Methods for evaluating the potential effects of marine protected areas on adjacent fisheries

by

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RESEARCH PROJECT SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

Master of Resource Management

In the
School
of
Resource and Environmental Management

Project No. 396

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SIMON FRASER UNIVERSITY

Spring 2006

Approval

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Degree:	Master of Resource Management
Project No.:	**396**
Title of Research Project:	Methods for evaluating the potential effects of marine protected areas on adjacent fisheries

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Abstract

Marine protected areas (MPAs) are proposed for a range of fisheries and ecosystem management objectives, including stock recovery and protection of critical benthic habitat. However, MPAs are often opposed by fishers, who expect reductions in the catch in nearby grounds. Therefore, information is needed to establish the likely short-term effects of MPAs on adjacent fisheries. I used spatial models of a fish population targeted by a fishing fleet, to develop methods for predicting the fishery effects of MPAs. My findings suggest that the decline in catch rates is not equivalent to the proportion of the catch nominally protected by the MPA. Further, although fish movement is important, low precision estimates may be adequate to predict MPA effects. Detailed catch and effort data can be used to predict the effects of MPAs on catch rates. These methods will help stakeholders evaluate the costs and benefits to the fishery of establishing MPAs.

Dedication

To my husband, Matt, who was always there for me.

Acknowledgements

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1 Introduction

1.1 The use of marine protected areas as management tools

The continuous and mounting human pressure on marine systems has led to increasing interest in the establishment of marine protected areas (MPAs), for a range of ecosystem and fisheries management objectives (Guenette et al. 1998, Hilborn et al. 2004). In this paper, MPAs are defined as "no-take" zones, which are areas closed to all fishing and established for two main objectives: conservation benefits, and fishery benefits. The terms 'MPA' and 'marine reserve' are used synonymously.

It has been well established that MPAs are useful to protect critical benthic habitats such as nursery and spawning areas, and areas of high species diversity (e.g., Allison et al. 1998, Guenette et al. 1998, Hilborn et al. 2004). Fishing techniques such as bottom trawling constantly disturb benthic habitats, shifting the ecosystem over time from assemblages of long-lived, larger species to short-lived, smaller species (Horwood et al. 1998). MPAs are becoming popular as a spatial management tool to allow benthic areas to recover from disturbance. For example, in the coastal waters of British Columbia, several MPAs designed to protect critical habitats including rare sponge reefs, seamounts, and other unique areas of high species diversity are in process or have already been established (Wallace and Boyd 2000). The use of MPAs to protect species with a sedentary adult phase is also gaining in popularity. Over a hundred small areas were recently protected in British Columbia to protect declining stocks of inshore rockfish (Yamanaka et al. 2004). Worldwide, there is a steady increase in the establishment of

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MPAs, particularly for conservation of tropical reefs or other "hotspot" areas of high fish abundance and diversity (Allison et al. 1998, Bohnsack 1996, Schmidt 1997). Fewer reserves have been established in prime fish habitat in temperate regions (Gerber et al. 2002), although there is evidence that a well-placed MPA could create (or recreate) a fish hotspot (Schnier 2005). Many studies have reported increased fish abundance and diversity inside MPAs after their establishment (Allison et al. 1998, Guenette et al. 1998, Hilborn et al. 2004, Lauck et al. 1998, Roberts et al. 2005, Smith 2004). Halpern and Warner (2002) reviewed monitoring studies of over 100 MPAs in both tropical and temperate locations, and concluded that there were general trends of increased average abundance, diversity, and organism size within MPAs over short (1-3 year) time periods. These increases persisted and in some cases improved over the long term (Halpern and Warner 2002).

The conservation benefits of MPAs are generally accepted, to the extent that reserves can reduce the impacts of fishing on benthic habitats and ecosystems and may provide protection for overexploited stocks (Hilborn et al. 2004). Further, MPAs are recognized for their role in providing data on long-term environmental change, as an insurance policy against uncertainty in environmental conditions and harvest rates, and as important reference tools for improving biological information (Bohnsack 1993, Hilborn 2004, Guenette et al. 1998, Lauck et al. 1998).

The potential of MPAs as spatial tools for fisheries management, on the other hand, has long been a subject of controversy in the literature (Willis et al. 2003). Beverton and Holt (1957) first explored MPAs using a yield-per-recruit model that they extended to examine spatial variation in fishing effort produced by "unfishable" areas.

They concluded that although there was potential to increase the yield of the stock in adjacent fished areas, it would be more practical to restrict fishing effort. Beverton and Holt (1957) concluded that an MPA would be have to be very large to produce any substantial increase in yield, the cost of finding fish would increase after MPA establishment, and in any case detailed information on fish movement would be required to assess benefits. Effort control was thought to be adequate to manage fisheries during the first half of the twentieth century, but the evolution of fishing technology now allows fishing in areas that were historically too remote or difficult to fish, so that there are now far fewer natural reserves able to provide protection from human ingenuity (Lauck et al. 1998). Managers and fisheries researchers are again examining the potential of MPAs to alleviate fishing pressure in order to allow overexploited populations to rebuild abundance and fecundity, in the hope of maintaining or improving fishery yields (Allison et al. 1998).

The results of some theoretical studies of MPAs and monitoring studies of specific marine reserves have suggested that MPAs have the potential to increase catch rates in areas adjacent to the reserve (e.g., Alcala et al. 2005, Quinn et al. 1993, Roberts et al. 2001, Rodwell and Roberts 2004). Other recent studies have concluded that MPAs have little or no effect on fishing yield (Gerber et al. 2002, Horwood et al. 1998), or that reserves and traditional fisheries management have equivalent effects on catch rates (Hastings and Botsford 1999). However, MPAs may not be the sole cause of increased biomass and fecundity inside reserves, since the impact of reserves is difficult to separate from the influence of other factors in empirical studies (Allison et al. 1998, Willis et al. 2003). Theoretical and empirical studies have suggested that the effect of MPAs on fish

abundance outside reserve boundaries may be contingent particularly upon fish

movement rates (Beverton and Holt 1957, Gerber et al. 2003, Guenette et al. 1998), the

exploitation level of the fish stock (Apostolaki et al. 2002, Guenette and Pitcher 1999,

Nowlis and Roberts 1999, Lauck et al. 1998), the life history characteristics of the

targeted species (Acosta 2002, Gerber et al. 2002, Guenette and Pitcher 1999, Walters

2000), and the response of fishing effort to MPA placement (Apostolaki 2002, Walters

and Bonfil 1999). The following sections give an overview of the current knowledge on

the importance of these factors with respect to the effect of MPAs on adjacent fisheries

(for comprehensive reviews, see Allison et al. 1998, Gerber et al. 2003, Guenette et al.

1998, and Willis et al. 2003).

1.1.1 Fish movement

Non-migratory species, or those with a sedentary adult stage would be most likely

to achieve conservation benefits from MPAs, since the population inside the protected

area would be expected to increase in spawning biomass after fishing pressure is removed

(Bohnsack 1996, Guenette et al. 1998, Hilborn et al. 2004). Sedentary species are defined

as those that move only short distances compared to the spatial scale of fishing and of

larval dispersal, such as most benthic invertebrates and reef fishes (Acosta 2002,

McGarvey 2004, Roberts et al. 2001, Quinn et al. 1993). In contrast, MPAs are likely to

be ineffective in increasing the abundance of mobile species. High transfer rates of fish

between the MPA and adjacent fishing grounds results in less protection afforded to fish

inside the reserve, so that fish become fully vulnerable to fishing (Halpern et al. 2004).

Marine reserves are therefore not generally designed to protect highly mobile species

(Hastings and Botsford 1999), but even relatively sedentary species can undertake

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seasonal migrations, and this type of movement between fished and unfished areas would alter the way production is exported outside MPA boundaries (Halpern et al 2004).

Several models have considered the importance of fish movement rates in determining the effect of MPA establishment on yields outside reserve boundaries. To examine the effectiveness of MPAs in controlling mortality from fishing, Polacheck (1990) used an age-structured yield-per-recruit model based on Beverton and Holt's original model (Beverton and Holt 1957) with random fish movements between a fished and unfished area. The study showed that the size of an MPA must compensate for the relative mobility of the fish, so that the faster the fish, the larger the reserve needed (Polacheck 1990). De Martini (1993) extended the model used by Polacheck (1990) to a study of coral reef fishes with different rates of mobility, and found that high-mobility species would not benefit from reserves due to constant emigration to fished areas, whereas low-mobility species would increase in biomass but would remain within the reserve and hence be invulnerable to fishing. De Martini (1993) suggests that species with a 'medium' rate of movement would benefit the most from MPAs, by remaining inside the reserve to build up biomass, but moving far enough to supply production to adjacent fished areas.

Guenette and Pitcher (1999) used an age-structured, non-equilibrium dynamic pool model with random movements to predict the effectiveness of MPAs for recruitment and protection against overexploitation. The study confirmed the results of Polacheck (1990) and De Martini (1993) and of course Beverton and Holt (1957), finding that increased mobility rates of fish decreased the benefits of marine reserves. However, Guenette and Pitcher (1999) did find slight improvements in the biomass of spawners

after an MPA, even with fast-moving species. Apostolaki et al. (2002) accounted for directed movement of fish populations, showing that the benefits of reserves are higher for low mobility, overexploited populations.

Hilborn et al. (2004) outlined the potential costs of liberal application of MPAs, warning that there is little evidence for increases in yield, for species with both low and high mobility. Clearly, faster rates of transfer would diminish the protection afforded by a MPA, and therefore would reduce the effect on catch rates (catch per unit effort, CPUE) in adjacent fishing grounds. Marine reserves established for conservation purposes such as protection of unique habitat areas should have little effect on adjacent fisheries for mobile species.

Fish movement is identified as a key source of uncertainty in how MPAs affect fishing yields, but it is not clear how important movement rates are in predicting the effects of potential MPAs on fisheries. The effects of fish movement may often be neglected in management policies because of this uncertainty, even though it should have an effect wherever fishing effort is not uniformly distributed over the range of the stock (Beverton and Holt 1957, Sibert et al. 1999). However, movement rates can be difficult to estimate from tag-recovery data (McGarvey 2004), and other methods may be prohibitively expensive and time-consuming. Determining the importance of fish movement on changes in catch rates will in turn determine the level of accuracy needed in estimating movement rates.

1.1.2 Life history attributes

In addition to the movement rate (migration) of fish, variation in the growth rate of the population, the extent of larval dispersal, and the carrying capacity may

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significantly affect catch rates after MPA establishment (Gerber et al. 2002). For

example, long-lived, low-mobility species may fail to recover in an MPA designed to

protect them, because the combination of a low growth rate and low transfer rate into the

reserve will cause abundance to dwindle, even with a very low rate of emigration

(Walters and Bonfil 1999). However, sedentary animals with widely dispersing offspring

may benefit the most from protection within a reserve, particularly if the population was

heavily exploited (Apostolaki et al. 2002, Roberts and Sargant 2002). The results of many

studies have suggested that density will increase within an MPA in the case of low

productivity and a high harvest rate (De Martini 1993, Gerber et al. 2002, Polacheck

1990, Quinn et al. 1993). Release from fishing mortality can allow populations to rebuild

abundance, and increases survival of older, larger individuals with higher fecundity

(Bohnsack 1992, Roberts et al. 2001). However, sedentary populations that increase in

biomass inside an MPA may be unable to replenish adjacent fisheries, except, in some

cases, through larval transport (Gaines et al. 2003, Halpern et al. 2004).

Gerber et al. (2002) used a Ricker model with life history attributes that included

adult density-dependence, larval dispersal and loss from a common larval pool. The

model tracked abundances of fished and unfished populations, and examined the

effectiveness of MPAs in terms of conservation of spawner biomass as well as fishery

yields. Their results showed that for over 90% of the combinations of life-history

parameters and harvest regimes simulated, the MPA did not improve fishery yield. MPAs

were most likely to increase yield when the harvest rate was very high and the area

protected was "not too large". They examined MPA effectiveness over a wide range of

parameter combinations, and suggested that environmental variability should be included

in future MPA models. However, Gerber et al. (2002) noted that building elaborate models to account for a diversity of life history types was less useful than simply focusing on key parameters, which they identified as growth rate and fishing pressure.

Quinn et al. (1993) used a logistic, spatial- and age-structured model based on sessile invertebrates that included larval dispersal, and found that the required size and location of MPAs depended upon the larval dispersal capabilities. They concluded that the ideal MPA design would include multiple MPAs spaced closer together than the average dispersal distance of the target species (Quinn et al. 1993). Gaines et al. (2003) also found that larval transport by currents may play a large role in the efficacy of reserves, and that multiple reserves may be most effective to protect spatially disjunct populations.

Clearly, the spatial distribution of fish habitat is important in determining the effects of MPAs. Fish are rarely distributed uniformly over a fishing ground, and habitat is rarely homogenous, but many models assume uniform fish distribution and no variation in habitat (Roberts and Sargant 2002, although see Walters and Bonfil 1999). High quality habitats where fish can maximize their reproductive potential are likely to have high local carrying capacity and large aggregations of fish. Therefore, the location of an MPA relative to the main fish concentration should significantly affect the change in catch rates in fished areas.

1.1.3 Level of exploitation

Most studies showed that yields improved after MPA placement only if the fishery was already overexploited (Polacheck 1990, Guenette and Pitcher 1999, Nowlis and Roberts 1999). Lauck et al. (1998) used a "model of uncertain harvests" of a closed

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stock with logistic growth and no movement, illustrating that MPAs could assist in the recovery of overexploited stocks by acting as insurance measures against sources of uncertainty. They pointed out that even very conservative harvesting strategies will fail if they are too difficult to control, whereas MPAs that protect a large enough proportion of the stock can also produce higher catches by allowing more intense fishing outside the reserve (Lauck et al. 1998). Nowlis and Roberts (1999) used a size-structured model with larval dispersal, and found that MPAs would likely cause yields to decline for underexploited species, but could help prevent overfishing if effort was high enough to cause recruitment overfishing. Apostolaki et al. (2002) developed a size-structured spatial model with seasonal migration to show that MPAs led to increased resilience of a fished stock to overexploitation, particularly for low-mobility species. In a study of Atlantic code, Guenette and Pitcher (1999), used an age-structured dynamic pool model, and found that at low exploitation rates, MPAs resulted in decreased fishery catch. However, when exploitation rate increased past the level of maximum sustainable yield (MSY) the biomass of female spawners in the reserve was higher, thereby sustaining the catch (Guenette and Pitcher 1999). They concluded that even for mobile fish, reserves would improve the resilience of exploited fish populations.

