Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover?

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ABSTRACT

Marine protected areas (MPAs) are considered as an effective tool in marine coastal management, and considered able to enhance local fisheries through adult fish spillover. Indirect evidence of fish spillover could be obtained by horizontal gradients in fish abundance. To address this question, the existence of gradients of fish abundance and biomass across marine reserve boundaries was assessed in six Mediterranean MPAs using underwater visual censuses performed at various distances from the core of the MPA, in integral reserve (IR), to buffer zone (BZ) and fished areas. A reserve effect was evidenced with higher values of fish species richness (×1.1), abundance (×1.3), and biomass (×4.7) recorded inside MPAs compared to adjacent fished areas. Linear correlations revealed significant negative gradients in mean fish biomass in all the reserves studied after the effect of habitat had been removed, whereas negative gradients in abundance were less conspicuous. Generalized additive models suggested two main patterns of biomass gradients, with a sharp decrease at the IR–BZ boundary or at the BZ–fished area boundary. It was estimated that fish spillover beneficial to local fisheries occurred mostly at a small spatial scale (100s of metres). The existence of regular patterns of negative fish biomass gradients from within MPAs to fished areas was consistent with the hypothesis of adult fish biomass spillover processes from marine reserves and could be considered as a general pattern in this Mediterranean region.

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1. Introduction

Marine protected areas (MPAs) are widely promoted as a conservation tool for biodiversity and habitats and are used to protect or restore fish species populations, but they are also predicted to benefit adjacent fisheries through two main mechanisms: net emigration of adult and juvenile fishes ("spillover effect", Rowley, 1994), and export of pelagic eggs and larvae from restored spawning stocks inside the MPA (Roberts and Polunin, 1991; Gell and Roberts, 2003; Alcala et al., 2005). Previous studies have demonstrated a positive effect of MPAs on adjacent fisheries, mainly in coral reef areas, by analysing long-term data (Russ and Alcala, 1996; Roberts et al., 2001; Russ et al., 2004) or measuring gradients of biomass through the marine reserve border (Rakitin and Kramer, 1996; Chapman and Kramer, 1999; Kaunda-Arara and Rose, 2004; Abesamis et al., 2006). If analysing the effect of fish spillover on a time scale gives the best evidence of fish spillover (Russ et al., 2003; Abesamis and Russ, 2005), such studies need longer-term efforts compared to studies performed at a horizontal spatial scale (Halpern et al., 2004).

Gradients of fish abundance and biomass have been advocated as a simple tool for evidencing fish spillover across reserve boundaries and assessing the distance of influence of the reserve (Rakitin and Kramer, 1996; McClanahan and Mangi, 2000; Ashworth and Ormond, 2005; Abesamis et al., 2006). A theoretical evaluation of the significance of gradients was recently modelled by Kellner et al. (2007) who proposed that emigration of fish from MPAs, as well as home range movements and relocation of fish, can be expected to produce a gradient of abundance across marine reserve boundaries. Their model showed that considering the effect of harvesting and the diffusion rate of species, the distribution of abundance or biomass with increasing distance from an MPA should produce a gradient in the form of a curve with a lower negative slope as the diffusion process becomes more important or as the fishing pressure increases. These negative gradients of fish abundance or biomass through MPA boundaries could be interpreted as evidence of spillover of adult fish beneficial to fisheries.

Mediterranean MPAs have been established mainly to meet conservation benefits in zones that already harbour structurally complex habitats like islands and capes (Francour et al., 2001). Numerous studies conducted in Mediterranean MPAs demonstrate an increase in the abundance, biomass and size of fishes inside marine reserves (Bell, 1983; García-Rubies and Zabala, 1990; Harmelin et al., 1995; Reñones et al., 1997; García-Charton and Pérez-Ruzafa, 1999; Macpherson et al., 2002; García-Charton et al., 2004). Their role in sustaining local fisheries in the Mediterranean has been recently confirmed for the spiny lobster, *Palinurus elephas*, from gradients of abundance in experimental and commercial catches along with tagging experiments in the Columbretes Islands (Goñi et al., 2006). However, to date no study has been carried out in the Mediterranean to look for evidence of fish biomass gradients which are needed to test the hypothesis of fish spillover through marine reserve boundaries. Most studies on MPAs are performed on single reserves, making it difficult to assess general trends in fish distribution across MPA boundaries (Halpern and Warner, 2002;

Halpern, 2003). Evidence of fish spillover and estimation of the spatial extent of fish export require sampling fish communities at many sites across a gradient of distances from the reserve border, both outside and within the reserve (Halpern et al., 2004).

The objective of this study was therefore to provide evidence of the export of adult fishes from six Mediterranean marine reserves by directly assessing the existence of gradients of abundance and biomass across the MPA boundaries, and estimate the distance at which fish spillover might occur. The working hypothesis was that if fish export is taking place between the MPAs and surrounding fished areas one can expect abundance and biomass of fishes to be higher inside the MPAs, and negative gradients of these parameters to occur across the MPA boundaries, following Rakitin and Kramer (1996) and Ashworth and Ormond (2005).

