The effects of marine protected areas over time and species’ dispersal potential: a quantitative conservation conflict attempt

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Abstract. Protected areas are an important conservation measure. However, there are controversial findings regarding whether closed areas are beneficial for species and habitat conservation as well as for harvesting. Species dispersal is acknowledged as a key factor for the design and impacts of protected areas. A series of agent-based models using random diffusion to model fish dispersal were run before and after habitat protection. All results were normalized without the protected habitat in each scenario to detect the relative difference after protecting an area, all else being equal. Model outputs were compared with published data regarding the impacts over time of MPAs on fish biomass. In addition, data on species’ dispersal potential in terms of kilometres per year are compared with model outputs. Results show that fish landings of species with short dispersal rates will take longer to reach the levels from before the Marine Protected Areas (MPAs) were established than landings of species with long dispersal rates. Further, the establishment of an MPA generates a higher relative population source within the MPA for species with low dispersal abilities than for species with high dispersal abilities. Results derived here show that there exists a feasible win-win scenario that maximizes both fish biomass and fish catches.

1 Introduction

Habitat protection is a complex issue which has only recently achieved high public visibility (UN, 2010). In marine environments it covers many aspects, such as conservation of juvenile fish habitats, protection of corals, and development of marine recreational parks or dive sites. Fishing is often seen as a destructive force, and habitat destruction by fishing practices has to be considered in any comprehensive management plan (Jones et al., 2011). Habitat protection can be total or partial. Total closures are often associated with Marine Protected Areas (MPAs) and the designation of certain areas for alternate uses such as recreation.

Closing an area affects several stakeholders. Closed areas are of interest to biologists, conservation scientists, land use planners, but also to fishermen and the fishing industry in general as well as the tourism industry (Ami et al., 2005; Rees et al., 2010b). While there are cases where closed areas are beneficial for species and habitat conservation (Jones et al., 2011; Seytre and Francour, 2014), there are also studies that question the benefits of closures from an economic perspective regarding fish landings (Gårdmark et al., 2006; Jones et al., 2011). This in turn has implications for both food security (Pauly et al., 2005) and economic impacts on fisheries (Eide et al., 2003, 2011; Jentoft and Eide, 2011). Thus a win-win scenario in terms of both increased fish biomass and increased fish landings after establishing an MPA is ideal (Rees et al., 2010a) but questionable.

The design of MPAs involves specifying the total surface area to be protected, the distribution in space of that area, and its connectivity (Moustakas and Silvert, 2011). That leaves a fairly wide range of choices: there is controversy about whether single large reserves are more effective than several smaller ones of the same total area, whether edge effects diminish their efficacy, and whether closely spaced reserves are more effective than distantly spaced ones (Mous-
takas and Silvert, 2011). It is acknowledged that dispersal is a key factor in designing MPAs (Coleman, 2013; Underwood et al., 2013). The reasons behind dispersal being a key factor (Lewis et al., 2013) are that (i) MPAs should be large enough so that adults can stay long enough inside them, but how large is large enough is clearly related to dispersal potential; (ii) MPAs should be close enough so that larvae can move between them, but how close is close enough is also related to dispersal potential.

Assuming dispersal to be an important factor in determining the ability of species to reach the protected areas, the impacts on species with different dispersal abilities may vary in time from the establishment of an MPA (Claudet et al., 2008; Silvert and Moustakas, 2011) for various reasons related to species growth rates or the ability of species to reach or remain within the MPA. Here, assuming all other factors that influence the efficacy of MPAs remain equal, the impacts of MPA(s) on biomass inside and outside the reserves, as well as on landings over time to species with different dispersal abilities, are investigated. In an effort to provide the relative differences in fish biomass and fish landings with and without MPAs, agent-based simulation modelling is used (Moustakas and Evans, 2015; Moustakas and Silvert, 2011) to model migration (Schönfisch and Kinder, 2002) via diffusion (Augustijn et al., 2016). Model outputs of each simulation scenario after the establishment of an MPA were normalized by model outputs of the same scenario prior to the establishment of an MPA in order to detect relative changes before and after closing an area.

