



# Modelling spatial and temporal scales for spill-over and biomass exportation from MPAs and their potential for fisheries enhancement

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## KEYWORDS

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## Abstract

Marine protected areas (MPAs) are considered as a tool for marine conservation and sustainable fishery resource management. Improvements in fishery yields should take place via the spill-over of individuals from the reserve. In general, it has been demonstrated that MPAs affect the density and biomass of the organisms within them, however, little evidence has been found in order to assess the exportation of individuals across their boundaries. In this study, a simple model involving population growth, harvest, and the diffusion coefficient for individuals was used to explore the effects of protection on populations inside the reserve and the spill-over of individuals to the fished area. The model showed that biological responses inside marine reserves appear to develop quickly, reaching mean levels within a short (1–5 year) time period. Mean population abundance is always higher inside the reserve and highlights the effectiveness of protection, particularly when there is strong fishing pressure outside the reserve. However, reserves smaller than 2000 m radius show significantly lower levels of abundance inside than larger sites. Large MPAs (i.e. about 2000 m in radius) offer nearly the maximum capacity for recovery (close to 100% of the system carrying capacity) and nearly the maximum flux of individuals per unit boundary length. Very large MPAs (i.e. larger than 6000 m in radius) could be a guaranteed means of providing resilience in order to prevent population crises, with the added advantage that the flux of individuals is slightly higher at larger distances from the boundary. However, in practice they provide no

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further advantage towards increasing the density of individuals or the exportation of biomass, and a network of smaller MPAs could be more beneficial, both from the point of view of conservation and of benefits to fisheries.

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## Introduction

Following the failure of traditional management measures (Waters, 1991), marine reserves have been strongly advocated as a tool for managing coastal fisheries (Agardy, 1994; Dugan & Davies, 1993; Gerber et al., 2002; Plan Development Team, 1990; Roberts & Polunin, 1991) and as a result a large number of marine protected areas (MPAs) aimed at the enhancement of local fisheries have been established around the world (Lubchenco et al., 2003). These marine fishery reserves are intended to protect critical spawning stock biomass, intraspecific genetic diversity, population age structure, recruitment supply, and ecosystem balance, while maintaining local fisheries (Plan Development Team, 1990). Marine fish dispersal that would benefit fisheries may occur via three mechanisms: egg and larval drift (Cowen et al., 2000); the trophic or reproductive migrations of adults; and home-range movements by individuals across reserve boundaries and home-range relocation as a consequence of density-dependent factors (Kramer & Chapman, 1999; Rakitin & Kramer, 1996; Russ & Alcalá, 1996). As well as serving as fisheries management tools, MPAs also protect sensitive habitats and their associated communities and ultimately halt their further deterioration (Jones, 2002).

The larval export role of MPAs has been emphasised as one of their major potential benefits which could enhance surrounding and distant fisheries and replenish depleted populations. However, despite the theoretical value of larval exports, published data are scarce and suggest that the ability of larvae to recruit back to their natal population may be a pervasive phenomenon among marine species (Jones et al., 2005; Patterson & Swearer, 2007; Swearer et al., 2002). Exportation via egg and larval dispersal has traditionally been considered an advective process dependent on the pattern and intensity of currents (González-Wangüemert et al., 2004; Pérez-Ruzafa et al., 2006). This was reflected in a review on this subject (Planes et al., 2000) which showed that studies are generally based on modelling fish eggs and larvae as passive particles moved solely by currents (Cowen et al., 2000; Roberts, 1997). But new findings show that active

movement (i.e. swimming), can also determine larvae dispersion (Cowen et al., 2006; Hogan & Mora, 2005). Due to the complexity of larval export processes it is currently impossible, in most cases (the exception would be species such as rockfish with very short larval cycles), to predict which areas may benefit from recruitment.

The effects of protection are more easily interpreted for adult fish. It is well established that fishing restrictions lead to an increase in the density, size structure, and biomass of fish populations (see reviews by García-Charton et al., 2000; Halpern, 2003; McClanahan & Mangi, 2000; Russ, 2002). Furthermore, marine reserves also act as insurance for the preservation of the gene pool and genetic diversity (Pérez-Ruzafa et al., 2006). Whether or not this increase in the abundance of individuals within MPAs leads to “spill-over” (permanent relocation of home-range outside MPA) or “leakage” (temporary movements over MPA boundary as part of daily home-range movements) that would benefit local fisheries remains difficult to determine (Sale et al., 2005). These movements would be expected to produce an abundance gradient across reserve boundaries whose slope would depend on the scale of species-specific displacements. Kramer and Chapman (1999) examined the implications of home-range size and the relocation of fish on marine reserve function and their ability to boost abundance outside reserve boundaries. They predicted that species with intermediate levels of mobility and density-dependent spatial use will provide the greatest spill-over benefits to nearby fisheries. If fishing pressure around MPAs is moderated, one can expect an abundance gradient to occur over reserve boundaries (Chapman & Kramer, 1999). On the contrary, if fishing pressure outside the MPA is extremely heavy, a sharp difference will be noted, both in abundance and mean individual size, between protected and unprotected zones. According to these authors, in the case of highly mobile and/or vulnerable species whose home-range clearly exceeds the MPA surface area, no gradient is expected to exist at all.

The only direct method currently available to explore export from MPAs is the tagging of fish inside an MPA to monitor their recapture outside.

Indirect evidence of biomass export from MPAs can also be obtained by detecting (i) a progressive increase over time in mean density and biomass of the target species, both within MPAs and in the surrounding areas (Russ & Alcala, 1996), and (ii) an abundance gradient and mean size for target species through the reserve boundaries (Chapman & Kramer, 1999; Rakitin & Kramer, 1996). The former method requires a great deal of time (>10 years) and associated expense, while the latter option, based solely on spatial sampling designs, would seem more feasible and could be carried out using direct underwater visual census (UVC) techniques, or via experimental, as well as commercial fisheries; these approaches having been used recently in the EU project BIOMEX (Q5RS-2002-00891). The results of this project on the basis of UVC show that negative fish biomass gradients from within MPAs to fished areas are a common finding in the six studied reserves, independent of the reserve size (Harmelin-Vivien et al., 2008). However, although these patterns are consistent with the hypothesis of adult fish biomass spill-over processes from marine reserves, the authors conclude that it is probably reduced to a few metres around the MPAs. The authors also recognise that the results are questionable as measuring spill-over distance depended on the sampling locations in each MPA (Harmelin-Vivien et al., 2008).

In view of the difficulties in detecting the exportation of biomass from MPAs to surrounding areas, modelling of MPA systems is a logical addition to the study of “spill-over” mechanisms. Most modelling studies conducted to date show that reserves have little effect on adjacent fisheries and produce minor improvements when compared with the best spatially uniform effort-control policies (Gerber et al., 2003) although other approaches suggest that no-take marine reserves always lead to maximised yields (Neubert, 2003). The aim of this study is to test the hypothesis that exportation of biomass produces an abundance gradient over reserve boundaries based on passive diffusion of individuals. We base diffusion rates on home-range movements and home-range relocation in a spatial concentration gradient whose main driving force results in a flux of specimens from regions with higher concentrations to those with lower concentrations. We analyse the form and behaviour of the abundance gradient under different conditions of reserve size, population intrinsic growth rate, rates of exportation, and degrees of fishing pressure, in order to facilitate the creation of hypotheses and the interpretation of results from studies on this topic.

## Methods

### Model equation and numerical technique

The model we have employed integrates three different mechanisms as contributors to changes in the concentration of specimens at a given point in space: diffusion; logistic growth; and, harvesting. Diffusion models the effect of a spatial concentration gradient resulting in a flux of specimens from regions with higher concentrations to those with lower concentrations. Logistic growth models the effect of the existing population on population growth, with a rate that decreases as the population increases, and depends on the carrying capacity of the habitat. The harvesting model adds the effect of fishing on logistic growth; in this case a decrease in the fish concentration is proportional to the fishing effort and the concentration itself.

We used a one-dimensional (1-D) model to simulate the influence that spatial variability has on fish concentration. This model is applicable to many situations; for instance, when fish movements occur parallel to the coast on a horizontal plane. Using  $x$  and  $t$  for position and time, respectively, the concentration of fishes,  $n$ , will be a function of both:  $n(x, t)$ . The model described above results in the following partial differential equation for the time rate of change of  $n$ :

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + r \left(1 - \frac{n}{K}\right) n - qEn \quad (1)$$

where  $D$  is the diffusion coefficient (units: length<sup>2</sup> time<sup>-1</sup>),  $r$  the intrinsic rate of population growth,  $K$  the carrying capacity of the habitat, and  $qEn$  the total catch harvested outside the MPA.

The proportionality constant  $q$  or catchability coefficient is, by definition, the proportion of the total stock caught by one unit of effort (Haddon, 2001; King, 1995). The fishing effort  $E$  can be given in units of number of days at sea, or of boats, men, length of nets, number of anglers, etc., operating in a given area per unit of time (Jennings et al., 2001). At the same time, catchability,  $q$ , is in practice far from constant (Gulland, 1983) as it is the result of several components such as gear efficiency, selectivity, habitat structure, fish behaviour, age of fish, time of day, season, etc. We have therefore used fishing mortality (Gulland, 1983) in the analyses of the outputs of the model as a parameter which integrates the variability in catchability and effort:  $F_t = qE_t$ .

$F_t$  assumes the dimension per time.