2. Materials and methods

2.1. Study sites

Six marine protected areas were studied in the Western Mediterranean, two located in France (Cerbère–Banyuls Marine Natural Reserve and Carry-le-Rouet Natural Park, hereafter referred as Banyuls and Carry-le-Rouet, respectively) and four located in Spain (Cabo de Palos – Islas Hormigas Marine Reserve, Cabrera Archipelago National Park, Medes Islands Marine Reserve, and Tabarca Island Marine Reserve, referred from now on as Cabo de Palos, Cabrera, Medes, and Tabarca) (Fig. 1). Common criteria used to select these MPAs were year of establishment (>10 years), high protection enforcement, degree of isolation (on mainland or island), and size (small and large; Table 1). Recent studies demonstrated that year of establishment is more important than size in detecting the effectiveness of MPAs (Dufour et al., 2007) along with a high level of enforcement (Samoilys et al., 2007). The six MPAs studied have been established for long enough and are well enforced by local rangers, therefore providing a good representation of reserve effects on fish communities in the Western Mediterranean. We selected MPAs that were at least 10 years old, as some studies have shown that a steady state is not reached before 6–10 years after their establishment (Russ et al., 2005; Claudet et al., 2006). Three reserves were located on mainland (Banyuls, Carry-le-Rouet and Cabo de Palos) and three were on islands (Cabrera, Medes and Tabarca) in order to look for patterns associated with reserve isolation state. All MPAs had an integral reserve area (IR) where all fishing activities (commercial and recreational) were forbidden, and all of them, with the exception of Carry-le-Rouet, also had a buffer zone (BZ) where only some controlled fishing activities were allowed (Francour et al., 2001).

2.2. Visual censuses

Fish species and their abundance and size were recorded in standardised sheets by underwater visual censuses using SCUBA diving on rocky substrates between 6 and 12 m depth using 25×5 m transects parallel to the coast. As *Posidonia oceanica* beds covered large areas around Tabarca Is-
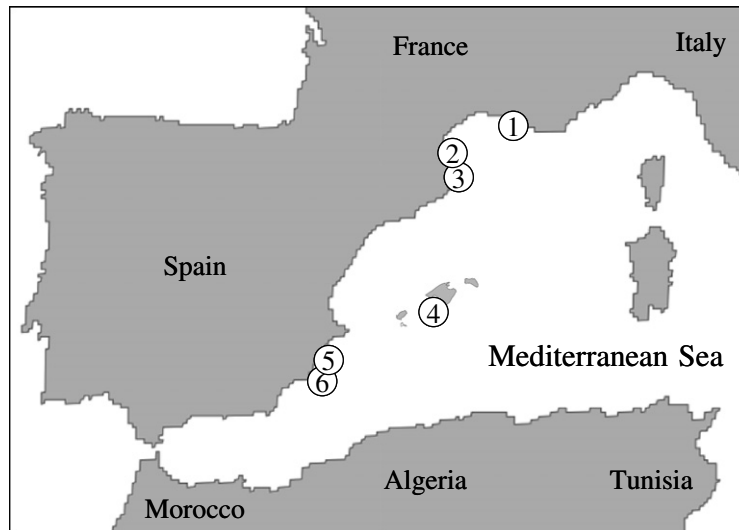
Fig. 1 – Localisation of the six marine protected areas studied in France (1, Carry-le-Rouet; 2, Banyuls) and Spain (3, Medes; 4, Cabrera; 5, Tabarca; 6, Cabo de Palos) in the Mediterranean Sea.

land, seagrass beds were also surveyed in this MPA, but on 50×5 m transects as fishes were more dispersed in this habitat. All fish species encountered were recorded, except small benthic species (e.g. blenniids, gobiids) and strictly pelagic species (e.g. clupeids, engraulids), which are little affected by protection. Actual observed number of fish was recorded up to 10 individuals, and higher numbers were ascribed to one of the abundance categories proposed in the literature (11–30, 31–50, 51–200, 201–500, >500 individuals) and usually used in visual censuses (Harmelin-Vivien et al., 1985). The size of individuals was recorded within 2-cm size classes. Fish weight was estimated from existing length–weight relationships for Mediterranean species (Bayle-Sempere et al., 2002).

Habitat structure is one of the factors to be called on to explain the small-scale spatial variability of Mediterranean fish assemblages (García-Charton and Pérez-Ruzafa, 2001) and may mask the effect of protection if protected areas present simpler habitats than non-protected ones (García-Charton et al., 2004). Thus, the main habitat characteristics were recorded on each transect, distinguishing between descriptors of habitat heterogeneity (measured as visual estimates of the percentage of cover by rock, pebbles, sand, and *P. oceanica*), and habitat complexity (estimated as the number of small, medium, and large rocky boulders; see García-Charton and Pérez-Ruzafa, 2001 for details). All data were subsequently recorded on the ECOCEN software developed by the University of Alicante (Bayle-Sempere et al., 2002).

Censuses were performed by the same team of well trained scientific divers from June to October 2003 in Cabo de Palos, Carry-le-Rouet and Tabarca, and from June to September 2004 in Banyuls, Cabrera and Medes. The warm season (June to October) is the most suitable period for visual counts in the Mediterranean, as fish communities are more diverse and stable during this period (Harmelin, 1987). The natural variance among replicates is reduced during this period, making it easier to detect spatial patterns of distribution and avoiding any seasonal effect in our study.