2 Methods

2.1 Model overview and rationale

A simulation model is used to predict the efficacy of MPAs as a function of species’ dispersal potential and different catch rates across two different MPA spatial design scenarios. All results presented here (regarding fish biomass and annual catch) were normalized to 100% in the steady-state situation without the MPA in each scenario. Thus, results presented here are presented as dimensionless numbers. Clearly, results from field studies are expected to differ in their values but in comparison with field data the shape of the curves should be at least similar. The model assumes that fish move around at random (Blackwell, 1997). Such a modelling attempt can serve as a null model (Silvert and Moustakas, 2011) and potentially as a minimal model for pattern formation (Petrovskii and Malchow, 1999). This is a conservative (and often an unrealistic) approach as many species exhibit directed dispersal by seasonal migration between feeding and spawning areas. However there are also species that exhibit such dispersal behaviour such as littoral fish species (estuarine fish, intertidal fish, coral reef fish), and the fishery that is mainly involved with this type of fishing is trawl and recreation fishing (Mant et al., 2006). In addition, habitat-dependent species like coral reef species (e.g. clownfish, anemonefish, and damselfish) are also characterized by this type of movement. The active fishery that is predominantly linked to this type of fish is artisan fishing (Campbell and Pardede, 2006).

2.2 Model description

The model follows previous modelling attempts in which a full description is provided (Moustakas and Silvert, 2011; Moustakas et al., 2006), modified accordingly here so that dispersal is random. The model is run on a square grid with $100 \times 100$ cells and each cell contains a fish biomass value $V(i, j)$. The initial fish biomass concentration was set to $V(i, j) = 100$ for all cells. Time step interval $t$ was set to 1 day and the total length of the simulation period $T$ was set to 10 years.

Population growth occurs at each time step with a constant (time- and space-independent) growth rate $G$. Fish landings (i.e. fish harvesting, thereby landings, $L$) occur at each time step with a rate of $L$. Landings are distributed over space (cells, $i, j$) at each time step $t$ such that higher fishing mortalities occur at cells with higher fish biomass concentration (Millischer and Gascuel, 2006). Consequently, fishing efforts (landings) are proportional to the concentration of fish (McClanahan and Kaunda-Arara, 1996). Thus, for a given annual mortality rate $M$, fishing mortalities are the same in scenarios with and without MPAs, but in scenarios that include MPAs fish harvesting (in the model landings) is spatially more intensive than the same effort distributed among fewer cells.

Fish movement is random with an equal probability of diffusing to the eight adjacent neighbouring cells. The probability of migrating to one of the eight neighbouring cells is multiplied by $D$ (dispersal) with values of $D$ close to 0, indicating small dispersal probability, thus a species with short dispersal potential, while $D$ values close to 1 indicate long dispersal.

For each time step $t$ and for each cell $i, j$, new biomass $V(i, j, t+1)$ values are updated in all cells prior to the establishment of MPA(s) or are introduced in all non-protected cells after MPAs. Biomass at the current cell is updated by adding growth, subtracting natural mortalities and fishing mortalities (landings), adding biomass that potentially diffused from any of the eight neighbouring cells and subtracting biomass from current cell that diffused to only one of the eight neighbouring cells:

$$V(i, j, t+1) = V(i, j, t) \times (1 + G - (M + L) \times V(i, j, t) + D \times \left(\frac{\left(V(i-1, j, t) \text{ or } V(i+1, j, t) \text{ or } V(i, i-1, j, t) \text{ or } V(i, i+1, j, t) \text{ or } V(i, j-1, t) \text{ or } V(i, j+1, t) \text{ or } V(i-1, j+1, t) \text{ or } V(i+1, j-1, t) \right)}{100} - V(i, j, t)\right) \text{ and landings } \times \left[1 \frac{\sum V(i, j, t)}{i} \text{ for } i, j \in \text{ all cells} \right] \times \left(\sum V(i, j, t) \text{ for } i, j \in \text{ all protected cells}\right)$$

while new biomass $V(i, j, t+1)$ values are updated in all
protected cells by \( V(i, j, t+1) = V(i, j, t) \times (1 + G + D \times ((V(i-1, j, t) \text{ or } V(i+1, j, t) \text{ or } V(i-1, j-1, t) \text{ or } V(i+1, j-1, t) \text{ or } V(i, j+1, t) \text{ or } V(i, j-1, t) \text{ or } V(i-1, j+1, t) \text{ or } V(i+1, j+1, t)) - V(i, j, t))) \).

There are no periodic boundary conditions meaning that fish located in the four corner cells of the simulation grid may move only to their three neighbouring cells.

