



Marine reserve spillover: Modelling from multiple data sources



Edwige Bellier ^{a,b,*}, Philipp Neubauer ^c, Pascal Monestiez ^a, Yves Letourneur ^d, Laurence Ledireach ^e, Patrick Bonhomme ^e, Frédéric Bachet ^f

^a INRA, UR 546 Biostatistics and Spatial Processes, (BioSP), F-84914 Avignon, France

^b Mediterranean Institute of Oceanology, University of Aix-Marseille II, Parc Scientifique et Technologique de Luminy, Case 901, 13288 Marseille Cedex 9, France

^c Institute of Marine and Coastal Sciences, Rutgers University, 71 Dudley Rd, New Brunswick, NJ, USA

^d Université de la Nouvelle-Calédonie, Laboratoire LIVE et LABEX "Corail", BP R4, 98851 Nouméa Cedex, New Caledonia

^e GIS Posidonie, Parc Scientifique et Technologique de Luminy, Case 901, 13288 Marseille Cedex 09, France

^f Parc Marin de la Côte Bleue, Observatoire du Parc, BP 42, 13620 Carry-le-Rouet, France

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ABSTRACT

The functional form of spillover, measured as a gradient of abundance of fish, may provide insight about processes that control the spatial distribution of fish inside and outside the MPA. In this study, we aimed to infer on spillover mechanism of *Diplodus* spp. (family Sparidae) from a Mediterranean MPA (Carry-le-Rouet, France) from visual censuses and artisanal fisheries data. From the existing literature, three potential functional forms of spillover such as a linear gradient, an exponential gradient and a logistic gradient are defined. Each functional form is included in a spatial generalized linear mixed model allowing accounting for spatial autocorrelation of data. We select between the different forms of gradients by using a Bayesian model selection procedure. In a first step, the functional form of the spillover for visual census and artisanal fishing data is assessed separately. For both sets of data, our model selection favoured the negative exponential model, evidencing a decrease of the spatial abundance of fish vanishing around 1000 m from the MPA border. We combined both datasets in a joint model by including an observability parameter. This parameter captures how the different sources of data quantify the underlying spatial distribution of the harvested species. This enabled us to demonstrate that the different sampling methods do not affect the estimation of the underlying spatial distribution of *Diplodus* spp. inside and outside the MPA. We show that data from different sources can be pooled through spatial generalized linear mixed model. Our findings allow to better understand the underlying mechanisms that control spillover of fish from MPA.

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1. Introduction

Marine protected areas (MPAs) provide refuges where populations of exploited species can recover and habitats modified by fishing can regenerate. Such MPAs aimed at the enhancement of local fisheries have recently been established around the world (Gray and Campbell, 2009; Lubchenco et al., 2003; White et al., 2008). These MPAs are intended to protect critical spawning stock biomass, intraspecific genetic diversity, population age structure, recruitment supply, and ecosystem balance while maintaining local fisheries (Cadiou et al., 2009; Halpern et al., 2008, 2010; Pelletier et al., 2005; Roberts and Polunin, 1991; Roberts et al., 2001).

Evidence from theoretical models and empirical studies suggests that higher abundances of fish inside MPAs can lead to spillover of fish beyond the boundaries of the MPAs (Goni et al., 2008; Halpern et al., 2009; Harmelin-Vivien et al., 2008; Januchowski-Hartley et al., 2013; Perez-Ruzafa et al., 2008; Rakitin and Kramer, 1996). Furthermore,

frequency-dependent models of animals' distribution such as the Ideal Free Distribution (Fretwell and Lucas, 1970) predict that animals should prefer to move from areas where their density is high relative to resources to areas where it is lower. If fish emigration from reserves is an important factor determining the distribution of fishes, abundance should be maximal in the centre of the reserve decreasing gradually beyond the boundaries (Gell and Roberts, 2003; Roberts and Polunin, 1991). Rakitin and Kramer (1996) proposed hypothetical effects of marine reserves on the spatial distribution of fishes based on their mobility and catchability. Kellner et al. (2007) used a theoretical model to project the spatial patterns that would likely be observed for species under different assumptions of mobility and spatial distribution in fishing pressure. Their results show that fishing around the MPA has a significant impact on the spatial patterns of fish density both within and outside the protected zone. Perez-Ruzafa et al. (2008) simulate potential spillover rates and distances by using a spatially-explicit population growth and harvest model. Abundance of fish decreases from the inside to the outside of the MPAs in function of the harvesting, the mobility (diffusion or passive diffusion) of fishes and population growth effects like density-dependence. The slope depends on the strength of the diffusion process, whereas the functional form of the gradient will depend on the spatial