The above partial differential equation is integrated numerically, with diffusion being the most

complex process to integrate by a finite difference procedure that involves treating space and time domains discretely. If the space ranges from  $x = 0$  to  $L$ , it is subdivided into a mesh of  $N$  equally spaced points with an interval:  $\delta x = L(N-1)^{-1}$ , with the objective being to compute the concentration,  $n$ , at the points  $x_i = i\delta x$ , where  $i$  takes values from 1 to  $N$ . This must be performed at instants given by  $t_j = j\delta t$ ,  $j$  integer, where the time step  $\delta t$  is related to the space step  $\delta x$  via a stability condition, as described below. Defining a variable  $C$  to represent the different values  $C_{[i][j]}$  that the concentration  $n(x, t)$  takes at  $x = x_i$  and  $t = t_j$ , after discretising the diffusion equation leads to:

$$C_{[i][j+1]} = C_{[i][j]} + (D\delta t(\delta x\delta x)^{-1}) \times (C_{[i+1][j]} - 2C_{[i][j]} + C_{[i-1][j]}) \quad (2)$$

in which a forward difference scheme for the time derivative and a 3-point finite difference for the second spatial derivative have been used. Starting from a known profile concentration at instant  $t_0$ ,  $C_{[i][0]}$ , the concentration at the following instants can be obtained by an iterative process based on the previous equation. For this algorithm to be stable the following relation has to be accomplished:

$$\delta t < \delta x\delta x(2D)^{-1} \quad (3)$$

The other two terms of the evolution equation, logistic growth and harvesting, can then be easily included in the iteration algorithm:

$$C_{[i][j+1]} = C_{[i][j]} + (D\delta t(\delta x\delta x)^{-1})(C_{[i+1][j]} - 2C_{[i][j]} + C_{[i-1][j]}) + rC_{[i][j]} \times (1 - C_{[i][j]}K^{-1}) - qEC_{[i][j]} \quad (4)$$

The implementation of the numerical integration was carried out by means of Ejs (Easy Java Simulations), an authoring tool useful for building Java simulations in different scientific and technical fields.

Eq. (4) states that the rate of change of population density at a given location is controlled by three processes: population growth; diffusion via a density gradient across the MPA boundaries; and, harvesting due to fishing activity. In this study, the habitat is assumed to be uniform, so that the carrying capacity is uniform along the gradient. In this model the final term described as harvesting, the fishing effort and catchability, or at least the resulting fishing mortality rate, is also constant throughout the gradient and thus the harvest rate at a given location is proportional to the stock size.

### Estimate of the diffusion coefficient in marine organisms

Among the above-mentioned mechanisms of fish and invertebrate dispersion from a marine reserve we have focused on home range and home-range displacement in a density gradient maintained by fishing mortality outside the reserve as the main factors leading to a spatially defined biomass gradient at small and medium scales. As in previous studies (Neubert, 2003) it was assumed that random home-range movements at the boundaries of a protected area and home-range relocation as a consequence of density-dependent factors could be adequately described by diffusion models.

The term “home-range area” is defined as the area in which an animal spends its typical activity cycle (Jones, 2005). Estimation of home-range area is usually made as the expected net squared displacement for each  $n$  moves observed in a given time in tracking or mark-recapture studies, taking into account distance moved (Eristhee & Oxenford, 2001; Hereu, 2005; Jadot et al., 2006) and in some cases turning angles (Acosta, 2002). However, it must be taken into account that as home-range area is defined in function of time it coincides with home-range *sensu stricto* for short periods of time (equivalent to an activity cycle) or when the population is distributed uniformly, but includes home-range displacement and relocation of home-range centre for longer periods when spatial differences in population density and competence by the space exists. For a fish or invertebrate moving in randomly changing directions, the diffusion coefficient may be parameterised by:

$$D = \frac{3\pi}{16\sqrt{2}} \bar{v} l_{mfp} = 0.420\bar{v} l_{mfp} \quad (5)$$

where  $l_{mfp}$  is the mean free path of the animal in its home-range displacement and  $\bar{v}$  the mean speed during random movement. In the same way  $D$  can be obtained from the *Einstein-Smoluchowsky* equation:

$$A_{HR} = 2dDt \quad (6)$$

where  $A_{HR}$  is the expected net squared displacement,  $d$  the number of dimensions of trajectory data and  $t$  the time. As we have mentioned, in a population density gradient,  $A_{HR}$  coincides with home-range for short periods of time (equivalent to an activity cycle) and includes home-range displacement and relocation for longer periods.

A derivation of this equation has been used by Acosta (2002) in his study of dispersal dynamics of *Palinurus argus* and *Strombus gigas* in the Caribbean.

Here Eq. (6) has been used to estimate the range of variation of  $D$  in several marine species for which data on home range and random movement patterns were available. Eq. (5) has also been used when mean velocity and mean path length of trajectories were also available in order to test the consistency of the previously obtained  $D$  values (Table 1).

In order to establish range bounds for the model, maximum, minimum, and mean  $r$  (instantaneous rate of population growth) were obtained from 1354 species from seven families of fish targeted by fishing: Sparidae; Mullidae; Mugilidae; Serranidae; Labridae; Syngnathidae; and, Gobiidae (<http://www.fishbase.org/>).

In the case of population density or abundance (number of individuals per unit area) the values obtained for the fish assemblage of seven localities in the western Mediterranean were used, each one including a reserve and a non-reserve area (García-Charton et al., 2004) and expressed as individuals per 100 m<sup>2</sup>. For the purpose of this study, carrying capacity ( $K$ ) has been assumed to be the maximum observed density for a given species.

## Analyses of data

For each simulation state variables were set at time 0, considering a situation without protection but with overfishing which would result in a mean abundance of 1.8 individuals per 100 m<sup>2</sup> for a carrying capacity of 10 individuals per 100 m<sup>2</sup>. These values are within the range for natural populations in the western Mediterranean (García-Charton et al., 2004).

We have assigned integral reserve (IR) to the no-take zone or the length of the gradient with no harvesting activity, to differentiate it from other types or zones of reserves in which regulated or recreational fishing are permitted. In this work, reserve and integral reserve are used with the same meaning. Different combinations of integral reserve size (IR-size),  $r$  (instantaneous rate of population growth),  $D$  (diffusion coefficient), and  $F$  (instantaneous fishing mortality rate) were tested. These were kept constant in each simulation and according to the ranges shown in Table 2.

Gradients of abundance (density of individuals) from the integral reserve were simulated up to a distance of 16 km from the centre of the reserve. Simulations were run for a 50-year period to analyse the effect of individual variables ( $r$ ,  $F$ , and  $D$ ) on the shape of the curves, the slope of the gradient, and the time required to reach a steady state. State variables *abundance* and *flux* of

individuals were recorded at 50 m intervals along the entire gradient at yearly intervals. We performed 260 simulations for different reserve sizes and random combinations of  $D$ ,  $r$ , and  $F$  in order to analyse the multivariate effect of parameters on the exportation of individuals across the reserve boundary, the slope of the gradient and effectiveness of the protection measured as the percentage of the mean abundance inside the integral reserve relative to its carrying capacity. The duration of each simulation was random, but only after the steady state was reached. Resulting data were analysed using multiple regression analyses with stepwise selection of variables in a Generalised Linear Model (GLM).

The influence of the reserve size on the effectiveness of protection, both in maintaining the abundance of individuals inside the reserve as close as possible to the carrying capacity and to maximising the flux of individuals to the fishing zone, was analysed using a three-way Analysis of Variance (ANOVA) considering factors “Integral Reserve Size” with six levels (100, 500, 1000, 2000, 6000, and 12,000 m radius), influence of “Protection”, with four levels (integral reserve, boundary, nearby non-protected area up to 2000 m from the boundary, and far non-protected area more than 2000 m from the boundary) and “Diffusion” with five levels (100, 500, 1000, 2000 and 5000 m<sup>2</sup> day<sup>-1</sup>), while maintaining the state variables  $r$ ,  $K$ , and  $F$  constant.

## Results

### Model simulations

Figure 1 shows some of the model simulation outputs for an MPA consisting of an integral reserve of 1000 m radius. Figure 1a represents a situation with a low fishing mortality ( $F = 0.001$  day<sup>-1</sup>) in relation to an also relatively low population growth rate ( $r = 0.003$  day<sup>-1</sup>) and high diffusion ( $D = 5000$  m<sup>2</sup> day<sup>-1</sup>), starting from a low population density (three individuals 100 m<sup>-2</sup>). In the first year, after the establishment of the MPA, the population reached a mean density of 8.57 ( $\pm 0.065$ ) individuals 100 m<sup>-2</sup> inside the protected area, and 6.5 ( $\pm 0.072$ ) individuals 100 m<sup>-2</sup> in the nearby non-protected zone. Equilibrium of the system was reached in the fourth year (8.86  $\pm$  0.066 individuals 100 m<sup>-2</sup> inside, and 6.82  $\pm$  0.070 individuals 100 m<sup>-2</sup> in the nearby outer zone) remaining constant for the next 50 years. Figure 1b shows the same initial values but with higher fishing pressure

