RESEARCH ARTICLE

Revealing the coral habitat effect on benthopelagic fauna diversity in the Santa Maria di Leuca cold-water coral province using different devices and Bayesian hierarchical modelling

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Abstract

1. Data from two experimental longline surveys and two video inspections carried out in Santa Maria di Leuca cold-water coral province (Mediterranean Sea) during spring–autumn 2010 were used in order to compare the benthopelagic abundance and diversity between coral and non-coral habitats and between different devices. The sampling was carried out in two types of habitat: a coral habitat with carbonate mounds and a non-coral habitat characterized by intermound sea floor.

2. A Bayesian hierarchical modelling approach to accommodate factors influencing community assemblages was used considering the number of species, the Shannon–Wiener diversity index and the two most abundant species represented by the European conger (*Conger conger*) and blackbelly rosefish (*Helicolenus dactylopterus*).

3. A relevant effect of the habitat factor was observed for both the number of species and the diversity index, showing a higher species number and diversity index in the coral habitat than in the non-coral habitat. Concerning the relevance of fixed effects from the model on the probability of observing non-zero (positive) abundances, the devices considered, longline and baited lander, did not show different influence for either *C. conger* or *H. dactylopterus*. In the case of positive abundance, a relevant device effect was only observed for *H. dactylopterus*, showing higher abundances for longline than for baited lander. A habitat effect was detected, with positive abundances for both species in the coral habitat.

4. This study proves that structurally complex habitats generated by cold-water corals influence the distribution and diversity of the benthopelagic fauna, and that the use of different devices can provide complementary useful results. Increased knowledge about the role of cold-water corals in the associated benthopelagic fauna could lead to better conservation of one of the most important hot spots of biodiversity in the Mediterranean Sea.

1 | INTRODUCTION

During the last three decades, the role of cold-water coral (CWC) reefs as biodiversity hot spots has been established (Buhl-Mortensen et al., 2010; Buhl-Mortensen, Buhl-Mortensen, & Purser, 2017; Costello et al., 2005; D'Onghia et al., 2011; Henry & Roberts, 2017; Jensen & Frederiksen, 1992; Jonsson, Nilsson, Floruta, & Lundälv, 2004; Mastrototaro et al., 2010; Reed, 2002; Rogers, 1999; Ross & Quattrini, 2007, 2009). CWC communities are used by commercial and non-commercial fishes and invertebrates for shelter, feeding, growing, spawning, and as nursery areas, providing essential fish habitat (EFH) (e.g. Baillon, Hamel, Wareham, & Mercier, 2012; Buhl-Mortensen et al., 2010; Busby, Orr, & Blood, 2006; Capezzuto, Ancona, et al., 2018; Cau et al., 2017; D'Onghia, 2019; D'Onghia et al., 2010, 2016; D'Onghia, Sion, & Capezzuto, 2019; Etnoyer & Warrenchuk, 2007; Freiwald, Fosså, Grehan, Koslow, & Roberts, 2004; Gomes-Pereira et al., 2017; Henry et al., 2013; Roberts, Wheeler, Freiwald, & Cairns, 2009). For these reasons CWCs are impacted by commercial fishing (e.g. D'Onghia et al., 2017; Fabri et al., 2014; Fosså, Mortensen, & Furevik, 2002; Grehan, Unnithan, Olu, & Opderbecke, 2005; Hall-Spencer, Allain, & Fosså, 2002; Orejas et al., 2009; Roberts, Harvey, Lamont, & Gage, 2000; Rogers, 1999; Söffker, Sloman, & Hall-Spencer, 2011), and their protection is necessary in order to combine biodiversity conservation and fisheries management objectives.

The benthopelagic fauna associated with CWCs has been investigated by various authors using different devices (e.g. Buhl-Mortensen et al., 2010; Costello et al., 2005; D'Onghia et al., 2010; Heifetz, 2002; Husebø, Nøttestad, Fosså, Furevik, & Jørgensen, 2002; Krieger & Wing, 2002; Kutti, Fosså, & Bergstad, 2015; Linley et al., 2017; Lumsden, Hourigan, Bruckner, & Dorr, 2007; Mastrototaro et al., 2010; Milligan, Spence, Roberts, & Bailey, 2016; Quattrini, Ross, Carlson, & Nizinski, 2012; Reed, Shepard, Koenig, Scanlon, & Gilmore, 2005; Roberts, Henry, Long, & Hartley, 2008; Ross & Quattrini, 2007; Söffker et al., 2011). Exploration of CWC ecosystems and the associated fauna is beset by many difficulties, however, mainly because of the irregular topographical setting and the risk of impacting vulnerable species, such as corals and sponges, and damaging the equipment used for such explorations (e.g. Kutti, Bergstad, Fosså, & Helle, 2014; Linley et al., 2017; Milligan et al., 2016; Pham et al., 2014; Taviani et al., 2017). In addition, the type of device used for such exploration can affect what species assemblages are identified, i.e. the use of different sampling equipment, such as video inspection or fishing gear, may lead to variations in the species composition recorded (e.g. Ayma et al., 2016; Capezzuto et al., 2012; Costello et al., 2005; D'Onghia et al., 2011, 2012; Kutti et al., 2014, 2015; Milligan et al., 2016; Ross & Quattrini, 2007; Söffker et al., 2011). Sampling variability is also tightly related to the behaviour of deep-sea fauna and to the size

and speed of sampling devices (D'Onghia et al., 2011; Lorance & Trenkel, 2006; Trenkel, Lorance, & Mahevas, 2004).

The studies of benthopelagic fauna carried out using fishing gear (bottom trawls, longlines, and traps) can damage the gear and can be harmful for habitat-forming organisms, such as corals, sponges, and other benthic species. Trawling destroys the reef, longlines are difficult to accurately locate over reefs, and traps, along with the previous two devices, are particularly selective for certain species and sizes (e.g. Costello et al., 2005; Durán Muñoz et al., 2011; Fosså et al., 2002; Husebø et al., 2002; Kutti et al., 2014; Mortensen, Hovland, Brattegard, & Farestveit, 1995; Sampaio et al., 2012). Among the fishing gear, experimental longlines, with a small number of hooks with respect to commercial longlines, seem to be the least harmful in fragile and structurally complex habitats (Pham et al., 2014). Furthermore, they are cost-effective and relatively easy to use (e.g. D'Onghia et al., 2012; Menezes & Giacomello, 2013).

