps was indicative of the accuracy of the method. The sand category had very high agreement between the two, i.e. 99.0% (0.50 km<sup>2</sup> with satellite imaging out of 0.51 km<sup>2</sup> by orthophoto maps), the seagrass meadows showed 75.5% agreement (0.58 km<sup>2</sup> out of 0.77 km<sup>2</sup>), while the reef category had 41.4% agreement (0.13 km<sup>2</sup> out of 0.31 km<sup>2</sup>). From the total of 1.59 km<sup>2</sup> of the assessed area, 0.38 km<sup>2</sup> (23.7%) were not classified in the satellite images. Taking into consideration the difference in scale (i.e. 30 m for the satellite images and 0.30 m for the UAVs orthophoto maps), this detection accuracy is considered satisfactory for the seagrass and sandy areas, but less so for the rocky areas. However, satellite images made it possible to produce relatively reliable coverage data at a large spatial scale. The hard-bottom class was affected by the limitation of the spatial resolution of the satellite images. For identifying and classifying an area as hard bottom, at least 900 m<sup>2</sup> (i.e.  $30 \times 30$  m) of almost continuous reef should exist at a relatively constant depth. Consequently, many small and fragmented hard-bottom areas (which are quite common) could not be identified at the resolution used (30 m).

### Occupancy modelling

The 'naïve' occupancy estimate is simply the proportion of sample units in which each target species was detected at least once, and ignores imperfect detectability. In our case, it ranged between 0 and 0.650 (Table 1). Nine of the target species were either not detected at all or detected less than 5 times and

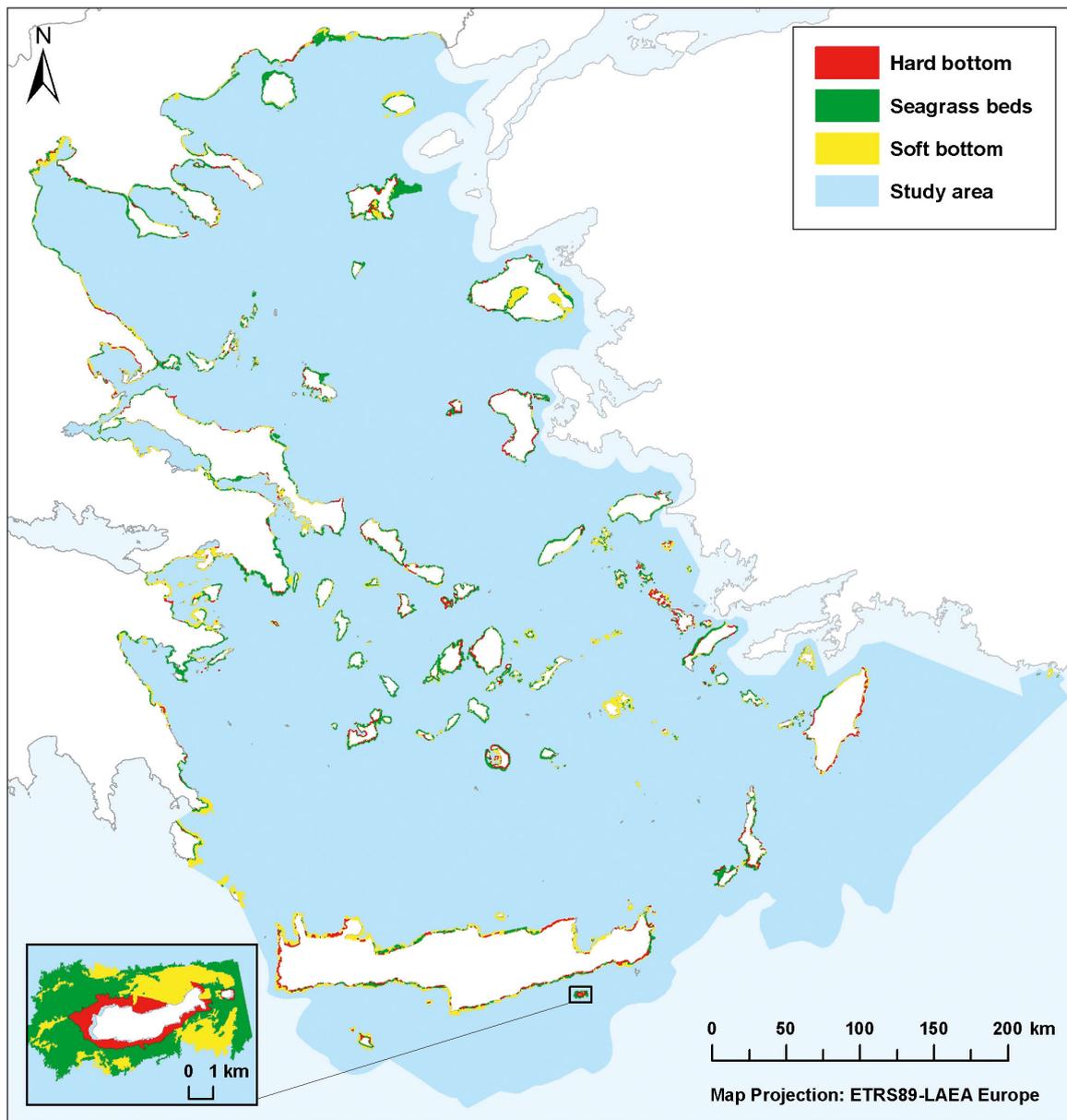


Fig. 2. Habitat mapping based on satellite imaging. Inset map: the island of Gaidouronisi, where the largest continuous patch of hard bottom was identified. The outlines of all polygons were intensified and hard bottom were overlaid on top for visual purposes. Maps at higher scale are provided in Fig. S7 in Supplement 2

thus it was not possible to model their occupancies due to insufficient data. Occupancy modelling was possible for 6 taxa (*Sarcotragus foetidus*, *Aplysina aerophoba*, *Cladocora caespitosa*, *Axinella cannabina*, *Centrostephanus longispinus*, and *Charonia variegata*). *Tethya* spp. occupied a single sampling station, *Ophidiaster ophidianus* was present at 5 stations, while the remaining target species were never observed at any of the sampling stations.

