



Novel methods for the design and evaluation of marine protected areas in offshore waters

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Abstract

There is strong international agreement on the need for marine protected areas to reverse pervasive human impacts on the oceans' biodiversity. However, their implementation is often hampered both by legal difficulties in defining reserves in international waters and the patchy nature of data in many offshore waters. We demonstrate the use of recent advances in statistical learning and conservation prioritization to produce MPA scenarios with varying costs and benefits for New Zealand's Exclusive Economic Zone, based on the analyses of distributions of 96 demersal fish species. MPAs based on our most cost-effective scenario would deliver conservation benefits nearly 2.5 times greater than those from equivalent-sized areas recently implemented at the request of fishers, and at lower cost to them. Such results demonstrate the power of quantitative, knowledge-based prioritization approaches, which can be applied at high resolution and at oceanic scales.

Introduction

Ongoing and pervasive declines in marine biodiversity at a global scale are driven by pressures including human exploitation, pollution, and environmental change (Roberts 2002; Thrush & Dayton 2002; Pandolfi *et al.* 2003; Stokstad 2006). Perhaps most seriously, persistent overharvesting has resulted in substantial declines in fish catch, and nearly one-third of fish stocks are now subject to unsustainable exploitation (Ormerod 2003). Although there is strong agreement on the need to establish a global network of marine protected areas (MPAs) to reverse these losses (Laffoley 2006), such areas currently protect only 0.6% of the world's oceans (Wood 2006). Their creation is hampered by a range of factors, including legal difficulties in defining and protecting reserves in international waters (Gjerde 2005), and/or a scarcity of comprehensive data describing biological patterns, particularly in offshore waters.

Various methods are being used to provide improved descriptions of habitats and/or biological values in marine ecosystems (e.g., Palumbi *et al.* 2003; Iampietro *et al.* 2005). These can serve as inputs to the growing range of analytical tools to aid reserve design (e.g., Marxan—Possingham *et al.* 2000; C-plan—Lombard *et al.* 2007) particularly in coastal and/or inshore waters (e.g., Sala *et al.* 2002; Airame *et al.* 2003; Leslie *et al.* 2003; Breen *et al.* 2004). In turn, other methods allow forecasts of fishery responses to reserves (Ecopath and Ecospace; Pitcher *et al.* 2002). This article describes a proof of concept analysis using a new combination of modeling methods that offer important features for marine reserve design in offshore waters, including: (1) realistic interpolation of species distributions based on biological and environmental data; (2) ability to handle relatively fine-scale data over large geographic areas; (3) obviation of the need for prior definition of planning units; and (4) identification of a nested set of reserve solutions that comprehensively describe

trade-offs between conservation benefits and reserve extent.

We use as our study area the oceanic waters of New Zealand’s Exclusive Economic Zone (EEZ), the fourth largest in the world, in which Government policy is to protect 10% of the total area as MPAs by 2010 (Anonymous 2000). We focus initially on the use of species distribution models (Guisan & Thuiller 2005) to interpolate catch data for widespread fish species from patchily distributed research trawls across all parts of the Exclusive Economic Zone with trawlable depths. We then analyze these species distributions using spatial prioritization software, deriving a range of MPA scenarios with widely varying conservation returns and costs to fishers. Our most cost-effective scenarios deliver conservation benefits that substantially exceed those delivered by areas recently set aside at the instigation of fishers.

Materials and methods

Predicting fish species distributions

While we had detailed fish catch data for 96 commonly caught, demersal (bottom-dwelling) fish species from more than 21,000 research trawls (Figure 1A),

the patchy spatial distribution of these required use of a robust interpolation procedure to provide geographically comprehensive descriptions of fish distributions. This was achieved using a statistical implementation of Boosted Regression Trees (BRT), a recently developed technique that uses stochastic gradient boosting to fit a model (Friedman *et al.* 2000; Friedman 2002), enabling sophisticated regression analyses of complex responses optimized for high predictive performance (Elith *et al.* 2006; Elith *et al.* 2008). This method differs from conventional regression in that, rather than fitting a single “best” model, it fits an ensemble of simple regression tree models. As a consequence, BRT draws on the strengths of regression trees, that is, their ability to handle continuous and categorical predictors while ignoring extraneous predictors, their accommodation of missing values in the predictors, and their fitting of interactions between predictors, while using boosting (the adaptive fitting of multiple models) to overcome their tendency to instability and lack of accuracy (Friedman & Meulman 2003).

To maximize the predictive performance of our BRT models, we chose environmental predictors that were functionally relevant to fish (Table S1, Leathwick *et al.* 2006). They included estimates of the trawl depth, temperature, and salinity at the sea floor, primary