Video inspections are less invasive for these fragile ecosystems and can provide information on small-scale species distribution, abundance, and behaviour (e.g. Bailey & Priede, 2002; Bo et al., 2015; Capezzuto et al., 2012; Costello et al., 2005; D'Onghia et al., 2011, 2018; D'Onghia, Capezzuto, Carluccio, et al., 2015; D'Onghia, Capezzuto, Cardone, et al., 2015; Fabri et al., 2014; Linley et al., 2017; Quattrini et al., 2012; Ross & Quattrini, 2007, 2009). They also have some limitations, however: survey via remotely operated vehicle (ROV) has been shown to influence results through species being attracted or repelled by the presence of the ROV (Costello et al., 2005; D'Onghia et al., 2011; Lorance & Trenkel, 2006; Ryer, Stoner, Iseri, & Spencer, 2009; Stoner, Ryer, Parker, Auster, & Wakefield, 2008; Trenkel et al., 2004).

Baited landers produce less disturbance, but predominantly attract scavenging fish and take a long time to achieve the correct positioning and operation. Furthermore, the use of landers can lead to some assumptions for estimating the benthopelagic abundance (Bailey, King, & Priede, 2007; Cousins et al., 2013; D'Onghia, Capezzuto, Carluccio, et al., 2015; Jamieson, Bailey, Wagner, Bagley, & Priede, 2006; Linley et al., 2017; Priede & Merrett, 1996; Roberts et al., 2005).

The Santa Maria di Leuca (SML) CWC province represents a well-structured coral ecosystem in the Mediterranean Sea made up of the reef-forming species *Lophelia pertusa* and *Madrepora oculata*. Dead and living colonies are widespread in an area of over 1200 km^2, between about 350 and 1100 m water depth, in the Northern Ionian Sea (southern Italy) (Bargain, Marchese, Savini, Taviani, & Fabri, 2017; Savini, Vertino, Marchese, Beuck, & Freiwald, 2014; Taviani et al., 2005; Tursi, Mastrototaro, Matarrese, Maiorano, & D'Onghia, 2004), playing an important role as nursery and spawning areas for several commercial benthopelagic species. In recent years many studies have been conducted in SML CWC province and the mobile fauna associated has been investigated using different sampling techniques,

from different fishing gear to video systems, both in coral and non-coral habitats (Capezzuto et al., 2012; Carlier et al., 2009; D'Onghia et al., 2010, 2011, 2012, 2016, 2017, 2018; Freiwald et al., 2009; Linley et al., 2017; Maiorano et al., 2013; Mastrototaro et al., 2010; Tursi et al., 2004). Corals play a fundamental role in providing a complex habitat that hosts a high variety of species and acts as a refuge area from fishing, enhancing the diversity in the deep sea (e.g. D'Onghia et al., 2010, 2011, 2012, 2016). In particular, D'Onghia et al. (2012) and Capezzuto, Ancona, et al. (2018) observed a coral habitat effect on benthopelagic abundance. The analysis conducted on longline data showed greater abundances of the fish species *Conger conger*, *Helicolenus dactylopterus*, and *Polyprion americanus* in coral habitat, and the fish *Pagellus bogaraveo* was only observed to be associated with corals. No significant differences were detected between the two habitats considering the average total catch per unit effort (CPUE), either in number or biomass, however. Only CPUE values coming from longline J-hook 9 showed significant differences between coral and non-coral habitats.

Using baited cameras on autonomous benthic landers, both on and off the coral mounds of the SML CWC province, Linley et al. (2017) did not detect significant differences in fish diversity between coral and non-coral habitats; however, *C. conger* was observed with much higher density within the coral areas. Faster arrival and higher peak numbers also indicate a greater abundance of *H. dactylopterus* in coral habitat than in non-coral habitat. Thus, these studies carried out in the SML CWC province revealed some differences between coral and non-coral habitats, but they did not provide clear and definitive results on the role of CWC habitat in influencing the distribution and diversity of the benthopelagic fauna.

As a result of the high level of biodiversity (e.g. Bongiorni et al., 2010; Mastrototaro et al., 2010) and the higher abundance of many commercial benthopelagic species inside the coral habitat (e.g. D'Onghia et al., 2010, 2011, 2012), as well as the resulting impact of trawling and other fishing gear, a fisheries restricted area (FRA) has been established in an area within the SML CWC province (GFCM-RAC/SPA, 2007). Nevertheless, even if towed dredges and bottom trawl nets have been prohibited in this FRA, data from observer programmes and from a satellite vessel monitoring system (VMS) have proven that trawlers often still fish inside the FRA (D'Onghia et al., 2017).

With this regard, the aim of this paper is to reveal the coral habitat effect on the benthopelagic abundance and diversity detected in the SML CWC province using data derived from two different sampling devices, an experimental longline and a baited lander, as well as using a different modelling approach with respect to previous studies. In this study data from different devices were used to consider how the type of device might influence either the diversity and number of species or the abundance of some species recorded. In particular, we investigated whether the presence of corals can affect the diversity of the benthopelagic fauna sampled with different devices. In order to achieve this goal, a Bayesian hierarchical modelling approach was adopted to accommodate factors influencing community assemblages. The Bayesian framework provides many advantages in terms of statistical accuracy and quantification of features of uncertainty affecting fish populations (Cressie, Calder, Clark, Hoef, & Wikle, 2009; Royle & Dorazio, 2008). It allows us to suitably model different kinds of effects affecting the relative abundances of species as well as the variation in species composition of communities, with the possibility of acknowledging the distributions of effects with appropriate priors throughout the hierarchy levels (Gelman et al., 2012).

In relation to the conservation difficulties of FRA within the SML CWC province (D'Onghia et al., 2017), a better knowledge of fish habitat use can enhance the conservation perspectives for this hot spot of biodiversity.

2 | METHODS

2.1 | Study area

The SML CWC province is located along the Apulian continental margin, a few miles off Cape Santa Maria di Leuca (Italy) in the Northern Ionian Sea (Central Mediterranean; Figure 1). It has the largest and deepest occurrence of a living deep-sea coral community currently known in the Mediterranean Sea (Bargain et al., 2017; Corselli, 2010; Freiwald et al., 2009; Savini et al., 2014).

Living colonies of *L. pertusa* and *M. oculata* have been collected at depths of 350–1100 m in the SML CWC province (Mastrototaro et al., 2010; Taviani et al., 2005; Tursi et al., 2004), and their westernmost presence was recorded by Freiwald et al. (2009) at depths of 603–744 m and 670–744 m, respectively.