2.3. Sampling design

The general sampling design applied in each MPA was the following: nine sectors, separated by 1000s of metres, were positioned at increasing distances from the core of the MPA (three inside the MPA and six in fished areas outside the MPA: three in one direction and three in the opposite direction) (Table 1). In each sector, three zones were haphazardly located at a scale of 100s of metres (Fig. 2). Finally, six transects (replicates) separated by 10s of metres were sampled in each zone. In three MPAs (Banyuls, Carry-le-Rouet and Cabo de Palos), gradients in fish parameters were studied in two opposite directions, whereas in the three MPAs located on islands (Cabrera, Medes, and Tabarca) only one direction (northward) could be studied due to the absence of suitable rocky habitats in the southern part of these islands. A total of 1026 underwater visual counts of fishes were performed during the 2003 and 2004 surveys.

2.4. Data analysis

The effect of protection was analysed on mean species richness, abundance and biomass of fishes per transect (125 m^2 for rocky habitats and 250 m^2 for *Posidonia* beds) to evidence the general trends of fish community distribution. The distribution pattern of individual fish species or groups of species will be detailed in an independent paper. Abundance and biomass were calculated excluding planktivorous species (Centracanthidae, Pomacentridae and the sparid *Boops boops*). These species are often abundant and gregarious, and their high variability in spatial distribution may mask the effect of protection or habitat (García-Rubies and Zabala, 1990; García-Charton and Pérez-Ruzafa, 2001).

To demonstrate a 'reserve effect' is a pre-requisite to analyse fish gradients, as an MPA has to be filled prior a spillover effect could be expected. Thus, mean values of species richness, abundance and biomass of fishes per transect inside and outside MPAs were compared using analyses of variance

Table 1 – Main characteristics of the six MPAs studied in the Western Mediterranean, direction of fish gradients analysed, sampling design (number of sectors, zones and replicates) and total number of fish species (Nb fish species) recorded in each MPA

MPA	Country	Year of establishment	Location	Size (ha)	Type of protection	Habitat sampled	Direction gradients	Maximum distance (m)	Nb sectors (in–out)	Nb zones	Nb replicates	Nb fish species
Banyuls	France	1974	ML	650	IR + BZ	Rocks	N + S	5370	9 (3–6)	27	162	43
Cabo de Palos	Spain	1995	ML	1898	IR + BZ	Rocks	N + S	8779	9 (3–6)	27	162	48
Cabrera	Spain	1991	Is	8680	IR + BZ	Rocks	N	22400	9 (6–3)	27	162	51
Carry-le-Rouet	France	1983	ML	85	IR	Rocks	W + E	2668	9 (3–6)	27	162	40
Medes	Spain	1983	Is	418	IR + BZ	Rocks	N	3058	7 (4–3)	21	126	51
Tabarca	Spain	1986	Is	1400	IR + BZ	Rocks	N	5448	7 (4–3)	21	126	41
Tabarca	Spain	1986	Is	1400	IR + BZ	Posidonia beds	N	1970	7 (4–3)	21	126	39

IR, integral reserve; BZ, buffer zone; ML, mainland; Is, island; N, north; S, south; W, west; E, east; Max dist., maximum distance sampled in fished areas from the IR border; in–out, number of sectors studied inside and outside the MPA.

(Underwood, 1997). The Cochran's test was used to test the homogeneity of variance for all variables (Cochran, 1951). Where significant differences were found, the data were transformed by $\sqrt{(x)}$ or $\ln(x + 1)$. When transformations did not remove heterogeneity, analyses were performed on the untransformed data since analysis of variance is quite robust to departures from their assumptions, especially when the design is balanced and contains a large number of samples or treatments (Underwood, 1997).

As Mediterranean MPAs were often established in naturally complex habitats that are more favourable to the development of abundant and diversified fish assemblages, the effect of habitat structure and protection could be confounded. It was thus important to discriminate between these two factors. To explore the relationships between habitat structure and fish community parameters, multiple regressions were performed between all habitat characteristics recorded and fish species richness, abundance and biomass, using generalized linear models (GLM; McCullagh and Nelder, 1989). Prior to regression analyses, the extreme and influential cases were detected and subsequently removed (McCullagh and Nelder, 1989; García-Charton and Pérez-Ruzafa, 2001). Because habitat characteristics may explain a large part of the data variation, we extracted first the variability due to the influence of habitat variables. Then, we used the residuals of regression analyses as dependent variables in the analyses of variance, linear regressions and GAMs with distance from MPA limits, to ensure that gradients were related to protection level and not to difference in habitat characteristics (Chapman and Kramer, 1999; García-Charton et al., 2004).

