ICES Journal of
Marine Science

ICES Journal of Marine Science (2018), 75(5), 1722–1732. 75(5), 1722–1732. doi:10.1093/icesjms/fsy010

Original Article

Sea pens in the Mediterranean Sea: habitat suitability and opportunities for ecosystem recovery

Azzurra Bastari[1,*], Daniela Pica[1], Francesco Ferretti[2], Fiorenza Micheli[2], and Carlo Cerrano[1]

[1]*Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, via Brecce Bianche, Ancona, 60131, Italy*
[2]*Biology Department and Woods Institute for the Environment, Hopkins Marine Station, Stanford University, 120 Ocean View Blvd, Pacific Grove, CA 93950, USA*

**Corresponding author: tel: 0712204649; e-mail: azzubast@univpm.it*

Bastari, A., Pica, D., Ferretti, F., Micheli, F., and Cerrano, C. Sea pens in the Mediterranean Sea: habitat suitability and opportunities for ecosystem recovery. – ICES Journal of Marine Science, 75: 1722–1732.

Received 10 July 2017; revised 8 January 2018; accepted 18 January 2018; advance access publication 23 February 2018.

The aim of this study is to synthesize available information on sea pens in the Mediterranean Sea and fill existing knowledge gaps through modelling of suitable habitat, with the overarching goal of informing strategies for protecting sea pen habitats from trawling impacts and facilitating their recovery. A review spanning the last 30 years was conducted to map the distribution of Mediterranean sea pen species. In the Adriatic Sea, presence–absence data were modelled with generalized additive models (GAMs) to identify potentially suitable habitats for *Funiculina quadrangularis*, *Virgularia mirabilis*, and *Pennatula* spp. Results show that sea pen distribution in the Mediterranean is mainly limited to continental northern shelves. Six species have been recorded throughout the Adriatic basin, where habitat suitability models confirm that its soft bottoms yield favourable conditions for sea pen assemblages. This information can help guide strategies for diminishing and reversing the impacts of bottom trawling on these vulnerable habitats.

Keywords: Adriatic Sea, conservation, Pennatulacea, species distribution models, trawling, vulnerable marine ecosystems

Introduction

Habitat-forming marine species, including seagrasses, maerl, sponges, corals, bivalves, and polychaetes support high local diversity by ameliorating physical conditions and providing refuge and food for a suite of associated species (Bertness and Callaway, 1994; Jones *et al.*, 1994, 1997; Cerrano *et al.*, 2006). These "foundation" species (Dayton, 1972) or "ecosystem engineers" (Jones *et al.*, 1994) are particularly important in soft sediment marine habitats, where they form tridimensional structures and patchiness in an otherwise homogeneous habitat. While much work has focused on a subset of important habitat formers, particularly corals and seagrasses, other organisms such as sea pens are relatively understudied and basic information on their distribution and ecology is largely lacking. Filling this gap is crucial for increasing our understanding of marine ecosystem functioning and services provision, as well as to conserve or restore them in the face of human exploitation and impacts.

Pennatulacea (Cnidaria, Octocorallia), known as sea pens, is a subclass of anthozoans adapted to live in soft bottoms, mainly muddy or sandy. Sea pens are gonochoric, with a 1: 1 sex ratio and broadcast gametes spawning was reported in *Ptilosarcus gurneyi* (Chia and Crawford, 1973), *Virgularia juncea* (Soong, 2005), *P. phosphorea* (Edwards and Moore, 2008), and *Funiculina quadrangularis* (Edwards and Moore, 2009). Larvae are not well described but are supposed to be lecithotrophic (Eckelbarger *et al.*, 1998; Soong, 2005; Edwards and Moore, 2008, 2009). Longevity and growth rates are not known for the Mediterranean sea pen species. Sea pens play a fundamental ecological role adding structural complexity to an otherwise homogeneous habitat, thereby increasing biodiversity (Tissot *et al.*, 2006; Porporato *et al.*, 2012; De Clippele *et al.*, 2015). They can act as substrate and refuge for eggs, larvae and juvenile fishes (Baillon *et al.*, 2012), and invertebrates (Krieger, 1993). They also alter water current flow, thereby retaining nutrients and entraining plankton near the sediment (Tissot *et al.*, 2006). They increase food delivery and decrease predation rates for closely associated species, such as rockfish (Pacific Ocean perch, *Sebastes alutus*) (Brodeur, 2001) and redfish (*Sebastes* spp.) (Baillon *et al.*, 2012), living in sea pen meadows with dense aggregation, particularly in these species' early life stages.

The important ecological role and the vulnerability of pennatulaceans to human activities have led to the classification of sea pen' forests as essential fish habitats (EFHs) and vulnerable marine ecosystems (VMEs) by the European Commission (Ardizzone, 2006; Greathead *et al.*, 2007; Rogers and Gianni, 2010). The conservation of key species such as sea pens is fundamental for an ecological point of view, but also offers management opportunities. In fact, sea pen and burrowing megafauna communities have been classified as "threatened and/or declining habitat" (OSPAR, 2004). The presence of sea pens and deep-sea corals supported the closure of marine areas for the protection of those fragile species (Cogswell *et al.*, 2011). The Resolutions 61/105 and 64/72 of Oceans and the Law of the Sea in the General Assembly of the United Nations stated the urgent need to identify and map VMEs in order to implement networks of marine-protected areas (MPAs). The Resolution A/RES/70/75 reaffirmed the urgent need to protect VMEs and address the impact of bottom fishing on them in order to effectively ensure the long-term conservation and sustainable use of marine resources.

The Adriatic Sea is one of the most exploited regions in the Mediterranean basin (Coll *et al.*, 2009; Lotze *et al.*, 2011; Micheli *et al.*, 2013a). Six of the 12 Mediterranean sea pen species, *Funiculina quadrangularis* (Pallas, 1766), *Pennatula phosphorea* Linnæus, 1758, *Pennatula rubra* (Ellis, 1761), *Pteroeides spinosum* (Ellis, 1764), *Veretillum cynomorium* (Pallas, 1766), and *Virgularia mirabilis* (Müller, 1776), have been recorded in the Adriatic Sea.

The presence of sea pen species in the Adriatic Sea has been well documented in the past (Linnæus, 1758; Richiardi, 1869; Paolucci, 1923; Pax and Müller, 1962; Kružić, 2007; Sánchez *et al.*, 2007). However, information about the current distribution, ecology, and abundance of Adriatic sea pens are very limited and scattered. Only recent scientific surveys started to take into account the presence of *F. quadrangualris* as an indicator of the quality of sandy-muddy habitats (Martinelli *et al.*, 2013). Due to the negative impact of bottom trawling on sea pens, it has been noted that pennatulids and their related habitat have declined in the Adriatic Sea (IUCN, 2014), following the same negative trend described for other regions of the world where trawling occurs.

Demersal fishing activities represent the greatest threat to the survival of sea pen colonies and may have had a significant influence on their reduction (Kinnear *et al.*, 1996; Troffe *et al.*, 2005; Cogswell *et al.*, 2011). *Funiculina quadrangularis*, *P. phosphorea*, *P. rubra*, and *P. spinosum* have been classified as vulnerable species in the Mediterranean basin (IUCN, 2016). Decline of *F. quadrangularis* and its associated community in areas with intense trawling has been reported in different areas of the Mediterranean Sea (Tunesi and Diviacco, 1997; Ardizzone, 2006; Rogers and Gianni, 2010). Moreover, species such as *F. quadrangularis* share the same habitat of commercially valuable species, in particular with the Norway lobster, *Nephrops norvegicus* (Linnæus, 1758), and the rose shrimp, *Parapenaeus longirostris* (Lucas, 1847) (Nouar and Maurin, 2001; Greathead *et al.*, 2007). Even if a direct and clear relationship between these crustaceans and sea pens has never been scientifically confirmed, cod, shrimp, and Norway lobster fisheries commonly have sea pens in their bycatch (Edinger *et al.*, 2007; Doyle *et al.*, 2015), suggesting habitat association between these species and sea pens.