There was no evidence of poor model fit in any case ( $p$ -values of the  $\chi^2$  test  $>0.05$ ). The null models

for occupancy,  $\psi(\cdot) p(\cdot)$  and  $\psi(\cdot) p(\text{obs})$ , assuming constant occupancy (O1), did not have substantial support in any case and were excluded from the 95% confidence sets of models (see Table S1 in Supplement 3). Hence, in all cases one or some of the explanatory variables substantially improved the occupancy predictions in comparison to the constant occupancy hypothesis.

Hypotheses O2 and O4 were not highly supported in any case, although they cannot be excluded from further consideration in the cases of *C. caespitosa*

Table 1. Target species of the present study and their protection status (gray shading). The species are ranked by descending occupancy (naïve estimate based only on the frequencies of detecting the species, i.e. ignoring imperfect detectability)

Phylum	Species	Barcelona Convention Annex II	Habitats Directive Annex IV	Bern Convention Annex II	Naïve estimate of occupancy
Porifera	<i>Sarcotragus foetidus</i> Schmidt, 1862				0.650
Porifera	<i>Aplysina aerophoba</i> (Nardo, 1833)				0.350
Cnidaria	<i>Cladocora caespitosa</i> (Linnaeus, 1767)				0.195
Porifera	<i>Axinella cannabina</i> (Esper, 1794)				0.187
Echinodermata	<i>Centrostephanus longispinus</i> (Philippi, 1845)				0.074
Mollusca	<i>Charonia variegata</i> (Lamarck, 1816)				0.039
Echinodermata	<i>Ophidiaster ophidianus</i> (Lamarck, 1816)				0.019
Porifera	<i>Tethya</i> spp. <sup>a</sup>				0.004
Porifera	<i>Axinella polypoides</i> Schmidt, 1862				0
Mollusca	<i>Luria lurida</i> (Linnaeus, 1758)				0
Mollusca	<i>Erosaria spurca</i> (Linnaeus, 1758)				0
Mollusca	<i>Pholas dactylus</i> Linnaeus, 1758				0
Mollusca	<i>Zonaria pyrum</i> (Gmelin, 1791)				0
Chordata	<i>Hippocampus guttulatus</i> Cuvier, 1829				0
Chordata	<i>Hippocampus hippocampus</i> (Linnaeus, 1758)				0

<sup>a</sup>Including *Tethya aurantium* (Pallas, 1766) and *T. citrina* Sarà & Melone, 1965

[ $w_+(O2) = 28.8\%$ ], *A. aerophoba* [ $w_+(O4) = 17.9\%$ ], *C. longispinus* [ $w_+(O4) = 18.5\%$ ], and *C. variegata* [ $w_+(O4) = 54.2\%$ ,  $w_+(O2) = 25.1\%$ ] (Tables 2 & S1). O3 was substantially supported by the data in the case of *S. foetidus* [ $w_+(O3) = 99.9\%$ ] and relatively less supported in the case of *A. cannabina* [ $w_+(O3) = 65.6\%$ ]. For *S. foetidus*, a significant increase of occupancy with  $T_{min}$  was predicted by all models supporting O3 (see Table S2 in Supplement 3 for the coefficients of the best model), indicating that minimum temperature can be a limiting factor for the distribution of the species. In contrast, occupancy of *A. cannabina* decreased with  $T_{min}$ , indicating a preference for low temperatures (Table S2). Simi-

larly, occupancy of *C. variegata* decreased with temperature ( $T_m$  or  $T_{max}$  depending on the model), indicating avoidance of relatively high temperatures (Table S2).

Hypothesis O5 was supported by the data in the cases of *C. variegata* [ $w_+(O5) = 84.0\%$ ] and *C. caespitosa* [ $w_+(O5) = 81.6\%$ ] and had less support in the case of *A. cannabina* [ $w_+(O5) = 63.3\%$ ] (Tables 2 & S1). Occupancy of *C. variegata* declined with Chl in all models supporting O5, indicating a preference for oligotrophic waters. In contrast, occupancy of *C. caespitosa* and *A. cannabina* significantly increased with Chl, indicating a preference for waters of higher productivity (Table S2).

Table 2. Relative importance of each hypothesis ( $k$ ) estimated by summing the Akaike weights across all the models in the set where each corresponding predictor variable occurs [ $w_+(k)$ ]. Hypotheses codes: (O1) occupancy was constant; (O2) occupancy depended on the annual average sea surface temperature ( $T_m$ ); (O3) occupancy depended on the annual minimum sea surface temperature ( $T_{min}$ ); (O4) occupancy depended on the annual maximum sea surface temperature ( $T_{max}$ ); (O5) occupancy varied with the annual average chl  $a$  concentration (Chl); (O6) occupancy differed among marine sub-areas (MAreas); (O7) occupancy varied with depth; (D1) detectability was constant across sampling stations and observer-independent; (D2) detectability was constant across sampling stations and observer-dependent. Values are provided as percentages; those >70% appear in **bold** and those >95% are shaded

Species	$w_+(O1)$	$w_+(O2)$	$w_+(O3)$	$w_+(O4)$	$w_+(O2, O3, O4)$	$w_+(O5)$	$w_+(O6)$	$w_+(O7)$	$w_+(D1)$	$w_+(D2)$
<i>Sarcotragus foetidus</i>	0.0	0.0	<b>99.9</b>	0.1	<b>100.0</b>	30.0	0.0	<b>89.7</b>	3.5	<b>96.5</b>
<i>Aplysina aerophoba</i>	0.0	3.6	2.6	17.9	24.1	29.7	<b>70.3</b>	28.3	64.8	35.3
<i>Cladocora caespitosa</i>	0.0	28.8	13.9	10.9	53.6	<b>81.6</b>	18.5	29.8	<b>78.1</b>	21.9
<i>Axinella cannabina</i>	0.0	0.1	65.6	0.1	65.8	63.3	34.3	<b>100.0</b>	17.2	<b>82.8</b>
<i>Centrostephanus longispinus</i>	0.0	0.8	4.0	18.5	23.2	18.5	<b>75.4</b>	<b>99.2</b>	4.5	<b>95.5</b>
<i>Charonia variegata</i>	0.1	25.1	7.5	54.2	<b>86.8</b>	<b>84.0</b>	0.1	28.2	<b>70.6</b>	29.3