Recently, habitat mapping based on bathymetric and backscatter data, has provided indications of complex topographic features, characterized by coral-hardground and coral mounds with living corals, over an area of about 2000 km^2 at depths of approximately 120–1400 m (Bargain et al., 2017; Savini et al., 2014). A total of 1902 coral mounds were recorded covering approximately 68 km^2 in total, with an average area of 35 000 m^2 per mound (Savini et al., 2014). More recently, a subset of 517 potential coral mounds was predicted using both geomorphometric proxies and the Maxent method (Bargain et al., 2017).

2.2 | Sampling devices and survey methodology

Data come from two different sampling devices, an experimental longline and a baited lander, both employed during spring and autumn seasons. Two experimental longline surveys were carried out in the SML CWC province during May–June and September–October 2010. A commercial fishing vessel was hired for these experimental surveys. The gear was armed with two types of hooks, J-hook 7 and J-hook 9. The sampling was carried out in two types of habitat: (i) a coral habitat characterized by a complex topography (C); and (ii) a non-coral habitat characterized by intermound sea floor (NC). In both habitats the depths examined were between 363 and 668 m. Six hauls with hook size 7 and three with hook size 9 were carried out in each habitat typology during each survey (Tables 1 and 2). More details about the survey methodology are given in D'Onghia et al. (2012).
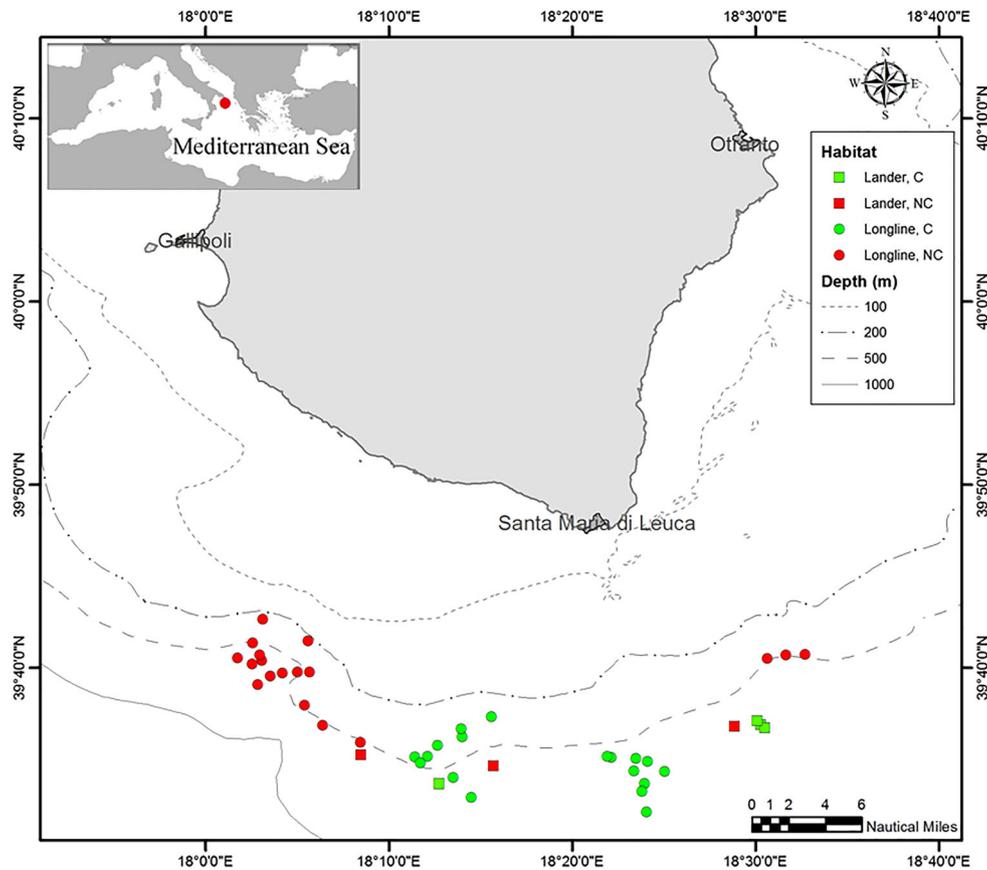
FIGURE 1 Longline and lander stations in the coral (C) and non-coral (NC) habitats of the Santa Maria di Leuca cold-water coral province (Northern Ionian Sea)

The MEMO (marine environment monitoring system) baited lander, equipped with two digital cameras, was deployed during two cruises carried out in June 2010 (CoralFISH project) and November 2010 (OBAMA project). A detailed description of this lander is reported in Capezzuto et al. (2012). The MEMO baited lander was also deployed in the C and NC habitats. Seven deployments were carried out between 547 and 648 m: four in C and three in NC habitats (Table 3).

The stations for the two different devices could not be coincident because of their different sampling coverage.

Video footage of 42 h 28 min and 31 h 27 min was recorded in C and NC habitats, respectively, with a total of 611 520 and 452 880 video frames taken by each camera in C and NC habitats, respectively. During each deployment, the lander was baited with fresh specimens of *Scomber scombrus*.

2.3 | Data analysis

Data analysis was carried out on benthopelagic fauna diversity and abundance, taking into account that the data were collected across time and space during heterogeneous surveys using different devices. Two aims were pursued: investigating the variation in benthopelagic biodiversity at the community level and inferring the relative abundance of selected species in the study area. From a statistical perspective, a suitable Bayesian hierarchical modelling approach is proposed for the two kinds of analyses in order to accommodate factors influencing community assemblages. Possible influencing factors are: the type of survey, classified as longline J-hook 7, longline J-hook 9, and baited lander (hereafter LL7, LL9, and video); the habitat, i.e. C and NC habitat; the season, i.e. spring or autumn (hereafter SP and AU); and finally the haul coordinates, i.e. longitude and latitude (hereafter lonUTM and latUTM).

Two different model specifications are proposed for assessing the peculiarities of the response variables (abundances and biodiversity), even though it is worth stressing that these models share a common structure in the spirit of the Bayesian hierarchical framework, which has many advantages in terms of statistical accuracy, providing the possibility of acknowledging the distribution of effects with specified priors and of quantifying the uncertainty of many features affecting fish communities.