The dramatic fish stock depletion documented for the Mediterranean Sea, and the Adriatic Sea in particular (Grbec *et al.*, 2002; Coll *et al.*, 2010) is highlighting the need to implement new strategies for sustainable exploitation of resources. Restoring the habitats and species on which key resources depend should provide efficient recovery of the whole marine environment. These efforts, however, are limited by a lack of robust baselines for conservation and restoration. Habitat suitability models have been used to predict the potential distribution of VMEs (mainly cold-water corals) and inform the design of protected areas for VMEs (Tittensor *et al.*, 2009; Davies and Guinotte, 2011; Tracey *et al.*, 2011; Yesson *et al.*, 2012; Knudby *et al.*, 2013). Studies of the distribution and habitat preferences of sea pens are scarce, globally (Greathead *et al.*, 2007, 2014; Krigsman *et al.*, 2012) and almost absent in the Mediterranean Sea (Lauria *et al.*, 2017). To fill this gap, we provide a synthesis of spatial knowledge of sea pens living in the Mediterranean Sea. Moreover, we report the first application of habitat suitability models for sea pens in the northern–central Adriatic Sea, where we have been able to collect a high number of sea pen records. Habitat mapping of Adriatic soft-bottom communities and of VMEs may contribute to the identification of priority areas in need of conservation, and support the development of an ecosystem base management (EBM) approach to support the recovery of the overexploited resources of the Adriatic Sea.

Material and methods

Mediterranean sea pen distribution

In order to describe the bathymetric and geographic distribution of Mediterranean sea pens, we performed a detailed review of published information spanning the last 30 years, from 1980 to 2017. Records of occurrence, together with the geographic location and bathymetric range were compiled for 12 species (see Supplementary Table S1). Coordinates were obtained and plotted using the open source software QGISS 2.4.0 (http://www.qgis.org/it/site/) to map the known distribution of Mediterranean sea pen species. A taxonomic identification at the species level was not possible for some records, in particular for data of publications describing deep benthic assemblages surveyed by ROV video (see Supplementary Table S1). In these cases, we plotted the distribution at the genus level.

Adriatic sea pen distribution and habitat suitability models

The Adriatic Sea is a semi-enclosed basin approximately 800 km long and 200 km wide located between Italy and the Balkan Peninsula, with a wide continental platform. Mean depths range from 35 m in the northern basin, to 130–150 m in the central portion. The depth rapidly increase in the southern region reaching a maximum of about 1200 m (van Straaten, 1970; Trincardi *et al.*, 1996). The Adriatic collects many freshwater inputs from the land, which creates one of the most productive basins of the Mediterranean Sea, with high levels of species richness and endemism (Lotze *et al.*, 2011). This triggers a complex system of anthropic pressures (Coll *et al.*, 2007, 2009; Lotze *et al.*, 2011; Micheli *et al.*, 2013a), of which fishing is one. Several authors have highlighted the urgent need to implement conservation actions in the Adriatic Sea (Micheli *et al.*, 2013b; UNEP/MAP-

RAC/SPA, 2015; Bastari *et al.*, 2016). One key method that could achieve effective management of Adriatic marine resources would be to map VMEs.

Sea pens dataset

We collected data on the distribution of sea pens in the Adriatic Sea from different sources: (1) a literature review for published occurrence records; (2) data from onboard observations of commercial fishing operations, and (3) presence/absence data extracted from published maps (Bastari *et al.*, 2013) of the distribution of sea pens collected during the SoleMon standardized scientific *rapido*-trawl survey (see Supplementary Materials for details on data extraction methods).

(1) The literature record was targeted to describe which species of sea pens live in the Adriatic Sea and where. The data comprised literature records from 1980 to 2016 (see Supplementary Table S1).

(2) Occasional catches recorded by the onboard observers of the Ancona semi-pelagic pair trawl fishery (personal observations). These data were collected in 2011, onboard of mid-water trawlers vessels, which mainly operate in the area offshore the Marche region.

(3) The scientific *rapido*-trawl surveys were carried out in the northern and central Adriatic Sea spanning the period 2007–2015, in the fall season (Bastari *et al.*, 2013; Salvalaggio *et al.*, 2016; Brunetti, unpublished). For each haul, all the collected specimens were classified to the lowest possible taxonomical level. Details on the gear used and sampling scheme of the trawl surveys are in Grati *et al.* (2013).

Data from all the three datasets (literature review, the opportunistic sampling on commercial vessels, and presence observation of sea pen species from the trawl surveys), were used to map the distribution of Adriatic sea pens and to visualize their geographic distribution. The *rapido*-trawl survey data were also used to create habitat suitability models through the use of generalized additive models (GAMs) (see below for a detailed explanation of data analysis and model construction). The rebuilt presence/absence dataset used in these analyses consists of 437 hauls in a depth range from 5 to 223 m. We extracted the latitude and longitude of the hauls indicating the sea pens' presence/absence from the maps in Bastari *et al.* (2013). We then merged the presence-absence dataset with an independently assembled environmental dataset (see below) to enrich the survey observation with environmental covariates useful to explain the presence-absence data.

Environmental dataset used for predictive models

The environmental variables used to identify suitable habitats for Adriatic sea pens were depth, salinity, temperature, and sediment composition in terms of the fraction of sand, mud, and gravel. Sediment compositions were extracted from the ADR_ONE database (http://instaar.colorado.edu/~jenkinsc/dbseabed/coverage/adriaticsea/adriatico.htm). Un-sampled locations were estimated by interpolation with a method described in Ferretti *et al.* (2013). The final grid resolution of the sediment dataset was of 0.02 degrees. The bathymetric data for the Adriatic Sea were downloaded from the European Marine Observation and Data Network (EMODnet) portal (http://www.emodnet.eu/). This bathymetric layer had a grid resolution of 0.016 by 0.016 degrees (approximately 4 km^2 grid size). Temperature and salinity data were obtained by the SeaDataNet portal (http://gher-diva.phys.ulg.ac.be/web-vis/clim.html) and had a resolution of 0.125 by 0.125 degrees (around 200 km^2 grid size). Monthly mean bottom values of temperature and salinity, corresponding to the month of the trawl surveys (obtained from Brunetti, unpublished), were extracted from the data portal. We used these environmental data to characterize depth, salinity, temperature, and sediment composition of the sampling stations of the surveys used for the analyses, by matching the station coordinates with the correspondent pixels of the above environmental rasters.

Data analysis

We fitted separate models for *F. quadrangularis* and *V. mirabilis*. For *P. phosphorea* and *P. rubra*, which can be difficult to identify by non-specialists, we ran a single model at the genus level (*Pennatula* spp.) including records of both Adriatic species.

The probability of detecting sea pens was modelled by fitting GAMs with binomial distribution and logit link function with the mgcv R package. The response variable was presence/absence of sea pen species, while the explanatory variables were latitude, longitude, depth, the log ratio between mud-sand and gravel-sand contents ($R_m = \log(\text{mud/sand})$, and $R_g = \log(\text{gravel/sand})$), temperature, and salinity. These variables were selected because deemed important to explain the variability of sea pens abundance (Greathead *et al.*, 2014; Lauria *et al.*, 2017). All variables were tested for collinearity using the variance inflation factor (VIF) (Zuur *et al.*, 2010). Only latitude and longitude revealed strong collinearity (VIF > 2; Supplementary Figure S1). To represent both terms in the model, we ran a linear regression of the terms against each other and we used longitude and the residuals of the linear regression in lieu of latitude to exploit the explanatory potential of the uncorrelated portion of this variable (Graham, 2003). In order to select the best subset of variables describing the habitat of the focal species, we used an information-theoretic approach by using the MuMIn package in R (Barton, 2015). From a saturated model having all variables listed above

$$Y_i = \alpha + f_1(X_i) + f_2(Z_i) + \ldots + f_n(W_i) + \varepsilon_i, \text{ where } \varepsilon_i N(0, \sigma_2)$$

where $f_1(X_i)$, $f_2(Z_i)$ and $f_n(W_i)$ are smoothing functions of the explanatory variables X_i, Z_i, W_i (i.e. depth, salinity, temperature, etc.) respectively, we fitted exhaustively all combination of terms, considering only the main effects and no interactions.