* Corresponding author at: Norwegian Institute for Nature Research-Postboks 5685 Sluppen, 7485 Trondheim, Norway. Tel.: +47 73 80 15 52; fax: +47 73 80 14 01.

E-mail address: edwige.bellier@nina.no (E. Bellier).

distribution of fishing pressure. When the diffusion process becomes important, the slope of the spillover is expected to be weakly negative, whereas it becomes highly negative with increasing fishing pressure. Hypotheses on the factors leading to different shapes of negative gradients can be discussed (Chapman and Kramer, 1999; Halpern et al., 2009; Kellner et al., 2007; Rakitin and Kramer, 1996).

Data issued from monitoring programmes of MPAs are issued most often from different sampling methods because sampling techniques inside and outside the MPA might be different. For instance, data are collected by experimental or artisanal fishing outside a MPA, while inside a MPA, the data can only be collected from underwater visual censuses. The data issued of these kinds of sampling are not normally distributed because counts are discrete and have a positive skewed distribution. Moreover, spatial autocorrelation is rarely taken account explicitly in studies that evidence spillover and its spatial extent (Abesamis et al., 2006; Harmelin-Vivien et al., 2008; La Mesa et al., 2011; Roberts et al., 2001). This may produce misleading results when traditional statistical methods are used to analyse such data. In this case, hierarchical modelling is a promising alternative model building strategy where data can enter at different levels of the hierarchy (Clark, 2007; Clark and Gelfand, 2006; Cressie et al., 2009). Integration of multiple sources of data, collected to analyse the same ecological process, leads to reduce the uncertainty associated to the parameters estimation (Cressie et al., 2009). In a hierarchical model, the levels correspond to either observations or conceptual, but unobservable, latent processes. A spatial latent variable describes an unobservable process which influences the realization of a random variable. The latent variable and the observed variable are linked by a sampling model that allows accounting for measurement errors.

In this paper, we developed our framework from a spatial generalized mixed effect model (Diggle et al., 1998). This model offers the possibility to estimate a spatial underlying density conditioned by an observed variable for which the distribution can be non-normal. This hierarchical spatial model is casted in a Bayesian framework, implemented by Markov chain Monte Carlo method, to solve the prediction problem of the underlying density, making a proper allowance for the uncertainty in the estimation of the parameters of the model. Here, we included different functional shapes of spillover in the spatial generalized mixed effect model and used a model selection procedure to discriminate between the different shape functions of spillover. We combine multiple data sources in a single model to improve the robustness of the estimation of the spillover parameters with respect to the

results found for individual datasets. These different data sources came from different sampling techniques but reflect the same ecological process, specifically the spatial distribution of a harvested fish species in and out of a protected area. We implement our hierarchical spatial model to evidence the shape of the spillover of *Diplodus* spp. from the MPA of Carry-le-Rouet (Mediterranean, France). The selected model allows us to propose some hypotheses on the different processes that can lead to observe such shape of spillover of *Diplodus* spp. from the MPA of Carry-le-Rouet.

2. Methods

2.1. Case study system

The MPA of Carry-le-Rouet, in the French Mediterranean coasts was created in 1982 and covers a surface area of 85 ha (no-take area) from 0 to 30 m of depth (Harmelin-Vivien et al., 2008). *Posidonia oceanica* meadows and rocky substratum are the main habitats down to 30 m depth. Below, sandy bottom is predominant. In the MPA of Carry-le-Rouet, all fishing activities (professional and recreational) are forbidden since its creation. Anchoring and scuba diving are forbidden since 1990.