Hypothesis O6 was substantially supported by the data in the cases of *C. longispinus* [ $w_+(O6) = 75.4\%$ ] and *A. aerophoba* [ $w_+(O6) = 70.3\%$ ], while it cannot be excluded from further consideration for *A. cannabina* [ $w_+(O6) = 34.3\%$ ] and *C. caespitosa* [ $w_+(O6) = 18.5\%$ ] (Tables 2 & S1). In the models supporting O6 for these species, the marine sub-areas with highest occupancies were the Evoikos-Pagositikos Gulfs for *A. aerophoba*, *C. caespitosa*, and *A. cannabina*, and the South Aegean for *C. longispinus*.

Hypothesis O7 regarding depth-related variation in occupancy was substantially supported by the data in the cases of *A. cannabina* [ $w_+(O7) = 100\%$ ], *C. longispinus* [ $w_+(O7) = 99.2\%$ ], and *S. foetidus* [ $w_+(O7) = 89.7\%$ ] (Table 2). O7 had relatively little support (but cannot be excluded from consideration) in the cases of *A. aerophoba* [ $w_+(O7) = 28.3\%$ ], *C. caespitosa* [ $w_+(O7) = 29.8\%$ ], and *C. variegata* [ $w_+(O7) = 28.2\%$ ]. A significant increase of occupancy with depth was predicted by all models supporting O7 for *A. cannabina* and *C. longispinus*, while a significant decrease with depth was predicted for *S. foetidus*.

Regarding detectability, the hypothesis of varying detectabilities among observers (D2) was supported more by the data than the hypothesis of observer-independent detectability (D1) for *S. foetidus* [ $w_+(D2) = 96.5\%$ ], *C. longispinus* [ $w_+(D2) = 95.5\%$ ], and *A. cannabina* [ $w_+(D2) = 82.8\%$ ]. The opposite was true for *C. caespitosa* [ $w_+(D1) = 78.1\%$ ], *C. variegata* [ $w_+(D1) = 70.6\%$ ], and *A. aerophoba* [ $w_+(D1) = 64.8\%$ ].

In terms of an overall average estimate of occupancy for all surveyed sites, *S. foetidus* had the highest occupancy estimate ( $\hat{\Psi} = 0.679$ ), followed by *A. aerophoba* ( $\hat{\Psi} = 0.361$ ), *C. caespitosa* ( $\hat{\Psi} = 0.243$ ), *A. cannabina* ( $\hat{\Psi} = 0.198$ ), *C. longispinus* ( $\hat{\Psi} = 0.119$ ), and *C. variegata* ( $\hat{\Psi} = 0.040$ ). These estimates were higher, as expected, than the naïve estimates (Table 1), which ignored detectability issues. Without accounting for imperfect detectability, occupancy for the 6 target species would have been underestimated by up to 38% (in the case of *C. longispinus*). The detection probabilities were  $>0.5$ , with the exception of the detection probabilities of *C. longispinus* by one of the observers.

### Mapping priority areas for the conservation of target species

Priority areas for the target species, as identified by the PHI, are areas where both the occupancy of the species on suitable habitat (i.e. hard bottom at a spe-

cific depth zone) and the coverage of this suitable habitat are simultaneously high (Figs. 3 & S8–S13 in Supplement 4). The habitat maps produced suggest that extensive rocky reefs are more prominent in the island-dominated South Aegean sub-area compared to the North, where continuous rock has a patchier distribution. For most species, suitable habitats were found to occur along a considerable part of the Aegean coastline, usually with a low PHI value (i.e. low importance). In contrast, areas of medium to high importance varied among species. For *A. aerophoba*, several high PHI cells were indicated in all Aegean sub-areas, but with a notable low probability along most of the Cretan coastline (Fig. S9.9); *A. cannabina* had higher PHI scoring sites in specific areas of the continental Aegean (Fig. S11.1, S11.5) and northern Crete (Fig. S11.8, S11.9). For *C. caespitosa*, the cells with the highest PHI scores were found within Pagasitikos Gulf and the northeastern Aegean (Fig. S10.2, S10.3). In the southern and eastern Aegean, several high PHI cells were observed for *C. variegata* (mainly in insular areas: Fig. S13.4, S13.7, S13.8, S13.9). The most important areas for *C. longispinus* were predicted in the South Aegean sub-area (Fig. S12.5, S12.7, S12.10), and for *S. foetidus*, mainly in Crete (Fig. S8.8, S8.9). Following an overall assessment in the above context, specific areas of the Aegean ecoregion emerge as combining different key elements, thus identifying areas of potentially high conservation interest. Among these areas are (1) Evoikos and Pagasitikos Gulfs, exhibiting a higher possibility of presence for *A. aerophoba*, *A. cannabina*, and *C. caespitosa*; (2) Lemnos Island, characterized by extensive and continuous seagrass meadows and higher probability of presence of *A. aerophoba* and *C. caespitosa*; and (3) the southern insular clusters and Crete, characterized by extensive rocky formations and a higher probability of presence of *C. longispinus*, *C. variegata*, and *S. foetidus*. The percentage of the PHI that is covered by the Natura 2000 network of protected areas ranges between 14.7% (for *S. foetidus* and *C. longispinus*) and 28.5% for *C. caespitosa* (Table 3).