Models were ranked on the basis of their relative Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). Hence, we selected a 95% confidence set of equally plausible models describing the data and from these, we calculated an average model. In particular, we extracted a list of fitted models, which the cumulative sum of the model weights were <=.95 (Burnham and Anderson, 2002) and then we averaged these models based on the AIC.

Species distribution data often display spatial autocorrelation, indicating that variables recorded in nearby locations are more similar than those recorded further apart. This aspect violates the GAMs assumption that residuals are independent and identically distributed. Although we included the samples' spatial coordinates to address this aspect, we further checked for spatial autocorrelation by plotting the residuals of the global model versus their spatial coordinates (Zuur et al., 2009) and produced a variogram of the residuals (Supplementary Figure S2 and Figure S3).

Because the majority of data were available for the central and northern basin of the Adriatic Sea, we fitted the models and predicted values only for latitudes greater than 42.5°N, in order to exclude model fitting and predictions in areas scant of observations. To assess the accuracy of the predictive model we calculated the area under curve (AUC). AUC values above 0.7 indicate an acceptable level of model performance (Fielding and Bell, 1997). Because spatial autocorrelation may inflate AUC values (Vierod *et al.*, 2014) we also ran a *k*-fold cross validation as additional criteria to evaluate the predictive performance (i.e. accuracy) of the models, using the CVgam function of the R package gamclass (http://cran.r-project.org/web/packages/gamclass/index.html). The CVgam function generates an estimate based on the complete data (called scale parameter, GAMscale). Moreover, it produces an estimate of mean-squared error scale parameter from cross-validation (CV-mse-GAM), representing an unbiased estimate of accuracy (Robertson *et al.*, 2015). When model assumption holds and the accuracy of the model is good, the mean square estimate will be slightly larger than the scale estimate.

Salinity and temperature were at a resolution coarser (around 200 km^2 grid size) than the other environmental variables used in the model (approximately 4 km^2 grid size). In order to test whether using average values of these variables had an effect on model results and evaluate the influence of deviations around these means on the parameter estimates we refit our best model 1000 times, when temperature and/or salinity were present in the best model. Each time we randomly sampled temperature and salinity of each observation drawing from a normal distribution with mean T_i or S_i and standard deviation equal to their associated standard error. We then calculated the deviance explained and the AUC for each refitted model. The full range of the variation of the models' performances has resulted to be small (Supplementary Figure S4). Thus, we can assume that the use of average values of temperature and salinity variables did not affect model results.

All the analyses were performed by using the open source statistical software R (3.3.1) (https://www.r-project.org/). We used the open source software QGISS 2.4.0 to produce and visualize the final maps of the predicted probability of the sea pen species in the northern–central Adriatic. We ran an interpolation using the algorithm inverse distance weighted (IDW) within the raster tool in QGISS. The IDW is a well-known interpolation method where points are weighted inversely by some measure of distance from the target data (Fortin and Dale, 2005). This method allows predicting a value for any unmeasured location. As the distance increases, the weight of the distant points decreases on the unknown value during the interpolation process.

Results

Sea pens in the Mediterranean Sea

Most of the Pennatulacea records detected from 1980 to 2017 are localized on the continental shelves of the northern Mediterranean Sea (Figure 1). Information for the central and eastern Mediterranean basins is limited, and it is mainly from the Strait of Sicily, the Adriatic and North Aegean Seas. Recent records are also available from the Mediterranean coasts of Egypt (Abdelsalam, 2014). No scientific reports are available for the majority of the southern regions of the Mediterranean Sea.

Six species, in the genera *Funiculina*, *Pteroeides*, *Pennatula*, and *Veretillum*, showed similar spatial distribution (Figure 1a–d) being recorded in the whole Mediterranean Sea across a wide depth range (from 20 up to 1000 m, see Supplementary Table S1). The only exception is *Pennatula aculeata* Danielssen, 1860, recorded only along Granada coast and Gibraltar Strait (Figure 1c and Supplementary Table S1). Species belonging to the genera *Cavernularia*, *Kophobelemnon*, *Crassophyllum*, and *Protoptilum* were recorded less frequently with a scattered distribution or in a single area. For example *Crassophyllum thessalonicae* Vafidis and Koukouras, 1991 has been recorded only in the Aegean Sea, and *Protoptilum carpenteri* Kölliker, 1872 was reported for the first time in the Mediterranean Sea in Santa Maria di Leuca area in 2014 (Mastrototaro *et al.*, 2014; Figure 1e and Supplementary Table S1). The species *Virgularia mirabilis* (Müller, 1776) showed a widespread distribution in the north-west and north-central Mediterranean, and up to now, it is the most common sea pen recorded in the Adriatic Sea (Figures 1f and 2 and Supplementary Table S1).

Sea pens in the Adriatic Sea: known distribution and habitat suitability models

Reported distribution

Of the 12 Mediterranean sea pen species, six species (belonging to five genera: *Funiculina*, *Pennatula*, *Pteroeides*, *Veretillum*, and *Virgularia*) have been reported in the Adriatic Sea. Most of the records we analyzed were in the central and northern Adriatic, declining in abundance southward (Figure 2).

Funiculina quadrangularis was recorded in offshore areas of the northern–central Adriatic from 40 to 270 m, in the Pomo (Jabuka) Pits, while in the southern basin it was reported in the offshore area of Montenegro up to 500 m (Figure 2). The two species of *Pennatula* (*P. rubra* and *P. phosphorea*) and the species *Pteroeides spinosum* were recorded both in coastal and offshore areas of the basin. The offshore presence of these three species mainly overlaps, while there are differences in records in coastal areas. In particular, *P. rubra* was recorded along the Apulia (Italy) Montenegro and Albania coasts, while *P. phosphorea* in Croatian shallow waters (Supplementary Table S1). The coastal distribution of *P. spinosum* is instead limited to the coast of Istria, Croatia, and Albania (Figure 2 and Supplementary Table S1). The species was recorded also in deep waters of the south Adriatic Pit (up to 800 m depth). The species *Veretyllum cynomorium* was reported only in the Telašćica Nature Park, in Croatia, in shallow waters (around 15–25 m depth) (Figure 2 and Supplementary Table S1). Finally, *Virgularia mirabilis* is mainly distributed in the northern Adriatic and along the Italian coasts. Few records exist from Albania and Croatia shallow waters (Figure 2). The bathymetric depth range of the species in the Adriatic basin is 10–74 m depth.