**Table 1.** Parameters for the estimation of the diffusion coefficient in different marine species.

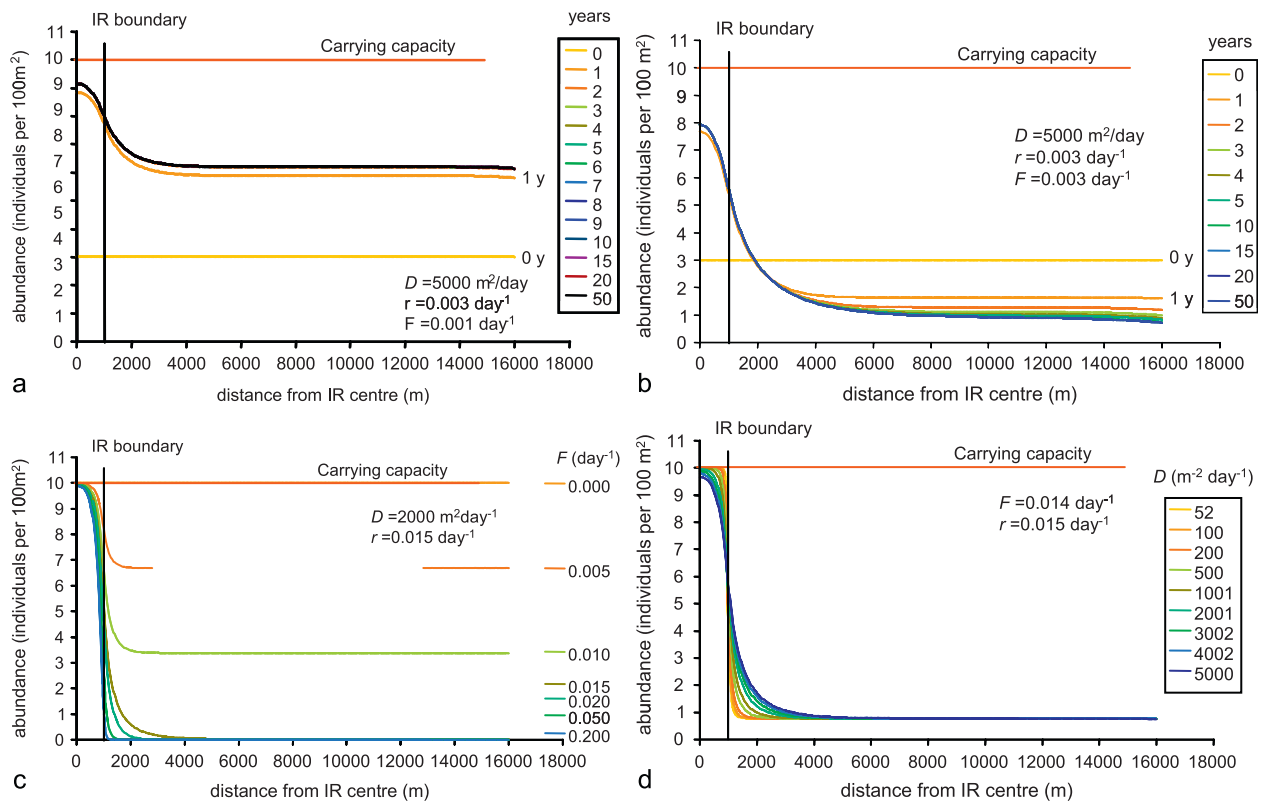
Species	Taxonomic group	Reference <sup>a</sup>	Mean linear distance per track (m)	Total linear distance (m)	Mean velocity (m day <sup>-1</sup> )	Home-range area (m <sup>2</sup> )	Time (days)	<i>D</i> (m <sup>2</sup> day <sup>-1</sup> )	<i>D'</i> (m <sup>2</sup> day <sup>-1</sup> )
<i>Strombus gigas</i>	Mollusca (Gastropoda)	4	8.50	87.30	8.50	7300	30	60.83	30.35
<i>Palinurus argus</i>	Crustacea (Decapoda)	4	29.43	268.10	9.93	14,900	27	137.96	122.73
<i>Clibanarius laevimanus</i>	Crustacea (Decapoda)	7	2.00			4	15	0.07	
<i>Mithrax spinosissimus</i>	Crustacea (Decapoda)	7	4.00			3038	112	6.78	
<i>Paracentrotus lividus</i>	Echinodermata (Echinoidea)	1	1.51	3.79	0.04	6	90	0.0167	0.0267
<i>Kyphosus sectatrix</i>	Fish (Kyphosidae)	2	547.36			34,423	21.46	401.01	
<i>Halicoeres</i> spp	Fishes (Labridae)	5				84.825	0.028	763.43	
<i>Semicossyphus pulcher</i>	Fish (Labridae)	10			1357.38	16,655.5	1	4163.88	
<i>Cephalopholis cruentata</i>	Fish (Serranidae)	3				2120	1.8	295.13	
Several spp	Fish (Serranidae, Lutjanidae, Lethrinidae)	9				<1500	0.5	<750.00	
<i>Sarpa salpa</i>	Fish (Sparidae)	6	422.79	14,031.52	1.90	40,082.86	20.79	482.10	337.39
<i>Phycodurus eques</i>	Fish (Syngnathidae)	8	80.55	1134.56	266.93	109,411.11	6.22	4395.98	9030.26
<i>Sparisoma viride</i>	Fish (Sparidae)	2				497			
<i>Epinephelus guttatus</i>	Fish (Serranidae)	2				1700			
<i>Plectropomus leopardus</i>	Fish (Serranidae)	2				12,000			

*D* has been estimated using Eq. (6), and *D'* using Einstein-Smoluchowsky Eq. (5) (see text).

<sup>a</sup>1 Hereu (2005). 2 Eristhee and Oxenford (2001). 3 Popple and Hunte (2005). 4 Acosta (2002). 5 Jones (2005). 6 Jadot et al. (2006). 7 Vannini and Cannicci (1995). 8 Connolly et al. (2002) 9 Zeller et al. (2003). 10 Topping et al. (2005).

**Table 2.** Description, units and numerical values of parameters used in the model obtained for different species from bibliographic sources.

Parameter	Name	Definition	Units	Values range (mean)	Geographic area	Taxonomic group	Data source
$n$	Abundance/density	Population size per unit of area	Individuals $100\text{ m}^{-2}$	0–212 (8.23)	Western Mediterranean	Fishes	García-Charton et al. (2004)
$r$	Intrinsic rate of increase or instantaneous rate of population growth		$\text{day}^{-1}$	0–0.11 (0.02)	World	Fishes (Gobiidae, Serranidae, Syngnathidae, Labridae, Mugilidae, Mullidae, Sparidae)	Fishbase ( <a href="http://filaman.ifm-geomar.de/search.php">http://filaman.ifm-geomar.de/search.php</a> )
$K$	Carrying capacity	Maximum number of individuals per unit of area that support a given habitat	Individuals $100\text{ m}^{-2}$	212	Western Mediterranean	Fishes	García-Charton et al. (2004)
$F$	Instantaneous fishing mortality	$= qE$	$\text{day}^{-1}$	0–0.11			
$q$	Catchability coefficient	Proportion of the population caught per unit of effort		0–1			
$E$	Fishing effort	Number or size of fishing gear per area, power of engines, time at sea, etc.					
$D$	Diffusion		$\text{m}^2\text{ day}^{-1}$	0.017–9030.26 (654)	World	Benthic invertebrate and fish species	See Table 1
$t$	Time		day				
$x$	Distance	Distance from the integral reserve centre	m	0–20,000			



**Figure 1.** Gradients of abundance from the integral reserve core (IR) of a 1000 m radius MPA to a distance of 16,000 m outside. The slope through the boundary of the reserve is directly related to the flux of individuals from the reserve to the fished zone. Each figure responds to different conditions. (a) and (b) show the 50 years evolution of the gradient for a species with a diffusion coefficient  $D = 5000 \text{ m}^2 \text{ day}^{-1}$  and instantaneous population growth rate  $r = 0.003 \text{ day}^{-1}$  under two different fishing mortalities ( $F = 0.001 \text{ day}^{-1}$  and  $F = 0.003 \text{ day}^{-1}$ , respectively). (c) and (d) show the effect of varying fishing mortality and diffusion coefficient, respectively, on the form of the gradient after a period of three years since the establishment of the reserve. The population instantaneous growth rate was  $r = 0.015 \text{ day}^{-1}$  in both cases. In (c)  $D$  was maintained constant at  $2000 \text{ m}^2 \text{ day}^{-1}$ . In (d)  $F$  was constant and took the value of  $0.014 \text{ day}^{-1}$ .

( $F = 0.003 \text{ day}^{-1}$ ). In this case the system also exhibited a quick response in the first year but the maximum mean abundance inside the reserve only reached  $7.32 (\pm 0.014)$  individuals  $100 \text{ m}^{-2}$  due to the higher harvesting in the non-protected area coupled with the high diffusion rate. The effect was also manifested outside the reserve as a decrease in abundance to  $3.09 (\pm 0.16)$  in the nearby area and to  $0.93 (\pm 0.18)$  in the far outer area after the fifth year. The system reached a steady state very rapidly for all simulations performed, in most cases between the second and fourth year, and always before the tenth year.

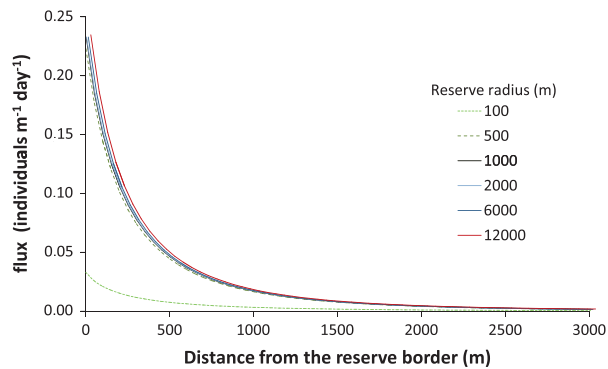
Figures 1c and d show the effect of varying fishing mortality and diffusion coefficients, respectively, on the shape of the gradient for an MPA with a radius of 1000 m. The instantaneous population growth rate was maintained constant at  $r = 0.015 \text{ day}^{-1}$  in both cases. In the former case  $D$  remained constant at  $2000 \text{ m}^2 \text{ day}^{-1}$  and in the latter  $F$  was constant and took the value of  $0.014 \text{ day}^{-1}$ .