Abundance of *Diplodus* spp. (mainly *D. sargus* and *D. vulgaris*) was recorded in standardised sheets by underwater visual censuses (hereafter, UVC's) using 25 × 5 m belt-transects parallel to the coast on rocky substrates between 6 and 12 m depth and 50 × 50 m on meadows of *P. oceanica*. Actual observed number of fish was recorded up to 10 individuals, and higher numbers were ascribed to one abundance category (11–30, 31–50, 51–200, 201–500, >500 individuals) often used in UVCs (as recommended by Harmelin-Vivien et al. (1995), we used the median values in the analysis). A total of 162 censuses were performed by the same team of well-trained scientific divers from June to October 2003. The warm season (June to October) is the most suitable period for assessing fish abundances in the Mediterranean, as fish communities are more diverse and do not vary strongly in density during this period (Harmelin, 1987). The variance among replicates was thus reduced during this period making it easier to detect spatial patterns of distribution and avoiding any significant seasonal effect. The general sampling design applied was the following: six sectors, separated by about 1000 m, were positioned at increasing distances from the core of the MPA (three inside the MPA and three in fished areas outside the MPA). In each sector, three zones were randomly chosen and located at a scale of 100 m (Fig. 2 in Harmelin-Vivien et al. (2008)).

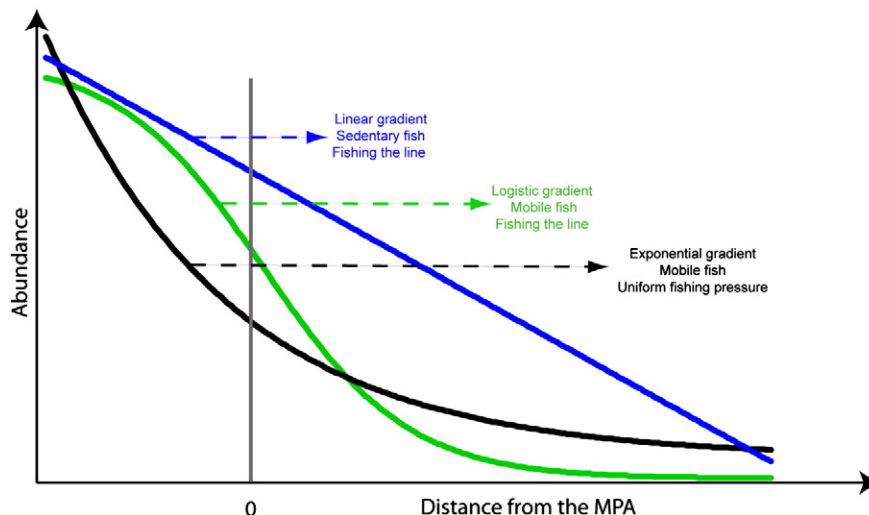


Fig. 1. Hypotheses on the different shapes of spillover deduced from Rakitin and Kramer (1996) and Kellner et al. (2007).

Table 1

Diplodus spp. counted by UVCs or caught by the artisanal fishing with different gears (in italic> for different classes of distances from the MPA boundary (negative values indicate samples inside the MPA).

Distance from MPA (in metres)	-300	-150	150	300	600	900	>900
Visual census	546	273	61	192	98	64	95
Artisanal fishing			68	14	11	12	34
<i>Trammel net</i>			0	12	11	0	2
<i>Gillnet</i>			0	0	0	2	24
<i>Combined net</i>			68	2	0	10	8

Finally, six transects (replicates) separated by 10 m were sampled in each zone (Fig. 2). The whole visual census sampling is composed of 108 transects inside and outside of the MPA.

The fishing fleet operating around the MPA of Carry-le-Rouet is constituted of 11 boats, mainly working with traditional coastal metiers (using trammel nets, gill nets, and combined nets). The sampling design focused on the metiers evoked above, and targeting *Diplodus* species which were known to show a positive reserve effect (Garcia-Charton and Perez-Ruzafa, 1999; Harmelin-Vivien et al., 1995).