## DISCUSSION

The development of broad-scale, cost-effective tools for the spatio-temporal assessment and monitoring of biodiversity is emerging as an important priority for the rigorous application of ecosystem-based management (Danovaro et al. 2016). This study provides a novel method to assess the spatial distribution of

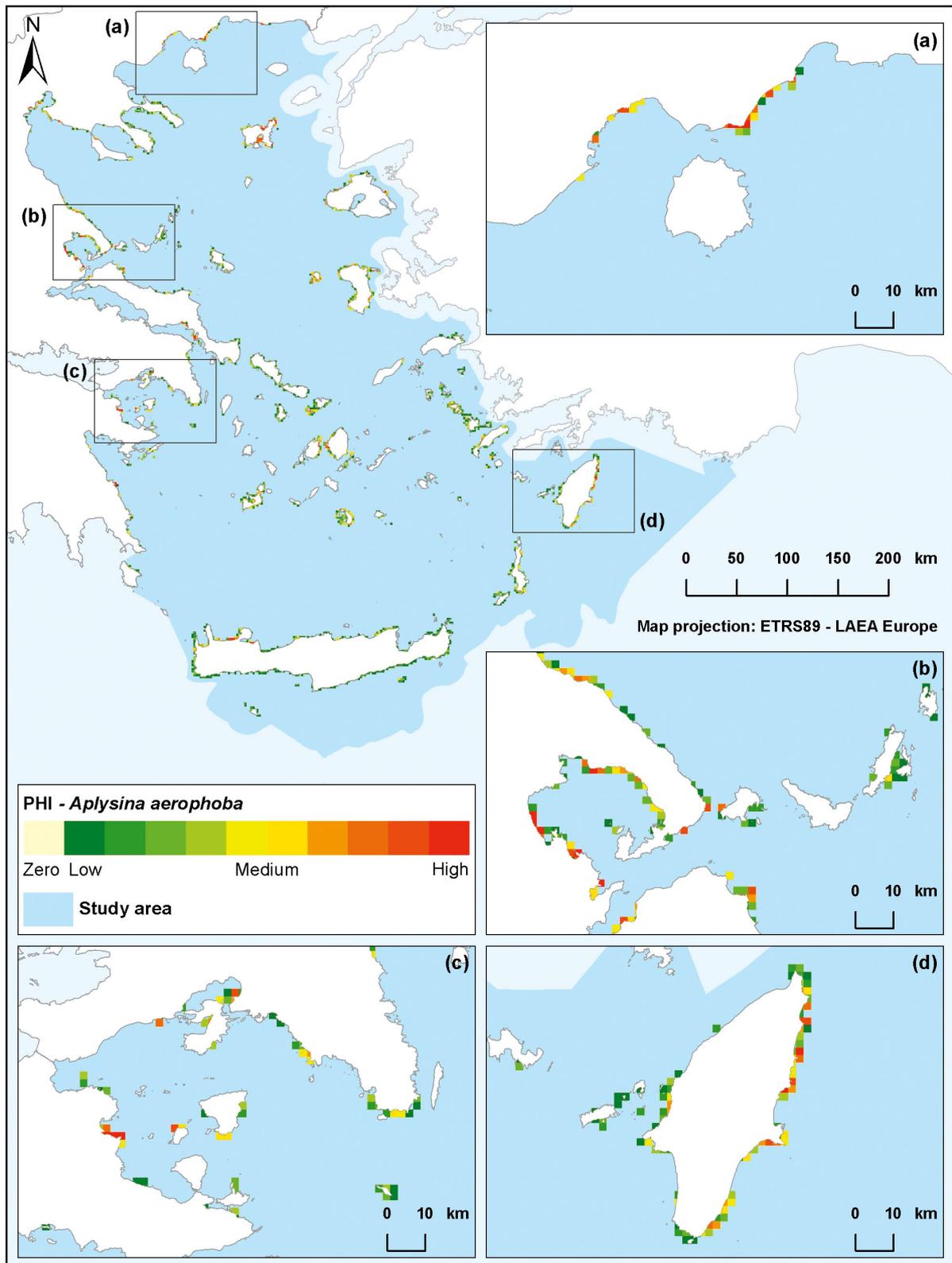


Fig. 3. Identification of priority areas for the conservation of *Aplysina aerophoba* populations, based on the potential habitat index (PHI). Color classification is based on natural breaks. See Figs. S8–S13 in Supplement 4 for maps of all target species at a higher scale

Table 3. Overlap of the priority areas identified in this study for the conservation of target species and the existing Natura 2000 network of protected areas, estimated as the percentage of the sum of the potential habitat index (PHI) within the Natura 2000 areas over the total sum of the PHI

Species	% in Natura areas
<i>Sarcotragus foetidus</i>	14.7
<i>Aplysina aerophoba</i>	18.8
<i>Cladocora caespitosa</i>	28.5
<i>Axinella cannabina</i>	19.2
<i>Centrostephanus longispinus</i>	14.7
<i>Charonia variegata</i>	15.8

marine species over extensive coastal areas. The combined use of habitat mapping through satellite telemetry and species occupancy modelling based on a restricted set of quantitative field data offers a practical and relatively low-cost (see Supplement 5) approach to obtain ecological information whilst overcoming data limitations at large scales. The estimated cost of obtaining and modelling a more informative state variable such as population density would be approximately double, while the necessary strip transect or line transect surveys would demand approximately 3 times more field effort (Tables S3 & S4 in Supplement 5).

Furthermore, strip transect sampling, which is the most commonly applied method of underwater visual surveys, suffers from the often inevitable violation of its main assumption of perfect detection of all individuals and species within the surveyed area (Katsanevakis et al. 2012). Although imperfect detectability is a major source of error (Yoccoz et al. 2001, Williams et al. 2002), many monitoring programs ignore it or deal with it ineffectively. The method developed in the present study properly accounts for imperfect detectability, providing improved accuracy in occupancy estimations by jointly accounting for detectability.

The main objective of the PHI approach for prioritization of sites for conservation actions is to improve the simplistic use of habitats as surrogates of biodiversity. Without any information on species occupancy, conservation targets in the framework of systematic conservation planning would be set on the entire coverage of the associated habitats. With the PHI approach, each unit area of the associated habitat is differentially valued proportionally to the probability of presence, and thus prioritization of sites is substantially improved. Although there are many other approaches based on species distribution modelling, it is argued that the PHI approach is useful

and beneficial due to the low associated cost and effort for data collection and processing and because detectability issues are accounted for.