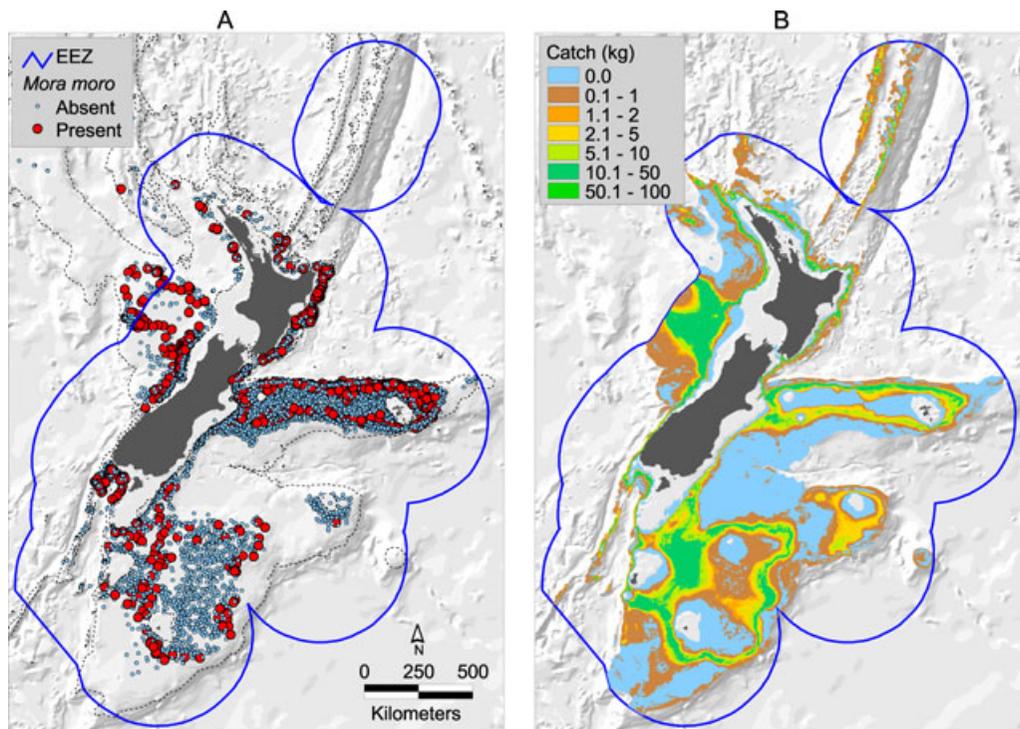


Figure 1 Geographic distribution of a typical species (*Mora moro*). Shown are: A. The actual presences and absences in the research trawls—note the uneven geographic distribution of these. B. The predicted catch per unit effort. In A, dashed lines indicate the 200 and 1950 m depth contours, which define the limits within which analyses were performed.

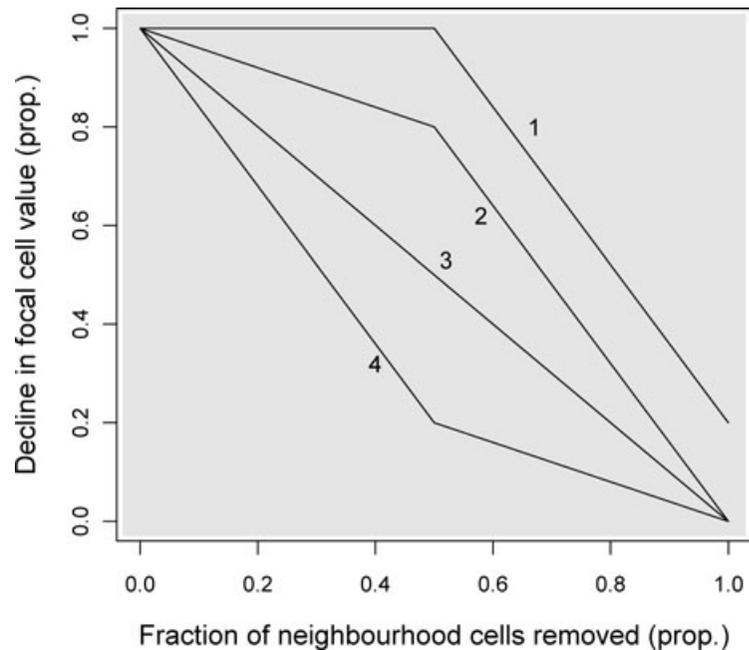


Figure 2 Species-group responses describing the decline in conservation value of focal cells as cells in their neighborhood are removed from the solution.

productivity at the ocean surface, and zones of ocean mixing and tidal currents. Estimates of sea floor water temperature and salinity were based on the World Oceans Atlas (Boyer *et al.* 2005). Estimates of suspended particulate matter, dissolved organic matter, and chlorophyll-*a* concentration were all derived from satellite imagery (Pinkerton & Richardson 2005). Data describing trawl distance, speed, and mesh size were included to allow standardization of catch success by taking account of differences in trawl parameters. While it would have been desirable to calculate the area swept for each trawl, lack of consistent collection of data describing net door spread, and headline height precluded this.

Because of the large number of trawls, we randomly split them into two sets—the first contained 17,000 trawls and was used for model fitting, while the second (4,314 trawls) was used solely for validation. Species catch data described the weight in kilograms of all species caught in 1% or more of trawls. Given the highly skewed (zero-inflated) distribution of the catch data, we fitted two BRT models for each species, and combined them using a delta-log-normal approach (Venables & Dichmont 2004). The first model for each species predicted its probability of catch using the presence/absence transformed data from all trawls in the training dataset, assuming binomial errors. The second was fitted to data only from those trawls in which a catch for a species occurred, and predicted the log of the catch, assuming normally distributed errors.

All regressions were fitted in R (R Development Core Team 2006) with the “gbm” library (Ridgeway 2006), and using a tenfold cross validation procedure to optimize model complexity for prediction (Elith *et al.* in press). The predictive performance of the final regression models was evaluated in two ways. First, estimates of predictive performance were calculated as part of the cross-validation procedure used to optimize model complexity. Second, we independently estimated the performance of all models by predicting for the evaluation data set both the probability of occurrence for each species (all trawls, $n = 4,314$), and its catch (trawls in which each species were caught). These predictions were then compared with the actual values using the area under the Receiver Operating Characteristic curve (AUC) statistic (Fielding & Bell 1997) for the predictions of occurrence, and the Pearson’s correlation coefficient for the catch estimates.