2.2. Modelling approach

Count data of animals cannot be modelled directly by a normal distribution because these data are discrete and positively skewed (Flechter et al., 2005). Here, we introduced a spatial generalized linear mixed model (Diggle et al., 1998) to account explicitly of the spatial dependence of our ecological data, their non-normal nature and the observation process. Spatial generalized linear mixed models are an extension of the conventional geostatistical method, it allows for modelling observed counts with a Poisson distribution with intensity (i.e. mean). λ be distributed as a lognormal variable. This generalization forms the basis of many models for spatially referenced counts (Moller et al., 1998; Royle et al., 2007; Thogmartin et al., 2004; Wikle, 2003; Wolpert and Ickstadt, 1998). The observed number of individuals N at location i is modelled using an homogeneous Poisson process so that $N_i \sim Poisson(\lambda_i)$ where λ is the expected number of observation or catch by sampling unit,

$$N_i \sim Poisson(\lambda_i) \tag{1}$$

$$h(\lambda_i) = \beta m_i + S_i + \varepsilon_i \tag{2}$$

where h is the link function that links the linear predictor to the expected value at the data point. In our model the link function is the logarithm function \log , m can be an environmental covariate or a gradient function of distance d as in our study, β is a parameter to be estimated which gives information on the incidence of the slope of the model, the more the value was high and negative, the more the gradient had a

Table 2

Estimated parameters and their 95% credibility intervals of the parameters of models M1, M2 and M3 fitted from artisanal fishing and visual census data on the west part of the marine protected area of Carry-le-Rouet and their deviation information criterium (DIC) values. The selected model is highlighted in bold. The inclusion point β_1 gives the shape to the model M2 and M3, the sign of the logistic gradient is given by β_2 . The variance the Gaussian spatial field S is s , and the scale parameter is a (effective scale is $3a$). The scale parameter a is given in metres.

Model	Parameters	Artisanal fishing			DIC	Visual census			DIC
		$q_{0.025}$	Median	$q_{0.95}$		$q_{0.025}$	Median	$q_{0.95}$	
M1	β_1	-0.9	-0.6	-0.3	112.35	-3.3	-1.1	0.4	10715
	s	1.86	4.07	10.98		0.71	3.76	7.2	
	a	0.5	1.5	43		5.7	16	203	
M2	β_1	-1.11	-0.98	-0.8	110.48	-1.2	-0.67	0.06	5898
	s	1.81	3.94	11.98		0.35	1.84	3.52	
	a	0.5	2.4	51		4.8	12.7	169	
M3	β_1	-17	-5.2	-2.9	110.92	-6.9	-5.1	-4	6349
	β_2	2.14	2.7	3.27		-0.22	1.17	2.43	
	s	2.23	4.09	6.83		0.56	2.85	5.02	
	a	1.2	5.9	245		1.7	5.3	104	

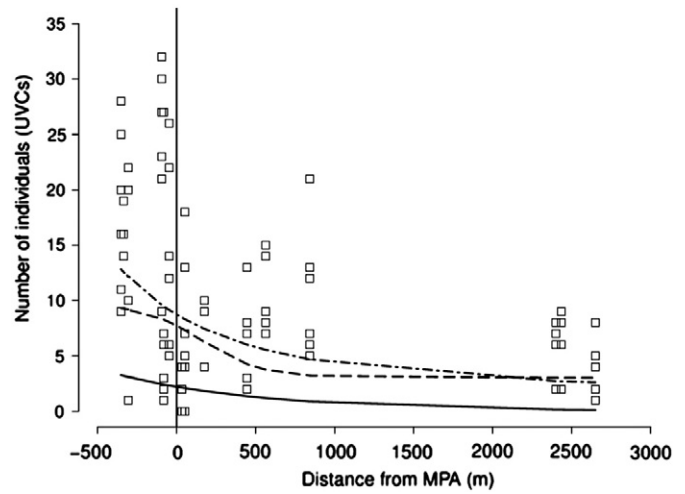


Fig. 2. Number of individuals of *Diplodus* spp. counted by UVCs in relation to the distance (in m) from the boundary of the MPA. The vertical line at distance zero indicates the MPA boundary; plain line: linear model (M1), dotted line: exponential model (M2), point dotted line: logistic model (M3).

steep slope. The latent Gaussian spatial process S_i is estimated from an exponential spatial covariance model

$$\rho(u) = s * \exp\left(-\frac{u}{a}\right)$$

where u is the Euclidian distance, s is the variance of the spatial Gaussian field, and a is the spatial scale parameter. The Gaussian noise ε_i has a mean equal to 0 and a variance σ^2 .