The example of the Aegean Sea underlines the utility of the proposed method as a tool to provide baseline information in data-poor regions, where logistical constraints related to time and resource availability for data acquisition hinder the urgent need for meaningful management decisions. Considering the extensive coastline of the Aegean Sea, to date, spatial patterns of marine biodiversity remain largely under-explored, and can only be inferred from a scrupulous review of past studies, which vary in space, time, and thematic scope. Most importantly, even though the currently assessed species have been protected for decades, there has been no previous effort to map their distribution and identify priority areas for conservation in order to assist decision makers in acting to protect them. The presented methodological approach enabled the identification of specific sub-areas of prominent conservation interest scattered throughout the Aegean ecoregion, further supporting the current perception that the diverse ecological components of the Aegean Sea result in distinct hot spot areas for different conservation elements (see Voultsiadou et al. 2013).

The estimated overlap of priority areas with the Natura 2000 sites is substantial; however, in a systematic conservation planning context, specific operational targets should be agreed upon in order to secure the conservation of the species. Furthermore, management actions in the protected areas should be based on the specific species to be protected at each site. In the Aegean Sea, management plans are absent from most of the Natura 2000 sites, which should rather be considered as 'paper-parks'. In the future development of management plans, the maps as produced in the present study would prove useful.

The present work was conducted within the framework of the MARISCA project ([www.marisca.eu](http://www.marisca.eu)), which aims to propose a network of MPAs in the Aegean Sea by expanding the existing Natura 2000 network, for the conservation of marine biodiversity. In the framework of MARISCA, the systematic conservation planning tool 'MARXAN with Zones' was applied (Watts et al. 2009), based on the distribution of 10 important marine habitats, 58 protected species, and the distribution of all main human activities and existing management plans (these results will be published elsewhere). Distribution maps of species were created by integrating information from a wide range of sources, such as scientific and grey literature, past research projects, online databases, and

new data collected in dedicated field surveys, as presented here. The distributions of the 6 species of the present study were included in this effort through their standardized PHI, i.e. for each species, the operational conservation targets were applied to the sum of standardized PHI values across all planning units.

In this study we investigated the presence of protected species on rocky substrates at a bathymetric range of 0 to 30 m; this depth zone is under the direct pressure of cumulative human impacts and natural stressors, and thus, the need for management actions is more urgent (Parravicini et al. 2013, Marbà et al. 2015). In all cases, the occupancy modelling results rejected the uniform distribution hypothesis, suggesting that the majority of the modelled species exhibit specific distribution trends in relation to environmental or geographical variables. The latter appear from our modelling to strongly shape the presence of the sponge *Aplysina aerophoba* and the echinoderm *Centrostephanus longispinus*, the 2 species whose distributions exhibit a significant correlation with marine sub-area. This trend (high population density in some areas and absence or rarity in others, irrespective of latitudinal gradient per se) has not been reported before for *C. longispinus*, a cryptobenthic species lacking broad-scale distribution studies in the eastern Mediterranean Sea. This finding highlights that, for some species, certain marine areas could potentially form important spots for their populations, and these should be prioritized in future protection initiatives.

Concerning correlation of species' distribution to environmental variables, the higher probability of presence of the dictyoceratid sponge *Sarcotragus foetidus* at southern (warmer) latitudes is supported by both 'in-the-field' experience and bibliographic data, suggesting that this species is quite prolific in the South Aegean sub-area, while being rarer in the North. Voultsiadou (2005) studied the distribution patterns of sponge diversity across different marine regions of the eastern Mediterranean and found that dictyoceratid sponges, which are mainly distributed in warm waters worldwide, had a greater contribution to the regional sponge fauna of the South Aegean, compared to that of the northern sector. Similarly, the highly supported correlation with chlorophyll (hypothesis O5) for the scleractinian *Cladocora caespitosa* is in accordance with previous studies underlining the species' preference for areas characterized by increased water turbidity and productivity levels such as the Evoikos and Pagasitikos Gulfs (Laborel 1961, Sini et al. 2015). Temperate symbiotic corals, such as *C. caespitosa*, shift from autotrophy in summer to

heterotrophy in winter in response to light limitation of the symbiont's photosynthesis (Tremblay et al. 2012). This physiological trend presumably limits the presence or growth of these scleractinians in the increasingly oligotrophic southeast Aegean (Morri et al. 2000), since the inherently low productivity levels seem insufficient to support *Cladocora* populations in the cold season.

The resulting bathymetric differences of occupancy also reflect the species' known niches. Both *Axinella cannabina* and *C. longispinus*, which had higher occupancy in deeper waters, are typical sciaphilous species commonly occurring in coralligenous habitats and marine caves (Antoniadou et al. 2006, Ballesteros 2006, Gerovasileiou et al. 2015, Sini et al. 2015). On the other hand, *S. foetidus*, whose occupancy appeared to decrease with depth, is a photophilic species, most commonly found in shallow rocky reefs (Pérès 1967). The fact that 3 of the modelled species showed substantial depth-related differences in occupancy underlines the importance of considering distinct depth zones in studies focusing on distribution patterns. Extending the bathymetric range of future surveys would enable a more representative mapping of species with a preference for deeper waters.

The 30 m spatial resolution of satellite images worked well for the mapping of soft substrates and seagrass meadows. The present estimate of seagrass coverage (1590 km<sup>2</sup>) substantially improves previous estimates, which, due to a lack of data from 92% of the Greek coastline, reported only 449 km<sup>2</sup> of *Posidonia oceanica* meadows for both the Aegean and Ionian Greek waters (Telesca et al. 2015). However, the cover of hard substrates was underestimated, since small reefs or discontinuous areas of rock could not be detected. Consequently, a considerable number of existing rocky reefs were left out from the habitat maps, and were unavoidably excluded from the calculation of the PHI. The use of finer spatial resolution images (e.g. Sentinel-2 data of 10 m spatial resolution, which were recently made freely available) could greatly improve the detection capacity of hard substrates with high confidence, and subsequently lead to a better delineation of priority areas for associated species.