Habitat suitability models

Considering the best model for *F. quadrangularis*, *Pennatula* spp. and *V. mirabilis*, none of explanatory variables were statistically significant in the best model of *F. quadrangularis's* distribution. The ratio between gravel/sand content (R_g) and salinity were presents, but with no statistical significance (Table 1). The variables that mainly influenced the presence/absence of *V. mirabilis* were depth, salinity and the residuals of the linear regression between latitude and longitude (rll). None of explanatory

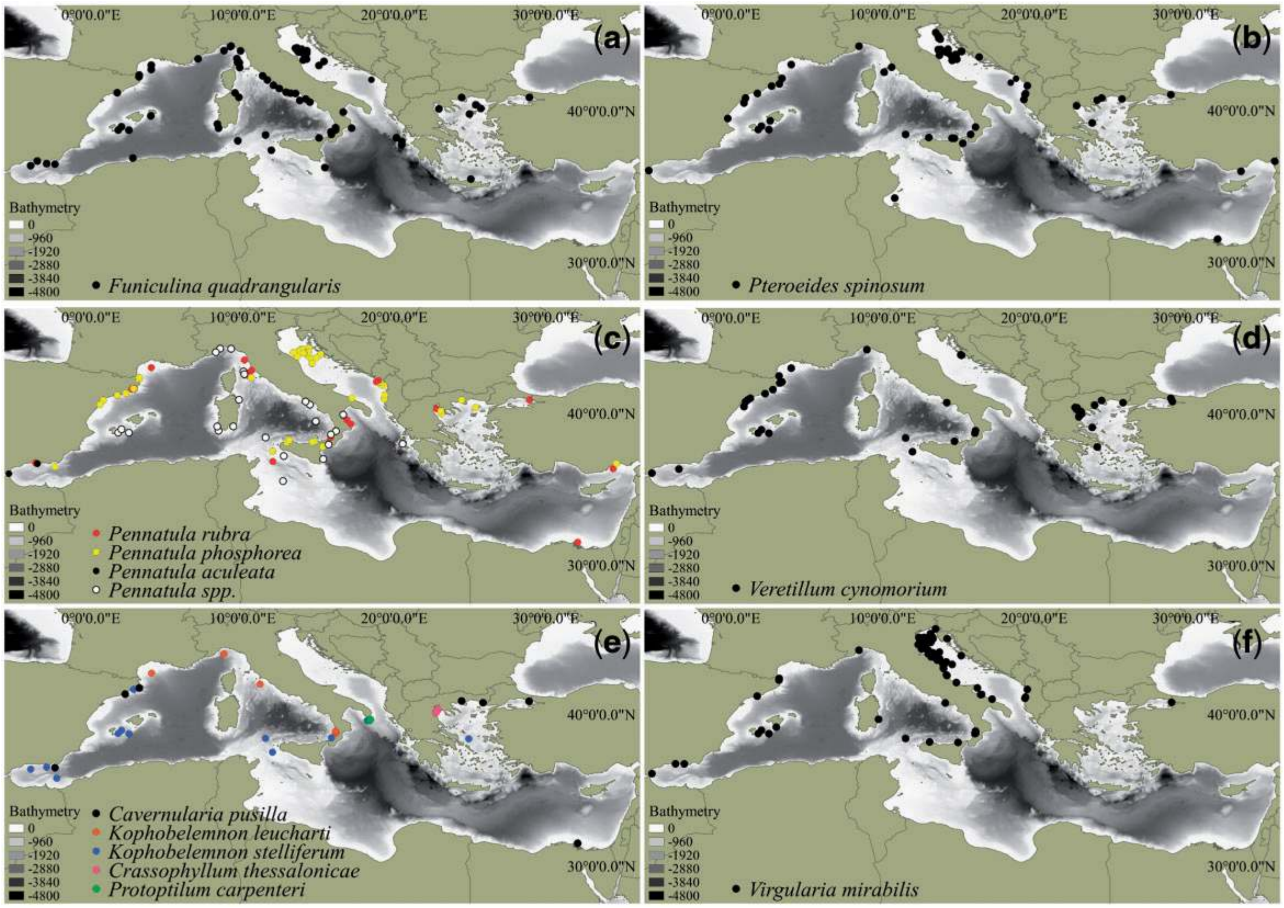

Figure 1. Distribution maps of the Mediterranean sea-pen species. Different symbols represent different species, when data were available at the species levels. Rare genera were aggregated. (a) *Funiculina quadrangularis* records; (b) *Pteroeides spinosum* records; (c) *Pennatula phosphorea*, *P. rubra*, *P. aculeata*, and *Pennatula* spp. records; (d) *Veretillum cynomorium* records; (e) *Cavernularia pusilla*, *Kophobelemnon leucharti*, *K. stelliferum*, *Crassophyllum thessalonicae*, and *Protoptilum carpenteri* records; (f) *Virgularia mirabilis* records.

variables were statistically significant in the best model of *Pennatula* spp's distribution (p-value > 0.05; Table 1).

Presence/absence models indicated the most suitable habitats for different sea pen species, and highlighted different species-specific preferences (Fig. 3). In our case, the habitat suitability models obtained using the average of the models with a confidence set of the 95% suggested that *F. quadrangularis* and *Pennatula* spp. have the highest probability to be found in areas deeper than 40 m, in the central offshore areas of the basin (Fig. 3). The most suitable habitats for *V. mirabilis* were mainly localized in shallow areas of the northern – central basin (Fig. 3).

The estimated AUC values of the models range from 0.8–0.9, indicating an excellent level of model performance (Table 1).

Discussion

This study is the first to compile and summarize the distribution of all the 12 known sea pen species in the Mediterranean Sea. Overall, our review highlights that little is known about the abundance and distribution of sea pens in the region. A few studies are available for large Mediterranean areas, with the exception of a recent work in the Strait of Sicily (Central Mediterranean Sea) (Lauria *et al.*, 2017) and virtually none from the southern and eastern regions. Moreover, all species' records are limited to continental shelves, leaving deep-water habitats of the Mediterranean basin poorly known (IUCN, 2014). Thus, there is a need to improve the data collection of sea pen species, in particular for southern, offshore, and deep areas, in order to improve the identification of Mediterranean VMEs.

The detailed analysis on sea pens distribution in the Adriatic Sea showed that pennatulids colonized a wide bathymetric range and all the different sub-regions of Adriatic bottoms. Variation among the six sea pen species distribution is related to their different ecological requirements and morpho-functional features. *Virgularia mirabilis* has a large muscular peduncle that allows colonies to retract completely and rapidly inside sediments (Greathead *et al.*, 2014). This allows *V. mirabilis* to colonize more unstable habitats, with a high content of gravel sediments, usually typical of shallow waters (Greathead *et al.*, 2007), as confirmed also in the Adriatic. Moreover, the withdraw capacity of *V. mirabilis* may make this species more resilient to trawling disturbance compared to other sea pen species that are probably more easily entangled in nets and removed by trawlers. *Funiculina quadrangularis*, for example, has no withdraw capacity and can protrude up to 1 m above the seafloor, making it one of the sea pen species that are most vulnerable to bottom trawling (Huges, 1998; Eno *et al.*, 2001; Greathead *et al.*, 2007). Information about *P. phosphorea* hightlights that usually this species shares the same habitat of *V. mirabilis* and *F. quadrangularis* (Eno *et al.*, 2001;

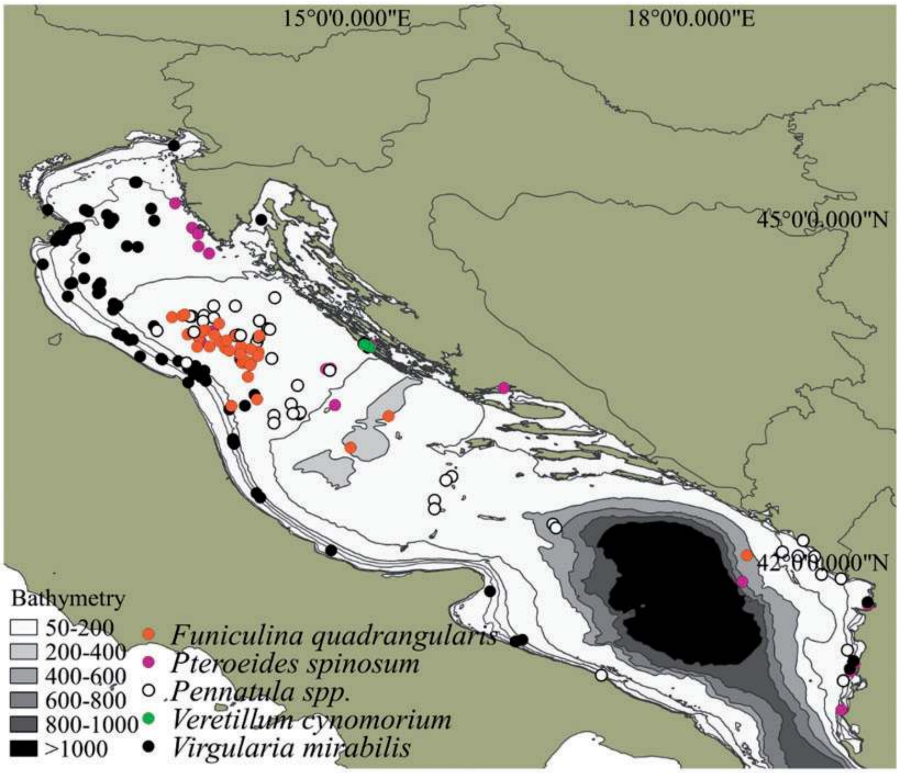

Figure 2. Adriatic distribution of sea pen species from 1980 to 2016. *Pennatula phosphorea* and *Pennatula rubra* have been mapped at genus level (*Pennatula* spp.).