Finally, the presence/absence and catch models were used to make environment-based predictions of the catch per unit effort for each species for 1.59 million grid cells, each of 1 km² (Figure 1B). In making these predictions, we assumed fixed trawl parameters, that is, a trawl distance of 4.26 km, a speed of 5.92 km/h, and a codend mesh size of 75 mm. These predictions covered all of New Zealand’s Exclusive Economic Zone with depths between 200 and 1950 m, including the 1.57 million grid squares for which no trawl data were directly available. Separate predictions were made

of the probability and the amount of catch for each species, with the latter back-transformed with correction (Duan 1983) so that final values were in kilograms. Probability and catch predictions were then multiplied together to form one predictive data layer (kg/standard trawl) for each species.

MPA design and evaluation

In the second phase of our analysis, we used the reserve selection software Zonation (Moilanen *et al.* 2005, Appendix S1 in Supplementary Material) to design and evaluate a range of potential MPA configurations, based on the predicted fish distribution data layers created in the first phase of our analysis. Zonation is based on the specification of priorities and connectivity responses for biodiversity features (Moilanen 2007) rather than on setting conservation targets as for most other conservation planning methods (Sarkar *et al.* 2006). It is particularly suited to the analysis of very large data sets (Kremen *et al.* in press) and provides solutions that have both high conservation value and are well balanced with respect to representation levels, connectivity, and spatial patterns for species (Moilanen 2007).

The Zonation meta-algorithm (Moilanen *et al.* 2005; Moilanen 2007) starts by assuming that the full landscape is protected, and proceeds by progressively identifying and removing cells that cause the smallest marginal loss in conservation value. Removing grid cells of least conservation value first leaves the areas of highest value until last, and these areas are the most relevant for conservation. The critical part of the algorithm is the definition of marginal loss, which also allows species weighting and species-specific connectivity considerations to be applied. Here, we used the core-area definition of marginal loss (Moilanen *et al.* 2005; Moilanen 2007), which in simple terms embodies the following principles: (1) of two otherwise equal locations, that with a lower occurrence for the most important species is removed first; (2) assuming two otherwise equal locations, that with the occurrence of a lower-weight species is removed before that with an equal occurrence for a high-priority species; (3) assuming two identical locations with identical original occurrence levels for two different species, the one is retained that contains a species that has lost more of its distribution; (4) of two otherwise identical locations, that with higher cost is removed first. Mathematically, marginal loss in core-area Zonation is defined as

$$\delta_i = \max_j \frac{Q_{ij}(S)w_j}{C_i} = \frac{p_{ij}w_j}{C_i * \sum_{k \in S} p_{kj}} \quad (1)$$

where w_j is the weight of species j , p_{kj} is the occurrence level of species j in site i , and C_i is the cost of adding cell

i to the reserve network. The critical part of equation (1) is $Q_{ij}(S)$, the proportion of the remaining distribution of species j located in cell i in the remaining set of cells, S . When a part of the distribution of a species is removed by cell removal the proportion located in each remaining cell goes up. In this manner, Zonation tries to retain high-quality core areas for all species until the end of cell removal, even if the species is initially widespread and common (Moilanen *et al.* 2005). Other variants of Zonation cell removal implement conservation planning based on additive value (Arponen *et al.* 2005) and specification of targets (Moilanen 2007), but we used core-area Zonation as it guarantees the retention of high-quality areas for all species, including those that occur in otherwise species poor areas.

All Zonation analyses used the predicted distributions of 96 fish species as their primary input. Nineteen endemic species were given higher priority in all analyses by allocating them a weight of five, while all other species were given a weight of one. An analysis of the sensitivity of outcomes to use of differential species weightings is provided in Appendix S1. To take account of the likely impacts of fragmentation on species protection provided by MPAs, we applied boundary quality penalties that allow the value of a target cell for a particular species to be reduced as cells in some surrounding neighborhood are removed (Moilanen & Wintle 2007). Losses were assessed in neighborhoods of varying size and at varying rates (Figure 2), depending on the known habits of species. For species living predominantly on the sea floor, mostly flat fish and eels, we used a 3 by 3 cell neighborhood, and a relatively slow loss of value (curve 1 in Figure 2), that is, 50% of the surrounding cells can be removed without loss of value in the target cell, but beyond this, removal of surrounding cells results in a linear decline to a value of 0.2 when all surrounding cells were removed. For species living immediately above the sea floor but caught largely as solitary individuals we used a 5 by 5 cell neighborhood and a slightly steeper loss curve (curve 2 in Figure 2). For species living above the sea floor but caught frequently as schooling aggregations we used a 7 by 7 cell neighborhood and a loss curve that declined linearly to a value of zero when all neighboring cells are removed (curve 3 in Figure 2). Finally, for the most mobile, semi-pelagic and schooling species we used a 9 by 9 cell neighborhood and a loss curve in which the value of a target cell diminishes to 20% when 50% of the surrounding cells are removed, and to zero when all surrounding cells are removed (curve 4 in Figure 2). A sensitivity analysis demonstrating the effects of these settings is provided in Appendix S1. One major algorithmic option in the software, uncertainty analysis (Moilanen *et al.* 2006), was not used here, but provides the capability to adjust the

optimization process where greater uncertainty is associated with species predictions for some regions, for example, in the far north-east of our study area where there are only a few trawls.