Trends and significance of gradients of fish abundance and biomass across MPA boundaries were calculated by linear correlations. Negative correlations would indicate that abundance and biomass of fishes decreased from the core of the MPA to distant fished areas. The border of the integral reserve was defined as zero, so negative distances indicated zones located inside the integral reserve (IR) and positive distances zones located outside the IR. Gradients of fish abundance and biomass were analysed by linear correlations on raw data and on residuals of multiple regressions with habitat characteristics to check how differences in these characteristics may affect the gradients. We used GAMs to describe the shape of the relationships of the residuals of biomass with distance to the boundaries of the reserve, as biomass was the most pertinent parameter in our study. Distance to the integral reserve boundary was introduced as a continuous smooth variable modelled non-parametrically using a loess smoother (lo(distance)). To model the relationship between dependent variables and predictors, we used the Gaussian variance and the identity link functions. F-tests were used to determine whether the distance to the reserve explained a significant portion of the model deviance. To fit the GAMs, we used the routines contained in the S-Plus (MathSoft Inc.) programming environment based on Hastie and Tibshirani (1990) and functions developed by Venables and Ripley (2000).

To measure at which spatial scale fish spillover might occur, we calculated the minimum distance between the studied zones located on each side of the MPA border where a sharp difference in mean fish abundance and biomass was observed inside versus outside the reserve.
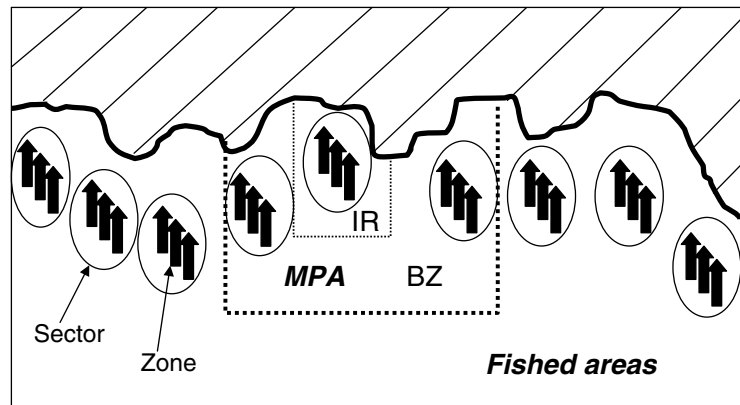
Fig. 2 – Spatially nested sampling design for studying fish gradients around MPA boundaries. MPA, marine protected area; IR, integral reserve; and BZ, buffer zone. The MPA boundary was indicated by dashed lines. Sectors were represented by ellipses and zones by black arrows. In each zone, six transects were studied.

3. Results

3.1. Effect of protection

In Cabo de Palos, Medes and Tabarca-*Posidonia*, all fish community parameters (species richness, abundance, and biomass) were significantly higher inside than outside the MPAs, whereas no significant difference existed in Tabarca-rocks (Table 2). The only non-significant parameters between protected and unprotected areas were mean abundance in Banyuls, and mean species and abundance in Cabrera and Carry-le-Rouet. Thus, a 'reserve effect' was observed for fish biomass in all MPAs, except in Tabarca-rocks, whereas the effect on fish abundance was less conspicuous.

3.2. Influence of habitat

Habitat structure showed a significant influence on all parameters in Banyuls, Cabo de Palos and Medes, whereas it was less important in Cabrera where only fish abundance responded significantly (Table 3). In Carry-le-Rouet and Tabarca-rocks fish biomass was not affected by habitat structure. It was interesting to observe that in Tabarca-*Posidonia* beds subtle differences in habitat structure in this apparently

Table 2 – Mean (SD) fish species richness (SP, number of species), abundance (AB, number of individuals) and biomass (BIO, fish biomass in kg) per transect of fish recorded inside and outside the six MPAs studied with results of ANOVAs

MPA		Inside MPA	Outside MPA	F	p	
Banyuls	SP	11.2 (3.2)	10.8 (2.5)	2.53	0.048	*
	AB	79.2 (61.2)	70.5 (55.5)	1.40	0.263	ns
	BIO	16.3 (30.3)	4.0 (19.3)	34.91	0.002	**
Cabo de Palos	SP	12.9 (3.2)	9.8 (2.7)	3.69	0.010	*
	AB	99.0 (66.0)	60.1 (50.2)	9.35	<0.001	***
	BIO	28.2 (28.3)	2.9 (5.8)	36.13	<0.001	***
Cabrera	SP	14.1 (2.5)	13.9 (2.7)	0.38	0.536	ns
	AB	93.0 (77.2)	71.6 (29.6)	3.82	0.052	ns
	BIO	13.6 (18.6)	2.7 (1.7)	18.46	<0.001	***
Carry-le-Rouet	SP	13.1 (3.0)	12.4 (2.8)	1.84	0.135	ns
	AB	99.3 (80.1)	64.1 (41.7)	1.29	0.306	ns
	BIO	16.3 (40.9)	2.4 (9.1)	4.12	0.006	**
Medes	SP	13.8 (3.6)	10.2 (2.4)	3.24	0.033	*
	AB	61.1 (34.2)	31.5 (23.0)	5.46	0.004	**
	BIO	17.5 (14.9)	2.7 (4.3)	15.00	<0.001	***
Tabarca-rocks	SP	12.3 (2.7)	13.3 (1.9)	1.97	0.139	ns
	AB	113.6 (69.7)	98.3 (52.0)	1.31	0.314	ns
	BIO	9.4 (9.0)	5.3 (0.1)	1.37	0.291	ns
Tabarca-*Posidonia*	SP	10.1 (2.8)	7.7 (2.4)	4.73	0.008	**
	AB	89.3 (68.4)	49.0 (44.0)	8.80	<0.001	**
	BIO	4.5 (11.2)	0.7 (0.8)	7.44	0.001	**

ns, not significant; *, significant at $p < 0.05$; **, significant at $p < 0.01$; ***, significant at $p < 0.001$.