2.4 | Bayesian hierarchical model for biodiversity measures

The investigation of factors affecting the community composition in each haul refers to the number of species (S) and to the Shannon index (H) as a measure of diversity (Magurran, 1991). S is the number of observed species in each haul, from longline and lander, whereas H

TABLE 1 Sampling stations, with mean depths and geographic coordinates, carried out using longline in coral habitat (C) and in non-coral habitat (NC) in the Santa Maria di Leuca (SML) coral province during May–June 2010

			START			END		
Date	Station	Habitat	Depth (m)	Latitude (N)	Longitude (E)	Depth (m)	Latitude (N)	Longitude (E)
28/05/2010	a1	C	396	39°37.355	18°15.599	460	39°36.268	18°13.999
	a2	C	460	39°36.268	18°13.999	437	39°35.171	18°12.116
	a3	C	437	39°35.171	18°12.116	499	39°35.544	18°11.115
29/05/2010	a4	NC	487	39°35.948	18°08.457	503	39°36.880	18°06.380
	a5	NC	503	39°36.880	18°06.380	551	39°37.987	18°05.410
	a6	NC	551	39°37.987	18°05.410	512	39°38.270	18°04.761
30/05/2010	a7	NC	561	39°39.790	18°05.029	594	39°39.103	18°02.848
	a8	NC	594	39°39.103	18°02.848	561	39°40.571	18°01.750
	a9	NC	561	39°40.571	18°01.750	503	39°41.762	18°00.977
31/05/2010	a10	C	512	39°35.135	18°22.134	524	39°34.916	18°24.122
	a11	C	524	39°34.916	18°24.122	594	39°33.692	18°23.950
	a12	C	594	39°33.692	18°23.950	545	39°34.375	18°22.726
07/06/2010	a13	NC	450	39°40.740	18°31.660	470	39°40.545	18°30.647
	a14	NC	470	39°40.545	18°30.647	450	39°40.230	18°28.950
	a15	NC	450	39°40.760	18°32.710	460	39°40.740	18°31.660
08/06/2010	a16	C	550	39°35.060	18°23.480	580	39°33.290	18°23.810
	a17	C	580	39°33.290	18°23.810	620	39°32.150	18°24.050
	a18	C	620	39°32.150	18°24.050	650	39°31.130	18°24.270

TABLE 2 Sampling stations, with mean depths and geographic coordinates, carried out using longline in coral habitat (C) and in non-coral habitat (NC) in the Santa Maria di Leuca (SML) coral province during September–October 2010

			START			END		
Date	Station	Habitat	Depth (m)	Latitude (N)	Longitude (E)	Depth (m)	Latitude (N)	Longitude (E)
17/10/2010	b1	C	404	39°36.692	18°13.953	431	39°35.790	18°12.652
	b2	C	431	39°35.790	18°12.652	479	39°35.153	18°11.423
	b3	C	479	39°35.153	18°11.423	470	39°35.953	18°12.235
29/09/2010	b4	NC	430	39°39.794	18°05.664	594	39°39.744	18°04.182
	b5	NC	594	39°39.744	18°04.182	462	39°40.428	18°03.063
	b6	NC	462	39°40.428	18°03.063	495	39°41.764	18°02.850
23/09/2010	b7	NC	414	39°42.686	18°03.130	512	39°41.385	18°02.583
	b8	NC	512	39°41.385	18°02.583	552	39°40.245	18°02.534
	b9	NC	552	39°40.245	18°02.534	577	39°39.256	18°03.599
15/10/2010	b10	C	528	39°34.368	18°25.032	533	39°34.370	18°23.363
	b11	C	533	39°34.370	18°23.363	524	39°35.191	18°21.903
	b12	C	524	39°35.191	18°21.903	552	39°34.595	18°19.626
24/09/2010	b13	NC	363	39°41.490	18°05.605	594	39°39.588	18°03.535
	b14	NC	594	39°39.588	18°03.535	495	39°40.744	18°02.959
	b15	NC	495	39°40.744	18°02.959	487	39°42.076	18°03.069
16/10/2010	b16	C	528	39°34.817	18°11.716	668	39°32.964	18°14.488
	b17	C	668	39°32.964	18°14.488	530	39°34.013	18°13.500
	b18	C	530	39°34.013	18°13.500	467	39°34.700	18°12.445

TABLE 3 Marine environment monitoring system (MEMO) lander deployments in the Santa Maria di Leuca (SML) cold-water coral community during the CoralFISH and OBAMA cruises in the Mediterranean Sea. C, coral habitat; NC, non-coral habitat

Cruise	Date	Deployment-site	Habitat	Latitude (N)	Longitude (E)	Depth (m)	Time of video record (h, min)
CoralFISH	16/06/2010	St. 1-MS08	C	39°33.6900	18°12.7300	547	14, 09
CoralFISH	17/06/2010	St. 2-MS04	C	39°36.9101	18°30.3000	622	05, 24
CoralFISH	17/06/2010	St. 3-MS04	NC	39°36.8300	18°28.8699	620	15, 37
OBAMA I	05/11/2010	St. 1-MS04	C	39°36.7543	18°30.5021	648	18, 17
OBAMA I	06/11/2010	St. 2-MS04	C	39°37.1367	18°30.1182	610	04, 38
OBAMA I	06/11/2010	St. 3-MS08	NC	39°34.6595	18°15.7071	624	13, 02
OBAMA I	07/11/2010	St. 4-off MS08	NC	39°35.2782	18°08.4744	615	02, 48

is the negative sum of the relative abundances of species multiplied by their natural logarithm in each haul, from both devices.

The two measurements represent different kinds of response variables, and thus S is assumed to follow the Poisson distribution, suitable for counting data, whereas H follows the Gaussian distribution. According to their specifications, both measurements are properly modelled by spatial generalized additive mixed models, with mean values depending upon the fixed effects of the covariates device, habitat, and season, on the interaction between survey and season, and on a smooth function of the spatial coordinates given by a linear combination of spline-like basis functions at a number of knots (Wood, 2017). To accommodate the residual spatial variation, a spatial random component was also considered, in order to improve the accuracy of predictions (Banerjee, Carlin, & Gelfand, 2004). This component has a multivariate normal distribution with zero mean and covariance matrix built by an exponential covariance function (Gneiting, 2002).

2.5 | Bayesian hierarchical model for abundances

Relative abundances of the European conger, *C. conger*, and the blackbelly rosefish, *H. dactylopterus*, were considered as response variables in the Bayesian hierarchical model, as they were the two most abundant species in both types of surveys. The choice of these two species is corroborated by previous results from both longline and lander used in the studied area, where the most abundant species were *C. conger*, *H. dactylopterus*, and *P. bogaraveo* (D'Onghia et al., 2012; Maiorano et al., 2013); *P. bogaraveo* was only found in the coral area and was not considered in the analysis.