1.1.4 Fleet dynamics

In the case where total effort remains the same following the establishment of an MPA, effort redistribution following reserve establishment results in the same number of fishers in a smaller area, resulting in lower catch rates (Halpern et al. 2004). Catch rates can be sustained despite increased effort if fish are mobile. Halpern et al. (2004) developed a simple generalized model with uniform distribution of adult fish and settling

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of larvae with independent larval mortality. They found that when transfer rates between MPAs and fished areas were high, the export of production from the MPA could compensate for increased fishing pressure outside the reserve, even if the MPA protected up to half the exploitable stock.

The redistribution of fishing effort will also be affected by spatial differences in catch rates and other variables specific to area, such as the relative cost of fishing, level of depletion, and distance from ports (Hilborn and Walters 1987). In the unrealistic case that fishers have perfect knowledge on where the best catch rates would be obtained, the distribution of the fleet would mirror that of the targeted fish population (Gillis 2003). Leaving aside the effects of fishing vessel interactions and gear saturation, it is realistic to assume that after the establishment of an MPA, effort from within the MPA is likely to be redistributed according to historic knowledge of the relative profitability of surrounding areas.

Few MPA studies have considered the spatial effects of fishing fleet behaviour on a dynamic fish population (Guenette et al. 2000, Walters 2000, Walters and Bonfil 1999). Hilborn and Walters (1987) evaluated the effect of fleet movement on spatially discrete, sedentary stocks by adapting a surplus fish production model with recruitment that also simulated fleet movement between fishing grounds. Fishing grounds closer to the "home port" were weighted to be more attractive to fishers. The catch rate declined more slowly than abundance until all stocks were depleted because each stock was sequentially fished (Hilborn and Walters 1987). A later study by Walters and Bonfil (1999) developed a multi-species spatial model to evaluate management strategies for trawl fisheries, where more profitable areas with higher catchability were more attractive to fishers. Their

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model predicted that rapid collapse of stocks was unlikely because effort would shift away from depleted areas. Hilborn et al. (2004) stated that for a large reserve with a sedentary stock, the spatial shift in effort after MPA designation would result in catch reductions that are directly proportional to the relative size of the area protected, an effect not found in the current study. For mobile stocks, the interactions between effort reallocation and relative abundances may produce considerably different results.

1.2   Addressing opposition to MPA establishment

The main obstacle to the widespread acceptance of MPAs is the uncertainty in their fisheries effects, and the subsequent opposition to their establishment by fishers (Apostolaki et al. 2002, Halpern and Warner 2002). The opposition to MPAs is based on the fear that catch rates will be significantly reduced over the short-term (Gerber 2003). The essential question is therefore not whether abundance will increase inside the MPA, but whether the increased abundance will be able to compensate for the losses associated with the closure of fishing grounds (Halpern et al. 2004, Sanchirico and Wilen 2001). Fishers may assume that the immediate reduction in catch rates is equivalent to the area removed from fishing, and this is possible if the targeted population is sedentary or otherwise confined to the reserve (Halpern et al. 2004; Hilborn et al. 2004). The socioeconomic effects of MPA creation must be explicitly considered; fishers are likely to oppose proposals to establish MPAs that are based solely on biological criteria, particularly if they are not adequately represented in the consultation process (Sanchirico and Wilen 2001). To reduce opposition, the effects of MPAs should be close to economically neutral over the short-term (Sumaila et al. 2000), either by placing MPAs to minimize losses in catch, or by providing compensation to fishers.

1.3 Study objectives

The objective of this study is to identify information that would be useful in addressing the concerns of the fishing industry over the establishment of MPAs. I assume that a potential MPA is established for a conservation purpose such as protection of critical benthic habitat, and not primarily for a fisheries management objective. In situations where the fishing industry is included in the consultation process, decision-makers are more likely to achieve industry consent if the MPA is placed to minimize losses in catch, or if adequate compensation is available to fishers. Protected areas may provide long-term benefits to fisheries, but fishers are likely to be concerned chiefly with the short-term fishery losses caused by MPA establishment. Thus, my goal is to predict the short-term effects of potential MPAs on catch rates, before the MPA is established. Providing information on the likely effects of MPAs will reduce the concerns of fishers, and will inform decision-makers on appropriate compensation if a reduction in catch rates is likely. To that end, the study addresses the following specific questions:

- What effect does the placement of a potential MPA have on catch rates in an adjacent fishing ground?

- Is the rate of fish movement important in predicting changes in catch rates, and if so, how accurately does movement need to be estimated?

- What other factors are important in determining the effects of potential MPAs on catch rates?

- Is fishery-dependent information adequate to reasonably predict the effects of MPA placement on the catch and catch rates of nearby fisheries, or, is high-resolution data required?

1.4 Study approach

I used simulation models of the fish population and the fishery to calculate the potential changes in catch and catch rates (CPUE) after the establishment of an MPA. The models were spatially explicit, dividing a region into a grid of connected spatial cells. The models simulated the spatiotemporal dynamic behaviour of a single hypothetical fish population and a fishing fleet, with or without an MPA placed over different portions of the fishing ground. The simulation models allowed for an "experimental" approach to MPA placements that would be prohibitive in cost and time in an empirical study. The models were used to evaluate the change in CPUE for a number of MPA placements, ranging from regions covering a negligible proportion of the catch, through to regions coinciding with the most productive fishing grounds. The different placements were characterized in terms of the proportion of the catch in the pre-MPA period that was contributed by the region to be covered by the MPA.

Short-term (10-year) and long-term (100-year) simulations were performed in order to collect catch and effort data within each grid cell. This information was used to calculate the change in CPUE after the establishment of different MPAs, which was identified as the performance indicator of primary interest to the fishing industry. Additional factors were varied for each MPA, including the rate of fish movement, the spatial geometry of the fish population, and the level of exploitation of the fishery. I then

ranked the power of various parameters to predict the change in CPUE resulting from the

introduction of the MPA.

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2 Methods

2.1 Model overview and general assumptions

I used a flexible, dynamic spatial model written in the R language (Ihaka and Gentleman 1996) that I developed collaboratively with my supervisor, W.K. de la Mare. This model simulates the behaviour of a single fish population, distributed over a spatial grid of cells and targeted by a fishing fleet. The spatial grid is a set of (x, y) locations measured in distances between cell midpoints, so that distances in the model are scale invariant. The model is spatially explicit, and could be linked to real physical locations in future simulations. Each spatial cell is represented as an element in a matrix, containing a proportion of the total fish population abundance (**N**), and a proportion of the total fishing effort (**E**). The matrix-based model simulates separate trajectories of local fish abundance and fishing effort over time for each spatial cell, over a daily time step (t), and yearly time step (Y).

The fish population is distributed over the spatial grid according to the relative desirability (attractiveness) of spatial cells. Desirability is a function of the current local densities and the local intrinsic rate of increase of the fish population in each cell. In order to have spatial variation in desirability, habitat quality is not homogeneous over the grid. Fish seek out and remain in high quality habitats that maximize their reproductive potential, where the local carrying capacity and the intrinsic rate of increase are both high. Animals exercise density-dependent habitat selection, and will move to poorer

habitats only when numbers in high quality areas approach local carrying capacities (MacCall 1990). The distribution of the fish population therefore approximates an Ideal Free Distribution over time (IFD; Fretwell and Lucas 1969); that is, the population will approach an equilibrium whereby all areas have the same relative desirability. In each grid cell at a given moment the fish population has a different rate of increase, with the corollary that the contribution of each cell to the reproductive output of the population is also different. The rate of increase in each cell depends on the local habitat quality and density. The desirability of each grid cell is continually updated as the local density changes.

Fish move daily between cells by diffusion and directed movement. After the daily movement of fish, losses from natural mortality are removed and the productivity of the fish population is updated. The productivity of the population in each spatial cell is logistic; productivity slows in individual cells as abundance nears carrying capacity. New recruits are added to the fish population at year-end, based on the cumulative productivity of the fish population in the previous year. Recruits are distributed by large-scale transport processes, originating from a common pool of larvae produced by all adults. Recruits disperse at year-end, and settle proportionally to the carrying capacity of the local population in each cell. This ensures that the distribution of fish is stable at carrying capacity.

The distribution of the fishing fleet is based on maximization of profit. Similar to the fish population, the fishing fleet behaves as an aggregate unit. A proportion of the total fishing effort is expended daily in each spatial cell, as long as the area remains profitable. The daily level of fishing effort in each cell changes depending on the degree

to which fishing was profitable the previous day. Profitability in turn depends on the price of fish and cost of fishing, which are kept constant, and the local catch rate. The model can allow the effort to decline exponentially when there is no profit made, and to recover towards the initial total effort when the fishery is profitable. In the results presented here, total effort is constant; there is no "mortality" of vessels or "recruitment" of vessels to the fishery.

Fleet movements also approximate an ideal free distribution (IFD; Fretwell & Lucas 1969). According to the assumptions of the IFD, fishing will always be located wherever the catch rate (or in this model, profit) is highest. When the area with the highest profitability becomes depleted to the level of the second highest ground, the fleet splits in two equally between both grounds until profits drop to the level of a third area, and so on (Gillis and Peterman 1998). As the model approaches an equilibrium state, all areas will have equal profitability and the distribution of the fleet becomes stable.

The fishing fleet is assumed not to experience interference; the entire fleet can crowd into the area with the highest profitability. The cost of fishing is constant in each spatial cell in the results presented here, although costs would realistically vary over time and according to vessel type (Gillis 2003). Many other factors such as regulations, gear restrictions, market fluctuations and individual preferences influence where fishers choose to fish (Gillis 2003, Holland and Sutinen 1999). However, to reduce complexity the behaviour of the fishing fleet in the current model depends purely on profitability.

The same basic form of movement model was used for both the fish population and the fishing fleet. This allows the fleet to track fish movement, concentrating effort in fishing "hotspots" where the fish population is densest. A parametric approach was

chosen to describe movement. The fish abundance and fishing effort in each spatial cell in the grid is indexed to an array of movement probabilities to the remaining cells, and the corresponding movement probabilities are updated daily for the number of years of the simulation.

I initialized the model by running it close to equilibrium, to find the Ideal Free Distribution of fishing prior to establishing an MPA. Prior to initialization, the fleet is distributed uniformly across the grid, and the fish population is in unexploited equilibrium. The fleet moves over time based on diffusion and directed movement to the best fishing locations. The model simultaneously simulates the dynamic behaviour of the fish population and the fishing fleet. Starting with stable distributions of the fish and the fleet, a marine protected area (MPA) is placed in various locations relative to the main fish concentration. The "size" of the potential MPA is represented by the proportion of the total catch that is within the protected area. When an MPA is present, total fishing effort redistributes among the remaining spatial cells according to their relative profitability. The fishing fleet is assumed to be perfectly compliant in avoiding the MPA.

The following sections describe the methods outlined above in detail, including the population dynamics of the fish population, the diffusive and directed movement of the fish and the fleet, model simulations including parameters varied, and performance measures. Figure 1 illustrates the sequence of operations performed by the models and the general path of data flow.

2.2 Notation

Each element within a matrix represents an individual location or cell in a spatial grid. Thus, multiplication and division of matrices are element-by-element in the model. For example, multiplication of matrices is denoted by *, so that:

$$\begin{bmatrix} x_{1,1} & x_{1,2} \\ x_{2,1} & x_{2,2} \end{bmatrix} * \begin{bmatrix} y_{1,1} & y_{1,2} \\ y_{2,1} & y_{2,2} \end{bmatrix} = \begin{bmatrix} (x_{1,1})(y_{1,1}) & (x_{1,2})(y_{1,2}) \\ (x_{2,1})(y_{2,1}) & (x_{2,2})(y_{2,2}) \end{bmatrix}$$

Matrices are denoted by bold capital letters, in order to distinguish them from other parameters. For example, C_t is a matrix of catches for each spatial cell, at timestep t. Similarly $C_{i,j}$ refers a single spatial cell within the catch matrix at location (i,j), and C_i refers to the cells within row i of the catch matrix. Arrays or matrices of probabilities are in lower case, while arrays of abundance are in upper case. Model operations are performed for each spatial cell, except where noted. The summation operator (Σ) sums all elements in a vector, matrix or array. Table 1 contains a full list of the notation used in this paper.

2.3 Fish population dynamics

2.3.1 Abundance

The fish population abundance matrix (N) is calculated for each spatial cell over a daily time step (t), using a simple biomass dynamic model of the general form:

(1) $N_t = (N_{t-1} - C_{t-1})\, S$

Where $\mathbf{N}_t$ is the current population abundance, $\mathbf{N}_{t-1}$ is the fish population abundance on the previous day, $\mathbf{C}_{t-1}$ is the catch removed by the fishing fleet on the previous day, and S is the daily survival rate, $S = e^{\frac{-M}{365}}$.

2.3.2 Recruitment

Recruitment to the fish population is characterized by logistic growth:

$$(2) \qquad \mathbf{R}_y = \mathbf{N}_{Y-1}(1-S)\left[1 + \bar{p}\left(1 - \frac{\mathbf{N}_{Y-1}}{\mathbf{K}}\right)\right] * s$$

Where $\mathbf{R}_Y$ is the total annual number of recruits added at year end to the fish population, $\mathbf{N}_{Y-1}$ is the total abundance of the fish population in the previous year, S is the survival rate $(S = e^{-M})$, $\bar{p}$ is the weighted mean productivity of the fish population in the previous year, $\mathbf{K}$ is the initial total number of fish, and s is the expected settlement pattern of recruits.