Table 3 – Summary of multiple linear regressions (GLMs) of mean species richness, abundance and biomass of fishes against linear, quadratic and cubic terms of all habitat characteristics together, as tested in the six MPAs

	Banyuls	Cabo de Palos	Cabrera	Carry-le-Rouet	Medes	Tabarca-rocks	Tabarca-*Posidonia*
Species richness	0.256[***]	0.347[***]	0.198 ns	0.278[**]	0.330[***]	0.262[***]	0.203[**]
Abundance	0.124[*]	0.269[***]	0.290[**]	0.233[*]	0.281[***]	0.204[**]	0.025 ns
Biomass	0.211[***]	0.605[***]	0.209 ns	0.206 ns	0.191[**]	0.102 ns	0.286[***]

Values of adjusted R^2 and the level of significance of each analysis were indicated; ns, not significant.
[*] Significant at $p < 0.05$.
[**] Significant at $p < 0.01$.
[***] Significant at $p < 0.001$.

'homogeneous' seagrass environment influenced significantly the species richness and biomass of fish. We removed then the effects of habitat in all MPAs when analysing gradients to be sure that the patterns observed were due to differences in protection and not to differences in habitat structure.

3.3. Gradients of abundance and biomass

Correlation coefficients (*r*) and probability levels (*p*) of these coefficients for abundance and biomass are presented in Table 4. Most correlations (35/40) were negative, which implied that fish abundance and biomass decreased from the core of the MPA to fished areas, and 23 of these negative correlations were statistically significant. Only five correlations were positive (increasing abundance and biomass in fished areas), but none of them were significant. The number of significant negative correlations was higher with biomass than with abundance, and higher when computed on raw data than on residuals. These results suggested that protection has greater influence on biomass than on abundance, and could be confounded with the effect of habitat structure in some cases.

Results of GAMs of the residuals of fish biomass, as a function of distance to reserve boundaries yielded significant nonlinear relationships in 8 out of 10 cases studied (Table 5). The deviation explained by the models was generally low with a maximum of 31% in Tabarca-*Posidonia*. Representation of fitted values for the GAMs showed two main patterns of biomass gradients (Fig. 3): mean biomass declined abruptly inside the MPA, at the IR–BZ boundary (Banyuls, Medes, and

Tabarca-*Posidonia*) or declined mainly outside the MPAs at the BZ–fished area boundary (Cabo de Palos, Cabrera, and Tabarca-rocks). In Carry-le-Rouet, biomass decreased abruptly at the IR–fished area boundary, as no buffer zone was established in this MPA.

3.4. Mean distance for spillover

The mean distance estimated for fish spillover was 510 ± 562 m ($n = 10$) from the six MPAs studied, ranging from a minimum of 107 m at Carry-West to a maximum of 1959 m at Banyuls-North. Results of GAMs provided a visual confirmation of these estimates with a depletion of biomass close to the reserve boundaries (<1000 m), with the exception of Cabo de Palos where the depletion was observed at a greater distance (3000 m) (Fig. 2). Therefore, the mean distance for fish spillover estimated in this study probably occurred at a scale of 100s of metres in five out of the six MPAs studied.

4. Discussion

4.1. Effects of protection

Our data indicated that significantly higher values in mean species richness, abundance or biomass of fishes occurred inside the six marine protected areas studied. The non-significant pattern observed for Tabarca-rocks originated probably from a synergy between two local characteristics: rocky areas were scarce and isolated among seagrass beds around Tabarca Island, and the fishing pressure was centred on *Posidonia*

Table 4 – Results of linear correlations performed on raw data of abundance (AB raw data) and biomass (BIO raw data), and on residuals after extracting the effects of habitat (AB residuals and BIO residuals)

MPA	AB raw data (*r*)		AB residuals (*r*)		BIO raw data (*r*)		BIO residuals (*r*)	
Banyuls-North	−0.069	ns	−0.104	ns	−0.387	***	−0.200	*
Banyuls-South	−0.040	ns	−0.126	ns	−0.203	*	−0.141	*
Cabo de Palos-North	−0.194	*	+0.020	ns	−0.492	***	−0.141	*
Cabo de Palos-South	−0.353	***	+0.067	ns	−0.624	***	−0.010	ns
Cabrera	−0.056	ns	−0.001	ns	−0.157	*	−0.459	***
Carry-le-Rouet-East	+0.037	ns	+0.190	ns	−0.021	ns	+0.033	ns
Carry-le-Rouet-West	−0.256	*	−0.228	*	−0.201	ns	−0.319	**
Medes	−0.575	***	−0.122	ns	−0.664	***	−0.356	***
Tabarca-rocks	−0.236	**	−0.022	ns	−0.242	**	−0.147	ns
Tabarca-*Posidonia*	−0.509	***	−0.312	***	−0.604	***	−0.352	***

The correlation coefficient (*r*) is given with its statistical significance; ns, not significant; *, significant at $p < 0.05$; **, significant at $p < 0.01$; ***, significant at $p < 0.001$.