Figure 1c shows that, under the conditions given for diffusion and reserve size, changes in  $F$  mainly affected the abundance at the MPA boundary and outside the reserve limits, but very few in the internal part of the integral reserve, leading to the extinction of the population in the far outer zone when fishing mortality was higher than the population growth rate. On the other hand, the diffusion coefficient (Figure 1d) affected the slope of the gradient and the abundance both inside the protected area and in the nearby outer zone as far as 5000 m from the boundary.

### Biomass export

Flux of individuals over the reserve boundary reached a maximum of 2.11 individuals per metre of transversal length per day in a reserve of 1000 m radius for a species with an instantaneous growth rate of  $0.11 \text{ day}^{-1}$ , a diffusion coefficient of





**Figure 2.** Mean flux of individuals over the distance gradient from the reserve boundary to the fished area as a function of the integral reserve size.

$4939.35 \text{ m}^2 \text{ day}^{-1}$  and under a fishing mortality of  $0.2 \text{ day}^{-1}$ . The mean flux of individuals over the reserve boundary under all simulated conditions reach  $0.26$  ( $\text{MSE} \pm 0.05$ ) to  $0.27$  ( $\text{MSE} \pm 0.06$ ) individuals per metre of transversal length per day in reserves of  $500 \text{ m}$  to  $12,000 \text{ m}$  radius, respectively. However, the mean flux of individuals over the reserve boundary in a reserve of  $100 \text{ m}$  radius was only  $0.03 \text{ individuals m}^{-1} \text{ day}^{-1}$  ( $\text{MSE} \pm 0.007$ ) (Figure 2). While for all the reserve sizes the flux of individuals could reach up to  $10 \text{ km}$  from the reserve boundary, this only affected the observed abundance gradient significantly within the first  $2000\text{--}3000 \text{ m}$ . This “area of influence” was affected by reserve size and became significantly shorter as the size of the reserve became lower than  $500 \text{ m}$  radius.

### Combined effect of parameters on the shape of gradients, the exportation of individuals and effectiveness of the MPA

The slope of the gradient and the flux of individuals across the reserve boundary did not show any significant correlation (Table 3). However, both were explained by nearly the same parameters, as shown by the regression models with stepwise selection of variables (Tables 4 and 5, Figure 3). Both were influenced by the diffusion coefficient, the fishing mortality outside the reserve and the population growth rate. In addition, the slope was affected by the size of the reserve. Small reserves tended to show shallower slopes due to their difficulty in maintaining high densities of individuals inside their limits. In fact, the possible combinations of slope and flux determined a well-defined set of relationships (Figure 4a) delimited by and organised along lines representing an equal

diffusion coefficient ( $D$ ) (Figure 4b). For each  $D$ , the lines represented increasing values of fishing mortality.

The factors determining the effectiveness of protection on maintaining a population density inside the reserve were studied by analysing the parameters which allowed the population to reach or approach the maximum percentage of the reserve’s carrying capacity (Table 6). The regression model with stepwise selection of variables included integral reserve size (IR-Size), as a factor that favours reaching the carrying capacity, and the diffusion coefficient, the slope at the boundary and the instantaneous fishing mortality-population growth rate ( $Fr^{-1}$ ) as factors that precluded or limited the MPA’s effectiveness. The flux across the boundary was also selected by the model as a positively related factor, but in fact this would be more a consequence than an effect.

### Effect of the size of the protected area on the effectiveness of the reserve

In the context of this work, effectiveness of protection from fisheries has two components: (1) recovery of the populations’ density to reach the habitat carrying capacity inside the reserve; and, (2) maximising the flux of individuals to the fished area. In general all MPAs showed a rapid and effective response to protection from fisheries. Figures 5a and b show the form of abundance gradients with increasing distance from the MPAs after 10 years of protection in MPAs with a radius ranging from  $100 \text{ m}$  to  $12,000 \text{ m}$ . Diffusion-coefficient values applied were  $500 \text{ m}^2 \text{ day}^{-1}$  (Figure 5a) and  $5000 \text{ m}^2 \text{ day}^{-1}$  (Figure 5b). In both cases the population growth was  $0.015 \text{ day}^{-1}$  while exposed to a high fishing mortality ( $F = 0.014 \text{ day}^{-1}$ ). The outputs of the model show that reserves with a radius of more than  $2000 \text{ m}$  reached their population carrying capacity in both situations. Reserves of a  $1000 \text{ m}$  radius accounted for  $97.7\%$  of their carrying capacity for populations with a low diffusion coefficient ( $D = 500 \text{ m}^2 \text{ day}^{-1}$ ) but only  $88.6\%$  of their carrying capacity when the diffusion coefficient was  $5000 \text{ m}^2 \text{ day}^{-1}$ . MPAs with a radius of less than  $500 \text{ m}$  had serious difficulties in maintaining their populations at  $20\%$  or  $30\%$  of their carrying capacity with both medium or high diffusion coefficients.

The results of ANOVA showed a significant effect for all factors analysed and their interactions ( $p < 0.0005$ ) on abundance (Table 7, Figure 6a). Mean assemblage abundance was always higher inside the MPA than in any other zone and the

reserve effect on abundance and the corresponding abundance gradient were observable for any fishing pressure outside the reserve. However, reserves with radii of less than 2000 m had a significantly lower abundance in the integral reserve, while no significant differences were observed outside the reserve. This effect was more evident in reserves with a radius of less than 500 m in which not only the integral reserve, but also the boundary and the nearby outer area exhibited significant differences compared to larger reserves under the same fishing conditions.

Regarding the effect of the reserve size on the flux of individuals across the reserve boundary, the ANOVA also showed significant differences for all factors and their interactions (Table 7). That means each analysed factor has a significant effect but acting in a different way. Logically the maximum flux took place across the MPA boundary and was at a minimum in the far outer zone and inside the reserve. On the other hand, the reserve size significantly affected the flux of individuals but with different patterns depending on the situation. The largest MPAs showed the highest export rates, though differences were small once reserves exceeded 1000 m radius, while as expected, reserves with a radius of less than 100 m radius showed significant lowest fluxes (Figures 2 and 6b). For reserve sizes from 100 to 500 m radius the flux of individuals increases in all the zones as reserve size is increased. However, in reserves larger than 1000 m radius the flux decreases in the integral reserve core and increases at the boundary and in the nearby protected area. Only in reserves larger than 6000 m the flux of individuals reach the far non-protected zone. The flux of individuals and the

distance at which it can be observed increases with the diffusion rate of the species, except in reserves smaller than 100 m, in which the flux of individuals decrease at highest diffusion rates due to the decrease of abundance in the integral reserve.

**Table 4.** General model explaining the slope of the gradient of abundances through an MPA boundary.

Effect	Coefficient	P (two tail)
CONSTANT	-0.01145	0.000
IR_SIZE	-6.882E-06	0.000
<i>D</i>	2.838E-06	0.000
<i>F</i>	-0.39878	0.000
<i>r</i>	0.09221	0.000

Models were generated by multiple regression analyses with stepwise selection of variables. *D*: diffusion coefficient, *F*: fishing mortality, *r*: population instantaneous growth rate, IR\_SIZE: integral reserve radius. (*n* = 180; adjusted *R*<sup>2</sup> = 0.74).