A transformation scaling abundance data to the time unit (1 hour) was adopted (*N/h*), giving right-skewed non-negative continuous responses characterized by zero inflation (Figure 2). For each species the relative abundances were modelled by gamma Hurdle models, assuming zero and non-zero data as being generated by two different processes (Hilbe, 2007; Lee, Joo, Song, & Harper, 2011). The basic idea is that abundances are modelled as a mixture of a Bernoulli distribution that governs the binary outcome (zero/non-zero) and a Gamma distribution, suitable for non-negative continuous data. In this framework, zeros and positive realizations can be modelled with different predictors. We assume that the probabilities of zero outcomes depend on the fixed effects of survey, habitat, and season covariates. In PARTICULAR, a marginal effect of the factor habitat on the probabilities of zero abundances might be first suggested by the inspection of the frequency distributions in Table 4.

The means of the non-zero abundances are assumed to depend on the fixed effect of the type of survey and on a latent component that
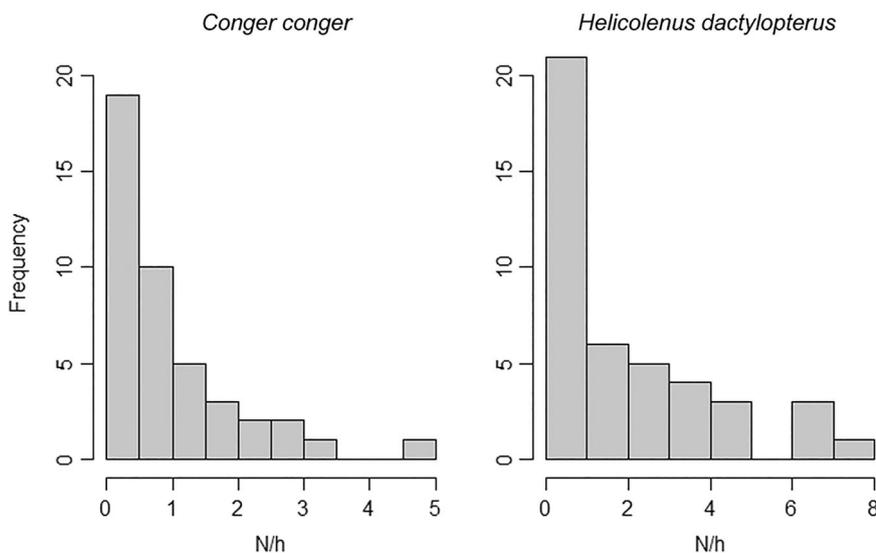

FIGURE 2 Distribution of species relative abundances (*N/h*)

TABLE 4 Distribution of zero and positive abundance values for *Conger conger* and *Helicolenus dactylopterus*, distinguishing between type of habitat

| | | *Conger conger* | | *Helicolenus dactylopterus* | |
		Coral	Non-coral	Coral	Non coral
N/h	0	1	7	1	10
	>0	21	14	21	11

can be considered as the random variation of the relative abundance common to the different surveys. At a lower level of the model hierarchy, this spatially correlated random latent component follows a Gaussian distribution, with its mean depending on the fixed effects of habitat and season, and on a smooth function of the spatial coordinates and spatial correlation given (as specified in Section 2.4).

At the lower level of the model hierarchy, the specification of priors for fixed effects, decay parameter, and precision share the same structure used for the Bayesian hierarchical model for biodiversity measurements, as discussed in Section 2.4.

2.6 | Implementation

For both kinds of models, Bayesian Markov chain Monte Carlo (MCMC) estimation was obtained with JAGS software (JUST ANOTHER GIBBS SAMPLER; Plummer, 2003), which extends standard Gibbs sampling, using further algorithms to sample from the target posterior distribution (Wood, 2016). JAGS obtains samples from the posterior distribution of the model parameters according to five main steps: model definition, compilation, initialization, adaptation/burn-in, and monitoring. Among the existing packages that provide an interface

TABLE 5 Presence/absence of species sampled in coral and non-coral habitats with longline and baited lander

| | | LONGLINE | | BAITED LANDER | |
		coral	non-coral	coral	non-coral
CEPHALOPODS	*Todarodes sagittatus*	–	–	✓	✓
CRUSTACEANS	*Bathynectes maravigna*	–	–	✓	–
	Geryon longipes	–	–	✓	–
	Munida spp	–	–	✓	–
	Nephrops norvegicus	–	–	✓	–
	Paromola cuvieri	–	–	✓	✓
	Plesionika martia	–	–	✓	✓
CHONDRICHTHYES	*Centrophorus granulosus*	✓	✓	–	✓
	Dipturus oxyrinchus	✓	–	–	–
	Etmopterus spinax	✓	✓	✓	–
	Galeus melastomus	✓	✓	–	–
	Hexanchus griseus	–	–	✓	✓
	Leucoraja circularis	✓	✓	–	–
	Leucoraja fullonica	✓	–	–	–
	Prionace glauca	✓	–	–	–
	Pteroplatytrygon violacea	✓	✓	–	–
OSTEICHTHYES	*Brama brama*	✓	✓	–	–
	Conger conger	✓	✓	✓	✓
	Helicolenus dactylopterus	✓	✓	✓	✓
	Lampanyctus crocodilus	–	–	✓	✓
	Lepidopus caudatus	✓	✓	✓	–
	Merluccius merluccius	✓	✓	–	✓
	Micromesistius poutassou	✓	✓	–	–
	Molva dipterygia	✓	–	–	–
	Mora moro	✓	–	–	–
	Pagellus bogaraveo	✓	–	✓	–
	Phycis blennoides	✓	✓	✓	✓
	Polyprion americanus	✓	✓	✓	✓
	Xiphias gladius	✓	–	–	–
Total number of species		20	13	16	11

between R and JAGS, R2JAGS (Su & Yajima, 2015) was used to go through the first four steps, whereas the CODA package (Plummer, Best, Cowles, & Vines, 2006) was used to analyse the MCMC output. All models were run with three chains for 72 000 simulations per chain with a burn-in phase of 12 000 and a thinning interval of five to reduce autocorrelation among iterative samples and to improve the computational efficiency. A total number of 12 000 samples were saved to summarize the posterior distribution for each model. Convergence of the chains to the stationary distribution was determined by monitoring trace plots and computing Gelman–Rubin diagnostics (Gelman & Rubin, 1992).

3 | RESULTS

The list of the species sampled in C and NC habitats both with longline and with baited lander is reported in Table 5.

In the C habitat 20 species were sampled with longline (eight cartilaginous fishes and 12 teleost fishes) and 16 species were observed with the lander (one cephalopod, six decapod crustaceans, two cartilaginous fishes, and seven teleost fishes). In the NC habitat 13 and 11 species were identified with the longline and lander, respectively. In particular, five cartilaginous fishes and eight teleost fishes were sampled with the longline; one cephalopod, two decapod crustaceans, two cartilaginous fishes, and six teleost fishes were observed with the lander.