Some target species were either not detected or very few individuals were recorded, rendering any distribution modelling impossible. Although this may partly reflect the rarity of the species in the specific ecoregion, it may also be an artefact of the sampling design. Some ecological aspects of the target species, such as temporal or diurnal shifts in distribution, elusive behaviors, and cryptic habits were not thor-

oughly addressed by our general-purpose sampling protocol. For example, night surveys would allow a more dedicated search for the cryptic cowries (*Luria lurida*, *Erosaria spurca*, *Zonaria pyrum*) which are known to be more active during nighttime (Passamonti 2015). Similarly, expanding the survey to other habitat types could make up for the rare occurrences of certain species, such as *Tethya* spp. and *Hippocampus* spp., that thrive in other habitats as well.

The aforementioned issues regarding field survey design are associated with the common difficulties involved when sampling by SCUBA diving (Parravicini et al. 2010). Emerging technologies, such as mixed-gas (technical) diving (Bozanic 2007) or closed-circuit rebreathers (Sieber & Pyle 2010), can greatly expand the observers' operating depth range and bottom time limits, but require advanced training and experience, add complexity to the logistics, and increase the total cost of an expedition. Remotely operated vehicles (ROVs) are currently emerging as viable alternatives for underwater marine life surveys (e.g. Cánovas Molina et al. 2016, Zapata-Ramírez et al. 2013), especially as the platforms are getting increasingly compact and affordable. Yet again, the extent to which these technologies can actually replace direct visual census techniques is debatable, as there are trade-offs with regards to the maneuverability of the vehicles and the image resolution they can ultimately provide (Zapata-Ramírez et al. 2013).

Despite its limitations, the proposed approach provides a framework and a baseline in the Aegean Sea that can be ameliorated with future improved information. As the available resolution of satellite imaging improves, and additional survey data on the occurrences of species become available, they could be incorporated into new iterations of the analysis. The proposed approach for the estimation of the PHI can be applied to any other shallow-water benthic species in any marine region, provided that its main habitat can be mapped through satellite imaging, or habitat maps are available through other means.

It is commonly argued that policy makers should put off making important decisions in data-poor situations suffering from high uncertainty. But such a 'wait-until-information-greatly-improves' approach is unproductive, as it will prevent assessments and conservation actions from ever happening (Halpern & Fujita 2013, Katsanevakis et al. 2016). There will always be data gaps, especially in large-scale assessments. All decisions about complex natural resource management problems, such as decisions on designing networks of MPAs and on implementing management actions for the protection of vulnerable pop-

ulations, will suffer from some degree of uncertainty. Suspending any action in a pursuit of minimal uncertainty will lead to decision paralysis, and can cause the decline of many vulnerable populations threatened by cumulative impacts (Kellon & Arvai 2011).

A way out of the trap of decision paralysis is the adoption of an adaptive management approach (Kellon & Arvai 2011), in which decisions can be modified on the basis of new knowledge about the system and assessments of the effectiveness of previous management actions (Ludwig et al. 1993, Parma 1998). Irrespective of whether a change results from new data, technological improvements, 'in-the-field' experience, or as a result of external circumstances, ecosystem-based management practices must be periodically reviewed and updated where appropriate (Katsanevakis et al. 2011b). Nevertheless, large-scale targeted surveys and direct mapping of biodiversity are irreplaceable and highly necessary, especially in data-poor regions. Moreover, in an era of evidenced shifts in coastal ecosystems (e.g. Thibaut et al. 2015, Rilov 2016), there is an apparent need for regular updates of primary data series concerning biodiversity and assemblage composition. Funding for such surveys should increase to provide high-quality data, which are vital to improve our knowledge base and therefore the effectiveness of management decisions. Given that funds are currently often restricted, the methodology and field protocol presented here offer an alternative, cost-effective, and practical solution to mapping priority areas for species conservation. This can be valuable when management decisions based on recent data—even if incomplete—are urgently required.

*Acknowledgements.* The present study was conducted in the framework of the MARISCA project ([www.marisca.eu](http://www.marisca.eu)), co-funded (85%) by EEA GRANTS, 2009-2014, and the Public Investments Program (PIP) of the Hellenic Republic (15%). Special thanks to the following diving centers and tour operators for providing important information and technical support during fieldwork: Mystic Blue Eco-sailing & Diving, Thalassa Diving School, Lichadonisia Diving Center, Aquacore Diving Center, Azure Diving Center, Athos Scuba Diving Center, North Aegean Diving Center, Tortuga Diving Center Chios, Black Rock Lesvos Center, Notos Mare, Chania Diving, Creta's Happy Divers, and European Diving Institute. Copernicus Marine Service Products were used in this study.

#### LITERATURE CITED

- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaaki F (eds) Proc 2nd Int Symp Inf Theory, Akademiai Kiado, Budapest, p 267–281