With these commonalities, we carried out four analyses that explored conservation benefits and their costs under varying conditions:

Unconstrained or “no cost constraint” analysis.

Equal costs were used for all cells, that is, this analysis was driven solely by consideration of species distributions, connectivity and conservation value with no regard to potential costs to fishers.

“Full cost constraint” analysis.

Species weightings and boundary quality penalties were applied as in the previous analysis, but costs for grid cells varied depending on fishing intensity as recorded by fishers during the 2005 calendar year. The fishing intensity or “cost” data layer (Figure S1) was created by applying a kernel smoother with a 20 km smoothing neighborhood to the start locations of a completely independent set of 47,700 commercial trawls conducted during 2005. The resulting spatial data layer was then scaled to describe relative fishing intensity, with values ranging from zero for no fishing to 100 for maximum fishing intensity. Because Zonation requires all cost estimates to be greater than zero, we allocated nonfished grid cells a nominal value of 1.0e-6 for this analysis.

“Modified cost constraint” analyses.

Three modified cost analyses were run, each of which used differing modifications of the cost layer to alter the balance between costs for fished and nonfished cells and allowing a more comprehensive exploration of scenarios intermediate between our “no cost constraint” and “full cost constraint” scenarios. The modified cost estimates were calculated as:

$$C_i^{\text{modified}} = \begin{cases} a, & \text{for unfished cells} \\ a + 1 + \log_{10}(C_i), & \text{for fished cells} \end{cases} \quad (2)$$

where a is a parameter used to tune the influence of cost, and C_i is the true fishing opportunity cost estimate for the cell. Three analyses were carried out using modified cost layers with values for a set to 1, 2, and 5, higher values decreasing the importance given to protecting sites preferred by fishers when selecting optimal sets of sites for protection.

“BPA” analysis.

In a final analysis, we used Zonation to assess the costs and benefits of a set of benthic protection areas (BPAs)

recently implemented at the request of fishers that provide partial protection to benthic species through the exclusion of bottom trawling (Ministry of Fisheries 2007). These areas were selected by fishers to protect a representative range of ecosystems based on a broad-scale environmental classification of New Zealand’s marine environments, along with a number of particular high value sites. They avoided areas fished either currently or in the past (Seafood Industry Council 2008). Although the BPAs encompass 23.5% of New Zealand’s EEZ, substantial parts of them (72.2%) are located in waters that are too deep to trawl with current technologies (> circa 2000 m). We therefore restricted our analysis to those parts of the BPAs that are in offshore waters of trawlable depths (200–1950 m), where they comprise 16.6% of the geographic area. In this replacement cost analysis (Cabeza & Moilanen 2006), we required Zonation to retain those cells falling within the BPA’s until all other cells had been removed, enabling assessment of their conservation returns using the same criteria as in our other analyses.

In summarizing the conservation outcomes for each of the scenarios described above, we mostly use as a measure of performance the average percentage of species distributions protected in a given fraction of geographic area. We stress that this is an aggregate measure of performance that summarizes statistics describing the quality, extent, and spatial distributions of individual species (Moilanen 2007). Similarly, we also report the costs as a function of the fraction of the geographic area protected for each scenario: for the “full cost constraint” scenario, these costs were calculated as an integral part of the analysis, while costs for the remaining scenarios were calculated retrospectively using the fishing cost layer described above.

Results

Predicting fish species distributions

Depth, temperature, and salinity had the strongest contributions to the outcomes of regression models predicting the distributions of fish species (Table 1), together accounting for nearly half the variation in catch when averaged across species. A further 13% of variation in species catch was accounted for by variables identifying zones of high productivity and/or where food resources are concentrated (chlorophyll- a and SST-gradients). Three trawl parameters, trawl distance, trawl speed, and net mesh size, together contributed approximately 14%.

Distributional models fitted for species showed excellent predictive ability both when assessed using cross-validation and in predicting to independent trawls

Table 1 Average contributions (%) of predictors describing environment and trawl methods in statistical models predicting the presence/absence and catch of 96 demersal fish species. Predictors are ranked in decreasing order, based on their overall average contribution.

	Presence/ absence	Catch	Overall average
Trawl depth	33.5	17.9	25.7
Temperature	13.8	12.7	13.3
Salinity	8.2	10.6	9.4
Chlorophyll- <i>a</i>	6.6	7.6	7.1
Sea surface temperature gradient	4.6	7.3	6.0
Tidal current	4.8	6.8	5.8
Codend mesh size	5.2	6.3	5.7
Trawl distance	3.7	5.8	4.7
Sea-floor slope	3.5	5.4	4.4
Year effect	4.1	4.6	4.3
Suspended particulate matter	3.9	4.2	4.0
Trawl speed	3.0	4.6	3.8
Orbital velocity	3.1	3.4	3.3
Dissolved organic matter	2.0	2.8	2.4

withheld from model fitting. The two parallel sets of performance estimates for the presence/absence models had a correlation of 0.969, and those for the catch models a correlation of 0.913. The presence/absence models for all species had excellent discrimination of species occurrence (mean AUC score = 0.950, range 0.86–0.99). By contrast, the predictive performance of the regression models predicting species catch was more variable (mean correlation = 0.534, range 0.05–0.82), and was strongly influenced by the number of catch observations used in model fitting. All species whose catch models showed poor predictive performance (correlation < 0.3) were caught in less than 5% of trawls. Final spatial predictions for these species depended mainly on their presence–absence models, and within the geographic range predicted as occupied by any of these species, predicted values were generally close to the mean catch. By contrast, the mean correlation for species occurring in greater than 10% of trawls was 0.67 with a minimum of 0.46. Final spatial predictions of catch for these species showed much greater variation reflecting the influence of environment on both the probability of catch and the amount caught.