A preliminary data analysis of the marginal effect of habitat in describing differences in terms of diversity and number of species is shown in Figure 3. No marginal evidence for difference was found between the devices used for measurement or between seasons.

Figure 4 shows the estimates of fixed effects from Bayesian hierarchical models for the number of species and the Shannon–Wiener index. For the sake of simplicity, only the estimates of the main covariate effects are reported, ignoring the effect of haul location that proved not to be relevant for any of the models implemented. A
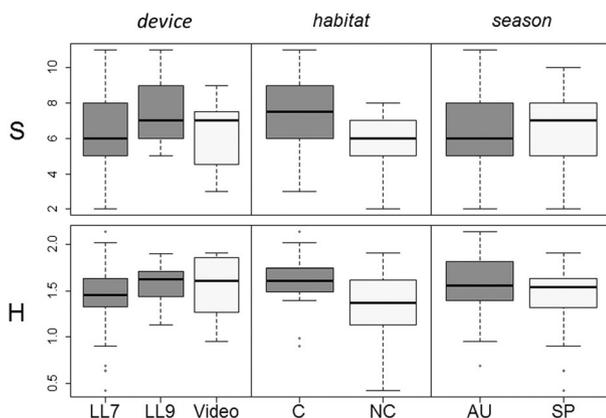

FIGURE 4 Posterior median values, and 95% and 90% confidence intervals (95% C.I. and 90% C.I.), of estimated fixed effects for the number of species (a) and the Shannon index (b). Abbreviations: LL7, longline J-hook 7; LL9, longline J-hook 9; NC, non-coral habitat; SP, spring; Video, baited lander survey

relevant effect of habitat is apparent for both measurements, supporting the preliminary results in Figure 3. In particular, NC habitats support a lower number of species and diversity than found in C habitats. The Shannon–Wiener index generally shows lower values for the spring season (Figure 4). This contrasts with the effect of the interaction between survey and season, showing larger diversity values for longline surveys with J-hook 7 in the spring season.

The estimates and credibility intervals of the main model parameters for the abundances of *C. conger* and *H. dactylopterus* are reported in Figure 5. Hurdle models explain the dependence of zero and positive abundances on different predictors. The left-hand panels of Figure 5 show the relevance of fixed effects on the probability of observing positive (i.e. non-zero) abundances. For both species the negative relevant effect of the NC habitat implies lower probabilities of positive abundances with respect to the C habitat. Evidence of this is obtained from the marginal frequency distribution of positive abundances in the two habitats (Table 4). The spatial distribution of predicted non-zero abundance probabilities (Figure 6) confirms that positive abundances are mostly detected in the C habitat for both species.

The three devices did not prove to have a different influence on the probability of positive abundances of *C. conger* and *H. dactylopterus* (Figure 5, left). Only for *C. conger* is there a higher probability of

FIGURE 3 Distribution of the number of species (*S*) and Shannon index (*H*) for potential factors affecting community composition. Solid horizontal lines represent median values. Abbreviations: AU, autumn; C, coral habitat; LL7, longline J-hook 7; LL9, longline J-hook 9; NC, non-coral habitat; SP, spring; Video, baited lander
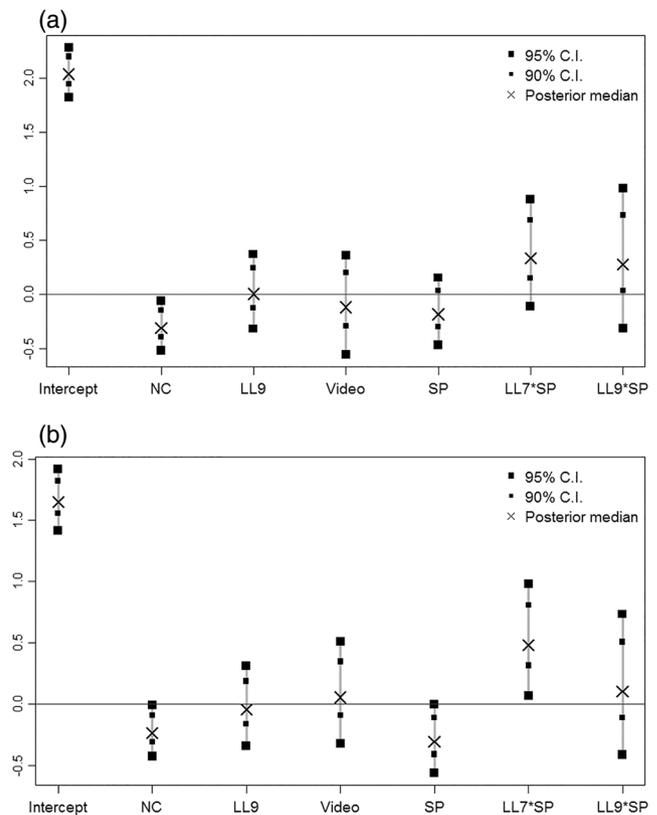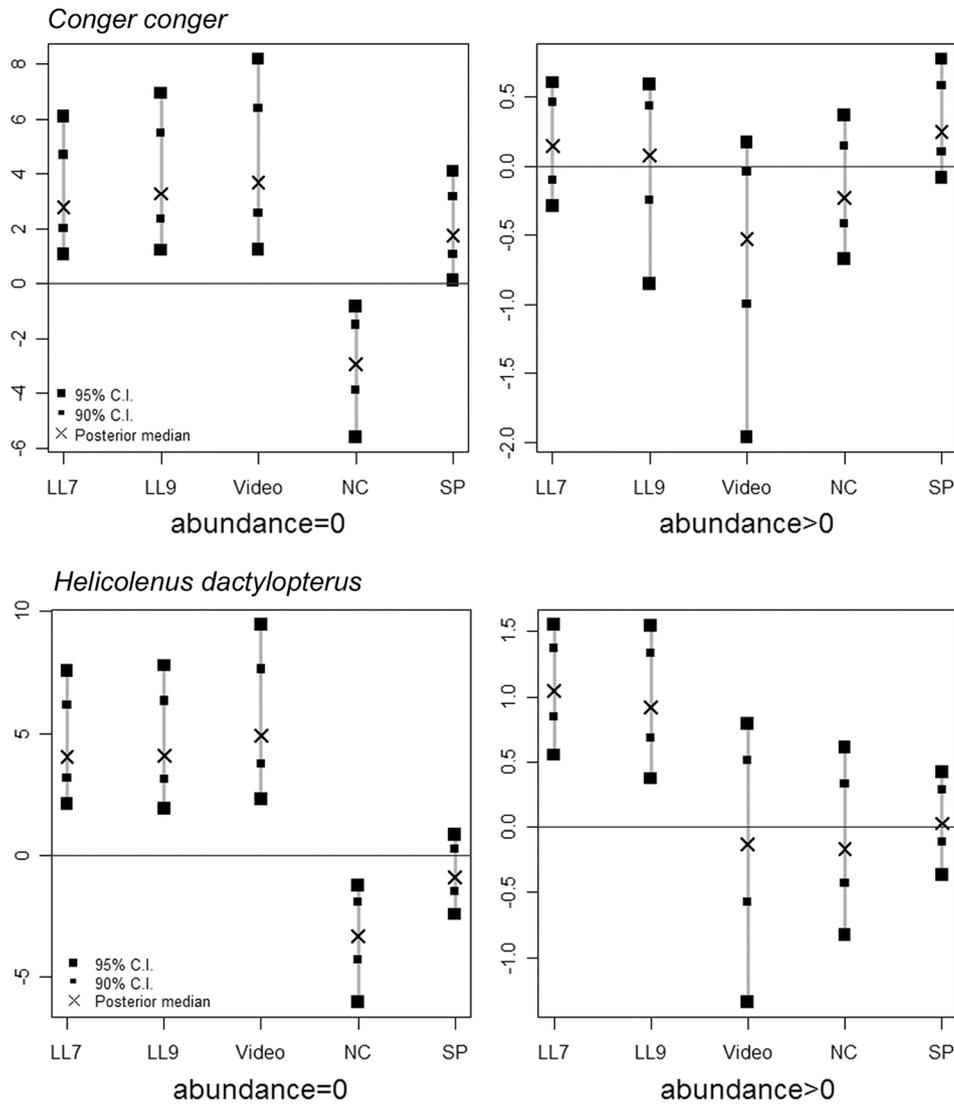
FIGURE 5 Posterior median values, and 95% and 90% confidence intervals (95% C.I. and 90% C.I.), of estimated effects from Hurdle models for *Conger conger* (above) and *Helicolenus dactylopterus* (below). Left-hand panels, effects on the probability of non-zero abundances; right-hand panels, effects on (positive) abundance values