The weighted mean productivity of the fish population in the previous year $(\bar{p})$ is calculated by multiplying the population productivity of the previous year (ρ_{t-1}) by the current fish abundance $(\mathbf{N}_t)$, summing the products to find the total productivity over all grid cells, and dividing by the total fish abundance (3). The total productivity of the fish population (ρ_t) is proportional to the carrying capacity $\mathbf{K}_t$ (4):

$$(3) \qquad \bar{p} = \frac{\sum(\rho_{t-1} * \mathbf{N}_t)}{\sum \mathbf{N}_t}$$

$$(4) \qquad \rho_t = \frac{\xi \mathbf{K}_t}{\mathbf{K}_{max}}$$

Where ξ is the maximum intrinsic rate of increase achievable by the fish species, and $\mathbf{K}_{max}$ is the matrix of maximum carrying capacities. Carrying capacity can vary in space and time but remains stable in the current study.

The initial settlement of recruits (s) is expected to be distributed in proportion to the initial spatial pattern of carrying capacity (**K**):

$$(5) \qquad s = \frac{\mathbf{K}_{t=0}}{\sum \mathbf{K}_{t=0}}$$

Finally, total annual recruitment ($\mathbf{R}_Y$) is added to the fish population at the end of each yearly time step (Y):

$$(6) \qquad \mathbf{N}_{Y+1} = \mathbf{N}_Y + \mathbf{R}_Y$$

2.3.3 Fish spatial parameters

The fish population is initially at carrying capacity, which is heterogeneous over the spatial grid. The carrying capacity of each cell determines the maximum density of fish, and the spatial pattern of carrying capacity can be entirely arbitrary. In the results reported here, two possible patterns were examined (Figure 2). In the first, the pattern of carrying capacity is a plateau, with fish concentrated in the highest quality habitat in the central area of the grid (Figure 2a). In the second, carrying capacity is a ridge configuration, with fish concentrated in a narrow band of highest quality habitat across the middle of the grid (Figure 2b). The pattern of carrying capacity is fixed across the days of the year, although it can be varied with the time of year to simulate seasonal environmental fluctuations.

Cumulative normal functions are convenient to define the distribution of the fish

population at carrying capacity, although logistic functions would also be appropriate.

For both the plateau and the ridge pattern, carrying capacity (**K**) is defined by a normal

cumulative function (Φ) multiplied with a reverse normal cumulative function (1- Φ) for

each row (i) and column (j), to obtain a plateau (Figures 2 and 3):

(7) $\quad \mathbf{K}_i = \left[\Phi\left(y_i, \mu_{y_1}, \sigma_{y_1}\right)\right] \times \left[1 - \Phi\left(y_i, \mu_{y_2}, \sigma_{y_2}\right)\right]$

(8) $\quad \mathbf{K}_j = \left[\Phi\left(x_j, \mu_{x_1}, \sigma_{x_1}\right)\right] \times \left[1 - \Phi\left(x_j, \mu_{x_2}, \sigma_{x_2}\right)\right]$

(9) $\quad \mathbf{K} = \kappa\left(\mathbf{K}_i * \mathbf{K}_j\right) + v$

Where y_i and x_j are the grid boundaries for each model row and column, μ_i and μ_j are the

midpoints of the row or column (the means of each cumulative normal function), σ_y and

σ_x are the standard deviations of the cumulative normal functions, κ is the equilibrium

stock size multiplier, and v adjusts the starting stock size to a specified number. The

vectors y and x define the longitudinal and latitudinal positions of each grid line,

respectively. Only the endpoints of the grid boundary vectors are used to determine the

pattern of carrying capacity. The endpoint that defines the upper bound of the left-hand

distribution (Φ) is also the lower bound of the right-hand distribution (1 – Φ). In the case

of the plateau configuration, $\sigma_y = \sigma_x$ (Figure 3), but for the ridge configuration, $\sigma_y \neq \sigma_x$

(Figure 4). In both configurations, fish density decreases out from the centre with a slope

determined by the standard deviation σ, which is constant in the results presented.

2.4 Fish movement

The daily movement of the fish population takes place in two steps. A portion of

the population in each grid cell first leave the "home" cell to explore neighbouring cells,

and then animals will either settle in the new cells or return to the home cell, depending on the relative desirability of the cell. A diffusion model determines the initial probabilities that fish will move from each grid cell, and a directed movement model updates the daily movement of the fish population (Figure 5).

2.4.1 Diffusion model

Diffusive movement in one dimension is based on a population version of a simple random walk, in which a population at a specific location N_i has an equal probability of moving either to the left (N_{i-1}) or to the right (N_{i+1}), with each step a constant distance (Okubo 2001, Sibert et al. 1999). Movement over time approaches a normal population density distribution $X{\sim}N(\mu_t, \sigma^2)$, where μ_t is the average position of the subject over time and σ^2 is the variance (Okubo 2001).

In two dimensions, movement relative to a set of coordinates can be described by a bivariate normal distribution without correlation:

$$(10) \quad p(x,y) = \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}}$$

Where $p(x,y)$ is the population density. The means of x and y are zero, and the marginal variances of x and y are equal.

In the current model, non-directed movement of the fish population is defined by an array of diffusion probabilities based on a bivariate normal distribution. The probability of diffusion to neighbouring cells is determined by the integral of the bivariate normal probability distribution over the spatially explicit grid boundaries. For a given cell, the distance to adjacent cells with a shared boundary is less than the distance

to cells on the diagonal. Consequently, movement to cells with a shared boundary is more probable (Figure 5).

For each cell ($N_{i,j}$), the model diffusion probability is the product of a normal distribution probability for the interval over row i with a normal distribution probability for the column j interval, to obtain a matrix (m) of combined probabilities of movement in two dimensions from each spatial cell to every other cell, defined by:

$$(11) \quad m_{i,j} = \left[\Phi\left(y_{i+1}, \mu_{y_{i+1}}, \sigma_{y_{i+1}}\right) - \Phi\left(y_i, \mu_{y_i}, \sigma_{y_i}\right)\right] \times \left[\Phi\left(x_{j+1}, \mu_{x_{j+1}}, \sigma_{x_{j+1}}\right) - \Phi\left(x_j, \mu_{x_j}, \sigma_{x_j}\right)\right]$$

Where Φ is the cumulative distribution function of a normal distribution, (x_j, x_{j+1}, y_i, y_{i+1}) are the grid cell bounds for the current cell, $\left(\mu_{x_j}, \mu_{x_{j+1}}, \mu_{y_i}, \mu_{y_{i+1}}\right)$ are the centre coordinates of the current and previous grid cell, and the standard deviations $\left(\sigma_{x_j}, \sigma_{x_{j+1}}, \sigma_{y_i}, \sigma_{y_{i+1}}\right)$ are the rates of diffusion from the current cell. The standard deviation is constant in all directions ($\sigma_x = \sigma_y$), and movement is independent in each axis. The tails of the normal distributions that fall outside the grid are included in the cells along the grid borders so that fish accumulate on the boundaries; fish cannot leave the grid (Figure 6).

The annual settlement of recruits in each spatial cell occurs after the catch has been extracted and the adult fish have moved. Recruit settlement is determined by a separate matrix of diffusion probabilities (r), which is structured identically to the bivariate normal distribution described above for adult fish. Recruits diffuse across the grid at the same rate as adults in the current study. Recruits to the fish population are assumed to originate from a common pool, settling at the end of each year according to the spatial pattern of unexploited abundance (K). The annual spatial distribution of recruits (R_Y) is therefore a function of the probability of recruit settlement in every cell

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(r) and the total recruitment from the previous year (R_{Y-1}), the latter determined in Equation 2:

(12) $R_Y = r * R_{Y-1}$

2.4.2   Directed movement model

A rule-based movement model advances the distribution of the fish population by one time step, by recalculating the desirability of each grid cell (Figure 7). The desirability (d_t) of grid cells determines whether animals stay in each cell or leave to explore neighbouring cells. Desirability is a function of the productivity of the fish population (ρ_t) and habitat quality (K_t):

(13) $d_t = \rho_t * \left(1 - \dfrac{N_t}{K_t}\right)$

Thus, the desirability of an area is measured by the reproductive output experienced by its occupants. As the population in each cell approaches the local carrying capacity, animals begin to leave the cell for better habitats. Fish movement is calculated cell by cell for each day, with the daily matrix of fish abundance updated when movement to and from all cells is complete. The probability that fish remain in each cell (h_t) is a function of the desirability of the cell (d_t) and the intrinsic rate of increase of the fish population (ζ):

(14) $h_t = \dfrac{d_t}{\zeta}$

When h_t is greater than zero, the number of fish exploring other cells (A_t) is based on the array of diffusion probabilities m_t ($A_t = m_t * N_t$, $h_t > 0$). When h_t is less than or equal to zero, the diffusion probabilities are amended so that all fish will leave the current cell and

none will return ($A_t = m'_t * N_t$, $h_t \leq 0$, where m'_t is the total number of fish in the current cell). Cell abundance will therefore not exceed carrying capacity. The number of fish staying in neighbour cells (**n**) at time (t) after moving from each home cell is:

(15) $n_t = h_t * A_t$

Thus, the number of fish returning home after exploring neighbour cells (n'_t) is:

(16) $n'_t = A_t - n_t$

Finally, after fish from the home cell explore the grid and settle in the best available habitat, the updated matrix of fish abundance (N_t) is:

(17) $N_{t+1} = N_t + n_t + \sum n'_t$

The numbers of fish exploring the grid, settling in new cells and returning to the "home" cell are accumulated as the calculations are performed for each cell. After fish movement is complete, the losses from natural mortality M (year^{-1}) are removed from the fish population for the current time step (t), and the distribution of the fish population is updated:

(18) $N_{t+1} = N_t S$

(19) $S = e^{\frac{-M}{365}}$

Where S is the daily survival rate.

2.5 Fishing fleet dynamics

In general, fleet movement is calculated using the same forms of model that describe fish movement. The initial distribution of the fishing fleet over the spatial grid is determined by arrays of diffusion probabilities, and the daily movement of the fleet is determined by a directed movement model. Diffusion probabilities of the fleet are based on the bivariate normal distribution as detailed in Section 2.4.1, with the implicit assumption that the fleet has perfect, universally shared information on the locations with the highest densities of fish. Therefore, the fleet is able to mimic closely the movement of the fish. The daily directed movement of the fleet follows the process in Figure 7, with the exception that there is no "mortality" of fishing vessels.

The fleet is initially distributed uniformly over the spatial grid. Although total effort (**E**) is constant, the distribution of effort is updated daily (**E**$_t$), and is determined by the relative profitability of each grid cell. Profitability (**P**$_t$) is a function of the catch rate in each cell (**c**$_t$):

(20) $\mathbf{P}_t = p\mathbf{c}_t - c$

Where **P**$_t$ is profitability, p is the selling price per fish, c_t is the daily catch rate, and c is the cost of fishing per day. The selling price (p) and cost (c) are constants in the results presented. Grid cells with the highest catch rates are the most profitable for the fishery. Consequently, the profitability of grid cells determines their desirability to the fleet:

(21) $\mathbf{d}_t = \mathbf{P}_t * \left(1 - \dfrac{\mathbf{E}_t}{\mathbf{E}_{max}} \right)$

Where $\mathbf{E}_{max}$ is the matrix of maximum carrying capacities for the fishing fleet. If $\mathbf{E}_{max}$ is set low, there is an upper limit to the fishing effort in each grid cell and the fleet experiences interference. In the current study, $\mathbf{E}_{max}$ is effectively unlimited.

The daily catch rate is a function of the population size ($\mathbf{N}_t$), the catchability (q) and the catch exponent (α):

(22) $\mathbf{c}_t = q\mathbf{N}_t^{\alpha}$

The catchability and the catch exponent are also assumed to be constant. The daily catch rate in each cell is used to calculate the distribution of the catch ($\mathbf{C}_t$) that is removed from the fish population (Equation 1). The catch is removed before movement of the fish and fleet takes place (Figure 1), and is a function of the catch rate ($\mathbf{c}_t$), fishing effort ($\mathbf{E}_t$), and an effort modulator (e_t):

(23) $\mathbf{C}_t = \mathbf{c}_t * \mathbf{E}_t e_t$

The effort modulator (e_t) allows the effort in each spatial cell to increase or decrease by a small increment each timestep, depending on whether fishing is profitable in the cell. In this study, $e_t = 1$.

The redistribution of the fishing fleet can be restricted by the inclusion of a no-take zone or marine protected area (MPA). The MPA is a block of spatial cells within the grid that is closed to fishing. In the presence of an MPA, the proportion of the total effort within the cells of the MPA is set to zero, and the effort from the MPA is redistributed over the remaining grid cells according to the relative desirability of cells to the fleet. The redistributed fishing effort produces new diffusion probabilities whereby the fleet completely avoids the MPA.

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2.6 Performance measures

I considered the total catch per unit effort (CPUE) in the final year of a 10-year simulation to be the performance indicator of primary interest to the fishing industry. I used this measure to evaluate the short-term effects of various MPA placements on catch rates. The final CPUE (U) is a ratio of the sum of the daily catches in the final year of the simulation (C_{10}) and the sum of the daily effort, in the final year (E_{10}):

$$(24) \qquad U = \frac{\sum C_{10}}{\sum E_{10}}$$

The "true" CPUE as calculated from the model was evaluated as a dependent variable against the following independent variables: the proportion of the total catch within each potential MPA, the rate of fish movement, and predicted CPUE from pre-MPA data:

1) **Proportion of total catch** - The proportion of the total catch that was within each potential MPA during the last year of each simulation was collected to evaluate the effect on ΔCPUE of different MPA placements relative to the main fish concentration. The measure is independent of the magnitude of the catch.

2) **Rate of fish movement** – The rate of fish movement was characterized by the probability that a fish would leave a particular MPA over the course of one day. The movement model was used to give a one-day matrix of movement probabilities, based on the fish abundance and relative desirability of each cell in a single day in the middle of the final year of each simulation. This measure is more meaningful than a rate of movement based on fish speeds because the probability of a fish leaving the protected area is contingent on both the overall movement rate and the habitat quality. The measure is also dimensionless and scale independent. Although the size of the

MPA and the actual rate of fish movement affect the probability of a fish leaving the MPA, these interact, and so the net effect is captured in the single probability metric.