	Term	Res.dev	Res.df	df	dev	F	p(F)	R²
Table 5 – Analysis of deviance for the generalized additive models (GAMs) fitted with the residuals of fish biomass								
Banyuls-North	Null	118.46	107					
	Lo(distance)	100.10	102	1	18.35	3.50	0.010**	0.16
Banyuls-South	Null	123.85	107					
	Lo(distance)	104.57	103	1	19.28	5.56	0.001***	0.16
Cabo de Palos-North	Null	84.73	107					
	Lo(distance)	69.30	101	1	15.42	4.61	0.001***	0.18
Cabo de Palos-South	Null	97.18	107					
	Lo(distance)	89.50	102	1	7.68	2.78	0.040*	0.08
Cabrera	Null	147.67	161					
	Lo(distance)	113.08	156	1	34.57	2.20	0.070 ns	0.23
Carry-le-Rouet-East	Null	157.12	83					
	Lo(distance)	119.97	79	1	37.15	7.74	<0.001***	0.24
Carry-le-Rouet-West	Null	102.49	83					
	Lo(distance)	71.43	78	1	31.06	6.27	<0.001***	0.30
Medes	Null	171.46	124					
	Lo(distance)	137.69	120	1	33.77	3.73	0.015*	0.20
Tabarca-rocks	Null	1.54	125					
	Lo(distance)	1.46	120	1	0.08	0.88	0.460 ns	0.05
Tabarca-*Posidonia*	Null	148.77	125					
	Lo(distance)	102.50	120	1	46.27	9.05	<0.001***	0.31

Res.dev. and Res.df are the deviance and degrees of freedom of the model, respectively. The probability column corresponds to the significance of the deviance portion of the residuals of biomass explained by the predictor. Lo(distance), locally weighted regression smoother 'loes'; ns, not significant.

* Significant at $p < 0.05$.
** Significant at $p < 0.01$.
*** Significant at $p < 0.001$.

beds instead of on rocky areas (Sánchez-Jerez and Ramos-Esplá, 1996). Difference in fish community parameters between inside and outside MPAs generally increased from species richness to abundance, and then to biomass. Mean values for the six MPAs were 1.1 times higher inside MPA than outside for species richness, 1.3 times higher for fish abundance (planktivores excluded) and 4.7 times higher for biomass. This implies higher fish weight in the MPAs than in fished areas. Mean fish weight of fishes, all species included, was estimated to be 3.4 times higher inside the MPAs than in fished areas. However, analysis at a species level is necessary to fully understand the differences in the patterns of the 'reserve effect' among fish communities. Higher abundance and biomass of fish inside MPAs was reported previously in Carry (Harmelin et al., 1995), Banyuls (Bell, 1983), Medes (García-Rubies and Zabala, 1990), Cabrera (Reñones et al., 1997), Tabarca (Bayle-Sempere and Ramos-Esplá, 1993), and Cabo de Palos (García-Charton et al., 2004). Results from the present study indicate the long-lasting effects of protection, and a further evidence that protection promotes an increase in fish species richness, abundance, and biomass in Mediterranean marine reserves, as observed for most tropical and temperate MPAs (see Halpern, 2003).

4.2. Evidence of gradients in fish abundance and biomass

Whereas visual counts were performed on rocky areas with habitat structure as comparable as possible, multiple linear regressions demonstrated that habitat characteristics at a fine spatial scale significantly influenced the fish community parameters (species richness, abundance, and biomass). The decrease in the number of significant linear correlations when calculated on residuals rather than on raw data was a confirmation of the need to take habitat characteristics into account to really analyse gradients related to protection, as evidenced by Chapman and Kramer (1999) and García-Charton et al. (2004).