Table 1. Summary of the parameters of accuracy of the GAMs models (AUC, GAM scale, and 10-fold MSE), and summary of the best GAMs models.

Species	AUC	GAM scale	10-fold MSE	Best model	
				Deviance explained (%)	Variable significance (*p*-value)
Funiculina quadrangularis	0.9	0.0122	0.0124	33.4	R_g 0.111 sal 0.242
Virgularia mirabilis	0.8	0.1058	859.95	17.3	rll 0.0203* depth 0.0196* sal 0.0168* temp 0.0832
Pennatula spp.	0.9	0.0256	0.0262	36.3	R_m 0.215 depth 0.565 sal 0.337

***p*-value < 0.005; **p*-value ≤ 0.05; ●*p*-value > 0.05 and < 0.1.

Greathead *et al.*, 2007). *Pennatula phosphorea* has been recorded in sandy or muddy sediments between 15 and 100 m and it is reported to be more widespread than *F. quadrangularis* (Greathead *et al.*, 2014). No ecological information are available for *P. rubra*. However, considering just the external morphology, the two *Pennatula* species can be easily confused, especially in the case of photo identification method (PIM). Thus, the actual distribution of *P. phosphorea* and *P. rubra* needs to be clarified because of possible misidentifications. However, the present study in the Adriatic Sea shows an overlap in the distribution between *Pennatula* spp. and *F. quadrangularis* as reported in the literature (Greathead *et al.*, 2014).

Habitat suitability models, with the production of maps predicting the probability of occurrence of VMEs by extrapolating information even into un-sampled locations (Hirzel *et al.*, 2002), may provide useful information to adequately address marine spatial planning and to focus management and conservation measures. Our maps show the most probable habitats for sea pen species in the norther and central Adriatic basin. The results suggest that the bottoms of central offshore areas and some shallower areas (from 15 m depth) host VMEs. Our habitat suitability models reveal with good approximation (AUC values >0.8; Table 1), that there is still a possibility to find and thus manage, sea pen habitats in several Adriatic areas. Surveys on sea pen discard from fisheries observations are commonly used to reconstruct soft corals presence, distribution, and fishing impacts (Greathead *et al.*, 2007; Cogswell *et al.*, 2011) but these data are scarce for the Adriatic Sea (Martinelli *et al.*, 2013). Traditional sampling with grab, trawl, or dredge can introduce sampling bias due to the

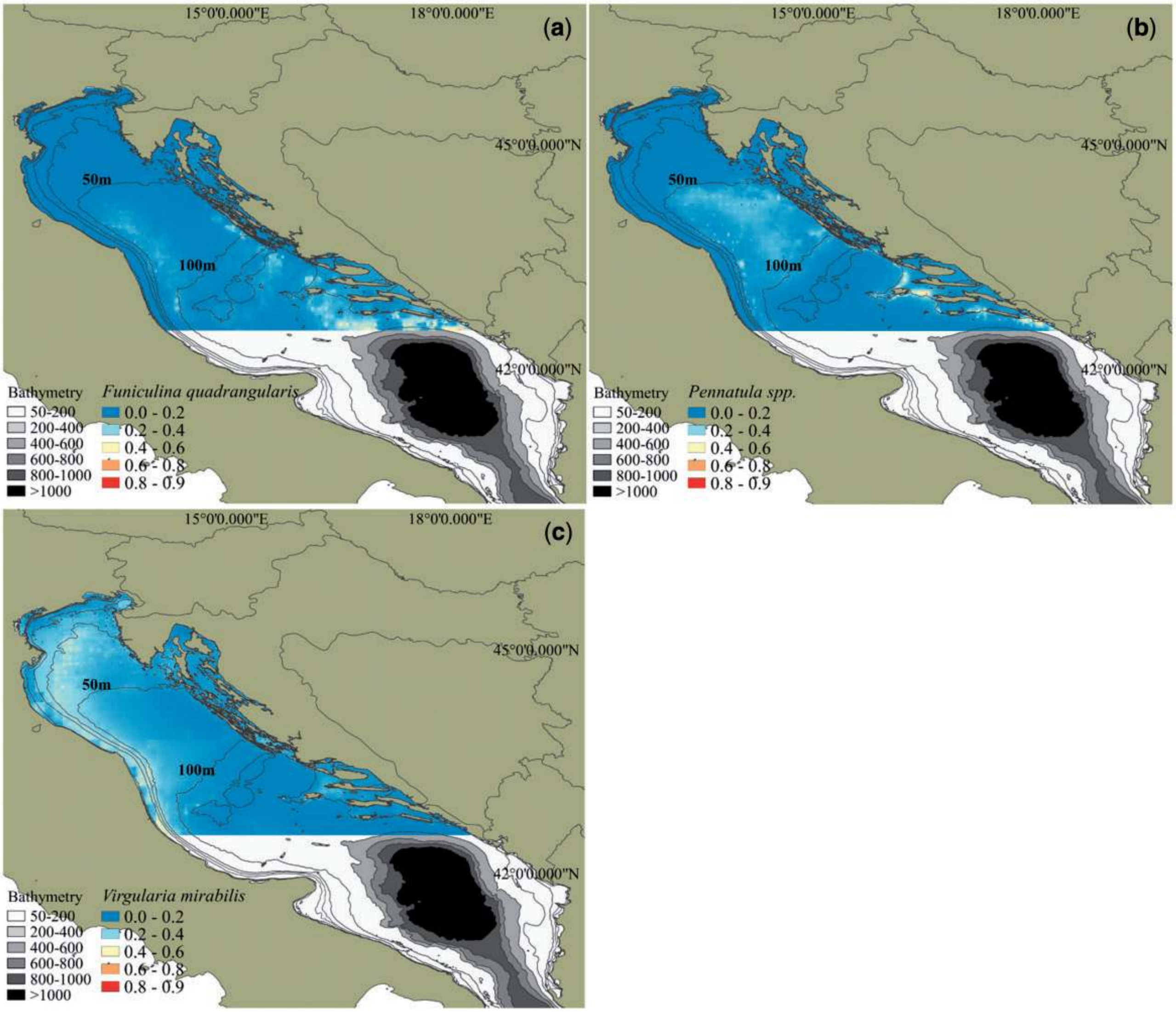

Figure 3. Predicted habitat suitability in the Adriatic Sea for (a) *Funiculina quadrangularis*; (b) *Pennatula* spp., and (c) *Virgularia mirabilis*. Values range from 0 (lowest probability to find sea pens in the area) to 0.9 (highest probability to find sea pens in the area). We limited the predictions to areas northern than 42.5°N.

patchy distribution of sea pens, and the species may not be adequately sampled by the gear with consequent underestimation. Several authors underlined that quality and quantity of available data and sampling gears are fundamental to produce robust habitat suitability models and consequently useful predictions of VMEs occurrence for the management of human activities (Cogswell *et al.*, 2011; Anderson *et al.*, 2016).