2.2.1. Modelling spillover with a spatial generalized linear mixed model

Mobility and catchability of fishes influence the effect of marine reserves on the spatial distribution of fish (Halpern et al., 2009; Rakitin and Kramer, 1996). Different shapes of gradient of abundances could emerge under the hypotheses of different spatial repartition of fishing effort around the MPA (Kellner et al., 2007). From these studies, we selected three shapes of gradient of abundance (Fig. 1). The shape function is included in a spatial generalized linear model formulation (Eq. 2),

$$M_1 : h(\lambda_i) = \beta_0 + \beta_1 * d_i + S_i + \varepsilon_i \tag{5}$$

$$M_2 : h(\lambda_i) = \beta_0 + \exp(\beta_1 * d_i) + S_i + \varepsilon_i \tag{6}$$

$$M_3 : h(\lambda_i) = \beta_0 - \frac{\beta_2}{1 + \exp((d_i - \beta_3) * \beta_1)} + S_i + \varepsilon_i. \tag{7}$$

From Rakitin and Kramer (1996), Kellner et al. (2007) and Halpern et al. (2009), we assume that a linear gradient (M_1) of abundance of

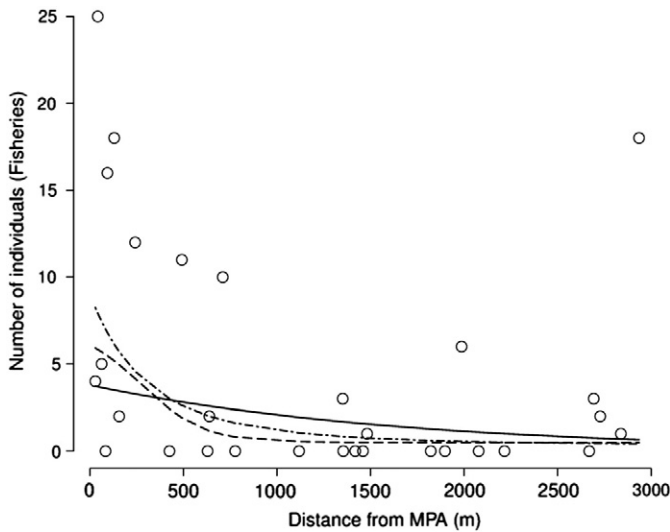


Fig. 3. Number of individuals of *Diplodus* spp. caught by artisanal fishing in relation to the distance (in m) from the boundary of the MPA; plain line: linear model (M1), dotted line: exponential model (M2), light point dotted line: logistic model (M3).

fish is expected for relatively mobile and moderately catchable fish under uniform fishing pressure, an exponential gradient (M_2) is expected for moderate mobile fish under uniform fishing pressure, a logistic gradient (M_3) is expected for sedentary highly catchable fish under uniform fishing pressure (Fig. 1).

2.2.2. Modelling spillover from multiple data sources

Since it is based on conditional probabilities, hierarchical modelling offers the opportunity to combine different sources of data, but quantifying the same ecological processes. The different data sets are independent conditionally to one or further parameters defining a single spatial latent variable,

$$Y_i = \text{Poisson}(\lambda_i) \tag{8}$$

$$h(\lambda_i) = \beta_0 v_i + \exp(\beta_1 * d_i) + S_i \tag{9}$$

where v_i are explanatory variables which can be factors that might represent different sampling techniques or quantitative explanatory variables and β_0 is the observability parameter.