The spatial design of MPA(s) included two different scenarios: a single large and two small MPAs totalling the surface of the single large MPA, and in each case the same total surface area was protected. The total protected surface area spanned from 1\% up to 20\% of the simulation area. In all cases mortalities \( M \) remain constant as prior to the establishment of MPA(s).

In order to examine relative differences with and without MPAs, each simulation scenario is replicated with a common parameter space, \( T, G, M, L, D \), in the first case without an MPA and in the second case with MPA(s). The model assumes that before the imposition of any MPA the fishery dispersing with a dispersal coefficient \( D \) had reached a steady state with the stock (only one stock is considered) growing at a rate of \( G \text{ day}^{-1} \) equal to the natural mortality of \( M \text{ day}^{-1} \) (\( G = M \) in the absence of landings \( L \)). Thus the explored fish stock exhibits mortality rates \( M + L > G \), which is an overfished population. Fish biomass \( V(i, j, t) \) and landings \( L(i, j, t) \) on cell \( i, j, \text{ time } t \), are recorded for every cell and time step for each identical simulation scenario (same \( T, G, M, L, D \)) pre- and post-MPA(s) establishment and sequentially divided as post-MPA(s) establishment results/pre-MPA(s) establishment results [\( V(i, j, t)_{\text{MPA}} / V(i, j, t)_{\text{noMPA}} \) and \( L(i, j, t)_{\text{MPA}} / L(i, j, t)_{\text{noMPA}} \)]. By doing this, the relative change before and after the establishment of MPA(s) is examined.

The simulation scenarios examined here (parameter space) include fish dispersal coefficients \( D \) varying from 0.1 to 0.2 with increments of 0.02, and from 0.1 to 0.5 with increments of 0.05. Landings were simulated for annual landing rates \( L = 1.1 \times G \), and \( L = 1.25 \times G \) (landings \( L \) up to 25\% larger than the growth rate \( G \)). The total protected surface area covered up to 20\% of the simulation space. The recorded variables included the development of fish catches over time and the spatial distribution (inside and outside the MPAs) of the simulated stock over time. Each parameter space scenario was replicated 10 times to account for stochasticity and results were averaged.

### 2.3 Model validation – confronting model outputs with data

In order to constrain model outputs with data (Moustakas and Evans, 2015), published data regarding fish biomass of fish species pre- and post-MPA establishment were used from the California Channel Islands, USA, including five fish species (see next paragraph for details regarding species) (Karpov et al., 2012) for model validation. The data included species-specific biomass data before and after MPA establishment (Karpov et al., 2012), allowing comparisons of impacts over time, as well as within and outside the protected area after the MPA was established from 2003 to 2008, allowing comparisons inside and outside the protected area after MPA establishment. Further, the data set also provides statistics on landings of commercial species before and 3 years after the establishment of MPAs.

The species-specific landings post-/pre-MPA establishment were regressed against their dispersal potential. Dispersal potential of each species was retrieved from the following published studies: Semicossyphus pulcher and Caulolatilus princeps from Kinlan and Gaines (2003); Atractoscion nobilis from Hervas et al. (2010), Ophiodon elongatus from Starr et al. (2004), and Paralichthys californicus from López-Duarte et al. (2012). In order to investigate the ratio of fish biomass inside and outside MPAs after the establishment of MPAs, the density (number of fish per 100 m²) of three targeted fish species was retrieved at the same time snapshot inside and outside MPAs and regressed against the species’ dispersal potential. The three fish species included Semicossyphus pulcher, Ophiodon elongatus, and Sebastes miniatus, and their dispersal potential was retrieved for the first two species as cited above. Dispersal potential of Sebastes miniatus was retrieved from Freiwald and Quinn (2012).

In order to link model predictions with marine species dispersal potential, thus predict the time impacts on landings of different species groups, analysis on (adult) marine taxa dispersal data was conducted. The data derived from a meta-analysis of 1897 publications (Moustakas and Karakassis, 2005, 2009): Within this data set a search regarding dispersal rate of species was conducted. From the 1897 publications, only the ones that explicitly mentioned dispersal rates per species and length of the study so that dispersal can be normalized as km yr⁻¹ were used. In total the dispersal rates of \( N = 553 \) marine taxa were available in the data set.