3) **Predicted CPUE** - To evaluate whether the change in CPUE after MPA establishment could be predicted from pre-MPA fishery-dependent data, a measure was developed to predict CPUE from catch and effort information in each spatial cell, without using any information on fish movement. This measure requires spatially resolved catch and effort data. For simplicity, I assume that the abundance of the fish population does not change over the final year as a result of fishing. Predicted CPUE was calculated by:

a) Averaging catch and effort data for each grid square over the final year of each simulation,

b) Resetting catch and effort within the potential MPA to zero,

c) Redistributing the total effort in the potential MPA over the remaining squares according to the proportion of effort already there,

d) Pro-rating the redistributed effort against the old effort so total effort remains unchanged.

e) Comparing the predicted ΔCPUE with the "true" ΔCPUE for all model simulations.

2.7 Model simulations

2.7.1 Initialization

To initialize the fish population and fishing fleet, the model first searches for a level of fishing effort that equilibrates the fish population closest to a specified target level g, which determines the historical level of depletion of the fish population. The target is a specified proportion of the initial carrying capacity. The level of effort that brings the fish population to the specified target level is used to bring the model to virtual equilibrium, by simulating the dynamics of the fish population and fleet for 200 years without the presence of an MPA.

2.7.2 Length of simulation

Since the fishing industry is likely to be concerned primarily with the short-term effects of MPA establishment on catch rates in adjacent fished areas, performance measures are evaluated over a further 10-year period for all parameter combinations described in the next section. I also ran the model for 100-year periods for a few limited parameter combinations, to explore the long-term effects of MPA placement on catch rates and fish population abundance.

2.7.3 Parameter variation

All parameter values used in the model simulations are listed in Table 2. In order to determine whether the predictors of MPAs are equally reliable under all conditions, I explored the model for variation in three key parameters:

1) **MPA placement** – I simulated the effects of seven different placements of potential MPAs relative to the main fish concentration (Figures 8 and 9). The location of an MPA in the grid simulated the degree of overlap between the MPA and the fishing ground. All MPAs covered the same number of spatial cells, but differed in "size" in terms of their contribution to the total catch. I did not consider the effects of multiple MPAs.

2) **Fish movement rate** – I explored nine rates of fish movement for the model, ranging from no movement (σ_i, $\sigma_j = 0.01$), at which no fish leave the spatial cell, to fast movement (σ_i, $\sigma_j = 2$), at which fish can move anywhere on the grid in a few days.

3) **Degree of exploitation** – To examine the effects of MPA establishment on the degree of exploitation, I explored the model for three levels of depletion from an unexploited abundance:

- Lightly depleted population (reduced to 75% of unexploited abundance)

- Moderately depleted population (reduced to 50% of unexploited abundance)

- Heavily depleted population (reduced to 25% of unexploited abundance)

The following parameters were then varied while the model was used to examine the effects of variation in MPA placements, fish movement rate and level of depletion:

1) **Productivity of fish population** – The productivity of the fish population is positively related to the intrinsic rate of increase (ζ). Increasing ζ improves the overall reproductive output of the fish population, so fish will be more productive in all habitats. Since the fleet closely follows the fish concentration, the exploitation rate of

the fishery increases with increased fish population productivity. The exploitation rate increases with productivity because the production of fish is higher in all areas of the fishing ground, thereby increasing the catch. I explored the model for low, moderate, and high overall productivity of the fish population, for different MPA placements, fish movement rates, and levels of depletion.

2) **Spatial configuration of the fish population** – I explored the effects of MPA placement, fish movement and level of depletion for two spatial configurations: a plateau, and a narrow ridge. The original configuration approximates a circle, which minimizes edge effects (Figure 8), while the alternative configuration approximates a ridge, maximizing edge effects by increasing the perimeter of the configuration relative to its area (Figure 9). The slope of the fish distribution and the density of fish is the same for both configurations. Placements of MPAs over the plateau configuration are square, while those over the ridge configuration are linear in form to mimic the specific geometries of the fish concentration.

3) **Population state** – Initial simulations were performed on a fish population in dynamic equilibrium. I also explored the effects of an MPA on a population in flux, where the total abundance was either increasing or decreasing as a result of changing the exploitation rate of the fishery. The models were initialized for 20 years to reach a specified target level of abundance with constant fishing effort. To produce a population with increasing abundance, the exploitation rate was then reduced to half of that required to maintain the population at the target level. The decreasing population was produced by doubling the exploitation rate that would maintain the

population at the target level. The dynamics of the fish and fleet were simulated for 10-year periods for different MPA placements and fish movement rates.

4) **Relationship between CPUE and fish abundance** – I examined the performance of the model with the catchability exponent α changed to 0.5, to produce nonlinear CPUE. The relationship between CPUE and abundance is weakened if CPUE declines at a slower rate than the fish population abundance.

3   Results

3.1   Low productivity fish population

The placement of MPAs over various portions of the fishing ground revealed an important finding regarding the rate of fish movement. For each MPA, the change in CPUE (ΔCPUE) was virtually unaffected until the probability of animals leaving the MPA approached zero, at which point ΔCPUE declined sharply (Figure 10). In the case of even a low mobility fish population, the transfer of animals between the MPA and the fishing ground continually replenished the fishery. Nonmobile fish had zero chance of leaving the MPA, which, as might be expected, caused a larger decline in ΔCPUE. Clearly, the rate of fish movement affected the change in catch rates, but only insofar as fish were mobile or nonmobile. Increasing the fish movement rate past a low mobility threshold had little effect on the model. Thus, I reduced the range of fish movement rates in subsequent scenarios to four, termed nonmobile, low, moderate and high mobility.

The probability that fish would leave the MPA clearly depended upon the exploitation rate (Figure 10). Animals were the least likely to leave all MPAs when the level of depletion was low (to 75% of the unfished abundance), because the fish population was close to its unexploited abundance (Figure 10). Animals occupied all areas near local carrying capacities, with the result that the desirability of all areas (and profitability, in the case of the fleet) was nearly equivalent over the grid. Thus, overall movement was low and both the fish population and the fishing fleet approached an Ideal Free Distribution (IFD: Fretwell & Lucas 1969). The change in catch rates was less in the

presence of high quality MPAs for the lightly depleted fish population, because animals were less likely to leave the MPA.

The change in catch rates was greater in the presence of high quality MPAs, in the case of a heavily depleted population reduced to 25% of the unexploited abundance (Figure 10). Fish were more likely to leave the MPA in these cases because the protected population was able to rebuild to near local carrying capacity. The fleet was concentrated over the best available habitat, close to the reserve, keeping densities in fished areas low. Fish subsequently moved out of the MPA to the lower density areas, resulting in higher ΔCPUE.

As expected, the Core MPA placement over the highest quality fish habitat caused the largest decline in ΔCPUE overall, while the placement of MPAs over lower quality habitats, such as the Marginal placement, had a slightly positive effect on ΔCPUE for most rates of fish movement (Figure 11). The change in catch rates was less when the reserve protected the best fish habitat because a large proportion of the population was unavailable to the fishery. The change in catch rates increased slightly when MPAs were placed over marginal areas, because some of the fleet effort that was previously within the marginal protected area was redistributed to higher quality fish habitats outside the MPA (Figure 11). This effect was more pronounced for a lightly fished population (to 75% of unfished equilibrium) since the larger stock supported a higher overall catch.

The proportion of the total catch inside the area of each potential MPA represented the relative size of each MPA. Both spatial configurations of the fish concentration produced similar proportions of the total catch for each MPA placement (Table 3). Values for the plateau configuration are used to examine the effect of MPA

placements in sections 3.1 and 3.2. The Core and Encroaching MPA placements accounted for an average of 25% and 22% of the total catch, respectively, while the remaining MPAs contained progressively smaller proportions (Table 3). The proportion of the catch within the high quality MPAs increased slightly when fish were mobile and heavily exploited (Figure 12). The change in catch rates declined as expected when the MPA protected more of the fish population. However, the reduction in ΔCPUE after MPA implementation was not equivalent to the proportion of the total catch inside the potential MPA, for both mobile and nonmobile fish. For example, with approximately 25% of the total catch inside the Core MPA, the decline in ΔCPUE was at most about 7% for nonmobile fish and 2% - 6% for mobile fish (Figure 12). The change in catch rates improved in all cases when fish were mobile (Figure 12). The change in CPUE was positive for mobile fish in the presence of low quality MPAs up to the Transitional placement, which nominally protected about 12% of the population and had a neutral effect on catch rates in mobile scenarios. The Transitional MPA acted as a pivot point between positive and negative effects on ΔCPUE for mobile fish (Figure 12). In contrast, only MPAs protecting less than about 7% of the catch produced positive effects on ΔCPUE for sedentary fish, and this was reduced when the population was more exploited (Figure 12).

The properties of the model produced some unexpected effects. At low rates of fish movement, ΔCPUE was observed to peak slightly in the Core MPA placement, equilibrating back to a lower level when the movement rate increased (Figure 10). This fluctuation was due to the discrete nature of diffusive movement in the model, and was apparent in the Core MPA because of the large number of fish moving. Fish were

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virtually nonmobile up to threshold values of approximately 0.15 for σ_i and σ_j. As the rate of movement jumped to the next increment, the probability of movement jumped above zero and there was a sudden influx of fish into adjacent cells.

3.2 Moderate and high productivity fish population

As in the case of the low productivity scenarios, the effect of establishing MPAs on fish populations with higher productivity depended upon the degree of exploitation and the rate of fish movement. The lightly depleted fish population retained a high overall abundance; therefore, animals were less likely to leave each MPA (Figure 13). Increasing the population productivity increased ΔCPUE for high quality MPAs, and decreased ΔCPUE for marginal MPAs, thereby reducing the differences between MPA placements observed in the low productivity scenarios. The ΔCPUE for nonmobile fish tended to decrease when productivity was higher, since the larger adult population remained inside the reserve and the settlement of recruits was virtually the sole source of replenishment to the fishery (Figure 13). The high quality MPA placements had the least negative effect on ΔCPUE when the fish population was mobile and highly productive, which was expected. The increased productivity also had a small effect on fish movement; low mobility fish were slightly more likely to leave the MPA due to the higher density, producing small changes in CPUE (Figure 13).

Since fishing effort was constant and directly related to the relative abundance of the fish population, the properties of the model were such that the exploitation rate of the fishery increased with population productivity (Figure 14). Mobile fish were able to take advantage of the high productivity areas depleted by the fishery. Therefore, the

exploitation rate for mobile fish was higher; in a heavily depleted, high productivity

population the exploitation rate was nearly 70% for mobile fish, in contrast with a rate of

about 40% for nonmobile fish at the same level of productivity and depletion (Figure 14).

The probability of fish leaving the protected area for the fishing ground increased as

population became more depleted, similar to observations for the low productivity

scenarios (Figure 15). Increasing the exploitation rate of the more productive fish

populations reduced ΔCPUE to near zero for mobile fish, for all MPA placements, while

ΔCPUE for nonmobile fish increased sharply for the highly productive population

(Figures 15 and 16).

The mobile, highly productive population transferred animals freely to the fishing

ground, thus compensating for the heavy rate of exploitation. Catch rates remained

unchanged for highly productive, mobile fish before and after MPA establishment. As

expected, the MPA provided no effective protection for a highly productive, mobile

population. Fish movement became irrelevant in the case of the heavily depleted

population because there were so few survivors after fishing. The fishery was replenished

through recruitment from the protected area, but the overall ΔCPUE remained low

because the population was already heavily depleted and was not allowed to recover.

The high quality MPAs did provide protection for a nonmobile, highly productive

population. Nonmobile fish were essentially undisturbed by the fishing fleet and were

able to build biomass within the protected area until the population approached local

carrying capacity. Since the population produced larvae from a common pool in the

model, and recruit settlement was density-dependent, the large population inside the

MPA boosted ΔCPUE in fished areas solely through the export of recruits. The change in

catch rates increased by about 25% for the Core MPA placement and less for reserves over lower quality habitat. The percentage increase in ΔCPUE in the nonmobile scenario was very close to the proportion of the total catch protected by the MPA (Figure 15).

3.3 Additional simulation scenarios

The following three sections detail additional scenarios that I examined with a limited number of parameter combinations. Changes in the geometry of the fish concentration and the MPAs, the fish population state, and the relationship between ΔCPUE and abundance were all simulated for a low productivity fish population only.

3.3.1 Geometry of fish population

I examined the effect of establishing a protected area for two possible geometries of the fish concentration. The plateau configuration was expected to be the more protective shape for fish, providing a better long-term conservation benefit (Figure 8). The ridge configuration was designed to maximize edge effects, and was therefore expected to cause an increase in ΔCPUE relative to the original configuration (Figure 9).

The proportion of the total biomass caught within each potential MPA was similar for both configurations, with slight differences due to limitations posed by the specific grid geometry (Figure 17). The change in CPUE was similar between the two spatial configurations for both mobile and nonmobile fish, although there was a small edge effect (Figure 18). The geometry of the fish concentration does not appear to be an important factor in estimating the effects of MPA placements on the change in catch rates.

3.3.2 Fish population state

Whether the fish population was stable, increasing, or decreasing at the time of MPA establishment had little effect on the change in catch rates; all population states produced similar results over the 10-year simulation period (Figure 19). The effect of increasing the rate of fish movement past a low mobility threshold was similar for all population states. The establishment of an MPA over marginal habitats caused a small increase in ΔCPUE for a mobile fish population, and a small decrease in ΔCPUE for a nonmobile population, for all population states (Figure 19a). The declining fish population returned slightly lower ΔCPUE than the other population states for the Marginal MPA placement. Animals would be sparser in the high quality habitats due to heavy exploitation of the declining stock, and the Marginal MPA would only afford protection to a small proportion of the population.

The MPA placement over the Core habitat resulted in a decline in ΔCPUE for all population states (Figure 19b). Mobile fish produced less of a decline in catch rates than sedentary fish. The declining, nonmobile fish population produced the lowest ΔCPUE following establishment of the Core MPA, as might be expected. The mobile fish population sustained CPUE in the fishing ground even when the population was in decline.