**Table 5.** General model explaining the flux of individuals through an MPA boundary.

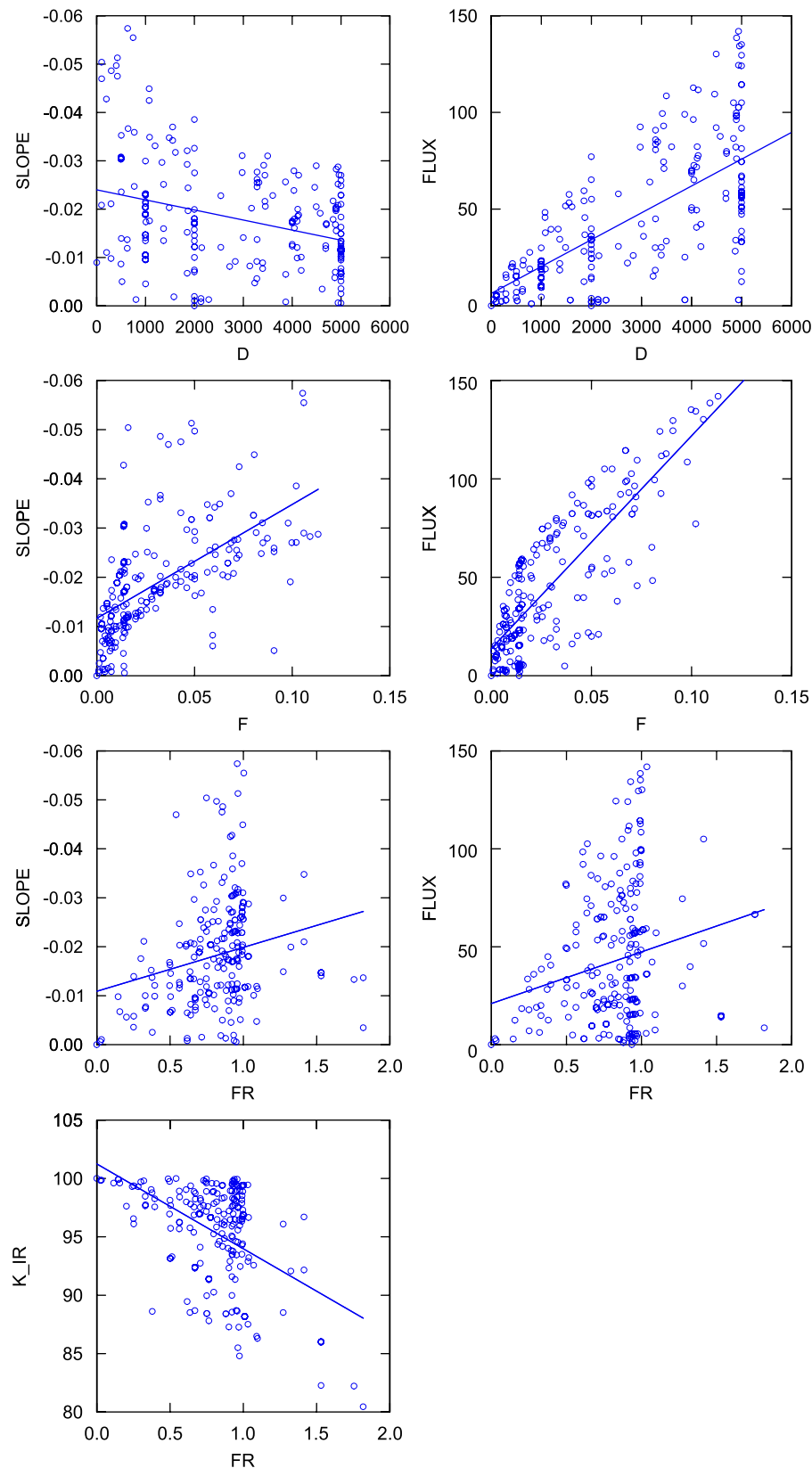
Effect	Coefficient	P (two tail)
CONSTANT	-5.35	0.000
<i>D</i>	0.01069	0.000
<i>r</i>	-2.13E+02	0.000
<i>F</i>	1.02E+03	0.000

Models were generated by multiple regression analyses with stepwise selection of variables. *D*: diffusion coefficient, *F*: fishing mortality, *r*: population instantaneous growth rate. (*n* = 230; adjusted *R*<sup>2</sup> = 0.91).

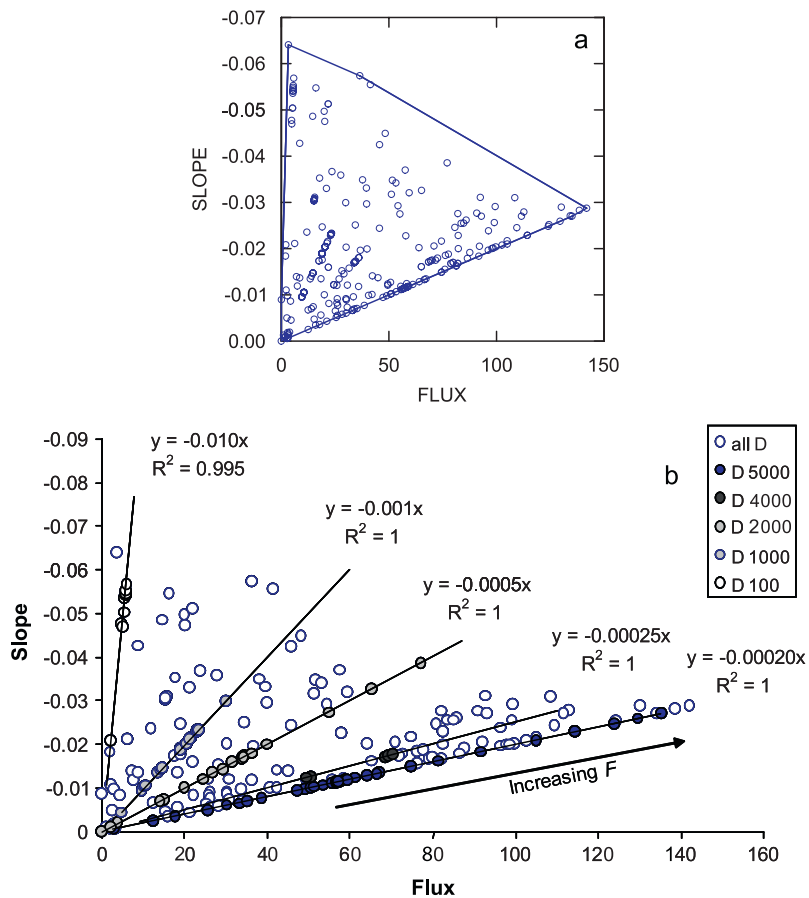
**Table 3.** Pearson correlation matrix between the biological parameters of species, reserve size, fishing mortality and the slope of the resulting gradient of biomass.

	IR_SIZE	<i>r</i>	<i>D</i>	<i>F</i>	Time	FLUX	SLOPE	<i>F r</i> <sup>-1</sup>	IR	NP_N	IR_NP
<i>D</i>		<b>0.25</b>									
<i>F</i>		<b>0.88</b>	0.23								
Time		-0.32		-0.26							
FLUX		<b>0.60</b>	<b>0.69</b>	<b>0.72</b>	-0.231						
SLOPE	-0.21	-0.30	<b>0.44</b>	-0.44							
<i>F r</i> <sup>-1</sup>							-0.25				
IR	<b>0.28</b>	0.22				<b>0.27</b>	-0.44				
NP_N				-0.31		-0.24	<b>0.45</b>	-0.888			
IR_NP	<b>0.24</b>			<b>0.38</b>		<b>0.39</b>	-0.69	<b>0.627</b>	<b>0.54</b>	-0.74	
IR_K	<b>0.28</b>	0.22				<b>0.27</b>	-0.44		<b>1</b>		<b>0.54</b>

Only significant figures are represented (*p* < 0.05, *p* < 0.005). *D*: diffusion coefficient, *F*: fishing mortality, time: time since the establishment of the MPA, FLUX: number of individuals crossing the boundary of the MPA, SLOPE: slope of the gradient of abundance in the boundary of the MPA, *r*: population instantaneous growth rate, IR\_SIZE: integral reserve radius, IR: mean abundance in the integral reserve, K\_IR: ratio between the IR\_K: ratio between the mean abundance in the integral reserve and the reserve carrying capacity, IR\_NP: integral reserve non-protected area mean abundance ratio, NP\_N: mean abundance in the nearby non-protected area.



**Figure 3.** Relationships between slope of the gradient at the reserve boundary, flux of individuals through the boundary, and percentage of the carrying capacity reached by the population in the integral reserve core respectively, with diffusion coefficient of the species (D), fishing mortality in the non-protected area (F), and fishing mortality/instantaneous population growth rate of the exploited population (FR). Straight lines respond to significant ( $p < 0.05$ ) linear regressions.



**Figure 4.** Relationship between slope of the gradient in the reserve boundary, flux of individuals through the boundary and fishing mortality outside the protected area. Slope-flux relationship determined a well-defined space (a) delimited by and organised along lines representing equal diffusion coefficient (b). For each diffusion coefficient  $D$ , the dots along the lines represented increasing values of fishing mortality.

**Table 6.** General model explaining the effectiveness of the reserve in terms of percentage of its carrying capacity reached by a population inside the integral reserve.

Dependent variable: IR\_K

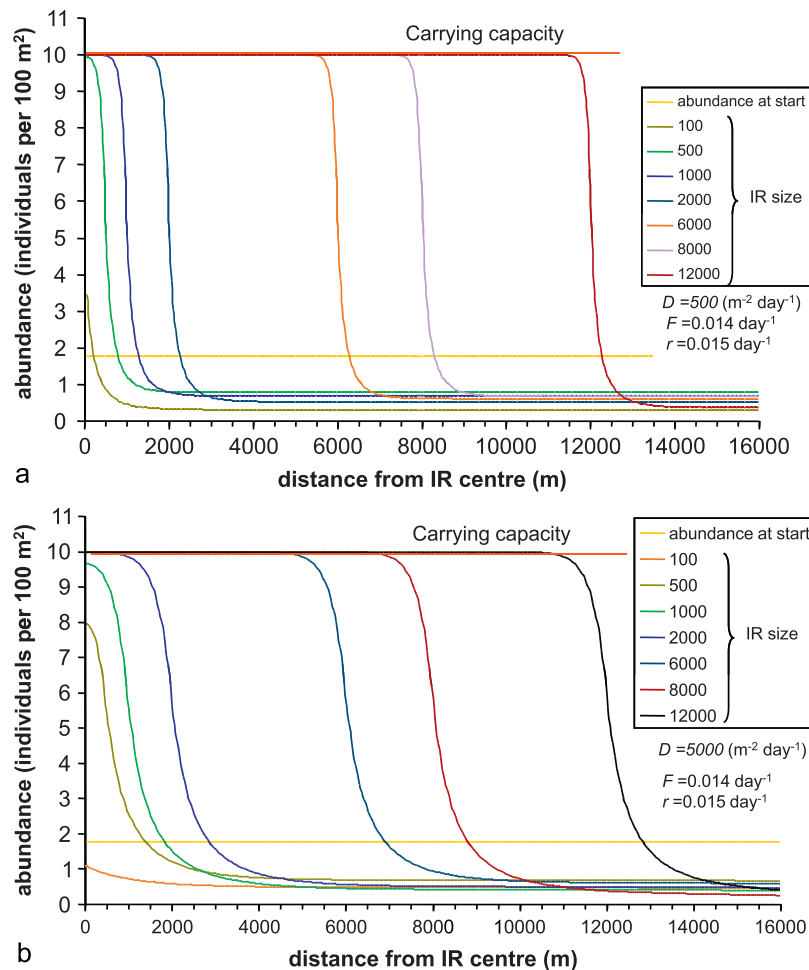
Effect	Coefficient	$P$ (two tail)
CONSTANT	100.109	0.000
IR_SIZE	0.001	0.000
$D$	-0.001	0.000
FLUX	0.058	0.000
SLOPE	-153.975	0.000
$Fr^{-1}$	-11.130	0.000

(IR\_K: ratio between the mean abundance in the integral reserve and the reserve carrying capacity in percentage). Models were generated by multiple regression analyses with stepwise selection of variables. IR\_SIZE: integral reserve radius,  $D$ : diffusion coefficient,  $F$ : fishing mortality, FLUX: number of individuals crossing the boundary of the MPA, SLOPE: slope of the gradient of abundance in the boundary of the MPA,  $r$ : population instantaneous growth rate. ( $n = 221$ ; adjusted  $R^2 = 0.75$ ).