- Akaike H (1983) Information measures and model selection. *Bull Int Stat Inst* 44:277–290
- Antoniadou C, Voultziadou E, Chintiroglou C (2006) Sublittoral megabenthos along cliffs of different profile (Aegean Sea, Eastern Mediterranean). *Belg J Zool* 136: 69–79
- ✦ Arvanitidis C, Bellan G, Drakopoulos P, Valavanis V, Dounas C, Koukouras A, Eleftheriou A (2002) Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes. *Mar Ecol Prog Ser* 244:139–152
- Ballesteros E (2006) Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanogr Mar Biol Annu Rev* 44:123–195
- Bozanic JE (2007) An evolution of scientific mixed gas diving procedures at the National Park Service Submerged Resources Center. In: Pollock NW, Godfrey JM (eds) *Diving for Science. Proc 26<sup>th</sup> Symp Am Acad Underwat Sci. Dauphin Island, AL*, p 143–154
- Burnham KP, Anderson DR (2002) *Model selection and multimodal inference*, 2nd edn. Springer-Verlag, New York, NY
- ✦ Cánovas Molina A, Montefalcone M, Bavestrello G, Cau A and others (2016) A new ecological index for the status of mesophotic megabenthic assemblages in the Mediterranean based on ROV photography and video footage. *Cont Shelf Res* 121:13–20
- ✦ Dalleau M, Andréfouët S, Wabnitz CCC, Payri C and others (2010) Use of habitats as surrogates of biodiversity for efficient coral reef conservation planning in Pacific Ocean Islands. *Conserv Biol* 24:541–552
- Danovaro R, Carugati L, Berzano M, Cahill AE and others (2016) Implementing and innovating marine monitoring approaches for assessing marine environmental status. *Front Mar Sci* 3:213
- ✦ Gerovasileiou V, Voultziadou E (2012) Marine caves of the Mediterranean Sea: a sponge biodiversity reservoir within a biodiversity hotspot. *PLOS ONE* 7:e39873
- ✦ Gerovasileiou V, Chintiroglou C, Vafidis D, Koutsoubas D and others (2015) Census of biodiversity in marine caves of the eastern Mediterranean Sea. *Mediterr Mar Sci* 16: 245–265
- Gotsis-Skretas O, Ignatiades L (2005) Phytoplankton in pelagic and coastal waters. In: Papathanassiou E, Zenetos A (eds) *State of the Hellenic marine environment*. Hellenic Centre for Marine Research, Athens, p 187–193
- ✦ Halpern BS, Fujita R (2013) Assumptions, challenges, and future directions in cumulative impact analysis. *Ecosphere* 4:art131
- ✦ Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952
- Hines JE (2006) PRESENCE2—software to estimate patch occupancy and related parameters. [www.mbr-pwrc.usgs.gov/software/presence.html](http://www.mbr-pwrc.usgs.gov/software/presence.html) (accessed Jul 2016)
- ✦ Hossain MS, Bujang JS, Zakaria MH, Hashim M (2015) The application of remote sensing to seagrass ecosystems: an overview and future research prospects. *Int J Remote Sens* 36:61–114
- ✦ Issaris Y, Katsanevakis S, Salomidi M, Tsiamis K, Katsiaras N, Verriopoulos G (2012) Occupancy estimation of marine demersal species: dealing with imperfect detectability. *Mar Ecol Prog Ser* 453:95–106
- ✦ Jackson S, Lundquist CJ (2016) Limitations of biophysical habitats as biodiversity surrogates in the Hauraki Gulf Marine Park. *Pac Conserv Biol* 22:159–172
- ✦ Katsanevakis S (2006) Modelling fish growth: model selection, multi-model inference and model selection uncertainty. *Fish Res* 81:229–235
- ✦ Katsanevakis S, Maravelias CD, Damalas D, Karageorgis AP, Anagnostou C, Tsitsika EV, Papaconstantinou C (2009) Spatiotemporal distribution and habitat use of commercial demersal species in the eastern Mediterranean Sea. *Fish Oceanogr* 18:439–457
- ✦ Katsanevakis S, Maravelias CD, Vassilopoulou C (2010a) Otter trawls in Greece: landing profiles and potential métiers. *Mediterr Mar Sci* 11:43–59
- ✦ Katsanevakis S, Maravelias CD, Kell LT (2010b) Landings profiles and potential métiers in Greek set longliners. *ICES J Mar Sci* 67:646–656
- ✦ Katsanevakis S, Zenetos A, Mačić V, Beqiraj S, Poursanidis D, Kashta L (2011a) Invading the Adriatic: spatial patterns of marine alien species across the Ionian–Adriatic boundary. *Aquat Biol* 13:107–118
- ✦ Katsanevakis S, Stelzenmüller V, South A, Sørensen TK and others (2011b) Ecosystem-based marine spatial management: review of concepts, policies, tools, and critical issues. *Ocean Coast Manage* 54:807–820
- ✦ Katsanevakis S, Weber A, Pipitone C, Leopold M and others (2012) Monitoring marine populations and communities: review of methods and tools dealing with imperfect detectability. *Aquat Biol* 16:31–52
- ✦ Katsanevakis S, Tempera F, Teixeira H (2016) Mapping the impact of alien species on marine ecosystems: the Mediterranean Sea case study. *Divers Distrib* 22:694–707
- ✦ Kellon D, Arvai J (2011) Five propositions for improving decision making about the environment in developing communities: insights from the decision sciences. *J Environ Manage* 92:363–371
- Laborel J (1961) Sur un cas particulier de concrétionnement animal. Concrétionnement à *Cladocora caespitosa* L. dans le Golfe de Talante. *Rapp PV Reun CIESM* 16:429–432
- ✦ Lourie SA, Vincent ACJ (2004) Using biogeography to help set priorities in marine conservation. *Conserv Biol* 18: 1004–1020
- ✦ Ludwig D, Hilborn R, Walters CJ (1993) Uncertainty, resource exploitation and conservation: lessons from history. *Science* 260:17–36
- ✦ Lyons MB, Phinn SR, Roelfsema CM (2012) Long term land cover and seagrass mapping using Landsat and object-based image analysis from 1972 to 2010 in the coastal environment of South East Queensland, Australia. *ISPRS J Photogramm Remote Sens* 71:34–46
- ✦ MacKenzie DI, Bailey LL (2004) Assessing the fit of site occupancy models. *J Agric Biol Environ Stat* 9:300–318
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) *Occupancy estimation and modeling*. Academic Press, San Diego, CA
- ✦ Manley PN, Zielinski WJ, Schlesinger MD, Mori SR (2004) Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecol Appl* 14:296–310
- Marbà N, Jordà G, Agustí S, Girard C, Duarte CM (2015) Footprints of climate change on Mediterranean Sea biota. *Front Mar Sci* 2:56
- ✦ Matthew MW, Adler-Golden SM, Berk A, Felde G and others (2002) Atmospheric correction of spectral imagery: evaluation of the FLAASH algorithm with AVIRIS data. In: *Proceedings of the IEEE Applied Imagery Pattern Recognition Workshop, Washington, DC, 16–18 October 2002*, p 157–163