3.3.3 Nonlinear CPUE

Decoupling CPUE from fish population abundance weakened the relationship, so that the change in catch rates decreased more slowly than abundance. The change in catch rates in the nonlinear case produced higher ΔCPUE for the high quality MPAs, but returned lower ΔCPUE for the more marginal MPAs (Figure 20). The fishing fleet thus

received a greater return in the best fish habitats if CPUE was nonlinear. The effect of nonlinear CPUE in the model was therefore to decrease ΔCPUE for MPAs situated over marginal habitats, and increase ΔCPUE for MPAs over high quality areas. Fish mobility had a reduced effect on catch rates; the relationship between the change in CPUE and the proportion of the catch inside the potential reserve was similar for mobile and nonmobile fish (Figure 21). In terms of fleet movement, the fishing fleet still preferred the best fish habitats, but tracked the fish concentration less closely. Since CPUE was coupled less tightly with abundance, the range of preferred fishing areas was expanded.

3.4 Prediction of ΔCPUE from pre-MPA data

Predicted ΔCPUE was calculated with spatially resolved catch and effort data for each grid cell, averaged over the final year of the simulation period. The following results explore the usefulness of predicted ΔCPUE as a crude estimator of the potential effects of an MPA, prior to establishment, and under several parameter combinations.

3.4.1 Low productivity fish population

The relationship between "true" and predicted ΔCPUE was roughly linear for high quality MPAs placed over a nonmobile fish population, but the predictor consistently underestimated the decrease in ΔCPUE (Figure 22a). The level of depletion of the fish stock also affected the predictor: as the level of depletion increased, the predictor became less accurate. Both true and predicted CPUE changed very little for the Transitional MPA, which was near the (0, 0) point on each plot. The Transitional MPA represented the threshold zone, where about 10% of the total catch was within the MPA and ΔCPUE remained unaffected.

For all mobile fish, the predicted ΔCPUE was very close to the "true" ΔCPUE collected from the model simulation over all MPA placements, producing a nearly 1:1 relationship (Figure 22b). The decrease in ΔCPUE was slightly overestimated for the high quality MPAs, while the reverse was true for the low quality MPAs. The change in CPUE was less affected by the level of depletion for the mobile population (Figure 22b). The CPUE crude estimator was most useful for mobile fish.

3.4.2 Moderate and high productivity fish population

Increasing the productivity of the fish population weakened the relationship between the true and predicted ΔCPUE. In the case of a nonmobile fish population, the ΔCPUE estimator was generally too optimistic in the moderate productivity scenario, underestimating the drop in ΔCPUE following the establishment of an MPA (Figure 23a). The linear relationship broke down further when I increased the exploitation level of the fishery (Figure 23a). The high productivity fish population was further affected by the level of exploitation. In the case of high productivity and a heavy level of depletion, predictive ΔCPUE was pessimistic for the high quality protected areas. For the Core placement, true ΔCPUE jumped to about 25% over the pre-MPA level, while predicted ΔCPUE stayed between 6% and 7% for all MPA placements (Figure 23b). The true change in CPUE was high because of recruit settlement. Since fish were nonmobile and could not leave the MPA, the highly productive population inside the MPA replenished the fishery. When the fish productivity and exploitation rate were both high, the fishery was able to deplete the fish population within the year. Therefore, predictive ΔCPUE failed in the heavily depleted case because the total abundance changed within the year, which violated one of the assumptions of the predicted CPUE algorithm.

The relationship between predicted and true ΔCPUE was linear but was not 1:1 for mobile fish under increasing productivity (Figure 24). Predicted ΔCPUE was affected by the level of depletion and the quality of the MPA; for example, although true ΔCPUE changed little for the heavily depleted fish population, the estimator predicted a decrease in ΔCPUE for high quality MPA placements.

3.4.3 Population state

The relationship between true ΔCPUE and predicted ΔCPUE was linear, but the predictor consistently underestimated the decrease in ΔCPUE for all population states when fish were nonmobile (Figure 25a). Predicted ΔCPUE was slightly more optimistic for the changing population states, when compared to the equilibrium scenarios. The changing population states showed little change in ΔCPUE for mobile fish, and the 1:1 relationship was maintained (Figure 25b). Thus, the crude CPUE predictor was robust to changing population abundance, under the parameter conditions simulated. However, the model simulation was designed to allow for only a small change in fish abundance of about 1% over the 10-year period. Larger losses or gains in abundance could further decrease the effectiveness of the CPUE predictor.

3.5 Ranking of factors affecting true change in CPUE

I used a linear model to rank the explanatory power of factors that appeared likely to affect ΔCPUE, to quantify my observations about the performance of the model under the various scenarios. I examined analysis of variance (ANOVA) tables for scenarios of high and low productivity, the geometry of the fish concentration, the population state, and nonlinear CPUE. The dependent variable was the true change in CPUE after MPA

establishment. The independent variables were the crude estimator of predicted ΔCPUE, the proportion of the total catch within the potential MPA, the probability that a fish would leave the MPA (a dimensionless proxy for fish movement), and the level of depletion from unexploited abundance. I used a simple regression of single factors as well as stepwise regression, with factors added sequentially as they became statistically significant. The objective was to determine whether a linear model could work as interpolation, and ultimately whether it would be a useful predictive tool for fishery management with respect to MPAs.

Analyses of the effect of increasing productivity and the geometry of the fish population suggested that the predicted ΔCPUE provided the best estimates of true ΔCPUE, as long as productivity remained low (Table 4). For the low productivity plateau population, the crude CPUE predictor by itself explained about 84% of the variation in the results, while the proportion of the catch inside the MPA by itself explained 70% of the variation. The sums of squares for the ridge configuration were slightly higher, with about 90% of the variation explained by predicted ΔCPUE and 76% explained by the MPA catch.

However, when evaluated for the high productivity stock in the plateau configuration, predicted ΔCPUE only explained about 29% of the variation in the results. The slope of the relationship between predicted ΔCPUE and true ΔCPUE for the highly productive population was variable, and there was a strong interaction between predicted ΔCPUE and the level of depletion (Figures 23 and 24). The proportion of catch in the MPA was also a very poor predictor for the high productivity stock. I added the fish movement rate and the level of depletion stepwise to a regression of true ΔCPUE against

predicted ΔCPUE, for low and high population productivity and both spatial geometries (Table 4). Both fish movement and the level of depletion had little effect on the fit of the model in all cases.

Predicted ΔCPUE explained more of the variation in the model than the proportion of the catch inside the MPA, in all cases. The predictor provided estimates that were close to true ΔCPUE for the nonlinear CPUE scenarios, but predicted ΔCPUE was less useful when the population state was changing (Figure 26). The high power of predicted ΔCPUE for the nonlinear CPUE scenarios was likely due to the partial decoupling of CPUE and abundance in those simulations. The predictor was weaker for the changing population states, in particular for the declining population. However, the performance of the predictor for increasing productivity was poor in comparison to all other scenarios examined, with at most 40% of the variation in the model explained (Figure 26). Overall, predicted ΔCPUE explained most of the variation in the model as long as fish productivity remained low. Adding factors stepwise to the regression of true ΔCPUE caused small improvements in the accuracy of the predictor, for all scenarios I examined (Figure 27).

3.6 Length of simulation

Although fishers and managers would likely focus on the short-term effects of a potential MPA on the fishery, the long-term effects of MPAs would also be of interest. I increased the period of the simulations to 100 years for a few parameter combinations, to determine the long-term effects of MPA establishment. The extent to which the reserve population can sustain or improve yields in fished areas over the long term is subject to the placement of the MPA, the initial exploitation level of the fleet, and to a lesser extent

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the mobility of the fish. Simulations of a heavily depleted stock with the MPA over high quality habitat produced a positive effect on CPUE over a 100-year period, while the change in catch rates for less depleted populations improved slightly but remained negative (Figure 28). These results also assumed total effort remained constant over 100 years. In contrast, MPAs over marginal areas reduced the change in catch rates over a 100 year period (Figure 29). The exception was the heavily depleted population, which produced a small increase for nonmobile fish.

Sedentary, heavily exploited populations increased the most, because recruitment from the fully protected population in the MPA steadily replenished the fishery through the settlement of recruits to all areas. Generally, the heavily exploited populations fared best because the stock slowly rebuilt over the long simulation period, while less depleted stocks were already closer to carrying capacity early in the simulation period. The increase in ΔCPUE was less for mobile populations in all cases, since the high transfer rates between the MPA and the fishing ground prevented the population inside the protected area from approaching carrying capacity. The long-term effects of MPA placement was the most beneficial to the fishery in the case of a nonmobile, heavily depleted fish population, with the MPA placed over high quality fish habitat. Marginal MPAs appeared to be beneficial to fishing yields in the short term, but the improvements diminished over the long term.

4 Discussion

The objective of this study was develop methods to evaluate the potential effects of marine reserves on adjacent fisheries, in order to address the concerns of fishers over the expected loss in catch and catch rates following the establishment of an MPA. I used dynamic, spatially explicit models of a hypothetical fish population targeted by a fishing fleet to estimate the change in CPUE. I investigated the effects of establishing MPAs in different locations over portions of a fishing ground, with changes in other factors such as fish mobility and the exploitation level of the fishing fleet. The models included spatial variation in carrying capacity, directed and diffusive fish and fleet movement, and redistribution of fishing effort following MPA establishment. The results of this study revealed two key findings. First, although the presence of an MPA rarely resulted in increased catch rates, the decline in ΔCPUE was not equivalent to the proportion of the total catch inside the potential MPA. Second, catch rates were little affected by fish movement above a low mobility threshold. Other factors such as the population state and the spatial geometry of the fish concentration also had little overall effect on the change in catch rates, although increasing the productivity of the fish population did increase ΔCPUE in some cases. Regression analysis of the factors affecting the change in CPUE suggested that fishery-dependent information could provide reasonable estimates of post-MPA catch rates, for low productivity fish. These methods may be helpful for providing quick assessments of potential MPAs, particularly where only fishery-dependent information is available.

The loss in catch rates following MPA implementation concurs with the findings

of other modeling studies (Apostolaki et al. 2002, Gerber et al. 2002, also see review by

Gerber et al. 2003). The reduction in available fishing grounds following the

establishment of an MPA has been found to depress the catch and catch rates in

remaining fished areas, assuming that total fishing effort remains the same (Halpern et al.

2004, Horwood et al. 1998). Hilborn et al. (2004) suggested that, in the case of a

sedentary stock with limited dispersal, a reserve covering 30% of a fishing ground should

reduce the potential catch in remaining areas by the same percentage. Put another way,

the drop in catch rates following the establishment of an MPA should be equivalent to the

proportion of the total catch inside the protected area. In contrast, the findings of the

current study showed that catch rates declined for sedentary stocks with all MPA

placements that protected more than about 7% of the total catch, yet the loss in ΔCPUE in

every scenario examined was far less than the proportion of the population protected by

the MPA. For example, the change in catch rates for sedentary fish fell by about 7%

when 25% of the total catch was inside the Core MPA. Therefore, the proportion of the

population nominally protected by the potential MPA was much larger than the

proportion that was actually protected. These results are similar to those of Daan (1993),

who conducted a simulation study of North Sea groundfish stocks and found that a

closure comprising 25% of the total fishing ground reduced fishing mortality by only

about 12%, assuming low dispersion rates. Clearly, the dynamic behaviour of the fish

population was able to compensate partly for the loss in ΔCPUE following MPA

implementation.

Two mechanisms were responsible for replenishment of the fishery: the transfer of adults and the export of production from the protected area to the fishing ground (Chapman and Kramer 1999, Gaines et al. 2003, Halpern et al. 2004). Russ and Alcala (1996) theorized that the transfer of adult fish outside the reserve, often termed in the MPA literature as "spillover", occurs when the population inside the protected area approaches higher densities than surrounding fished areas. The spillover of fish from MPAs has been documented in empirical studies of MPAs (e.g., Abesemis and Russ 2005, Roberts et al. 2001), but the effect can be difficult to distinguish from directed seasonal movements of fish (Murawski et al. 2005). However, Walters and Bonfil (1999) examined observer data from the British Columbia groundfish fishery and found no evidence of local depletions in areas of intense fishing, indicating rapid transfer between fished and unfished areas.

In the current study, the rate of fish movement determined the degree to which the fish population replenished the fishery. Mobile fish always returned a higher catch rate, which was expected and agrees with the findings of other modeling studies (Apostolaki et al. 2002, Rodwell and Roberts 2004). Mobile populations replenished fishing yields through the direct transfer of adults to fished areas and the settlement of recruits from production by the reserve population. The placement of the reserve relative to the fishing ground determined whether the change in catch rates was negative or positive for mobile fish. Although MPA placements protecting more than 20% of the total catch produced a small negative effect on catch rates in all mobile scenarios, MPAs over less than 20% of the catch tended to have neutral or slightly positive effects on ΔCPUE. In all cases, increasing the movement rate past a low mobility threshold had a negligible effect on

ΔCPUE. All simulations with mobile fish showed that catch rates remained stable when the movement rate was increased. Indeed, catch rates were stable even in the case of a declining fish population. Salthaug and Aanes (2003) demonstrated that CPUE can become hyperstable with decreasing population size, due to increased catchability. As the population declines the range of the fish population contracts, and fishers respond by concentrating their spatial effort over the diminishing fish stock (Guenette et al. 2000, Harley et al. 2001, Salthaug and Aanes 2003).

The reduction in ΔCPUE for sedentary fish tended to be a few percentage points lower than mobile fish for each MPA placement, with the difference attributable to the lack of adult movement from the MPA. The settlement of recruits was the sole mechanism compensating for the drop in catch rates following MPA implementation, for sedentary fish. This assumption is appropriate for low mobility species such as benthic invertebrates, or fishes with small territorial ranges such as many rockfish, when the MPA is larger than the spatial scale of adult movement (Kaplan and Botsford 2005). The processes of larval dispersal and settlement have been identified as likely key determinants of the fisheries benefits of marine reserves (e.g., Gaines et al. 2003, Gerber et al. 2003). Many species with sedentary adult phases have pelagic larvae, and ocean currents can transport larvae over vast distances (Halpern 2003, Kaplan and Botsford 2005). Therefore, the direction of currents relative to the location of marine reserves may be important in determining whether specific MPAs act as a sink (destination) or source for larval transport (Allison et al. 1998). In the case of low mobility species such as benthic invertebrates and reef fish, enhanced larval output and subsequent settlement may

be the primary benefits of MPAs (Acosta 2002, Horwood et al. 1998, Polacheck 1990, Nowlis and Roberts 1999).