## Discussion

### Effectiveness of MPAs in preserving species abundance

According to Halpern’s review (2003), MPAs are very effective at recovering the abundance and natural size structure of exploited populations. Amongst other things, the level of recovery and recovery rate should be influenced by the size of the MPA and by fishing pressure in surrounding waters. Our simulations show that marine reserves of all sizes can positively influence the abundances of fishes both inside and outside the MPA borders irrespective of fishing pressure outside the reserve, though smaller MPAs may not be able to reach their carrying capacity. Furthermore, for all the simulations performed the system reached a steady state very rapidly, in most cases between the second and fourth year, and always before the tenth year.



**Figure 5.** Effect of integral reserve size on the effectiveness of an MPA. The exportation of individuals through the reserve boundaries depends directly on the slope of the gradient. The capacity to preserve the abundance of the populations can be tested by comparing the abundance showed by the line with the carrying capacity of the system. The model outputs from left to right correspond to increasing reserve sizes.

As could be expected, response was fastest inside the reserve and in the non-protected area close to the boundaries, with some delay occurring as you move away from the MPA border. Once equilibrium is reached, the density inside the protected area remains stable over time (in simulations up to 50 years) irrespective of fluctuations in the harvesting regime within the fishing area. Our findings do not coincide with others, such as the ECOSIM dynamic mass-balance model that showed slow increase, or the negative response of biomass for some groups, such as crustaceans and molluscs, in simulations of short time periods of under three years (Watson et al., 2000). This is likely due to our model being applied to individual species and not taking into account interspecies relationships. In the case of the ECOSIM model the rapid response of top predators (many of them being target species for

fisheries) would explain the slow response of other prey species mentioned above. In line with our findings it is noteworthy that the ECOSIM model did predict that there would be a marked increase in biomass of most groups after 10 years. Our findings also agree with a review by Halpern and Warner (2002) of 112 independent measurements from 80 reserves which revealed that higher average values for density inside reserves (relative to controls) reach mean levels within a time period of 1–3 years for reserves that have been established for up to 40 years. This supports conclusions reached by Gerber et al. (2005) that the optimal monitoring time-frame for analysing the reserve effect in terms of protecting populations and enhancing fisheries, as well as making the best management decisions for marine reserves and improving estimates for optimum design, is rarely more than five years.

**Table 7.** ANOVA table for the dependent variables ABUNDANCE (number of individuals per 100 m<sup>2</sup> in the integral reserve) and FLUX (number of individuals per 100 m per day crossing the reserve boundary) analysed for the factors integral reserve size (IR\_SIZE with six levels: 100, 500, 1000, 2000, 6000, 12,000 m radius); protection status (PROTECTION with four levels: integral reserve, boundary, non protected close and non protected far) and diffusion coefficient of species (DIFFUSION with five levels: 100, 500, 1000, 2000, 5000 m<sup>2</sup> day<sup>-1</sup>) and their interactions.

Source of variation	df	Mean-square	F-ratio	P
Dependent variable: ABUNDANCE ( <i>n</i> : 10,479; $R^2 = 0.99$ )				
IR_SIZE	5	62.85	554.83	0.000
PROTECTION	3	3580.08	31,603.50	0.000
DIFFUSION	4	2.472	21.82	0.000
IR_SIZE × PROTECTION	15	25.64	226.35	0.000
IR_SIZE × DIFFUSION	20	2.16	19.050	0.000
PROTECTION × DIFFUSION	12	15.83	139.73	0.000
IR_SIZE × PROTECTION × DIFFUSION	60	1.78	15.74	0.000
Error	10,359	0.11		
Dependent variable: FLUX ( <i>n</i> : 10,479; $R^2 = 0.54$ )				
IR_SIZE	5	582.89	64.89	0.000
PROTECTION	3	13,167.77	1465.84	0.000
DIFFUSION	4	4522.68	503.47	0.000
IR_SIZE × PROTECTION	15	713.61	79.44	0.000
IR_SIZE × DIFFUSION	20	122.04	13.59	0.000
PROTECTION × DIFFUSION	12	1786.90	198.92	0.000
IR_SIZE × PROTECTION × DIFFUSION	60	176.46	19.64	0.000
Error	10,359	8.98		

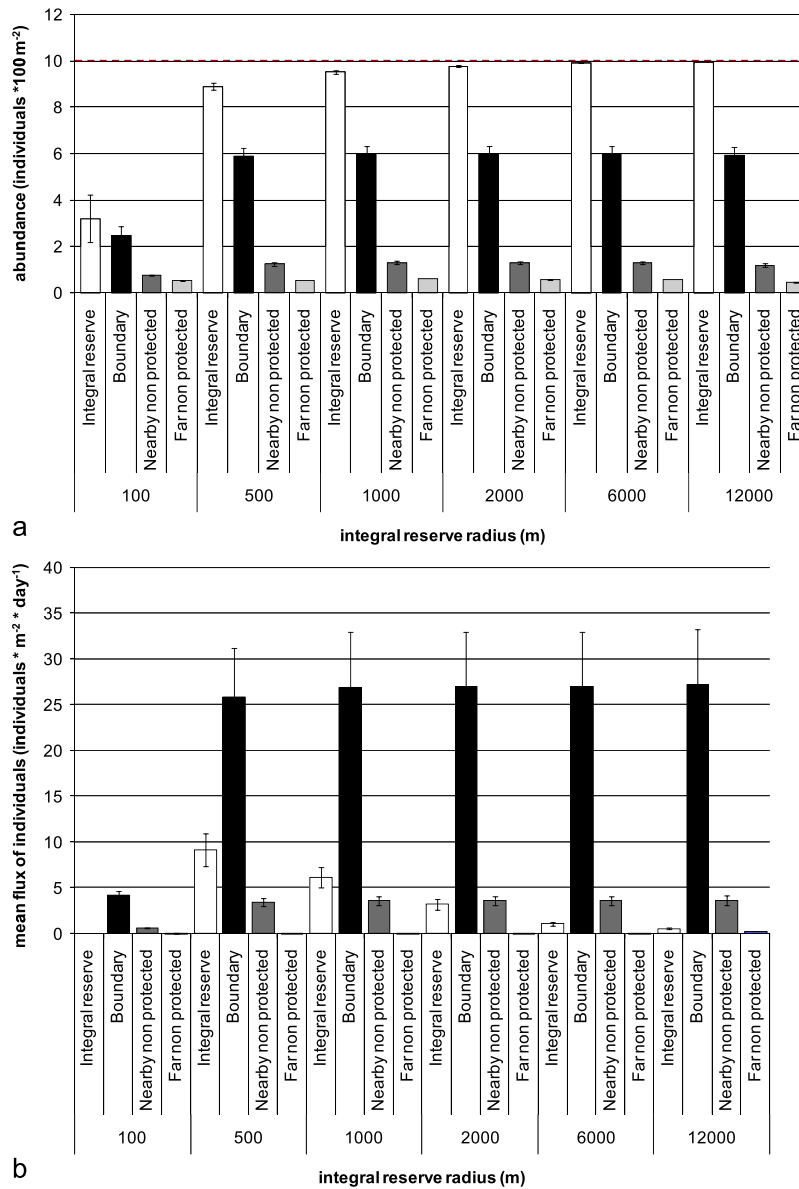
### Spill-over at the reserve boundary

As well as abundance and biomass of species increasing within the MPA, we would expect both “spill-over” and “leakage” to produce an abundance gradient across reserve boundaries. The slope of the gradient will depend on fish mobility and the scale of displacements. [Kramer and Chapman \(1999\)](#) examined the implications of fish home-range size and relocation on marine reserve function and their ability to increase abundance outside reserve boundaries. They predicted that species with intermediate levels of mobility and density-dependence of space use would provide the greatest spill-over benefits to nearby fisheries. Our results show that, for reserves larger than 1000 m radius, the flux of individuals increases with the diffusion coefficient of species, enhancing fisheries outside the reserve without negative consequences for the density of the protected populations in the integral reserve.

According to [Chapman and Kramer \(1999\)](#), if fishing pressure around an MPA is moderated, one can expect that a gradient of abundance will occur across the reserve boundaries. On the contrary, if fishing pressure outside the MPA is extremely heavy, abundance will show a sharp difference between protected and unprotected areas. However, in disagreement with these authors, as shown by simulations, gradients were always present except when there was no fishing activity at all. In the case

of highly mobile and/or vulnerable species whose home-range clearly exceeded the MPA area, some gradient was still expected to exist, although the populations inside the reserve reached less than 30% of the carrying capacity.