International criteria to define VMEs reject the use of bycatch data as sufficient criteria to map these habitats (Murillo *et al.*, 2011), but encourage multi-disciplinary approaches including visual ground truthing and multi-beam sonar mapping, and incorporating fishery footprints, to develop accurate VME maps. The need to develop multi-disciplinary approaches in VMEs mapping has also emerged in this study. The environmental variables used as predictors for habitat suitability models of the Adriatic sea pen were not always significant (Table 1). Sediment composition, salinity, and temperature did not explain the patterns in distribution of all the species and we suspect that Adriatic sea pen distribution may be affected by others variables, including anthropogenic impacts such as fishing. The Adriatic soft bottoms have been highly impacted by bottom trawling (Santelli *et al.*, 2017) for centuries (Lotze *et al.*, 2011). Intense bottom trawling destroys sessile organisms such as sea pens and corals, compromising an actual management of fishing resources. Thus, further analysis is needed to relate fishing effort and the effects of towed gears in particular, on the recovery of tridimensional soft bottoms habitats in the Adriatic Sea.

The high level of cumulative impacts affecting the Adriatic basin, in particular fishing activities (Lotze *et al.*, 2011; Micheli *et al.*, 2013a, b), may have contributed to shape the present composition and distribution of benthic assemblages, including sea pens. Historical data about abundances and distribution of Adriatic Pennatulacea are scant, and identifying a pristine, undisturbed condition is difficult because of the long history of use and alteration of these ecosystems. The abundances and distributions of Adriatic sea pens may have been decreasing in the same way that happened in other world regions (Hixon and Tissot, 2007), but a dearth of baseline data and experimental studies of the effect of trawling in the basin make this assessment difficult. Sea pens have declined in the Ligurian Sea, in the northwestern Mediterranean, where in the 1970s soft coral habitats were very common, but currently have disappeared from intensively trawled areas (Tunesi and Diviacco, 1997). Similar negative trends have been reported from Algeria, where otter trawling fisheries on muddy bottom targeting shrimp *Parapenaeus longisrostris* impacted the benthic habitats associated with *F. quandrangularis* (Tudela, 2004). Moreover, it is possible to infer that sea pen species may reach maturity at 5 or 6 years of age and may live for over a decade (Wilson *et al.*, 2002; Ager, 2003; Neves de Moura *et al.*, 2015). Because of their sessile, slow-growing and long-life cycles (Hixon and Tissot, 2007; Neves de Moura *et al.*, 2015), the recovery of sea pens from trawling disturbance is expected to be difficult and slow.

The development and implementation of EBM approaches, including the conservation of critical habitats, should be fundamental to the recovery of Adriatic and Mediterranean marine ecosystems and resources. The identification of areas where sea pens are currently present and might recover if protected from physical disturbance, may help the selection of priority areas (Murillo *et al.*, 2011). Current management of fisheries in the Mediterranean Sea has rarely taken into account soft bottom VMEs. The VMEs database created by the Food and Agriculture Organization (FAO) (http://www.fao.org/in-action/vulnerable-marine-ecosystems/en/) for the identification and the management of VMEs in areas beyond national jurisdictions (ABNJ) includes, for the Adriatic Sea, only areas deeper than 1000 m, where a trawl ban was implemented by the General Fisheries Commission for the Mediterranean (GFCM) in 2005 (Recommendation GFCM/2005/1). Recently, following several proposals to improve and expand management of Adriatic marine resources (Bastari *et al.*, 2016) stressing the importance of promoting the recovery of Adriatic stocks and soft bottom habitats, the GFCM has established a fishery restricted areas (FRA) in the Pomo (Jabuka) Pit (central offshore Adriatic). The FRA includes a no-take area of around 1400 km^2, and it has been in force for 3 years, with the possibility to extend this period depending on the outcomes of the trawling ban on stocks (GFCM, 2017). Monitoring and enforcement of the FRA will be fundamental to evaluate the effects of the trawl ban in a vast area of the central Adriatic Sea and for the study of the potential recovery of its communities.

Conclusions

Sea pens are important indicators for VMEs but have been poorly studied in the Mediterranean Sea. Data on their natural history, abundance, and distribution are urgently needed. Our work gives a first picture of the status of sea pens in the entire basin and it sets a baseline for future analysis and mapping of the soft bottoms VMEs of the Adriatic Sea and broader Mediterranean region. The habitat suitability maps of the Adriatic sea pen species presented here provide the first extended study about soft bottom habitat-forming species in the Adriatic basin. Sea pen habitats are one of the few soft bottom habitats to be classified as EFHs and VMEs, with increasing attention by international organizations on sand–mud seafloor ecosystems. These habitats should be taken into account in the selection of priority areas in need of protection. Our suitability models highlight a good (>0.5) presence probability of different sea pen species both in shallow and offshore areas of the Adriatic basin. However, to define an effective management strategy for sea pen and associated habitats, and to increase the accuracy of habitat suitability models predictions as indicator of VMEs, more detailed studies should be done, in particular including past and current fishing effort as explanatory variables in the models. The unregulated fishing practices and the lack of knowledge of the ecological role played by soft bottom habitats makes it difficult to define clear management and protection actions for the sustainability of Adriatic and Mediterranean marine resources. The established FRA could represent a fundamental step in promoting the recovery of Adriatic stocks and it represents a starting point for the recovery of the whole basin. However, the temporal scale of the trawling ban (3 years) could be not enough for the recovery of long-lived soft bottom species.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

The research has been supported by a grant of the Polytechnic University of Marche to Carlo Cerrano (Adriatic Marine Ecosystem Recovery [AMER] project) and co-funded by the Flagship Project RITMARE—The Italian Research for the Sea—coordinated by the Italian National Research Council and funded by the Italian Ministry of Education, University and Research within the National Research Program 2011–2013. Francesco Ferretti and Fiorenza Micheli acknowledge the support of the Lenfest Oceans Program, the Pew Charitable Trust, and Stanford's Woods Institute for the Environment.

References

Abdelsalam, K. M. 2014. Faunistic study of benthic Pennatulacea (Cnidaria, Octocorallia) from the Northern coast of Egypt. The Egyptian Journal of Aquatic Research, 40: 261–268.

Ardizzone, G. D. 2006, March. An introduction to sensitive and essential fish habitats identification and protection in the Mediterranean Sea. Working Document to the STECF. SGMED-06-01 sub-group meeting on Sensitive and Essential Fish Habitats in the Mediterranean (Rome).

Ager, O. E. D. 2003. *Funiculina quadrangularis*: the tall sea pen. *In* Marine Life Information Network: Biology and Sensitivity Key Information Reviews [on-line]. Ed. by H. Tyler-Walters and K. Hiscock. Plymouth: Marine Biological Association of the United Kingdom. Available from: http://www.marlin.ac.uk/species/detail/1154.

Anderson, O. F., Guinotte, J. M., Rowden, A. A., Clark, M. R., Mormede, S., Davies, A. J., and Bowden, D. A. 2016. Field validation of habitat suitability models for vulnerable marine ecosystems in the South Pacific Ocean: implications for the use of broad-scale models in fisheries management. Ocean & Coastal Management, 120: 110–126.

Baillon, S., Hamel, J. F., Wareham, V. E., and Mercier, A. 2012. Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment, 10: 351–356.

Barton, K. 2015. MuMIn: multi-model inference. R package version 1.15.6.

Bastari, A., Pica, D., Grech, D., Scarcella, G., and Cerrano, C. 2013. The last soft-bottoms habitat formers of the western Adriatic Sea.

XXIII Congresso SItE, Ancona, 16–18 Settembre 2013. https://www.academia.edu/27309796/The_last_soft-_bottoms_habitat_formers_of_the_western_Adriatic_Sea (last accessed 30 October 2015).

Bastari, A., Micheli, F., Ferretti, F., Pusceddu, A., and Cerrano, C. 2016. Large marine protected areas (LMPAs) in the Mediterranean Sea: the opportunity of the Adriatic Sea. Marine Policy, 68: 165–177.