MPA design and evaluation

Results from our “no cost constraint” Zonation analysis indicate both those cells with the highest conservation priorities (Figure 3A), and the progressive decline in species protection as cells of lower conservation value

are removed from the solution (blue line in Figure 3D). Note that these priorities are hierarchical, that is, the 10% of cells with the highest conservation value are contained within the top 20% of cells, which are in turn contained within the top 30% of cells, and so on. Results from this initial analysis indicate that setting aside 10% of the offshore parts of New Zealand’s EEZ with trawlable depths would protect, on average, 27.4% of the geographic range of each of the 96 fish species analyzed. At a species level, there is a general trend of greater protection for species of more limited geographic range (Figure 4A), that is, the spatial extent of a species’ geographic range sets the maximum amount of protection that it can receive under any given degree of geographic protection. Despite this inherent constraint, protection of 10% of New Zealand’s EEZ based on this scenario would protect 20% or more of the geographic ranges of half of the 96 species used as input to the analysis. Assignment of higher weights to endemic species was effective, resulting in them receiving nearly 70% greater protection than nonendemic species (40.8% versus 24.1%, F -statistic = 10.79, $P = 0.001$). Increasing the area protected to 20% would increase average species protection to 46.4% and 83 out of the 96 species would receive protection of 20% or more of their geographic ranges. Retrospective analysis of the costs of implementing MPAs based on this scenario indicate that protection of the 10% of cells with the highest conservation value would result in a 22% reduction in fishing opportunity (Figure 3D), reflecting the strong coincidence between sites targeted by fishers and those having the highest conservation values. Finally, use of neighborhood constraints for this analysis identifies much more tightly aggregated groups of cells to protect than when such constraints are not applied, that is, use of boundary quality penalties not only allows for varying degrees of species mobility, but also provides a more useful basis for the implementation of MPAs with shapes meeting practical management requirements (Leslie *et al.* 2003).

Use of the cost layer to influence cell selection in our “full cost-constraint” analysis resulted in a markedly different set of priority cells being identified (Figure 3B) than those selected in our initial scenario, with only two-thirds of the top-ranked cells (top 10%) in these two scenarios shared in common. This reflects the manner in which cells favored for fishing were removed early in the analysis, even if they had high conservation value per se. Despite this, MPA protection with 10% geographic coverage based on this solution (Figure 3D) would provide only slightly lower conservation returns (23.4%) than our ideal “no cost constraint” scenario (27.4%). Forty-four percent of species would still receive protection of 20% or more of their geographic ranges under this