More significant correlations were observed for fish biomass than for abundance. Overall, 70% of the linear correlations of fish biomass with distance were significantly negative, which implied that in most cases fish biomass significantly decreased from MPAs to fished areas. GAMs demonstrated that gradients were not linear in most cases, with sharp decrease in fish biomass near MPA boundaries. Few studies throughout the world have quantified up to now the actual shape of fish abundance or biomass gradients across MPA boundaries (e.g. Chapman and Kramer, 1999; Kaunda-Arara and Rose, 2004; Ashworth and Ormond, 2005; Guidetti, 2007). The present study, by encompassing a broad geographical extent, and including six MPAs with their own particularities, constitutes the biggest effort to date to quantify such gradients, and permits to generalize the results at the regional scale. It also provided evidence that decreasing gradients of abundance and biomass are not related to the location (on mainland or island) or size (small or large) of the MPAs.
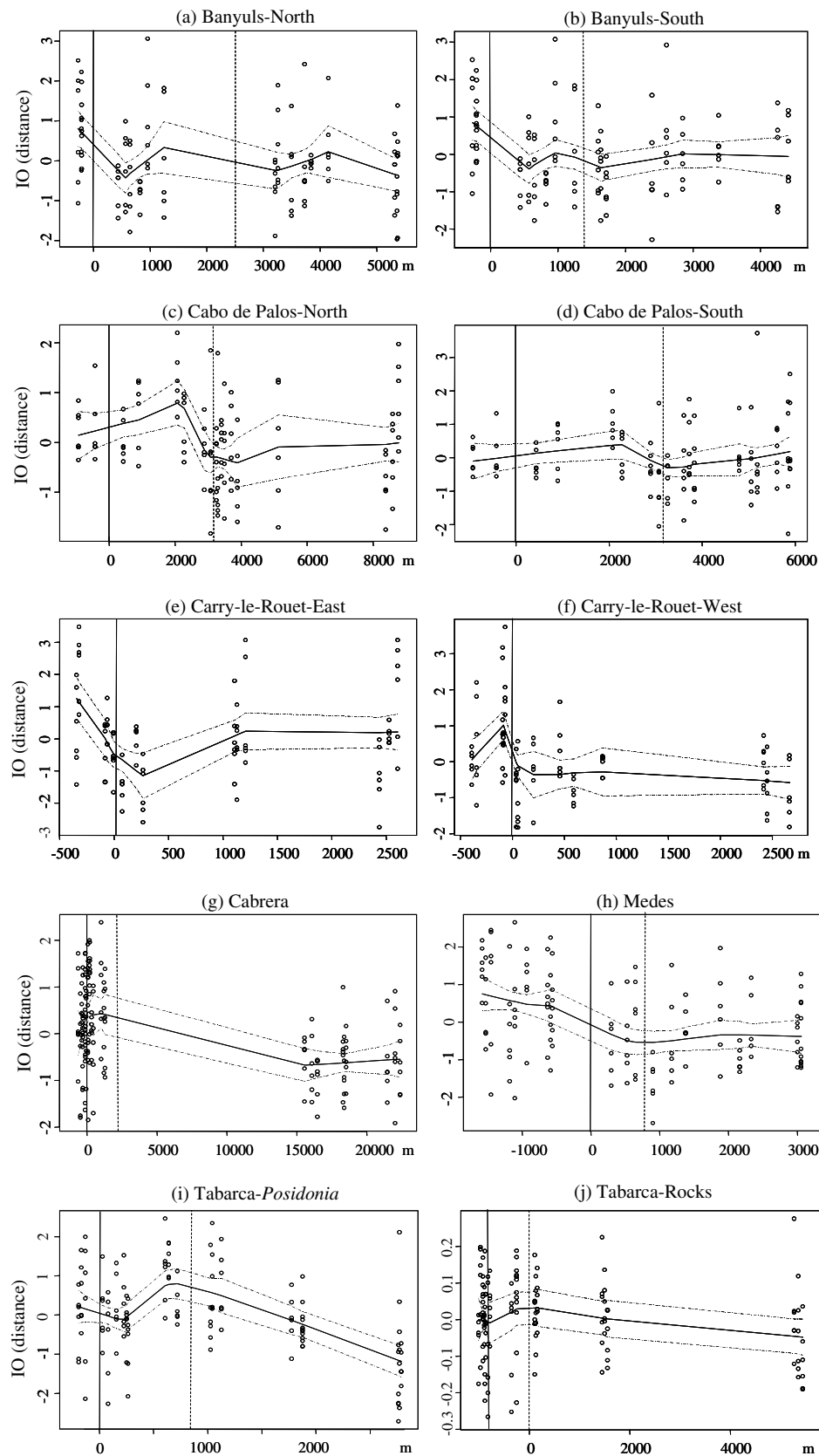
Fig. 3 – Fitted mean residuals of biomass as a function of the smooth variable distance (m) from sample to the integral reserve boundary derived from generalized additive models (GAMs), in the six Mediterranean MPAs studied. The y-axis is scaled so that zero corresponds to the mean in the log scale. Dashed lines indicate mean ± 2 standard errors. The vertical line indicates the limit of the integral reserve (IR) and the vertical dashed line the limits of the buffer zone (BZ).

In our analysis, two main patterns in the change of biomass with distance could be differentiated: one showed that mean biomass declined inside the MPA at the integral reserve–buffer zone boundaries, while in others mean biomass declined outside the MPA at the buffer–fished area boundaries. These two patterns may be related to spatial allocation of fishing effort allowed and effectively exerted in both the buffer zone and outside the different MPAs, diversity of gears used, and mobility and catchability of the main species forming the fish assemblage (Rakitin and Kramer, 1996; Kramer and Chapman, 1999; Kellner et al., 2007).