An empirical cumulative density function (ECDF) was used to evaluate the dispersal range of each species (in kilometres) against the percentage of species in the data set that have a dispersal potential less than or equal to that value. The ECDF \( F_n(x) \) is defined as follows:

\[
F_n(x) = \frac{\text{number of elements in the sample } \leq x}{n} = \frac{1}{n} \sum_{i=1}^{n} 1 \{t_i \leq x\}.
\]

In the case examined here the values of \( F_n(x) \) on the vertical axis define the percentage of all species \( t_i \) with a dispersal range less than or equal to the corresponding value on the horizontal axis, \( x \) in km yr⁻¹. For example the value on the vertical axis of 10 corresponds to the value \( x \) on the horizontal axis of the dispersal range in km yr⁻¹ of 10\% of all species. The ECDF resembles a cumulative histogram without bars and it is based on parameters estimated from the
original data (Van der Vaart, 2000). In this respect, an ECDF is similar to a probability plot, except both axes are linear and non-transformed (Van der Vaart, 2000). Further, 95% confidence intervals of the mean and median values of species’ dispersal rates were calculated.

3 Results

Model outputs showed that recovery of landings (in comparison to the levels of pre-MPA establishment) was faster for species with high dispersal rates than for those with low dispersal rates. This applies to both single large and multiple small MPA spatial designs for mortalities \((M + L)\) up to 25% larger than growth rates \(G\) and for 20% of the total protected surface areas (Figs. 1a, 2a). This implies that landings of species with low dispersal rates or short home rates will take longer to recover. Spatial distribution of species biomass within the MPA(s) increases with decreasing dispersal potential and this applies to both single large and multiple small MPAs for mortalities up to 25% larger than growth rates and for 20% of protected surface area (Figs. 1b, 2b). Results for mortalities \(M < 1.25 \times G\) produced higher recovery of landings and biomass (results not shown here). However, results for total protected surface area < 20% resulted in the recoveries of species with high dispersal rates only (results not shown here).

Statistical analyses of fish density data post- and pre-MPA establishment showed that landings of commercial fish species in post-MPA establishment divided by the
landings of the same species pre-MPA establishment regressed against the dispersal potential of each species. This showed that in the case of the five commercial fish species that were examined, the relative change in landings post-normalized by pre-MPA establishment was more pronounced in species with longer dispersal rates (Fig. 3a; $R^2 = 70.8\%$, $df = 1$, $p = 0.022$ formula: $\log_{10}(\text{after/before}) = -0.4725 + 0.1860 \log_{10}(\text{Dispersal})$). Relative fish density inside MPAs divided by fish density outside MPAs regressed against the species’ dispersal potential and showed that species with shorter dispersal rates have relatively shorter density inside MPAs than outside (Fig. 3b; $R^2 = 100\%$, $df = 1$, $p = 0.008$, formula: $\log_{10}(\text{fish density in/out from the MPA}) = 0.2785 - 0.05567 \log_{10}(\text{dispersal})$).

Highest dispersal potential is exhibited amongst the phyla of Gadiformes, Crustaceans, Perciformes, Echinodermata, Mollusca, and Pleuronectiformes (Fig. 4a). With the exceptions of Gadiformes and Pleuronectiformes, phyla with high dispersal rates have a high variation of dispersal rates between individual species within the phylum (Fig. 4a). The majority of phyla examined have dispersal rates of less than 1 km (Fig. 4a). From the species considered here, 48% have dispersal rates of < 1 km, while 90% have dispersal rates of < 200 km (Fig. 4b). Overall, dispersal rates between species was very high as indicated by differences between 95% confidence intervals of the mean = 54 km, [41, 68] and the median = 7 km, [4, 31].

4 Discussion

Model outputs derived here depict the relative time needed for fish landings to reach levels from before the establishment of an MPA. The method – normalizing outputs after a change in the system has been introduced by model outputs prior to the change – may serve as a valuable null model tool in ecology and biological sciences in order to investigate the relative effects of a key parameter (here, dispersal on the impacts of MPAs on both fish biomass and landings). Models are used when experiments are costly, require significant labour effort, ethics, and effects of spatial or temporal scales associated. Cellular automata and agent-based models are useful tools for addressing such issues (Bastardie et al., 2013; Convertino et al., 2015; DeAngelis and Yurek, 2015; Eide, 2012, 2014; Moustakas and Silvert, 2011; Moustakas et al., 2006).