Modeling studies often characterize larvae as arising from a common pool with random settlement (e.g., Hastings and Botsford 1999), which may be a fair approximation for low mobility species, such as rockfish of the genus *Sebastes* and benthic invertebrates (Carr and Reed 1993). However, many models do not include a larval stage at all, because of limited knowledge of larval movements (Gaines et al. 2003, Gerber et al. 2003). Recruits in our models arose from a common larval pool but settlement was density dependent. Recruits settled in fished areas when population density in the MPA was high enough that other areas were comparatively more attractive. I found that the export of production from the MPA had a large compensatory effect on catch rates for most of the scenarios examined, illustrating the importance of including a larval stage in MPA modeling studies.

The results for sedentary fish may be conservative, since adults in the sedentary population did not leave the MPA in the current study. In a study of the frequency and range of daily movement of lingcod, Starr et al. (2004) found that net movement was very low, but individuals travelled outside the MPA and returned over short periods in search of prey. Therefore, even populations that are considered relatively sedentary may supply adults to fished areas. In addition, low mobility animals may also undertake seasonal migrations (Egli and Babcock 2004). However, the transfer of animals from reserves is also likely to be site-specific. Spatial changes in habitat type can be barriers to fish movement, such as reef habitats separated by sandy areas (Chapman and Kramer 1999). I assumed that mobile fish transferred freely between areas of different habitat

quality through diffusive and directed movement, and recruits settled in any desirable

habitat with sufficient space. Fish movement was not restricted by changes in spatial

habitat in the model.

Theoretical and empirical studies since Beverton and Holt (1957) have suggested

that detailed information on the movement of fish between the closed area and the fishing

ground may be critical in estimating the impact of the MPA on fishery yield (e.g., Gerber

et al. 2003, Guenette et al. 1998, Starr et al. 2004). The findings of this study show that

fish movement is important in estimating the loss in ΔCPUE after MPA establishment,

but only to the point of determining whether fish are mobile or sedentary; that is, it may

only be necessary to determine whether fish are transferring out of the reserve to provide

reasonable estimates of MPA effects on fishing yields. These findings may have

significance for the use and cost of mark-recapture studies, in that low precision estimates

of fish movement are likely sufficient to predict the effects of MPAs on catch rates.

Fishing effort within the reserve was redistributed to other areas following MPA

establishment, which is reasonable as long as the profitability of the fishery is high

enough to support the increased effort (Sanchirico and Wilen 2001). I assumed a

conservative response by fishers, where the total fishing effort remained constant, so that

the extra effort from the MPA was partitioned into the remaining areas depending on

local profitability (Halpern et al. 2004, Murawski et al. 2005). Fishing pressure outside

the reserve therefore increased in some areas after MPA establishment, accelerating the

local rate of exploitation. In a comprehensive review of MPA models, Gerber et al.

(2003) stated that effort redistribution has not often been explored in the context of

spatial variation in habitat and directed fish movement. Exceptions include an early

simulation study by Hilborn and Walters (1987), and several studies since that have examined spatial adaptation by fishers following implementation of reserves, where fishing behaviour changes in response to closures (e.g., Guenette et al. 2000, Halpern et al. 2004, Sanchirico and Wilen 2001, Walters 2000, Walters and Bonfil 1999). The properties of our models were such that the fleet "explored" all areas of the grid in search of fish, but tended to concentrate in areas with the highest profitability (Hilborn and Walters 1987, Murawski et al. 2005). In the case of a reserve placed over high quality fish habitat, the fleet congregated around the edges of the reserve where profits were highest. Pelletier and Mahevas (2005) stated that effort allocation is highly dependent on spatiotemporal resource patterns; therefore, the tendency of the fleet to concentrate around the high quality MPA is probably a reasonable simplification of fleet behaviour. Fishers tend to return to familiar profitable grounds, and thus effort may be most concentrated near the closed area (Guenette et al. 2000, Walters and Bonfil 1999). The concentration of the fleet next to the MPA led to local depressions in fish density along the boundaries, increasing transfer rates outside the MPA. Walters (2000) previously found this effect in a multiple species ecosystem model with simple diffusive movement. The extra effort around the MPA reduces the conservation benefits of the MPA but stabilizes the catch, as was also found by the current study.

Catch rates improved slightly when the reserve was placed over areas of marginal fish habitat, due to an emergent property of the model where some of the fishing effort that was within the marginal MPA was redistributed to better quality areas after implementation. The fleet had perfect knowledge of the best fishing locations, and a portion of fishers moved to marginal areas whenever profits were reduced to comparable

levels in the best grounds. The cost of fishing is higher in marginal areas because fish are more likely to leave poor habitats, and the fleet expends more effort for lower returns. However, even in an open access fishery, many other factors may affect the selection of fishing grounds, including distance from port, fuel and opportunity costs of exploration, gear saturation in preferred fishing grounds, and imperfect knowledge of the location of fish aggregations (Gillis 2003, Gillis and Peterman 1998, Walters and Bonfil 1999). In any case, an MPA placed on marginal habitat would likely be the preferred placement choice for fishers, leaving the best fishing grounds open.

Although I focused on the short-term (10-year) effects of MPA establishment as being of primary interest to fishers and managers, a few simulations indicated that the long-term (100-year) effects of MPAs on catch rates were positive for depleted stocks, but remained negative for less depleted stocks. Total effort was constant in this study, even for the 100-year simulations. Realistically, fishing power may increase over time, in response to lower catches or lost grounds (Guenette et al. 1998). Assuming no regulations are in place, reductions in CPUE could trigger acceleration in gear improvements as the fleet competes for less fish (Guenette et al. 2000). Adding variability in fishing effort may be a more realistic treatment of fisher behaviour. I also did not consider seasonality in fishing patterns, which are likely for fisheries that target species with seasonal changes in behaviour (Pelletier and Mahevas 2005).

Several other interrelated factors affected the change in catch rates. Increasing the pre-MPA rate of exploitation increased the movement rate of the fish population; that is, the intense fishing activity depleted the population and increased the desirability of available habitats. The higher transfer rates from the reserve produced higher catch rates

from the depleted population when the MPA was over the best habitats. Previous studies have suggested that reserves may improve fishing yields for mobile populations when the level of effort has been high enough to cause recruitment overfishing (Apostolaki et al. 2002, Gerber et al. 2002, Lauck et al. 1998, Quinn 1993, Nowlis and Roberts 1999). Our findings showed catch rates improved for heavily exploited populations, but were still lower than those prior to MPA establishment.

The opposite effect was found for MPAs placed over marginal habitat areas: the change in CPUE was initially positive because the most productive fish habitat was fully available to the fleet, but this effect decreased as the exploitation level increased and the best areas were depleted. Marginal areas by definition had low carrying capacity for fish, and afforded little protection to the fish population which was thus unable to compensate for the heavy exploitation rate. Sedentary fish would also be unlikely to sustain and export production if only marginal areas were protected. This effect was demonstrated in an empirical study by Tegner (1993), who found little conservation benefit for Southern California abalone when reserves were placed in poor habitats.

Bohnsack (1992) noted that the structure of protected populations tended to shift toward larger, older individuals when fishing pressure was removed. The increased fecundity of older fish may boost the overall productivity of MPA populations, increasing the protected stock so that the reserve can become a source of adult and juvenile dispersal (Allison et al. 1998, Berkeley et al. 2004). In the current study, increasing the productivity of the fish population increased catch rates, because the model was structured so that the fleet exploited the highly productive population more intensely. However, the sedentary, highly productive and heavily depleted population produced the

only significant increase, where ΔCPUE increased by 25% for the Core MPA. Overall catch rates were extremely low in this scenario, both before and after MPA establishment. As shown by previous studies, it would seem reasonable that low mobility, highly productive species would benefit from an MPA in the case of heavy exploitation (Apostolaki et al. 2002, Gerber et al. 2002, Quinn et al. 1993).

The establishment of MPAs tended to have neutral or positive fishery effects for higher productivity populations. However, increasing productivity and exploitation rate reduces the ability to predict the effects of potential MPAs on catch rates. The CPUE predictor was calculated from averaging ΔCPUE within each spatial cell over the final year of the simulation. At low productivity, predicted ΔCPUE provided good estimates of the "true" simulated ΔCPUE, particularly for mobile fish. The CPUE predictor became less reliable as productivity was increased, because the intense fleet effort drastically reduced the population abundance in all areas within the first part of the year. Predicted ΔCPUE was generally pessimistic for highly productive populations, indicating the maximum expected reduction in the change in catch rates, or a lower bound to ΔCPUE. Thus, the predictor could be used as part of a precautionary approach to predict the effects of MPAs on fisheries for highly productive fish populations.

Overall, predicted ΔCPUE was less useful for heavily depleted stocks, and this was more evident as the population productivity was increased. However, a marine reserve used as a sole management tool would be unlikely to sustain a severely depleted stock unless the reserve was very large (Guenette et al. 2000). Other traditional management measures would presumably be in place, such as limits on the total catch or a quota system (Walters and Bonfil 1999). For overexploited stocks, marine reserves

would be most useful as spatial tools to complement existing management, such as for closures of spawning aggregations or other fish hotspots, or to limit the by-catch of vulnerable non-targeted species (Hilborn et al. 2004, Horwood et al. 1998).

An underlying goal of this study was to determine whether the activity patterns of a fishing fleet could provide inferences about the movement, numbers and behaviour of a targeted fish population. Under the assumptions of the models I used, annual catch and effort information for individual fishing locations (spatial cells) can provide reasonable estimates of predictive ΔCPUE after the placement of an MPA over various proportions of a fish population, as long as the exploitation rate remains low or moderate. In addition, only minimal information on the frequency and range of fish movement may be required. In light of the increasing popularity of MPAs as a tool to manage a range of ecosystem objectives, it is likely that many MPAs will be established in areas where stock assessments have not been completed or there is little fishery-independent data available. Participants in MPA processes often hope to see major improvements in fish abundance shortly after MPAs are established, and may be quick to press for other management alternatives if this hope is not sufficiently realized (Gerber et al. 2002). The methods described in this study may be useful for rapid assessments of a proposed MPA, in order to obtain reasonable estimates of the projected short-term costs to fishers from loss of fishing grounds, and to decide upon appropriate compensation.

The models used in this study are flexible, and can be tailored to examine a wide range of population dynamics and fleet behaviour. The models can be parameterized for seasonal spawning aggregations or migrations of fish, temporal shifts in carrying capacity, and adaptive behaviour of the fish or the fleet following MPA establishment.

Socioeconomic additions to the models could include variability in fisher behaviour, the introduction of a quota system, or allowing for market-driven price fluctuations. The simulations thus far have examined the effects of changing the size and shape of an MPA, represented by the proportion of the catch inside the reserve, and the comparison of linear and circular MPAs. The effects of multiple or seasonal MPAs, or multiple fish populations with different life histories, have not yet been examined. Also, the model is currently deterministic. Gerber et al. (2002) also used a deterministic model and found that reserves rarely increased fishing yields. Adding environmental variability should make the fishery benefits more obvious (Gerber et al. 2002). Finally, adding locational data would be straightforward since the model is already spatially explicit. Further research should include evaluating the models against a spatially explicit time series of catch and effort data for a commercial fish stock.

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Figure 1. Flow chart illustrating general path of data flow for model simulations: t is daily timestep; Y is yearly timestep; N, C and E are matrices of fish abundance, catch, and fishing effort, respectively. *Figure 7 describes the path of data flow in more detail regarding daily movement of the fish population. †Section 2.5 details fishing fleet dynamics.
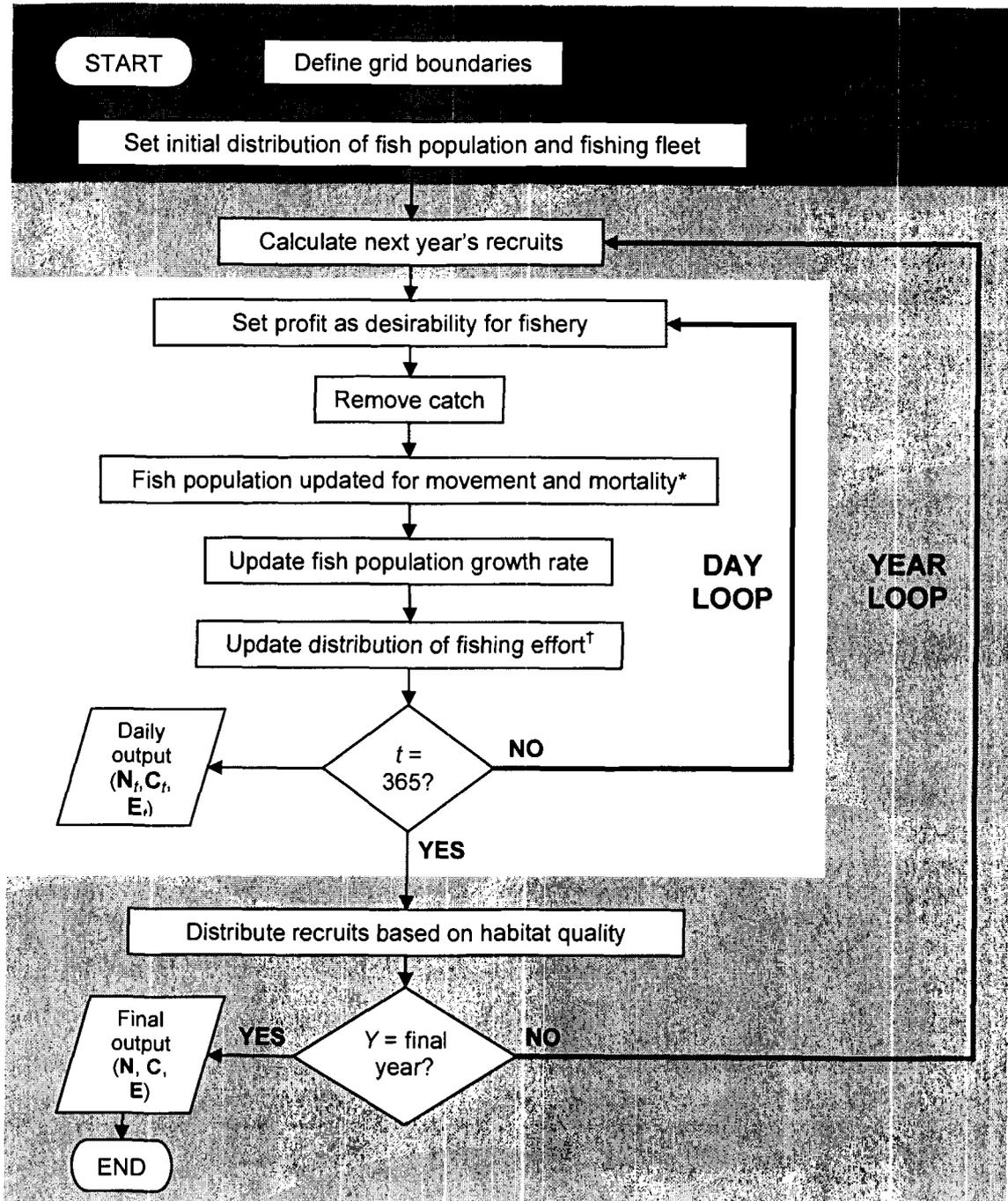
Figure 2. Two patterns of carrying capacity examined in this study. (a) Plateau configuration: 10-by-10 cell grid (b) Ridge configuration: 7-by-18 cell grid. Fish densities in each configuration are the same.