The difficulties in detecting the exportation of biomass from MPAs to surrounding areas could suggest that dispersal mechanisms are not as effective as expected for many littoral demersal fish, or more probably, that some limitations exist in an approach based on looking for straight lines in nature. In fact, the problem lies in that the gradient takes place at small spatial scales (a few hundred metres) on both sides of the reserve boundary and is usually much smaller than the scale at which sampling designs are applied ([Harmelin-Vivien et al., 2008](#)). Furthermore, this straight line is a particular case of the state of equilibrium of a gradient in which at one extreme (inside the integral reserve) the higher population density remains constant and at the other extreme, a continuous loss of individuals take place due to constant fishing effort. However, when harvesting due to fishing activity occurs along the gradient line with different fishing effort (as occurs outside the reserve border), such theoretical equilibrium is not usually reached and a new one based on polynomial functions would describe the gradient more adequately (see [Harmelin-Vivien et al. \(2008\)](#) for real gradients in different marine reserves).



**Figure 6.** Mean values of abundance of individuals (a) and flux (b) in the integral reserve (IR), at the boundary of the MPA, in the nearby non-protected area (<2000m from the boundary) and in the far non-protected area (>2000m from the boundary) in reserves of different sizes.

Thus, when describing the curve along the gradient two factors must be considered: the distribution of the fishing pressure outside the reserve; and, the rate of diffusion over the reserve boundary. Both factors determine the difference between the population abundance inside and outside the reserve, and the slope of the gradient. The percentage of the system's carrying capacity reached by a population is related to the slope of the gradient, and is determined by the flux of individuals and the instantaneous growth rate of the population. As found in recent works, MPA size

plays an important role in maximising the differences in abundance inside and outside its borders (Claudet et al., 2008). In our study, multiple regression models selected the reserve size as an explanatory variable of the reserve effectiveness both, in maximising the abundance in the integral reserve and the slope of the abundance gradient at the boundary. However, in practice, with the exception of very small MPAs, the differences in reserve size have little influence on the abundance within MPAs and spill-over to the fishing area.

### How big must an MPA be?

The size of the reserve is an important parameter when designing management strategies based on MPAs. However, meta-analytical studies comparing biological variables of fish communities inside and outside MPAs found no (Côté et al., 2001; Guidetti & Sala, 2007; Halpern, 2003) or positive effects (Claudet et al., 2008) for the size of marine reserves. Clearly, the effectiveness of a marine reserve in maintaining the population density as close as possible to the carrying capacity of the system with a critical number of spawners, so that the growth rate of the population due to recruitment and reproduction might compensate for the continuous loss of individuals over reserve boundaries, must be highly dependent on the total stock and therefore of the reserve's size and its carrying capacity. If this were not the case, and fishing pressure outside was high, the reserve would eventually become depleted and lose its functionality. In this context it is important to note that the size should be considered in relation to those habitats suitable for a given species and not only the total size of the reserve. On the other hand, recent empirical studies find thresholds indicating a general increase of the spatial scale affecting fisheries benefits, with increasing MPA sizes (Stelzenmüller et al., 2008).

According to our results, large MPAs (i.e. larger than 2000 m in radius) offer the maximum capacity for recovery (close to 100% of the system carrying capacity) and nearly the maximum flux of individuals per unit boundary length. Very large MPAs could be a guaranteed means of providing resilience in order to prevent population crises due to extremely high natural mortality or recruitment failure, with the added advantage that the flux of individuals is slightly higher at larger distances from the boundary. However, in practice they provide no further advantage towards increasing the density of individuals or the exportation of biomass, and therefore other management strategies could be more beneficial, both from the point of view of conservation and of benefits to fisheries. In fact, the carrying capacity is reached in all reserves larger than 1000 m radius with normal ranges of species diffusion (depending on home-range). This agrees with Lundberg and Jonzén (1999) which showed that, based on a different approach, optimal harvest rate remains unaffected by the size of the reserve. This is an important consideration to take into account when using MPAs to manage fisheries. The effectiveness of these protection measures is the same for a very large protected area as it is for several smaller ones

whose sum is equal in size. However, benefits for fisheries in the non-protected areas would be greater from a network of medium-sized MPAs separated from each other by a few kilometres. This is in agreement with the conclusions reached by Neubert (2003) who estimated that catch would be maximised by fishing the lines of multiple marine reserves. Furthermore, other studies performed in the EMPAFISH project show that total management costs increase with reserve size, and total cost per ha shows a minimum for integral reserves between 600 and 1500 ha (1400-2200 m radius) (Alban et al. 2008). Thus, the ideal size of no-take zones range between 600 and 1500 ha, and any further improvement should come from a network of several MPAs, each with an individual size of between 600 and 1500 ha, and taking into account that the effects on fisheries would be improved when the distance between MPAs is not higher than a few tens of kilometres.

### Biological factors determining the effectiveness of a marine protected area

Some of the key points of the effectiveness of a marine reserve according to this modelling approach are home range and its related diffusion coefficient estimations. Home-range size and spatial use by organisms are considered critical in determining the effectiveness of MPAs in terms of conserving biomass, or providing biomass for adjacent fisheries through spill-over (Eristhee & Oxenford, 2001; Kramer & Chapman, 1999; Russ & Alcala, 1996). According to our results the latter case holds true more-so than the former. Our results show that marine reserves larger than 1000 m radius maintain the abundance of their populations close to their carrying capacity, meanwhile the flux of individuals through the reserve boundary and the spatial range at which it can be detected are strongly affected by the diffusion coefficient. Nonetheless, critical information on movement patterns, spatial use, habitat preferences of the species harvested and to what extent home ranges vary within species are still scarce (Topping et al., 2005).

Home range is related to the diffusive capacity of individuals but few studies have established or quantified this relationship. According to the movement patterns of different species of decapods, Vannini and Cannicci (1995) classified the species into random-diffusive movement and non-random diffusive movement categories with some continual shifting of location during the study periods as well as non-random non-diffusive



movement categories, but no data are provided to quantify such differences. Furthermore, species can show differences in their diffusive capacity between sexes, the size of the individuals, depending on the time of the day or between unprotected areas and reserves (Connolly et al., 2002; Hereu, 2005; Jones, 2005). Here we have used a broad range of diffusive coefficients based on species for which data on home-range and random movement patterns are available. However, the particular values for these species cannot be considered accurate. Our estimates would only be useful in establishing a realistic range of possibilities to include in the model. In addition to diffusion based on home-range displacements, many benthic species show migratory movements from juvenile to adult habitats. Although the scale of movements ranged from metres to thousands of kilometres, most organisms ( $\approx 80\%$ ) move from kilometres to tens of kilometres (Gillanders et al. 2003). As these movements are non-random, either in time or space, they could probably produce deviations from the model's general predictions when comparing with abundance or fishery enhancement data in some areas.

Another important biological parameter to consider in the functioning of a MPA is the instantaneous population growth rate of the species. This affects the speed of recovery of the populations after cessation of fishing activity and the ability of the species to maintain abundances close to the carrying capacity inside the integral reserve. Furthermore and most importantly, it affects the population size in the fished area and therefore determines the fishing mortality that the population can support without collapsing. In our study, multiple regression analyses performed selected this parameter as an explanatory variable of the descriptors of the reserve functioning, slope of the gradient, flux of individuals at the boundary and percentage of the carrying capacity recovered in the integral reserve. It showed a positive coefficient when explaining the slope of the abundance gradient at the reserve boundary, and negative coefficient in the regression function when explaining the flux of individuals. When  $r$  increases, the slope becomes less negative and the flux of individuals through the boundary decreases. In all cases, the effect of  $r$  is strongly linked to its relation with fishing mortality rate.