4.1 Recovery after the establishment of an MPA as a function of dispersal

Model outputs derived here showed that fish catches are more likely to recover faster at the original levels pre-MPA(s) establishment and above. Statistical analysis of normalized post/pre-MPA establishment data exhibited a monotonic pattern and faster recovery of landings of long dispersers – data were available for 5 species and 5 years after closures.

4.2 Source–sink dynamics and biomass inside and outside MPAs

Source–sink theory has been applied to the spatial design and impacts of MPAs (Andrello et al., 2013; Seijo and Caddy, 2008). Results derived here exhibited that MPAs are increasingly acting as population sources as species’ dispersal range.
Figure 4. (a) Dispersal rates per different orders of species (in km yr\(^{-1}\)), data from a search in the data set described in Moustakas and Karakassis (2005, 2009). The solid line is the median, and the boxes are defined by the upper and lower quartiles (25th and 75th percentiles). The whiskers extend up to 1.5 times the interquartile range of the data. (b) Empirical cumulative density function (ECDF) of the dispersal range of each species (in kilometres) against the percentage of species in the data set that have a dispersal potential less than or equal to that value. ECDF shows the percentage of species that exhibit a dispersal range (km yr\(^{-1}\)) less than or equal to the value on the horizontal axis.

decreases. Species with shorter dispersal rates are likely to also be smaller in size and/or body mass (Alimov, 2003; Williams, 1999), thus they benefit more simply from the fact that in all scenarios MPAs had an equal total size. Clearly, home range areas of short dispersers will be smaller than those of long-distance dispersers (the model does not account for individual body length or mass). However, given that species with short dispersal potential have more restricted distributions (Bradbury et al., 2008; Curini-Galletti et al., 2012), overall it seems reasonable to expect that protecting the habitats of short dispersers will create larger population buffers within the protected area than when protecting the habitats of long dispersers. Data of movement of lingcod (Ophiodon elongates, a species with limited dispersal rates from the five examined species post-/pre-MPA landings) in and out of an area closed to fishing, showed that individuals left the reserve but were only absent for a short time (Starr et al., 2004). Model outputs from another study have also reported that modest dispersal rates of fish can reduce abundance within protected areas (Walters et al., 2007).

According to the results derived here, the abundance of species of phyla with very low dispersal rates such as Porifera, Rhodophyta, Bryozoa, and Anthophyta will be considerably higher within the MPA than outside. The majority of these species are not commercial (and would not be targeted by fishers) but a “blind” fishing method such as trawling would affect them (González-Irusta et al., 2013; Heery and Cope, 2014). Further, several of the short dispersing species are habitat-forming species (Lilley and Schiel, 2006). It should be noted, however, that these conclusions are based upon a fairly large data set (Moustakas and Karakassis, 2005, 2009), but this data set is not exhaustive.

In general the variables used in this work have no units, as they are normalized. However when comparisons with real fish species are made, since real \(D\) values are used, it would be interesting to use them to gain an insight into the real-life size of the grid, the subsequent grid cell size, and MPA size. The model is run on a simulation space of \(100 \times 100 = 10000\) cells. Assuming a perfectly directed dispersal (the opposite of random diffusion) from the upper left to the lower right corner of the simulation grid, which is the maximum straight line distance that can be made, fish can disperse into 141.42 cells, which is the diagonal. The minimum value of dispersal recorded in the data set was 0.0005 km yr\(^{-1}\), while the maximum was 527 km yr\(^{-1}\). After defining the diagonal distance by the largest dispersal value, 142 cells correspond to 527 km, thus the cell diagonal is \(\sim 3.7\) km, the cell side \(\sim 2.6\) km, the cell surface area \(\sim 6.9\) km\(^2\) and the simulated area \(\sim 6.8 \times 10^4\) km\(^2\). Note that these values are only listed as a gross rule of thumb as (a) species disperse randomly and not directed, and (b) the ABM model is not calibrated to a specific scale (Moustakas and Evans, 2015; Zhang et al., 2015).