positive abundances in the spring season. The right-hand panels of Figure 5 report estimates and credibility intervals of the model effects on positive relative abundance values. Although no relevant effects on positive abundance related to the different devices can be detected for *C. conger*, a relevant positive effect of longlines (both J-hooks) was detected for *H. dactylopterus*, implying higher abundances of this species for this type of fishing gear than for videos. The spatial distributions of predicted relative abundances are reported in Figure 7, notable confirming the greater abundance of *H. dactylopterus* obtained using longlines.

4 | DISCUSSION

Integrating data from different devices and applying Bayesian hierarchical modelling, these results provide a further contribution to our knowledge about the role of coral habitat in influencing the

benthopelagic diversity and abundance within the SML CWC province. A relevant effect of habitat was detected, showing a higher number of species and a higher diversity in C habitat than in NC habitat, thereby reinforcing previous results (D'Onghia et al., 2010, 2012; Linley et al., 2017; Maiorano et al., 2013). The higher value of the Shannon–Wiener index observed during spring using the longline J-hook 7 might be linked to an increase in evenness during this season. In fact, the Shannon–Wiener index takes into account the relative abundances of the different species; J-hook 7 is also less selective than J-hook 9 at the depths investigated, as it catches a wider range of fish species, and thereby increases equitability among the different species captured.

The devices considered in the model applied did not show different effects on the probability of non-zero abundance for both *C. conger* and *H. dactylopterus*. A relevant habitat effect was detected, with positive abundances for both species in C habitat, as confirmed by the spatial distribution of predicted non-zero abundance. The relevant
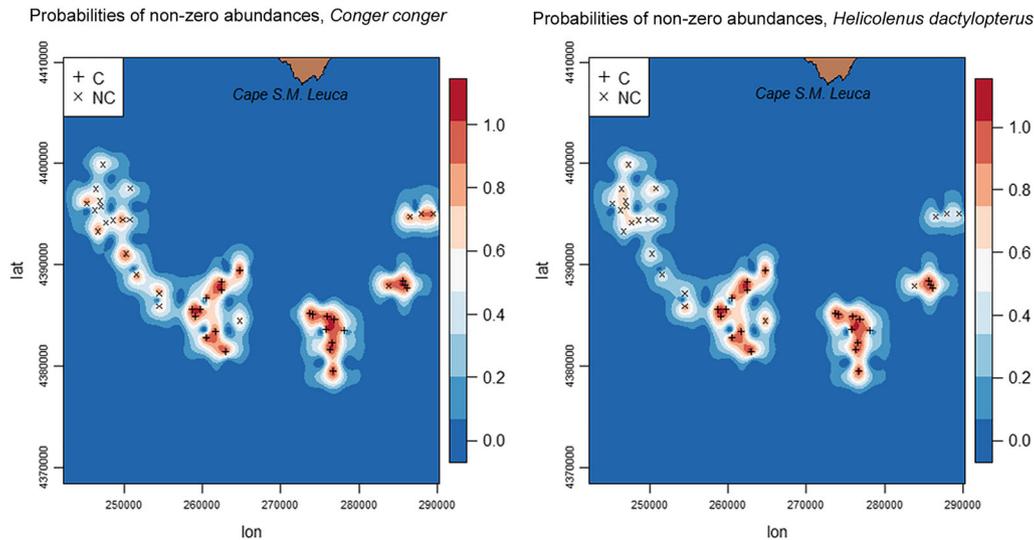
FIGURE 6 Spatial prediction of probabilities of non-zero abundances for *Conger conger* (left) and *Helicolenus dactylopterus* (right), distinguishing between coral (C) and non-coral (NC) habitats
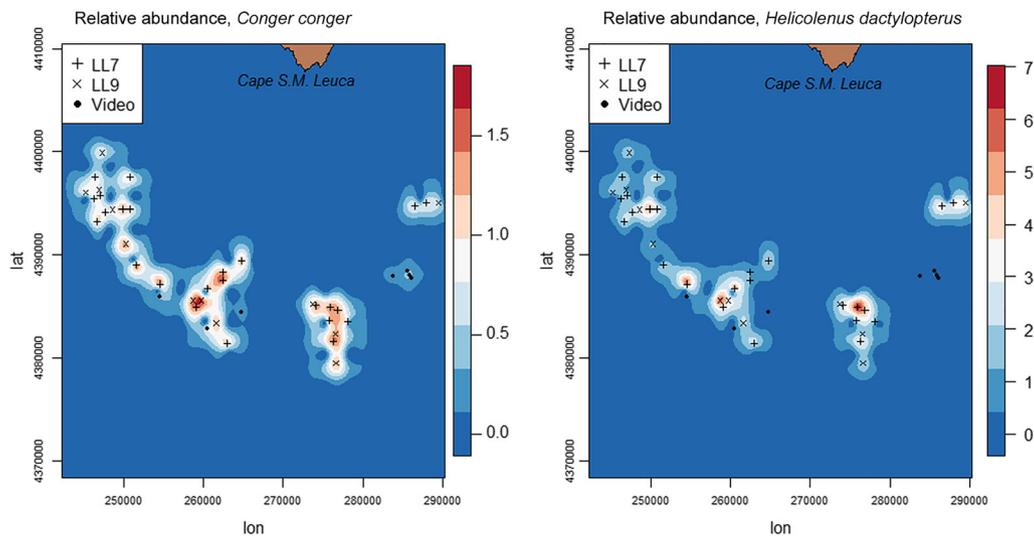