Modelling studies have suggested that spillover from marine reserves is likely to be higher under condition of high fishing pressure (Nowlis and Roberts, 1997). Abesamis et al. (2006) observed that density and biomass decreased abruptly across the reserve boundary in the Philippines and attributed this pattern to high fishing level. Furthermore, the fishing-the-line strategy, by being the more frequent spatial arrangement of fishing effort around Mediterranean marine reserves (Goñi et al., 2006), is likely to generate abrupt changes in the border limits (Kellner et al., 2007). Stelzenmüller et al. (2007) observed high levels of fishing effort and catch per unit of area (CPUA) by local artisanal fisheries near protection boundaries around Medes Islands, as well as significant decreasing trends with distance to those boundaries. As an example, in Cabo de Palos the total fishing effort (expressed as total length of longlines or nets soak in one year, averaged for 2003–2005) for bottom longline sharply decreased with distance to the no-use area from 72,330 to 36,800 m y^{-1} in 1 nautical mile (nm) to the north, and to 23,216 m y^{-1} in 2 nm to the south; in the case of rockfish trammel-net this difference was 76,410 m y^{-1} against 29,710 m y^{-1} in 1 nm to the north, and 34,680 m y^{-1} in 2 nm to the south (S. Polti and O. Esparza, Univ. de Murcia, Murcia, Spain, personal communication). This concentration of fishing effort along MPA limits can be used as evidence of spillover, provided that MPAs included in the present study are older than 10 years, hence precluding the confounding effect of redistribution of fishing effort after reserve creation, as indicated by Halpern et al. (2004).

Fish mobility and catchability are likely to influence the existence and shape of abundance and biomass gradients across MPA boundaries (Kramer and Chapman, 1999; Kellner et al., 2007). Thus, these gradients are expected to be sharper for low-mobility species and for species presenting high catchability. In some cases (Banyuls, Cabo de Palos-North, Carry-East, and Medes), we observed a sharp depression of the biomass of the observed fish assemblage. This could be due to an accumulation of fishing effort near the reserve boundary, in a multispecies fishery aiming to maximize CPUE of more mobile species and catching less mobile species at the same time (Kellner et al., 2007). Similarly, the depletion in biomass of lobsters observed around Columbretes Islands by Goñi et al. (2006) would indicate that fishing effort was higher near this MPA, as corroborated by their effort allocation data. On the other hand, fishing effort exerted in the vicinity of Mediterranean MPAs throughout the year is targeting a large array of fish species very efficiently, the mobility of these target species ranging from limited (e.g. Scorpaenidae) to high (e.g. Carangidae). This is due to the fact that artisanal fisheries within and around Mediterranean MPAs are usually seasonally rotating, multi-gear and multi-specific in nature, and they use a technology that has been evolving for centuries until achieving very high efficiency to obtaining aggregated catch of several, high-value species (Bas et al., 1985; Stelzenmüller et al., 2007). Such decreasing gradients of fish abundance and biomass across MPA boundaries were observed in a number of studies in tropical and temperate regions for fish and invertebrates targeted by local fisheries (Chapman and Kramer, 1999; Ashworth and Ormond, 2005; Goñi et al., 2006; Guidetti, 2007). General trends emerging from our results were in accordance with the initial hypothesis proposed by Rakitin and Kramer (1996) and the existence of such negative gradients seemed to be a good evidence of fish spillover from the six Mediterranean MPAs studied.

4.3. Spatial scale of MPA effectiveness for local fisheries

Even if individual fish of some species were able to swim long distances as shown by tagging experiments in this region (Chauvet et al., 1992), the benefit of fish spillover to local fisheries is likely to occur at small spatial scales (100s of meters), at least where the movement of sub-adults and adults by different mechanisms is concerned (home range relocation and/or migration). The small-scale (500 m in average) on which fish spillover from the six MPAs studied seemed mostly to occur was probably also related to the high fishing pressure existing outside these MPAs. Similar results were obtained for other marine reserves located in temperate (Guidetti, 2007) and tropical regions (Russ and Alcala, 1996; Roberts et al., 2001; Russ et al., 2003; Abesamis et al., 2006), where fish spillover from MPA was estimated to occur on the scale of a few 100s of metres. The procedure used in the present study was questionable as measuring spillover distance depended on the sampling design in each MPA but was used here as the best estimate available.

Tagging and telemetry studies recurrently revealed that movement of fishes across MPA boundaries are rare, extending from a few 10s to 100s of meters away from the marine reserves for sparids (Egli and Babcock, 2004), labrids (Topping et al., 2006), serranids (Lowe et al., 2003), mullids (Meyer et al., 2000), lutjanids (Meyer et al., 2007), and young sharks (Garla et al., 2006). Only for some carangids, the beneficial effect of MPAs beyond their boundaries can reach longer distances (e.g. James, 1980; but see Holland et al., 1996). In this framework, the question of what is the optimal fraction of coast to be protected, or other design aspects of MPAs in order to prevent fish populations from fishing depletion, remains open.

5. Conclusions

The existence of regular patterns in negative gradients of fish abundance and biomass across MPA boundaries to fished areas in the six MPAs studied was consistent with the initial hypothesis of export of adult fishes from MPAs to adjacent non-reserve sites, and could be considered to be a general pattern in the Western Mediterranean. Spillover, however, is probably reduced to a few 100s of metres around MPAs. Very little information is available yet to characterize home range

and diel, seasonal and ontogenetic migrations of Mediterranean coastal fish species, and hence this kind of information is urgently needed to properly design MPAs to achieve their management goals.

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