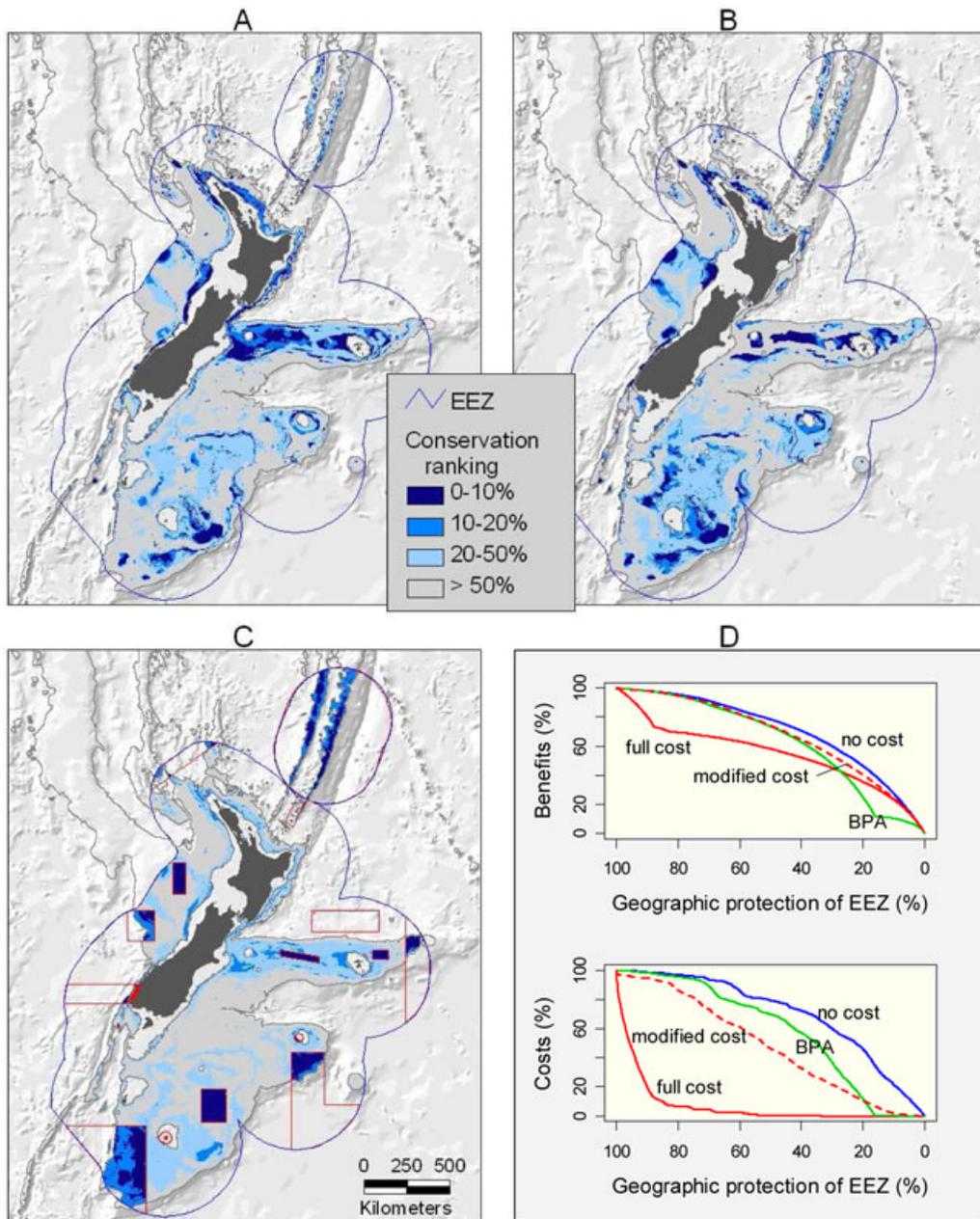


Figure 3 Zonation scenarios for marine protected areas in waters of trawlable depth in New Zealand's Exclusive Economic Zone, given varying constraints; highest conservation priorities are associated with low ranking scores. A. Initial "no cost constraint" analysis with weighting of endemic species and allowance for fragmentation effects; B. "full cost constraint"—as for A, but using a fishing intensity layer to constrain site

selection; C. "BPA"—as for A, but cells falling within Benthic protection areas (boundaries shown in red) were retained until all other grid cells had been removed; D. mean benefits (top) and costs (bottom) as a function of geographic protection of waters of trawlable depth in the Exclusive Economic Zone for four Zonation scenarios.

scenario (Figure 4B), and endemic species still receive 60% higher protection than widespread species (33.4% versus 20.9%, F -statistic = 9.91, P = 0.002). Importantly, these returns would be achieved with no loss of cur-

rent fishing activity. While this lack of impact on current fishing patterns is initially surprising, it reflects the manner in which Zonation removed practically all fished sites in the early stages of the analysis because of their low

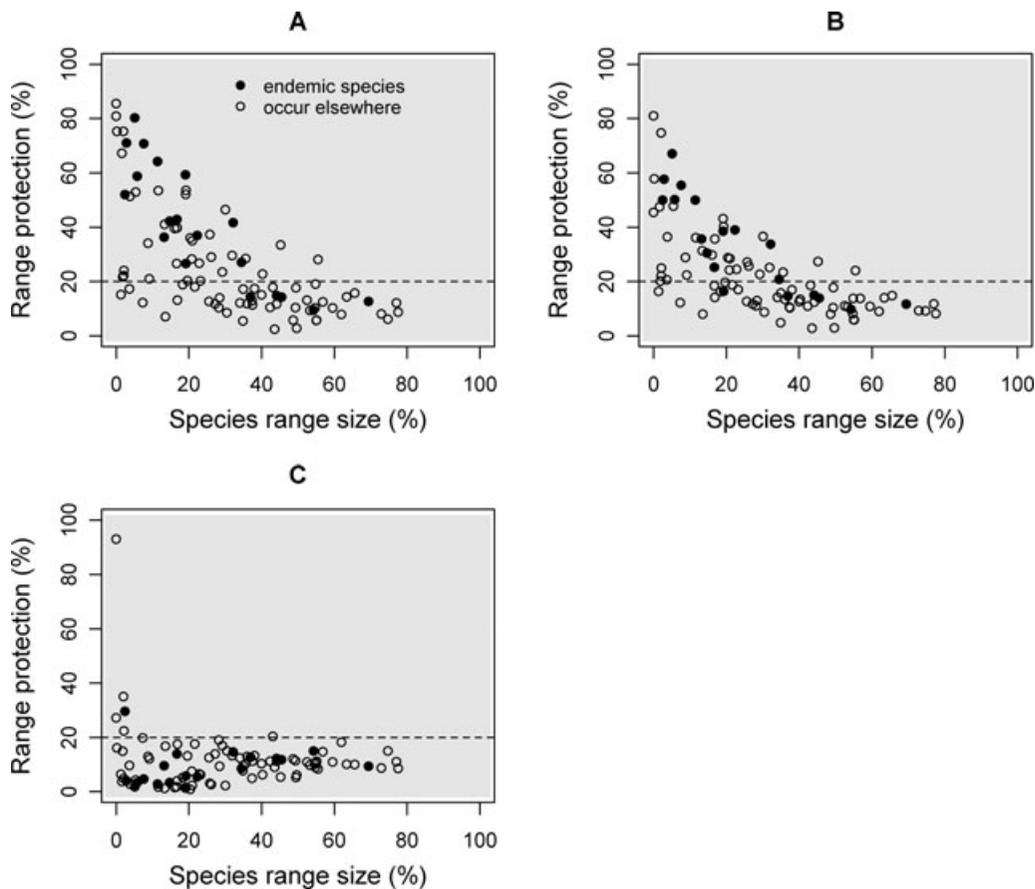


Figure 4 Comparison of the distributional range protection for species versus their range size, as provided by different Zonation scenarios, assuming 10% geographic protection: A—“no cost constraint”; B—“full cost constraint”; C—“BPAs.” Species range sizes are calculated as the percentage of the total extent of New Zealand’s EEZ with depths in the range 200–1950 m. Dashed horizontal lines indicate 20% species range protection.