Bertness, M. D., and Callaway, R. 1994. Positive interactions in communities. Trends in Ecology & Evolution, 9: 191–193.

Brodeur, R. D. 2001. Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Continental Shelf Research, 21: 207–224.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.

Cerrano, C., Calcinai, B., Bertolino, M., Valisano, L., and Bavestrello, G. 2006. Epibionts of the scallop *Adamussium colbecki* (Smith, 1902) in the Ross Sea, Antarctica. Chemistry and Ecology, 22: S235–S244.

Chia, F. S., and Crawford, B. J. 1973. Some observations on gametogenesis, larval development and substratum selection of the sea pen *Ptilosarcus guerneyi*. Marine Biology, 23: 73–82.

Cogswell, A., Kenchington, E., Lirette, C., Murillo, F. J., Campanis, G., Campbell, N., and Ollerhead, N. 2011. Layers Utilized by an ArcGIS Model to Approximate Commercial Coral and Sponge By-catch in the NAFO Regulatory Area. NAFO SCR Doc. 11/72. Available at: http://archive.nafo.int/open/sc/2011/scr11-072.pdf (last accessed 12 June 2013).

Coll, M., Santojanni, A., Palomera, I., Tudela, S., and Arneri, E. 2007. An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. Journal of Marine Systems, 67: 119–154.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. 2009. Food-web changes in the Adriatic Sea over the last three decades. Marine Ecology Progress Series, 381: 17–37.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. 2010. Ecosystem assessment of the North-Central Adriatic Sea: towards a multivariate reference framework. Marine Ecology Progress Series, 417: 193–210.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *In* Proceedings of the Colloquium on Conservation Problems in Antarctica, pp. 81–96. Ed. B. C. Parker. Allen Press, Lawrence.

Davies, A. J., and Guinotte, J. M. 2011. Global habitat suitability for framework-forming cold-water corals. PLoS One, 6: e18483.

De Clippele, L. H., Buhl-Mortensen, P., and Buhl-Mortensen, L. 2015. Fauna associated with cold water gorgonians and sea pens. Continental Shelf Research, 105: 67–78.

Doyle, J., Lordan, C., Fitzgerald, R., O'Connor, S., Fee, D., Butler, R., Stokes, D., Ni Chonchuir, G., Sheridan, M., and Simpson, S. 2015. Aran, Galway Bay and Slyne Head Nephrops Grounds (FU17) 2015 UWTV Survey Report and catch options for 2016. Marine Institute UWTV Survey report.

Eckelbarger, K. J., Tyler, P. A., and Langton, R. W. 1998. Gonadal morphology and gametogenesis in the sea pen *Pennatula aculeata* (Anthozoa: Pennatulacea) from the Gulf of Maine. Marine Biology, 132: 677–690.

Edinger, E. N., Wareham, V. E., and Haedrich, R. L. 2007. Patterns of groundfish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. Bulletin of Marine Science, 81: 101–122.

Edwards, D. C. B., and Moore, C. G. 2008. Reproduction in the sea pen *Pennatula phosphorea* (Anthozoa: Pennatulacea) from the west coast of Scotland. Marine Biology, 155: 303–314.

Edwards, D. C. B., and Moore, C. G. 2009. Reproduction in the sea pen *Funiculina quadrangularis* (Anthozoa: Pennatulacea) from the west coast of Scotland. Estuarine, Coastal and Shelf Science, 82: 161–168.

Eno, N. C., MacDonald, D. S., Kinnear, J. A., Amos, S. C., Chapman, C. J., Clark, R. A., Bunker, F., and Munro, C. 2001. Effects of crustacean traps on benthic fauna. ICES Journal of Marine Science, 58: 11–20.

Ferretti, F., Osio, G.C., Jenkins, C.J., Rosenberg, A.A., and Lotze, H.K. 2013. Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. Scientific Reports, 3: 1057.

Fielding, A. H., and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24: 38–49.

Fortin, M., and Dale, M. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, New York.

GFCM, 2017. 41th session of the General Fisheries Commission for the Mediterranean 16 October 2017–20 October 2017.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology, 84: 2809–2815.

Grati, F., Scarcella, G., Polidori, P., Domenichetti, F., Bolognini, L., Gramolini, R., Vasapollo, C., *et al.* 2013. Multi-annual investigation of the spatial distributions of juvenile and adult sole (*Solea solea* L.) in the Adriatic Sea (northern Mediterranean). Journal of Sea Research, 84: 122–132.

Greathead, C. F., Donnan, D. W., Mair, J. M., and Saunders, G. R. 2007. The sea pens *Virgularia mirabilis*, *Pennatula phosphorea* and *Funiculina quadrangularis*: distribution and conservation issues in Scottish waters. Journal of the Marine Biological Association of the United Kingdom, 87: 1095–1103.

Greathead, C., González-Irusta, J. M., Clarke, J., Boulcott, P., Blackadder, L., Weetman, A., and Wright, P. J. 2014. Environmental requirements for three sea pen species: relevance to distribution and conservation. ICES Journal of Marine Science, 72: 576–586.

Grbec, B., Dulcic, J., and Morovic, M. 2002. Long-term changes in landings of small pelagic fish in the eastern Adriatic possible influence of climate oscillations over the Northern Hemisphere. Climate Research, 20: 241–252.

Hirzel, A. H., Hausser, J., Chessel, D., and Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology, 83: 2027–2036.

Hixon, M. A., and Tissot, B. N. 2007. Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon. Journal of Experimental Marine Biology and Ecology, 344: 23–34.

Huges, D. J. 1998. Sea pens and burrowing megafauna. An overview of dynamics and sensitivity characteristics for conservation management of marine SACs David J. Hughes Centre for Coastal and Marine Sciences Dunstaffnage Marine Laboratory, Oban AUGUST 1998 Prepared for Scot. Science (August).

IUCN, 2014. Salvati, E., Bo, M., Rondinini, C., Battistoni, A., Teofili, C. (compilatori). Lista Rossa IUCN dei coralli Italiani. Comitato Italiano IUCN e Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Roma.

IUCN, 2016. The IUCN red list of Anthozoans in the Mediterranean. International Union for the Conservation of Nature and Natural Resources. *In* 19th Conference of the Parties to the Barcelona Convention, February 2016. Available at: http://cmsdata.iucn.org/downloads/anzothoa_fact_sheet_final_baja.pdf (last accessed 6 February 2017).

Jones, C. G., Lawton, J. H., and Shachak, M. 1994. Organisms as ecosystem engineers. Oikos, 69: 373–386.

Jones, C. G., Lawton, J. H., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology, 78: 1946–1957.

Kinnear, J. A. M., Barkel, P. J., Mojsiewicz, W. R., Chapman, C. J., Holbrow, A. J., Barnes, C., and Greathead, C. F. F. 1996. Effects of

Nephrops creels on the environment. Fisheries Research Services Report, 2: 96.

Knudby, A., Kenchington, E., Murillo, F. J., and Pronzato, R. 2013. Modeling the distribution of *Geodia* sponges and sponge grounds in the Northwest Atlantic. PLoS One, 8: e82306–e82320.

Krigsman, L. M., Yoklavich, M. M., Dick, E. J., and Cochrane, G. R. 2012. Models and maps: predicting the distribution of corals and other benthic macro-invertebrates in shelf habitats. Ecosphere, 3: art3.

Krieger, K. J. 1993. Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fishery Bulletin, 91: 87–96.

Kružić, P. 2007. Fauna koralja Parka prirode Telašćica (Jadransko more, Hrvatska). Natura Croatica, 16: 233–266.

Lauria, V., Garofalo, G., Fiorentino, F., Massi, D., Milisenda, G., Piraino, S., Russo, T., *et al.* 2017. Species distribution models of two critically endangered deep-sea octocorals reveal fishing impacts on vulnerable marine ecosystems in central Mediterranean Sea. Scientific Reports, 7: 8049.