FIGURE 7 Spatial prediction of relative abundance values for *Conger conger* (left) and *Helicolenus dactylopterus* (right), distinguishing between devices: longline J-hook 7 (LL7), longline J-hook 9 (LL9), and baited lander (Video). Note the different scales for relative abundance reported for the two species in this figure

association of *H. dactylopterus* and *C. conger* with corals is in agreement with several previous studies (Biber et al., 2014; Buhl-Mortensen et al., 2017; Costello et al., 2005; D'Onghia et al., 2010, 2011, 2012, 2016; Linley et al., 2017; Mytilineou et al., 2014; Reed, Weaver, & Pomponi, 2006; Roberts et al., 2008; Ross & Quattrini, 2007, 2009; Sulak et al., 2007).

An effect for season was only detected for *C. conger*, probably because of an increase in food availability during spring in the C habitat or the reproductive requirements of adult specimens during this season linked to corals as spawning habitats (D'Onghia et al., 2016). In fact, the European conger is an opportunistic predator and a scavenger living and foraging close to rocky areas, where it finds refuge during the day (Morato, Sola, Gros, & Menezes, 1999; Xavier, Cherel,

Assis, Sendão, & Borges, 2010). Sulak et al. (2007) report *Conger oceanicus* burrowing into the base of *Lophelia* clumps.

A relevant effect for device was only observed for *H. dactylopterus*, showing higher abundances (i.e. greater catchability) for longline than for baited lander. This is probably linked to the behavioural pattern of the blackbelly rosefish, which usually rests on the sea bed, being a typical sit-and-wait ambush predator, feeding mainly on benthic crustaceans, fish, and plankton (Consoli et al., 2010; D'Onghia et al., 2012; Mainzan, Mari, Prenski, & Sanchez, 1996; Nouar & Maurin, 2000; Sulak et al., 2007). For this reason, the longline bait lying on the bottom is more attractive for this fish than the bait of the lander set on a plate above the bottom. With its greater mobility and roaming behaviour, no difference was detected in the attractiveness of bait

between lander and longline devices for the European conger (D'Onghia et al., 2011).

The model highlighted that the presence of corals affects the diversity and abundance of the benthopelagic fauna in the SML CWC province, showing some differences between longlines and baited lander in detecting the distribution of two different fish species. Although both species may be considered scavengers, differences in their behaviour lead to differences in their abundance estimates via longline and baited lander.

Some authors report that behaviour influences the composition of deep-sea faunal assemblages and species relative abundances, subsequently affecting the biodiversity indexes calculated using different methodologies (Ayma et al., 2016). Consequently, as different devices differ in attractiveness for species because of the differing behaviours of the species, a proper analysis of the fauna assemblage would require the combined use of different devices in order to obtain better estimates of the diversity and abundance of the fauna associated with coral habitat.

Finally, the present study finds a significant influence of cold-water corals on the distribution and diversity of benthopelagic fauna and reinforces that the use of different methodologies may help to mitigate individual selectivity. At same time, different devices can also contribute to providing complementary information on the small-scale distribution of benthopelagic fauna as a consequence of behaviour. Although a direct linkage between benthopelagic fauna and corals has not been investigated in this study, the associations observed between fishes and habitats is of paramount importance in the development of a credible system of monitoring, control, and surveillance of the SML CWC province, in order to gain a better conservation perspective with ecosystem-based approaches to fisheries management (Rosenberg, Bigford, Leathery, Hill, & Bickers, 2000). The role of the CWC province as EFH with a beneficial influence on fisheries resources has been previously demonstrated (Capezzuto, Sion, et al., 2018; Capezzuto, Ancona, et al., 2018; D'Onghia, 2019; D'Onghia et al., 2019). The extensive three-dimensional CWC habitat hosts a great variety of species, for which it acts as a feeding, spawning, and refuge area from fishing (Baillon et al., 2012; Bo et al., 2015; Capezzuto, Ancona, et al., 2018; Capezzuto, Sion, et al., 2018; Cau et al., 2017; Costello et al., 2005; D'Onghia et al., 2016, 2019; Freiwald et al., 2004; Henry et al., 2013; Husebø et al., 2002; Kutti et al., 2014; Quattrini et al., 2012; Reed, 2002; Ross & Quattrini, 2007). Indeed, the presence of species at the top of the marine food web, such as *Centrophorus granulosus* and *Hexanchus griseus*, respectively considered Critically Endangered and of Least Concern in the International Union for Conservation of Nature (IUCN) European Red List of Marine Fishes (Nieto et al., 2015), and those of commercial interest such as *Helicolenus dactylopterus*, *Merluccius merluccius*, *Pagellus bogaraveo*, and *Polyprion americanus*, with *M. merluccius* considered Vulnerable in the IUCN Mediterranean Regional Red List (Relini et al., 2017), could emphasize the role of the SML CWC province as a partial refuge from fishing activity, and could stress the need for its protection. CWC communities are impacted by anthropogenic activities (Hinz, 2017). The major direct impacts are linked to deep-water fishing activities, which mainly include longlining and accidental trawling, discarded/lost gear, dumping, and littering. This also occurs in the SML CWC province where an FRA has been established (D'Onghia et al., 2017). A lack of monitoring, control, and surveillance could make the FRA ineffective. Therefore, management initiatives are urgently required to prevent further overexploitation and habitat loss (Capezzuto, Ancona, et al., 2018; D'Onghia et al., 2017; Grehan, Arnaud-Haond, D'Onghia, Savini, & Yesson, 2017).

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