benefit-to-cost ratio—note the rapid decline in costs in the early stage of cell removal for this scenario in Figure 3D. It also reflects the availability of alternative sites that have relatively high conservation value but are not fished, presumably because of their relative lack of commercial species or unsuitable conditions. This allowed Zonation to identify a set of alternative, nonfished sites with combined conservation values that are 85% of those protected when selection is made without cost constraints.

The spatial configurations produced by our “modified cost constraint” analyses provided a range of options intermediate between those produced by our “no cost constraint” and “full cost constraint” analyses (Figure S2). Assigning a value of 1 to the tuning parameter (*a* in formula 2) produces a spatial ranking that is most similar to that produced by our “full cost constraint” scenario, while assigning a value of 5 to the tuning parameter results in a spatial ranking much more similar to our “no cost con-

straint” scenario. The benefit and cost curves also occupy intermediate positions between the respective curves for the “no cost constraint” and “full cost constraint” scenarios, as shown for the scenario produced using a value of 2 for the tuning parameter in Figure 3D.

Use of Zonation to evaluate the conservation value of BPAs proposed by the fishing industry, which comprise 16.6% of the trawlable parts of the EEZ, indicate that these would deliver conservation benefits of 13.4% protection of species’ ranges if all fishing was prohibited within them. This would be achieved at a negligible fishing opportunity cost of 0.3%. The best quality parts of these reserves (Figure 3C and D), comprising 10% of the trawlable parts of New Zealand’s EEZ, could potentially deliver conservation returns of 10.4%, substantially less than would be delivered by equivalent areas based on our previous scenarios. At a species level, these best parts of the BPAs protect 20% or more of the geographic ranges of only six species (Figure 4C), all with limited

distributions. Endemic species receive the same average level of protection as those that are more widespread.

Discussion

Analytical issues

While our analysis is preliminary, it provides a powerful demonstration of the ability of emerging tools to integrate data and enable effective exploration of marine conservation scenarios over extensive offshore areas. Although statistical interpolation techniques are used widely to achieve spatially comprehensive predictions of species distributions in terrestrial settings, they are rarely implemented in marine environments. Here they allowed high-resolution prediction of species distributions over a large geographic area, and these predictions in turn facilitated use of a conservation planning tool that focuses on the design of networks optimized to provide balanced protection of species. Although we could have performed a similar analysis by target-based analysis using simulated annealing, initial trials indicated that, given the size of our study area, use of the most widely available implementation (Marxan) would have required substantial reduction in the spatial resolution of our data. Given the rapid changes in species composition along steep environmental gradients and marked local variation in fishing intensity, carefully controlled aggregation of data would be needed to minimize impacts on optimality of solutions (cf. Richardson *et al.* 2006). We preferred to retain all details and to use nested rather than target-based solutions for reserve selection.

Further development of several aspects of this analysis would be desirable to enable it to contribute better to operational planning. First, we assumed here that the commercial value of trawling in different locations is proportional to activity by commercial fishers, an approach also used in other studies (e.g., Sala *et al.* 2002). This was based on our understanding that spatial patterns of commercial fishing reflect strongly its profitability because strong economic constraints force fishers to focus their efforts in the most profitable locations. Use of information describing fishing patterns over longer time periods might be desirable, but recent patterns probably best describe current economic constraints, particularly those driven by recent increases in fuel costs. Use of more sophisticated profitability data would be possible, but would require a high level of industry cooperation. Further exploration is also required of the parameters used to describe the mobility of different functional groups of species to encourage geographically compact solutions, but this is challenging, given the general lack of information on movement of most offshore species. While our approach is empirical,

it allows biologically realistic aggregation with strongest effects applied to highly mobile species.

One potential limitation of our analysis is its reliance on biological data for only one functional group (demersal fish). However, evidence from at least one recent study (Colloca *et al.* 2003) supports the proposition that marine ecosystems with high fish diversity also support a high diversity of other functional groups. In addition, for many of the world's oceans, data describing fish distributions provides the only comprehensive description of biological patterns, and must therefore be relied upon as a surrogate for broader ecosystem patterns. Nevertheless, these methods are equally practicable if data for other biological groups are available for use either on their own, or in conjunction with fisheries data. Consideration should also be given to variation in the source-sink roles played by different parts of the geographic ranges of some species (Leslie 2005). For example, for species that congregate in large spawning aggregations, knowledge of where such spawning occurs could be used to insure the protection of these particularly high-value sites.

Use of catch data to define biologically rich areas could be problematic in heavily fished areas, particularly given the profound degree to which both the biomass and size-class structures of many species are likely to have been altered (Jennings & Blanchard 2004). In such systems, prediction of probability of catch alone might provide a more robust indication of former natural patterns than predictions of abundance. Alternatively, definition of MPAs in these settings might be more robust if based on representative protection of geographic units defined by bio-regionalizations defined using environmental factors driving ecosystem patterns (Snelder *et al.* 2006). Such approaches may also have to be used in waters deeper than around 2000 m, from which only limited biological data are generally available.