2.2.3. Bayesian estimation by Monte Carlo Markov chain

The parameters of the models are estimated in a Bayesian framework using Markov chain Monte Carlo algorithm. Non-informative priors were defined for the different parameters of the model (see Appendix) in the same manner with Diggle et al. (1998). The algorithm was developed in the free software package R (R Development Core Team, 2010) using conventional methods based on the Metropolis–

Table 3

Estimated parameters of the exponential function (M2) and their 95% credibility intervals by combining the visual census data and the artisanal fishing. Each observability ratio is related to each sampling technique.

Parameters	Artisanal fishing and visual census			DIC
	$q_{0.025}$	Median	$q_{0.95}$	
β_1	-4.3	-2.4	-0.38	11028
s	1.73	3.04	4.83	
a	1.3	6.3	351	
B_0 trammel net	-1.29	0.423	0.474	
B_0 gillnet	-0.759	0.158	1.164	
B_0 combined net	-0.17	0.406	0.959	
B_0 UVCs	-1.592	0.094	1.28	

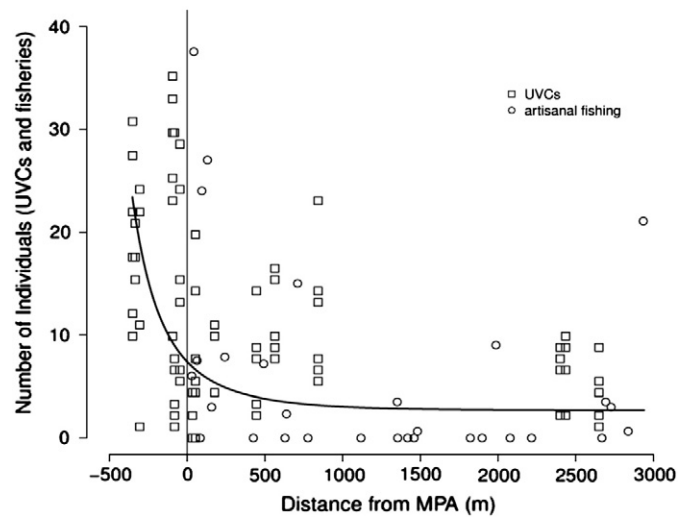


Fig. 4. Joint modelling of UVCs and artisanal fishing data. Dots are number of individuals of *Diplodus* spp. caught by artisanal fishing. Squares are number of individuals counted by UVCs. The vertical line at distance 0 indicates the MPA boundary. Plain line: exponential model fitted to UVCs and artisanal fishing data.

Hastings algorithm and Gibbs sampling (Robert and Casella, 1999). We generated two chains of length 200,000, discarding the first 100,000 as burn-in. The burn-in and the length of the chain needed have been obtained from the statistics defined by Raftery and Lewis (1995) included in the package R Coda (Plummer et al., 2009). The convergence was assessed using the Gelman and Rubin statistic (Gelman et al., 2004). We used the deviance information criterion (DIC) for the selection procedure of the different models (Spiegelhalter et al., 2002).

3. Results

For both datasets, the raw counts decreased when the distance from the MPA increased (Table 1), while a slight increase was observed for distance >900 m for the visual censuses. All the estimates of the median of the posterior distribution of the β_1 were negative (Table 2) for the 3 models fitted on both data set. The exponential model was associated for both dataset to the lower deviation information criterium value (110.48 for the artisanal fishing and 5898 for the UVCs). The slope of the exponential model decreased for UVCs (Fig. 2) and the artisanal fishing until ~1000/1500 m (Fig. 3) giving an approximation of the distance of the spread of the spillover. For the artisanal fishing, the 95% credibility intervals never included zero, which confirms that the slope of the gradient is clearly negative. For the UVCs the 95% credibility included zero for each model (Table 2). The logistic model had also a weak DIC (Table 2). The linear model had larger values compared to the exponential and the logistic models (Table 2). The joint modelling of the two datasets with and without explicative variables gave negative median estimates of the parameter β_1 (-0.0021, Table 3) and the 95% credibility intervals never include zero (-0.003 and -0.0021). The slope of the gradient is clearly negative (Fig. 4) and the scale of the spillover is estimated at 2000–2550 m (Table 3; Fig. 4). The estimation of the observability parameter β_0 gave information on how the different sampling methods affected the estimation of the spatial abundance of the species.