(a)   (b)
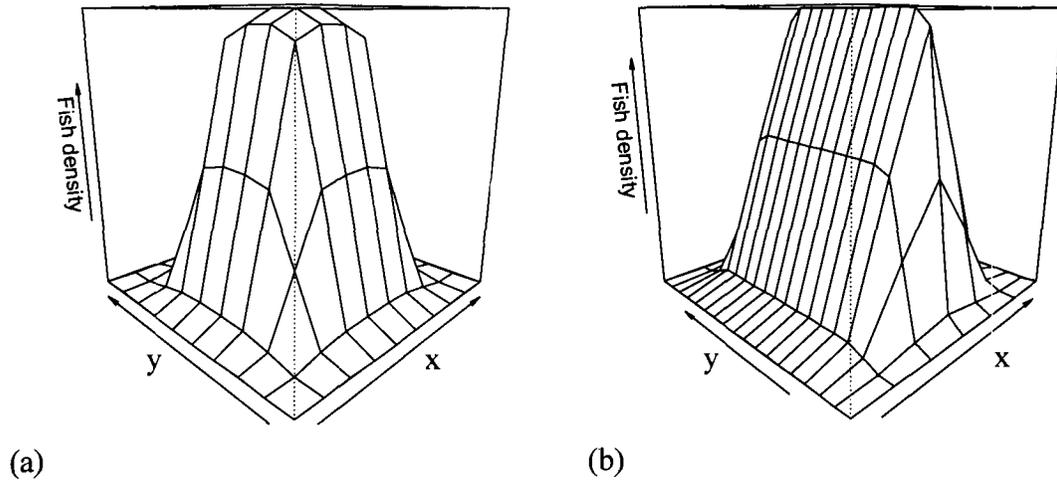
Table 1. Notation

Matrices

|	
A_t	Number of fish exploring other cells in spatial grid in time step t
C_t	Catch distribution in time step t
c_t	Proportion of fish population N caught in time step t
d_t	Desirability of cells for fish in time step t
E_t	Fishing effort (fleet abundance) in time step t
E_{max}	Maximum carrying capacity of the fishing fleet
f_t	Desirability of cells for fleet in time step t
h_t	Probability that fish or fleet stay in each "home" cell in time step t
K_t	Carrying capacity of the fish population in time step t
K_{max}	Maximum carrying capacity of the fish population
m_t	Movement of adult fish from each grid square in time step t
m'_t	" " " " " when N approaches K in time step t
N_t	Fish abundance in time step t
n_t	Fish or fleet that stay in other cells after exploring in time step t
n'_t	Fish or fleet that return home after exploring in time step t
P_t	Total profit in time step t
p_t	Productivity of the fish population in time step t
R_y	Total recruitment in year Y
r_t	Settlement probabilities of recruits in time step t
s_t	Expected recruit settlement in time step t
U	Final catch per unit effort (CPUE)

Parameters

α	CPUE exponent
c	Cost of fishing per unit effort
e_t	Effort growth or decay
g	Initial level of stock depletion
i	Index for matrix row
j	Index for matrix column
κ	Equilibrium stock size multiplier
M	Natural mortality rate
p	Selling price per fish
q	Catchability coefficient
$\bar{p}$	Weighted mean fish productivity
S	Survival rate
σ_i, σ_j	Movement rate (standard deviation of Φ) in row i and column j
t	Time step (day)
μ_i, μ_j	Means of the cumulative normal distributions in row i and column j
v	Carrying capacity adjustment parameter
ξ	Intrinsic rate of increase
x_j	Vector of grid cell boundaries in column j
y_i	Vector of grid cell boundaries in row i
Y	Time step (year)
Φ	Cumulative normal distribution

Figure 3. Pattern of carrying capacity in one axis for the plateau configuration. Solid line (—) shows cumulative normal distribution (Φ). Dotted line (---) shows reverse cumulative normal distribution (1 − Φ). Solid grey lines show the mean grid cell midpoint of each distribution (μ_1 and μ_2) at 50% density, and the slope of the distribution (σ_1 and σ_2). Steps illustrate the uniform probabilities of diffusion within each grid cell.
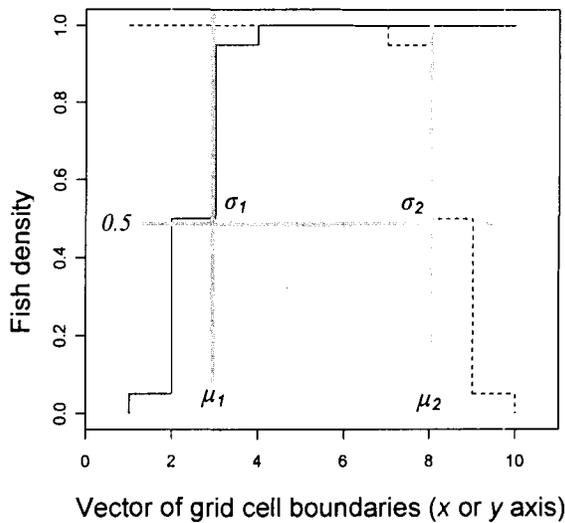

Figure 4. Pattern of carrying capacity in row i (a) and column j (b) for the ridge configuration. Parameters are the same as those in Figure 3, with the exception of grid bounds.
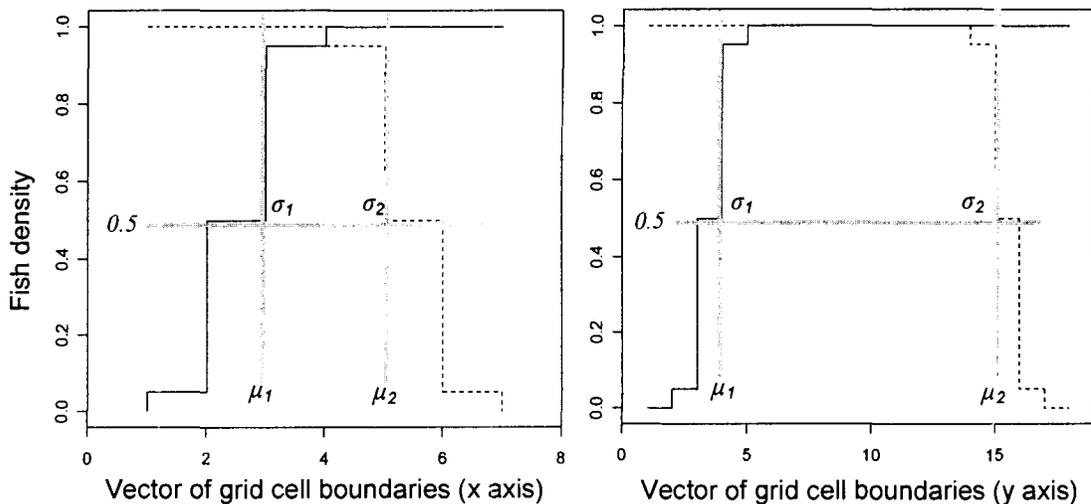

(a)   (b)

Figure 5. Calculation of fish (N) movement. Shading represents differences in habitat quality, with marginal habitats as darker cells around perimeter, and core habitat as white cells in centre. (a) Diffusion probabilities from cells $N_{1,1}$ and $N_{2,2}$. Thick arrows show the most probable paths of diffusion to closest cells ($N_{2,1}$, $N_{1,2}$); thin arrows show lower diffusion probabilities to more distant (diagonal) cells. (b) Directed movement from cell $N_{2,2}$ and $N_{3,3}$. Fish moving from $N_{2,2}$ to $N_{3,3}$ (thick arrow) will stay in $N_{3,3}$ due to higher habitat quality, but will diffuse back out to surrounding lower quality habitats (thin arrows) when numbers approach local carrying capacity.
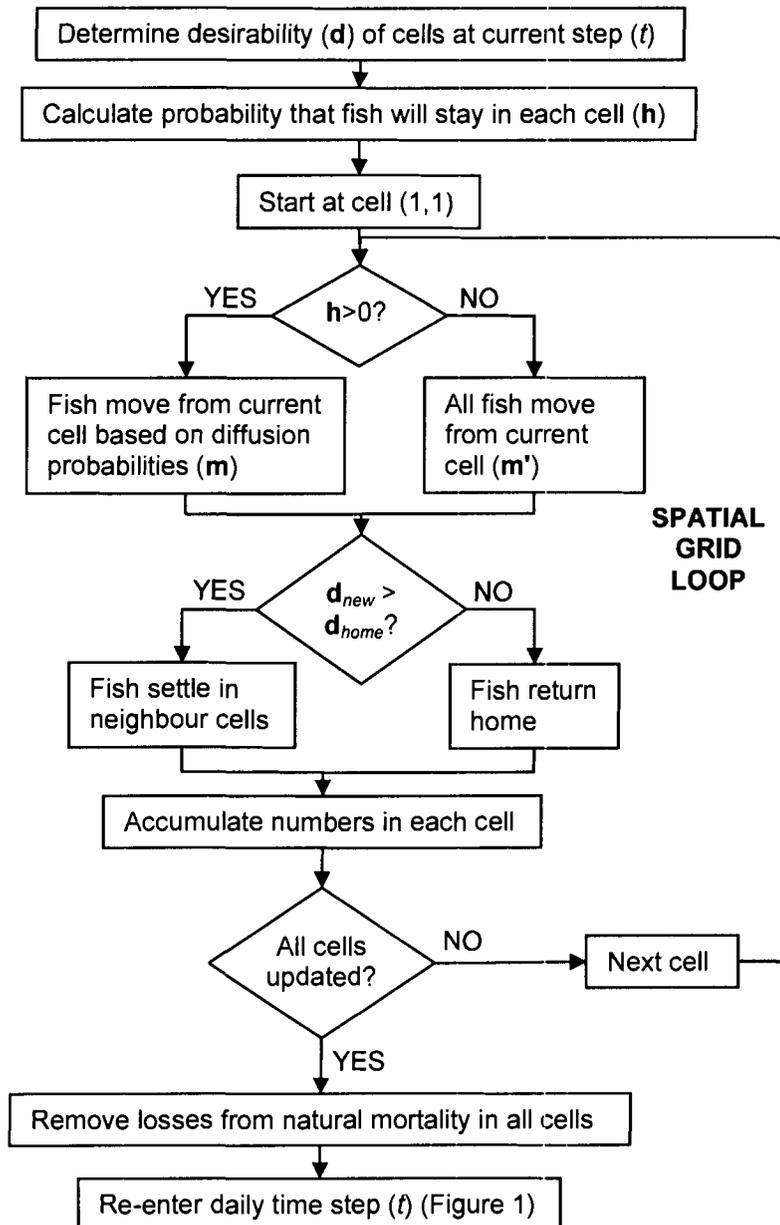

(a)   (b)
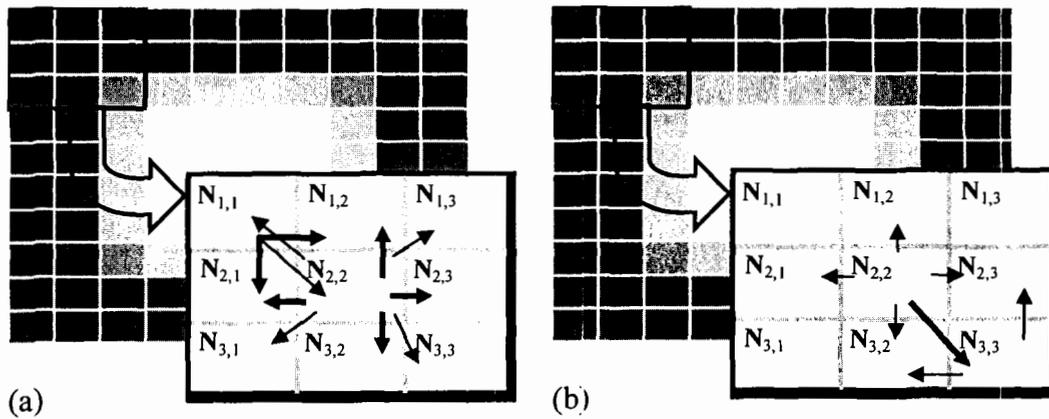
Figure 6. Diffusion probabilities of two representative grid cells, in one axis (plateau configuration). Dotted line (---) shows diffusion probabilities from a cell in the centre of the spatial grid. Solid line (—) shows adjusted distribution of diffusion probabilities for an edge cell. Solid grey lines show location of home cells for edge and internal cells. To prevent fish from diffusing off the grid, the tails of the distribution are adjusted so that fish are allowed to accumulate along the boundaries. Steps illustrate the uniform probabilities of diffusion within each grid cell.
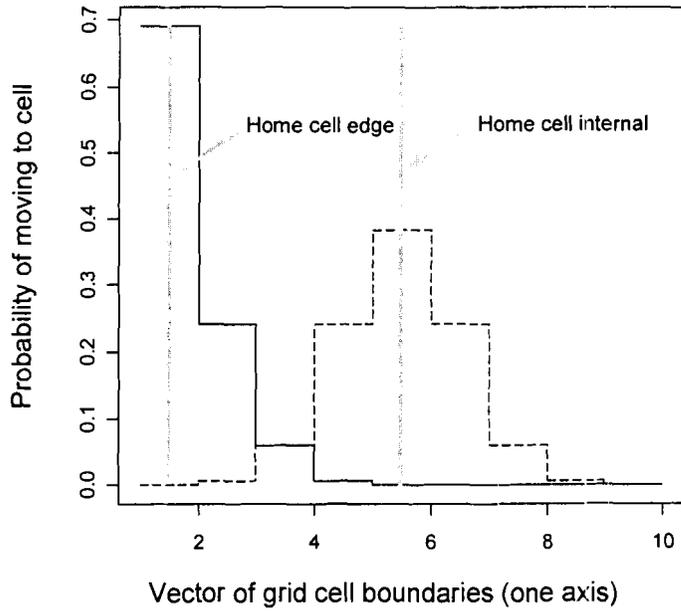
Figure 7. Flow chart illustrating calculation of fish movement and population redistribution: an expansion of the daily fish movement step shown in Figure 1. Movement of the fishing fleet uses the same form of model, without losses from mortality.