Management implications

Our results identify a range of potential MPA options that offer gradually increasing levels of protection to fish species distributions, albeit at increasing cost through loss of opportunity for fishing (Figure 5). Two particular features stand out. First, the stated policy objective of the New Zealand Government is to protect 10% of its EEZ, presumably reflecting a desire to balance conservation gains against the short-term costs incurred to resource-based industries by declaring reserves. Our results show that extending MPA coverage above this extent would not only deliver substantial increases in conservation benefits, but could also be achieved at minimal cost. For example, increasing the extent of MPAs based

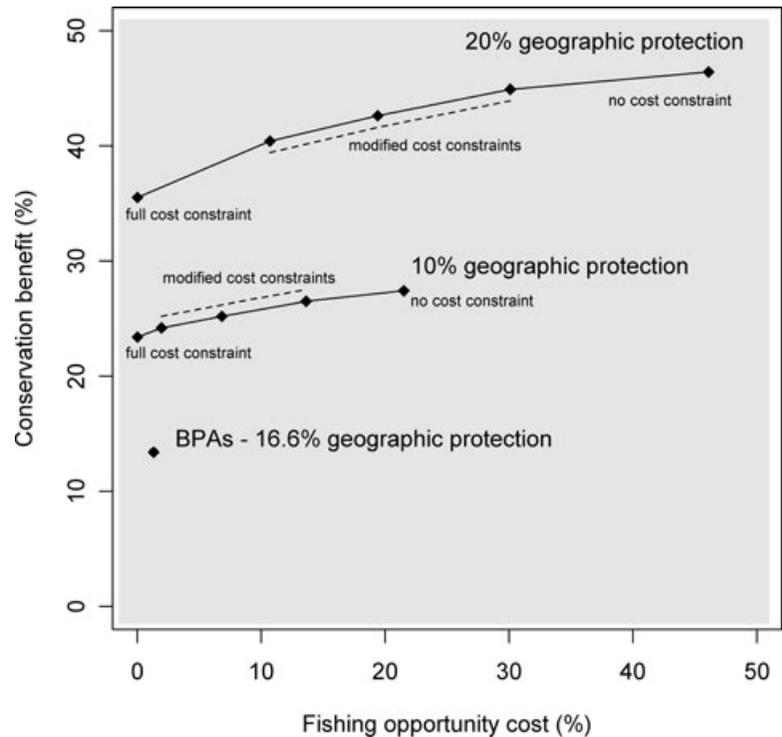


Figure 5 Costs and benefits of defining MPAs based on five Zonation scenarios in which cell selection was influenced to varying degrees by data describing spatial variation in fishing intensity during 2005. Cost–benefit curves are shown for 10% and 20% levels of geographic protection of waters with trawlable depths, with symbols indicating results from particular scenarios. The costs and benefits of reserves proposed by the New Zealand fishing industry (BPAs) are shown for comparison.

on our “full cost constraint” scenario from 10% to 20% geographic coverage would increase average species protection by 50% (left of Figure 5). Importantly, this could be achieved at minimal cost to the fishing industry, based on their current patterns of fishing. In addition, such benefits would exceed by almost 30% the best possible protection achievable when geographic protection is limited to 10%, that is, when no consideration is given to loss of fishing opportunity (our “no cost constraint” solution). That solution would reduce fishing opportunity substantially (22%), assuming fishing activity could not be relocated elsewhere.

Second, the alternative Zonation scenarios that we describe deliver substantially greater conservation benefits than BPAs recently implemented at the instigation of fishers, even though these were designed to meet similar objectives, that is, to provide representative protection across New Zealand’s EEZ while avoiding sites subject to fishing. By contrast, equivalent-sized MPAs based on our “full cost constraint” scenario would deliver nearly 2.5 times the conservation benefits while also completely avoiding areas currently fished. The little information that is available on how the BPAs were selected indicates that the process was essentially qualitative in nature. Given the similarity in stated objectives, we therefore conclude that these marked differences in outcome most likely reflect the choices of data and methods used for

selecting reserves. Suboptimal solutions associated with establishment of ad hoc reserves have also been reported in studies elsewhere (e.g., Stewart *et al.* 2003). Clearly, in this case the use of quantitative, data-driven tools would have allowed the identification of reserves having much greater representativeness, transparency, and efficiency (Pressey *et al.* 1993). In practical terms, the relative ease of use of the planning software that we used makes it ideally suited for use in collaborative approaches to MPA design involving a range of stakeholders, allowing conflicting objectives to be resolved in a transparent fashion to produce outcomes more likely to satisfy the objectives of all parties.

Finally, the most difficult challenges in defining MPAs are likely to be political rather than technical (Lawton 2007). This reflects a range of factors, including difficulties in defining protected areas in international waters, and resistance from those fishers who focus on the perceived short-term loss of fishing opportunity resulting from MPA creation, but with minimal acknowledgment of the long-term gains for wider ecosystem services. In the context of these challenges, our research demonstrates the ability of knowledge-based, cost–benefit analyses to create opportunities for win–win decision making that meets the objectives both of those with interests in marine conservation and those who derive a livelihood from the sea.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Additional methodological information about Zonation, including sensitivity analyses for species weighting and spatial effects.

Figure S1. Fishing intensity cost layer.

Figure S2. Zonation results when using modified costs layers.

Table S1. Environmental and trawl predictors.

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