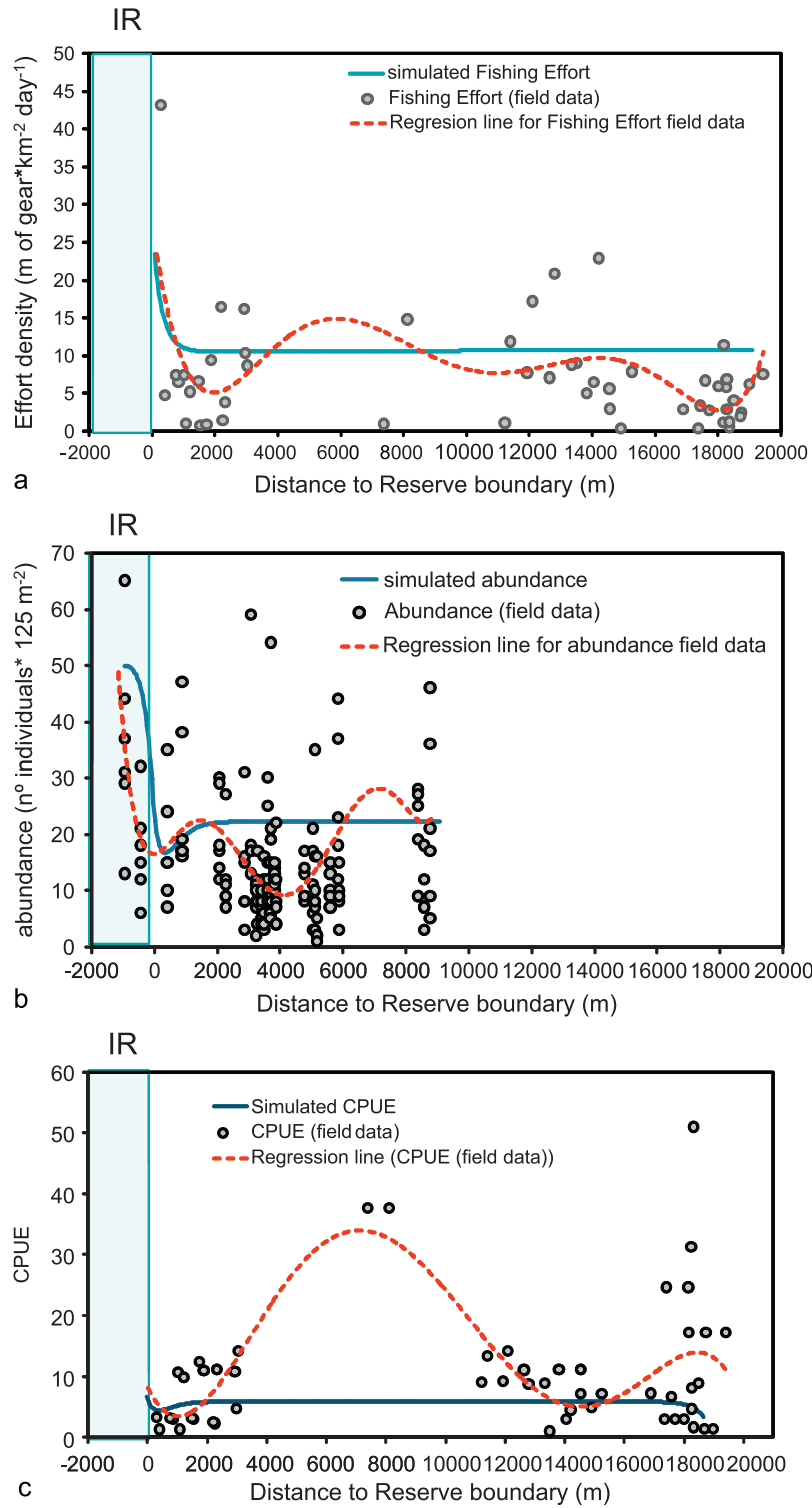
### Applicability of the model to management of real fisheries and marine protected areas

Fishing activity is a dynamic process both in time and space. Rarely is fishing effort distributed

uniformly in space. In fact, as recent studies have shown, fishing effort tends to concentrate in the proximity of reserve boundaries producing heterogeneous patterns and steep gradients of fishing effort within the study areas (Goñi et al., 2008; Hilborn et al., 2006; Murawski et al., 2005; Stelzenmüller et al., in press). In general, fishermen adjust their position to maximise the catch per unit effort (CPUE) according to the "fishing the line" strategy, so that a concentration of fishing effort close to the reserve boundary is interpreted as evidence of spill-over from the reserve. In general it has been considered that effort redistribution can be critically important to achieving management objectives, especially when fishing effort concentrates near the boundaries of a marine reserve or fishing closure (Halpern and Warner, 2003; Halpern et al., 2004), however, our results predict that this is only true for small MPAs (less than 500 m radius). The consequences of three fishing strategies (fishing effort is uniformly distributed, when a harvesting strategy with a fishing-the-line component is implemented for a competitive fishing industry, and in the case of a coordinated fleet) on the spatial patterns of fish density and CPUE in the vicinity of a marine reserve has been analysed in a recent theoretical study, published during the reviewing process of this work and based on the same modelling approach (Kellner et al., 2007).

We have compared a real case study in Cabo de Palos-Islas Hormigas, southeast Spain, with the outputs of the model for the same total fishing effort, and a negative exponential distribution with distance from the reserve boundary to the nearby non-protected zone, and constant in the far non-protected area (Figure 7). The reserve includes an integral reserve 270 ha in size (927 m radius) where all fishing activity is prohibited. Data on fish abundance of target and bycatch species through a gradient from the integral reserve to the fishing area were obtained by visual censuses using scuba-diving on rocky substrates with patches of sand and *Posidonia oceanica* beds, between 6 and 12 m depth (see Harmelin-Vivien et al., 2008 for details) and data from fishing effort and catches were obtained from field sampling on board the Cabo de Palos fishing fleet. In both cases abundance and catch data sets were recorded in 2004 and 2006 as part of the European project BIOMEX.

The conditions fed into the model reproduce the observed real conditions with a carrying capacity of 41 individuals per 125 m<sup>2</sup> for all the species considered, and a daily mean total fishing effort in the area of 3200 m of different fishing gears. Best fits of the model were obtained for  $r = 0.015$ ,



**Figure 7.** Spatial patterns (circles and dotted line) and model predictions at steady state (solid line), of fish abundance (B) and multispecies catch per unit effort (CPUE) (C) in the vicinity of a marine reserve (shaded area) based upon the fishing effort distribution showed in (A) for the real data (circles and dotted line) and the model (solid line), respectively. The parameter values used to fit the model were  $K = 41$  individuals  $125 \text{ m}^{-2}$ ;  $r = 0.015 \text{ day}^{-1}$ ;  $D = 4000 \text{ m}^2 \text{ day}^{-1}$ ;  $q = 0.33$ ;  $F = 0.0085 \text{ day}^{-1}$ .

$q = 0.33$ , a mean diffusion coefficient  $D = 4000$ . The resultant fishing mortality ( $qE$ ) was 0.009. The model outputs (Figure 7) are quite similar to the real data on assemblage abundance distribution in the nearby non-protected area and to the slope at the boundary, as well as the mean values through the complete gradient. Deviations from the field data can clearly be attributed to the spatial variability of fishing effort that, apparently, does not fit exactly with the fishing the line concept, or to spatial changes in the carrying capacity due to habitat complexity variability. Figure 7a shows a gradient of fishing effort from the reserve to the distant non-protected area with a strong concentration of effort close to the reserve boundary. However, secondary effort concentrations can be observed at 8 and 14 km from the reserve, coinciding with the main rocky outcrops in the area and an extensive field of anti-trawling artificial reefs. The increase in the carrying capacity of these sites due to their higher habitat complexity and lower fishing pressure than in the reserve boundary explain the higher than expected fish density and CPUE in these areas (Figure 7b and c).

The importance of habitat complexity on fish density has already been stated by García-Charton and Pérez-Ruzafa (1998, 1999, 2001) and García-Charton et al. (2000). According to these studies, habitat structure is one of the main factors used to explain the variability in Mediterranean fish assemblages. Therefore, in some cases, non-protected marine areas with naturally complex habitats may present even more diverse and abundant ichthyofauna than neighbouring protected areas with simpler habitats (García-Charton et al., 2004). Therefore, the expected habitat heterogeneity along transects from the integral reserve and the fishing area can preclude, or interfere with the detection of expected abundance gradients and should be incorporated in to models to predict the reserve effect and fishing fleet behaviour.

Furthermore, as Mediterranean marine reserves are established in areas that already harbour structurally complex habitats, they thereby support a more abundant and diverse fauna (García-Charton & Pérez-Ruzafa, 1999). The influence of the habitat can lie in a fixation effect being exerted on the assemblage, increasing the effectiveness of protection measures by increasing the carrying capacity inside the reserve but decreasing the practical (real/effective) difference in concentration of the diffusion equation, and acting as an attractor in the assemblage and fixing the home-range centre, thus reducing spill-over. This could explain the fact that small reserves, albeit with a significantly greater habitat complexity than in

surrounding zones (as is often the case in the Mediterranean), show a significant reserve effect when differences in abundance are compared inside and outside the reserve.

## Conclusions

Random home-range movements at the boundaries of a protected area and home-range relocation as a consequence of density-dependent factors can be adequately described by diffusion models and are probably the main driving force leading to a spatially defined biomass gradient at small and medium scales. This holds for organisms whose movement follows the assumptions of the model, i.e. undirected random dispersal with no directed migrations. Diffusion rates based on home-range displacement in a spatial concentration gradient result in a passive flux of specimens from regions with higher concentrations to those with lower concentrations. For all the reserve sizes the flux of individuals could reach up to 10 km from the reserve boundary, however this only affected the observed abundance gradient significantly within the first 2000 to 3000 m. This “area of influence” was affected by reserve size and became significantly shorter as the size of the reserve became lower than 500 m radius. At larger distances, exportation via egg and larval dispersal became the main mechanism to explain the connectivity between populations (González-Wanguemert et al., 2004; Pérez-Ruzafa et al., 2006).

The model showed that biological responses inside marine reserves appear to develop quickly, reaching mean levels within a short (1–5 year) time period. The effectiveness of the protection and the exportation of individuals per unit length through the boundary of the reserve depend on the size of the MPA. Mean abundance is always higher inside the reserve and highlights the effectiveness of protection, particularly when there is strong fishing pressure outside the reserve. However, reserves smaller than 2000 m radius show significantly lower levels of abundance in the integral reserve than larger sites. Large MPAs (i.e. about 2000 m in radius) offer nearly the maximum capacity for recovery (close to 100% of the system carrying capacity) and nearly the maximum flux of individuals per unit boundary length. Very large MPAs (i.e. larger than 6000 m in radius) could be a guaranteed means of providing resilience in order to prevent population crises, with the added advantage that the flux of individuals is slightly higher at larger distances from the boundary.

However, in practice they provide no further advantage towards increasing the density of individuals or the exportation of biomass, and a network of smaller MPAs could be more beneficial, both from the point of view of conservation and of benefits to fisheries.

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