4.3 Limitations and simplifications of the method

This study shows that in the explored parameter space a win-win scenario in terms of fish biomass and increase in landings after some years of closing an area is feasible, but it does not show what the actual parameter space leading to this result is. It only shows that this is mathematically possible. Despite the fact that the results presented here are unitless (ratio), the sensitivity to the scale of analysis has not been accounted for (Gautestad 2013) in terms of multiscale modelling (Duan et al. 2014). A ratio is scale-free, but the actual processes as they are defined here are not. There are several scales involved: \(D\) in the context of a diffusion process regards dispersal distance squared divided by time, thus both space- and timescales are involved (Gautestad and Mysterud, 2010). Due to the implicit scale of the grid cells (unit
5 Conclusions

There are very large differences in the dispersal potential of species as indicated by differences between mean (\(\sim 50 \text{ km yr}^{-1}\)) and median values (\(\sim 7 \text{ km yr}^{-1}\)) (von Hippel, 2005). The mean dispersal value is derived mainly by relatively few species with long dispersal potential. The median dispersal value rather reflects the dispersal potential of the majority of species. In addition the ECDF distribution values indicate that 50% of all species disperse no more than 1 km per year and 70% of all species no more than 50 km yr\(^{-1}\). Distances between MPAs are often not comparable to these values (Andrello et al., 2013). This indicates that there is no simple optimal conservation strategy if dispersal is a critical factor for the efficacy of MPAs. Large-bodied marine species are under greater threat of global extinction (Olden et al., 2007) and have longer dispersal rates (Bradbury et al., 2008). It is therefore difficult to design an MPA that will account for long dispersers, thus large-bodied threatened species, and simultaneously account for maximizing biodiversity within the MPA (based on dispersal as a biodiversity proxy) or maximizing slow-dispersing habitat-building species.

Introducing MPAs may lead to a temporary decline of landings, owing to stronger fishing effort outside the protected areas to compensate for lack of fishing inside MPAs. However, over time the source–sink effect – due to a gradual many-fold increase in fish abundance inside the MPAs – may not only gradually make landings from the unprotected fishing areas rise again but even overshoot the pre-MPA level. This result was achieved under overfishing, a 25% of total mortalities (natural and fishing mortalities) higher than the growth rate as it often happens in reality (Daskalov, 2002; Jackson et al., 2001). Thus, a win-win result is achieved (Rees et al., 2010a): fish and the local ecosystem are protected and can thrive inside protected areas, and the fishing industry will benefit from a net gain after a temporary decline while waiting for the MPA population(s) to increase sufficiently, so that it can become a strong provider of dispersing individuals (Rees et al., 2010a). This win-win scenario needs time (Rees et al., 2010a; Russ and Alcala, 2004), and in general an integration of science and stakeholder-based methods may facilitate such scenarios (Gall and Rodwell, 2016; Ruiz-Frau et al., 2015).

Fast recovery or even overshoot of landings relative to pre-MPA level basically depend – under the given model design – on two main aspects: dispersal rate \(D\) and number of MPAs (actually, the size of MPAs relative to \(D\); see below). Larger \(D\) and/or splitting of MPA into a set of smaller areas with the same total area both contribute positively to reducing the time it takes to regain a pre-MPA landing quantity. Thus, in the context of SLOSS, from the present results many small refuges seem to benefit both fish populations and exploitation. \(D\) is species- and habitat-dependent (and varies with age class, which is not accounted for here). However, the number of MPAs, their locations and sizes are manageable. This theme has been subject to much research, both empirically and through simulations, and results from meta-analyses have generally been non-conclusive due to the many-faceted system dynamics (Palumbi, 2004). Theoretical results have generally supported the a priori intuitive hy-
pothesis that strong dispersers are less protected by MPAs than more sedentary species (Micheli et al., 2004; Moustakas and Silvert, 2011; Moustakas et al., 2006). However the present results support the opposite: strong D leads to relatively fast recovery of landings after implementation of the refuge, while still maintaining a larger fish density inside the refuges relative to the pre-MPA level. Splitting the refuge into smaller entities improves recovery even more, and may lead to even better fishing yields in the long run.

At present MPAs generally cover much less than 20% of fishing areas; consequently this policy need revision in order to achieve the net fishing gain over time. Other studies suggested that the yield from the harvest effort is strongly affected by the fraction of area protected from harvesting and that maximum yield is independent of the size of the protected area unless the fraction is > 0.56 (Kaitala et al., 2004). The dependence on D is a key parameter here, and should be considered relative to (dispersal distance squared)/(time unit), MPA size, and an estimate of the fishing range in the actual area.

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