- ✦ McArthur MA, Brooke BP, Przeslawski R, Rayan DA and others (2010) On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuar Coast Shelf Sci* 88: 21–32
- ✦ Moilanen A (2002) Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos* 96:516–530
- Moilanen A, Wilson KA, Possingham HP (2009) *Spatial conservation prioritization: quantitative methods computational tools*. Oxford University Press, Oxford
- ✦ Morri C, Vafidis D, Peirano A, Chintiroglou CC, Bianchi CN (2000) Anthozoa from a subtidal hydrothermal area of Milos Island (Aegean Sea), with notes on the construction potential of the scleractinian coral *Madracis pharensis*. *Ital J Zool* 67:319–325
- ✦ Parma AM (1998) What can adaptive management do for our fish, forests, food, and biodiversity? *Integr Biol* 1: 16–26
- ✦ Parravicini V, Micheli F, Montefalcone M, Villa E, Morri C, Bianchi CN (2010) Rapid assessment of epibenthic communities: a comparison between two visual sampling techniques. *J Exp Mar Biol Ecol* 395:21–29
- ✦ Parravicini V, Micheli F, Montefalcone M, Morri C and others (2013) Conserving biodiversity in a human-dominated world: degradation of marine sessile communities within a protected area with conflicting human uses. *PLOS ONE* 8:e75767
- Passamonti M (2015) The family Cypraeidae (Gastropoda Cypraeoidea) an unexpected case of neglected animals. *Biodivers J* 6:449–466
- Péres JM (1967) Mediterranean benthos. *Oceanogr Mar Biol Annu Rev* 5:449–533
- ✦ Pierson JC, Barton P, Lane P, Lindenmayer DB (2015) Can habitat surrogates predict the response of target species to landscape change? *Biol Conserv* 184:1–10
- ✦ Pollock KH, Nichols JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105–119
- ✦ Rilov G (2016) Multi-species collapses at the warm edge of a warming sea. *Sci Rep* 6:36897
- Sakellariou D, Alexandri M (2007) Geomorphology of the Hellenic sea-floor. In: Papathanassiou E, Zenetos A, Vassilopoulou V, Tserpes G (eds) *State of the Hellenic fisheries*. Hellenic Centre for Marine Research, Athens, p 17–23
- Sakellariou D, Lykousis V, Karageorgis A, Anagnostou CH (2005) Geomorphology and tectonic structure. In: Papathanassiou E, Zenetos A (eds) *State of the Hellenic marine environment*. Hellenic Centre for Marine Research, Athens, p 16–20
- Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (2002) *Predicting species occurrences*. Island Press, Washington, DC
- ✦ Sieber A, Pyle R (2010) A review of the use of closed-circuit rebreathers for scientific diving. *Underwat Technol* 29: 73–78
- Sini M, Garrabou J, Koutsoubas D (2015) Diversity and structure of coralligenous assemblages dominated by *Eunicella cavolini* (Koch, 1887) in the Aegean Sea. In: Bouafif C, Langar H, Ouerghi A (eds) *Proc 2<sup>nd</sup> Mediterr Symp Conserv Coralligenous Calcareous Bio-Concretions*. RAC/SPA, Tunis, p 171–176
- ✦ Telesca L, Belluscio A, Criscoli A, Ardizzone G and others (2015) Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Sci Rep* 5:12505
- ✦ Thibaut T, Blanfuné A, Boudouresque CF, Verlaque M (2015) Decline and local extinction of Fucales in the French Riviera: The harbinger of future extinctions? *Mediterr Mar Sci* 16:206–224
- Thompson WL (ed) (2004) *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*. Island Press, Washington, DC
- ✦ Torres-Pulliza D, Wilson JR, Darmawan A, Campbell SJ, Andréfouët S (2013) Ecoregional scale seagrass mapping: a tool to support resilient MPA network design in the Coral Triangle. *Ocean Coast Manage* 80:55–64
- ✦ Tremblay P, Ferrier-Pagès C, Maguer JF, Rottier C, Legendre L, Grover R (2012) Controlling effects of irradiance and heterotrophy on carbon translocation in the temperate coral *Cladocora caespitosa*. *PLOS ONE* 7: e44672
- ✦ Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob Ecol Biogeogr* 21:272–281
- ✦ Velaoras D, Kassis D, Perivoliotis L, Pagonis P, Hondronasios A, Nittis K (2013) Temperature and salinity variability in the Greek Seas based on POSEIDON stations time series: preliminary results. *Mediterr Mar Sci* 14(3):5–18
- ✦ Voultziadou E (2005) Demosponge distribution in the eastern Mediterranean: a NW–SE gradient. *Helgol Mar Res* 59:237–251
- Voultziadou E, Gerovasileiou V, Dailianis T (2013) Extinction trends of marine species and populations in the Aegean and adjacent ecoregions. In: Briand F (ed) *Marine extinctions: patterns and processes*. 2013 CIESM Workshop Monograph No. 45. CIESM Publisher, Monaco, p 59–74
- ✦ Ward TJ, Vanderklift MA, Nicholls AO, Kenchington RA (1999) Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecol Appl* 9:691–698
- ✦ Watts ME, Ball IR, Stewart RS, Klein CJ and others (2009) Marxan with Zones: software for optimal conservation based land- and sea-use zoning. *Environ Model Softw* 24:1513–1521
- ✦ Weber D, Hinterman U, Zangger A (2004) Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. *Glob Ecol Biogeogr* 13:97–104
- Williams BK, Nichols JD, Conroy MJ (2002) *Analysis and management of animal populations*. Academic Press, San Diego, CA
- ✦ Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends Ecol Evol* 16:446–453
- ✦ Zapata-Ramírez PA, Scaradozzi D, Sorbi L, Palma M, Pantaleo U, Ponti M, Cerrano C (2013) Innovative study methods for the Mediterranean coralligenous habitats. *Adv Oceanol Limnol* 4:102–119
- Zervakis V, Theocharis A, Georgopoulos D (2005) Circulation and hydrography of the open seas. In: Papathanassiou E, Zenetos A (eds) *State of the Hellenic marine environment*. Hellenic Centre for Marine Research, Athens, p 104–111