4. Discussion

In this study, we qualified and quantified the spillover of a harvested fish in the Mediterranean. The exponential model was selected for both data sources quantifying the spatial abundance of *Diplodus* spp. inside and outside the MPA. Following the hypotheses exposed in Fig. 1, the selected functional shape of spillover of *Diplodus* spp. is consistent with

their mobilities and spatial distribution of fishing pressure around MPA (Harmelin-Vivien et al., 2008; La Mesa et al., 2011). Relatively mobile fish such as *Diplodus* spp. should exhibit a shallower gradient of abundance across the reserve boundaries such as an exponential shape, whereas sedentary fish should exhibit a steep gradient (i.e. linear gradient) and highly mobile fish a flat gradient (Fig. 1). The artisanal fishing pressure around the MPA of Carry-le-Rouet was relatively spatially uniform (Harmelin-Vivien et al., 2008). Uniform fishing is also associated to shallower gradient of spatial fish distribution outside and inside the MPA while “fishing the line” practices should lead to a linear gradient or a logistic gradient (Kellner et al., 2007).

Few empirical studies have documented explicitly spatial gradient in abundance across reserves and adjacent areas (Goni et al., 2008; Harmelin-Vivien et al., 2008; Murawski et al., 2005). Our results do not only confirm but reinforce the evidence of spillover already shown by Harmelin-Vivien et al. (2008) and Goni et al. (2008) in the NW Mediterranean area using generalized additive models. Our study allows giving a functional shape to spillover leading to a better inference on the processes producing exportation of fish from MPAs. Our models estimate a spillover distance of approximately 1 km from UVCs and artisanal fishing modelled independently and jointly. Our results in terms of shape and scale of spillover are in line with the results of the theoretical study of Perez-Ruzafa et al. (2008). By using a spatially-explicit population growth and harvest model, they show that the simulated spillover has an exponential form that vanish around 2000 m from the boundaries of the MPA. Furthermore, Roberts and Polunin (1991) and Russ (2002) concluded that the increase of the catches due to spillover should not exceed 1 km with an even more clear effect on short distance. The observed differences in the estimates of the scale of spillover from visual census and artisanal fishing could be explained by the behaviour of fish. Export of fishes naïve to exploitation from marine reserves has greater catchability leading to differences between underwater visual census and catch data (Januchowski-Hartley et al., 2013).

The estimation of the range of the exponential covariance function presents rather large uncertainty. One possible reason of this large uncertainty is the way of considering the sampling design when analysing the data. In this study the artisanal fishing sampling and the transect sampling are assumed to be “punctual location of sampling” which artificially reduced the spatial sampling effort and in turn can increase the uncertainty of the range estimation. Furthermore, the range of the exponential model is not finite but asymptotically infinite that leads often to large uncertainty in the estimates of this parameter (Webster and Oliver, 2007). Modelling spillover of fish explicitly from a distinct shape function is a way to model the non-constant spatial mean often observed in the spatial distribution of a species (Fortin and Dale, 2005). The latent spatial field estimated in this study corresponds to the underlying spatial constant mean of the harvested species. Local heterogeneity observed in the estimated latent density of *Diplodus* spp. might be due to factors acting at different scales on the species distribution (Garcia-Charton and Perez-Ruzafa, 1999). Habitat quality can be different inside and outside the MPA, schooling behaviour and territoriality can influence the spatial distribution of fish inside and outside of the MPA (Claudet et al., 2010). Fishes can differ in their response to protection depending on their size, habitat preferences or schooling behaviour.

5. Conclusion

Including functional shape in a spatial generalized linear mixed model allows selecting between different shapes of spillover and associating multiple sources of data to reduce the uncertainty on the estimation of the shape function. This might aid when management measures relative to harvested species have to be taken. Further work is required to extend this model to two dimensions in order to take into account in a more efficient manner the different fishing pressures outside the MPA.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2013.09.004>.

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