Linnæus, C. 1758. Systema Naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Salvius, Holmiæ, pp. 4–824.

Lotze, H. K., Coll, M., and Dunne, J. A. 2011. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. Ecosystems, 14: 198–222.

Martinelli, M., Morello, E. B., Isajlović, I., Belardinelli, A., Lucchetti, A., Santojanni, A., Atkinson, R. J. A., *et al.* 2013. Towed underwater television towards the quantification of Norway lobster, squat lobsters and sea pens in the Adriatic Sea. Acta Adriatica, 54: 3–12.

Mastrototaro, F., Chimienti, G., Capezzuto, F., Carlucci, R., and Williams, G. 2014. First record of *Protoptilum carpenteri* (Cnidaria: Octocorallia: Pennatulacea) in the Mediterranean Sea. Italian Journal of Zoology, 82: 61–68.

Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R., *et al.* 2013a. Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. PLoS One, 8:

Micheli, F., Levin, N., Giakoumi, S., Katsanevakis, S., Abdulla, A., Coll, M., Fraschetti, S., *et al.* 2013b. Setting Priorities for Regional Conservation Planning in the Mediterranean Sea. PLoS One, 8.

Murillo, F. J., Durán Muñoz, P., Altuna, A., and Serrano, A. 2011. Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. ICES Journal of Marine Science, 68: 319–332.

Neves de Moura, B., Edinger, E., Layne, G. D., and Wareham, V. E. 2015. Decadal longevity and slow growth rates in the deep-water sea pen *Halipteris finmarchica* (Sars, 1851) (Octocorallia: Pennatulacea): implications for vulnerability and recovery from anthropogenic disturbance. Hydrobiologia, 759: 147–170.

Nouar, A., and Maurin, C. 2001. Nature of and typical populations on the characteristic facies of substratum of *Parapenaeus longirostris* (Lucas, 1846) along the Algerian coast. Crustaceana, 74: 129–135.

OSPAR, 2004. Descriptions of habitats on the initial OSPAR list of threatened and/or declining species and habitats. OSPAR convention for the protection of the marine environment of the North–East Atlantic. OSPAR 2004-07, 7 pp.

Paolucci, C. 1923. Il primo esperimento governativo di pesca con battello a vapore nell'Adriatico. Rivista Di Pesca e Idrobiologia, pp. 33–60.

Pax, F., and Müller, I. 1962. Die Anthozoenfauna der Adria. Fauna Et Flora Adriatica, Split, 3: 1–343.

Porporato, E. M. D., De Domenico, F., Mangano, M. C., Rinelli, P., and Spanò, N. 2012. *Ebalia nux* (Decapoda, Brachyura) found among the leaves of *Pteroeides spinosum* (Anthozoa, Octocorallia). Crustaceana, 85: 125.

Richiardi, S. 1869. Monografia della famiglia dei Pennatularii. Archivio per La Zoologia, L'anatomia e La Fisiologia, Bologna, Serie, 2: 1–150.

Robertson, B. P., Gardner, J. P., and Savage, C. 2015. Macrobenthic–mud relations strengthen the foundation for benthic index development: a case study from shallow, temperate New Zealand estuaries. Ecological Indicators, 58: 161–174.

Rogers, A. D., and Gianni, M. 2010. The implementation of UNGA resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas. Management, p. 97. Available at: http://www.stateoftheocean.org/pdfs/61105-Implemention-finalreport.pdf (last accessed 15 May 2014).

Salvalaggio, V., Fabi, G., Punzo, E., Santelli, A., Strafella, P., Tassetti, N., Cvitkovic, I., *et al.* 2016. Distribution of the sea pens *Virgularia mirabilis* and *Funiculina quadrangularis* (Cnidaria Anthozoa) in the northern and central Adriatic Sea. Rapport Du 41[e] Congres De La CIESM—Commission International Pour L'Exploration Scientifique De La Mer Méditerranee, 41: 504.

Sánchez, P., Sartor, P., Recasens, L., Ligas, A., Martin, J., De Ranieri, S., and Demestre, M. 2007. Trawl catch composition during different fishing intensity periods in two Mediterranean demersal fishing grounds. Scientia Marina, 71: 765–773.

Santelli, A., Cvitković, I., Despalatović, M., Fabi, G., Grati, F., Marčeta, B., Punzo, E., *et al.* 2017. Spatial persistence of megazoobenthic assemblages in the Adriatic Sea. Marine Ecology Progress Series, 566: 31–48.

Soong, K. 2005. Reproduction and colony integration of the sea pen *Virgularia juncea*. Marine Biology, 146: 1103–1109.

Tissot, B. N., Yoklavich, M. M., Love, M. S., York, K., and Amend, M. 2006. Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fishery Bulletin, 104: 167–181.

Tittensor, D. P., Baco, A. R., Brewin, P. E., Clark, M. R., Consalvey, M., Hall-Spencer, J., Rowden, A. A., *et al.* 2009. Predicting global habitat suitability for stony corals on seamounts. Journal of Biogeography, 36: 1111–1128.

Tracey, D. M., Rowden, A. A., Mackay, K. A., and Compton, T. 2011. Habitat-forming cold-water corals show affinity for seamounts in the New Zealand region. Marine Ecology Progress Series, 430: 1–22.

Trincardi, F., Cattaneo, A., Asioli, A., Correggiari, A., and Langone, L. 1996. Stratigraphy of the late-Quaternary deposits in the central Adriatic Basin and the record of short-term climatic events. Memorie-Istituto Italiano Di Idrobiologia, 55: 39–70.

Troffe, P. M., Levings, C. D., Piercey, G. B. E., and Keong, V. 2005. Fishing gear effects and ecology of the sea whip (*Halipteris willemoesi* (Cnidaria: Octocorallia: Pennatulacea)) in British Columbia, Canada: preliminary observations. Aquatic Conservation: Marine and Freshwater Ecosystems, 15: 523–533.

Tudela, S. 2004. Ecosystem effects of fishing in the Mediterranean: an analysis of the major threats of fishing gear and practices to biodiversity and marine habitats. Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 74. Rome, FAO. 44 pp. http://www.fao.org/docrep/007/y5594e/y5594e04.htm#bm4.7 (last accessed 15 October 2014).

Tunesi, L., and Diviacco, G. 1997. Observations by submersible on the bottoms off shore Portofino Promontory (Ligurian Sea). *Atti 12° Congresso AIOL*, Isola di Vulcano, 18–21 Settembre 1996, I(Dl), pp. 61–74.

UNEP/MAP-RAC/SPA, 2015. Adriatic Sea: description of the ecology and identification of the areas that may deserve to be protected. By Cerrano, C. Ed. RAC/SPA, Tunis. 2015; 92 pp.

Vafidis, D., and Koukouras, A. 1991. *Crassophyllum thessalonicae* sp.n. (Octocorallia, Pennatulacea), from the Aegean Sea. Zoologica Scripta, 20: 201–205.

van Straaten, L. M. J. U. 1970. Holocene and late-Pleistocene sedimentation in the Adriatic Sea. Geologische Rundschau, 60: 106–131.

Vierod, A. D., Guinotte, J. M., and Davies, A. J. 2014. Predicting the distribution of vulnerable marine ecosystems in the deep sea using presence-background models. Deep Sea Research Part II: Topical Studies in Oceanography, 99: 6–18.

Wilson, M. T., Andrews, A. H., Brown, A. L., and Cordes, E. E. 2002. Axial rod growth and age estimation of the sea pen, *Halipteris willemoesi* Kölliker. Hydrobiologia, 471: 133–142.

Yesson, C., Taylor, M. L., Tittensor, D. P., Davies, A. J., Guinotte, J., Baco, A., Black, J., *et al.* 2012. Global habitat suitability of cold-water octocorals. Journal of Biogeography, 39: 1278–1292.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution, 1: 3–14.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Handling editor: Michel Kaiser