Fish population updated for movement and mortality:

Determine desirability (**d**) of cells at current step (*t*)

Calculate probability that fish will stay in each cell (**h**)

Start at cell (1,1)

h>0?
— YES
— NO

YES: Fish move from current cell based on diffusion probabilities (**m**)

NO: All fish move from current cell (**m'**)

SPATIAL GRID LOOP

$d_{new} > d_{home}$?
— YES
— NO

YES: Fish settle in neighbour cells

NO: Fish return home

Accumulate numbers in each cell

All cells updated?
— NO → Next cell
— YES

Remove losses from natural mortality in all cells

Re-enter daily time step (*t*) (Figure 1)

Table 2. List of parameter values

| Symbol	Parameter	Value
A	CPUE exponent	0.5, 1
c	Cost of fishing per unit effort	5
e_t	Effort growth or decay	± 0.01
g	Initial level of stock depletion	0.25, 0.5, 0.75
i, j	Number of rows and columns	(10,10) and (7,18)
κ	Equilibrium stock size multiplier	20000
M	Natural mortality rate	0.2
N_I	Initial total fish abundance	500000
p	Selling price per fish	3
q	Catchability coefficient	0.001, 0.1
r	Intrinsic rate of increase	0.6, 3., 6.
σ_i, σ_j	Movement rate, row i or column j	0.01, 0.1, 0.15, 0.2, 0.25, 0.3, 0.5, 1, 2.
υ	Carrying capacity adjustment parameter	0.001

Figure 8. MPA placements relative to the main fish concentration for the "Plateau" configuration. Shading represents differences in habitat quality, with marginal habitats as darker cells around perimeter, and core habitat as white cells in centre.


NO MPA

OUTSIDE

TOUCHING

FRINGE

MARGINAL

TRANSITIONAL

ENCROACHING

CORE
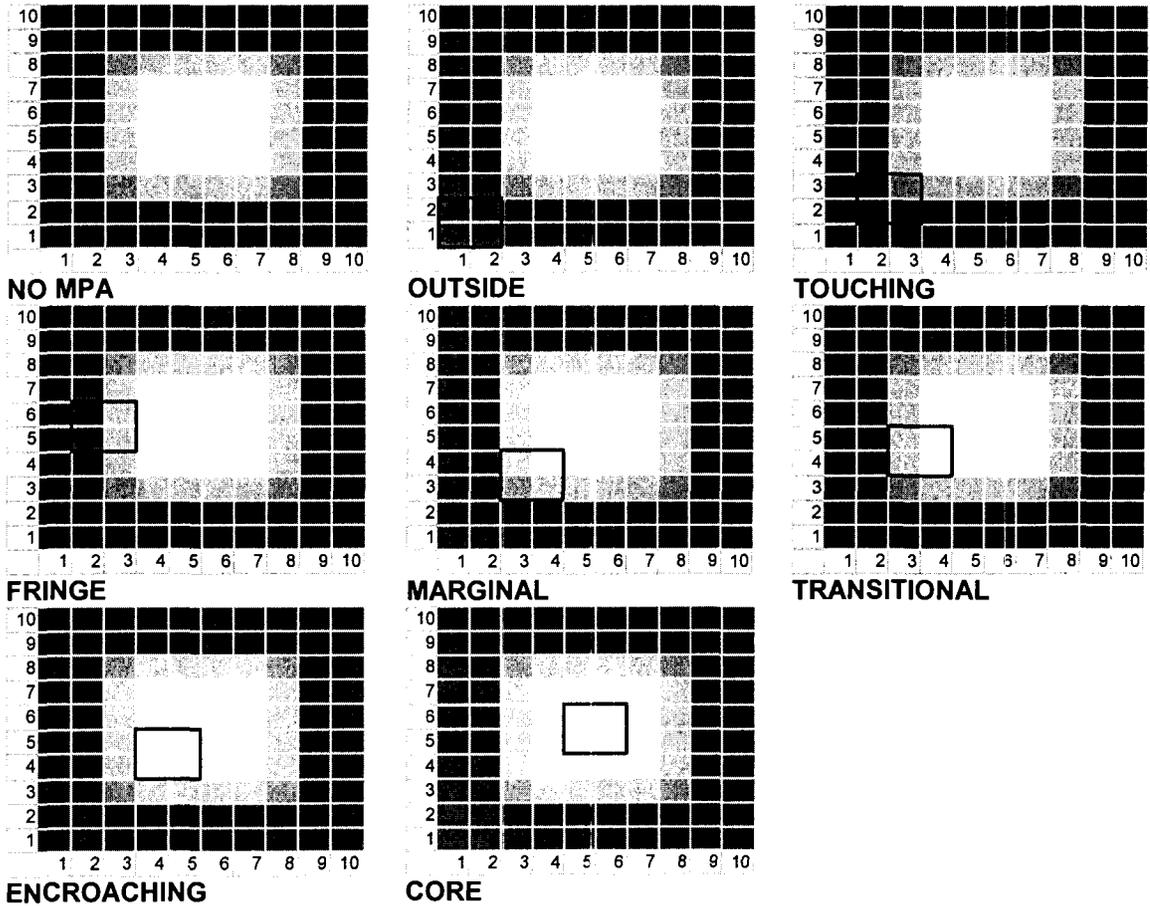
Figure 9. MPA placements relative to the main fish concentration for the "Ridge" configuration. MPAs are linear in this case.

NO MPA

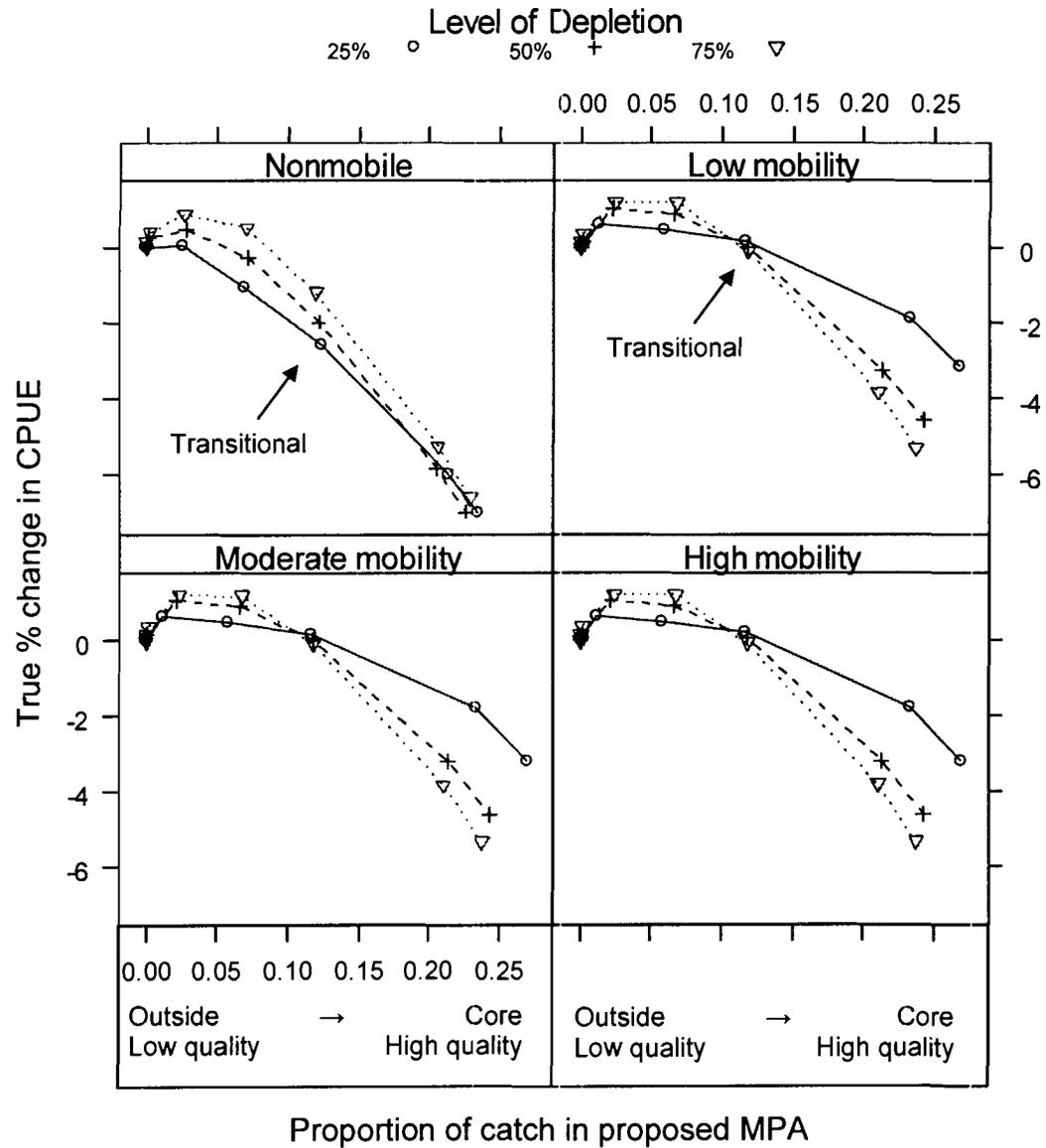OUTSIDE

TOUCHING

FRINGE

MARGINAL

TRANSITIONAL

ENCROACHING

CORE
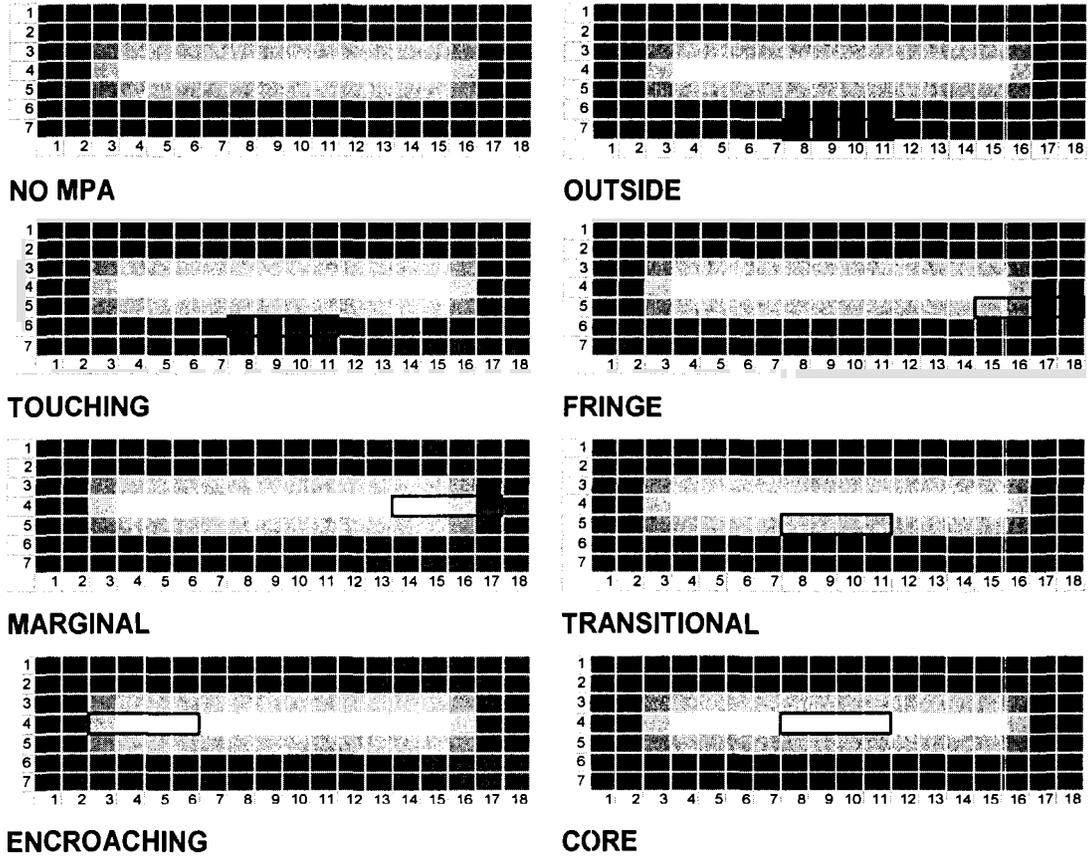
Figure 10. True ΔCPUE for different MPA placements over a low productivity fish population, for three levels of depletion (heavy: to 25% of unexploited abundance, moderate: to 50% of unexploited abundance, light: to 75% of unexploited abundance) and nine fish movement rates, ranging from nonmobile to highly mobile fish. The probability of a fish leaving the MPA in one day (x-axis metric) is a dimensionless proxy for fish movement, and the rate of movement increases from left to right in each panel. The Outside MPA placement has no effect on ΔCPUE in any scenario, and is not shown.
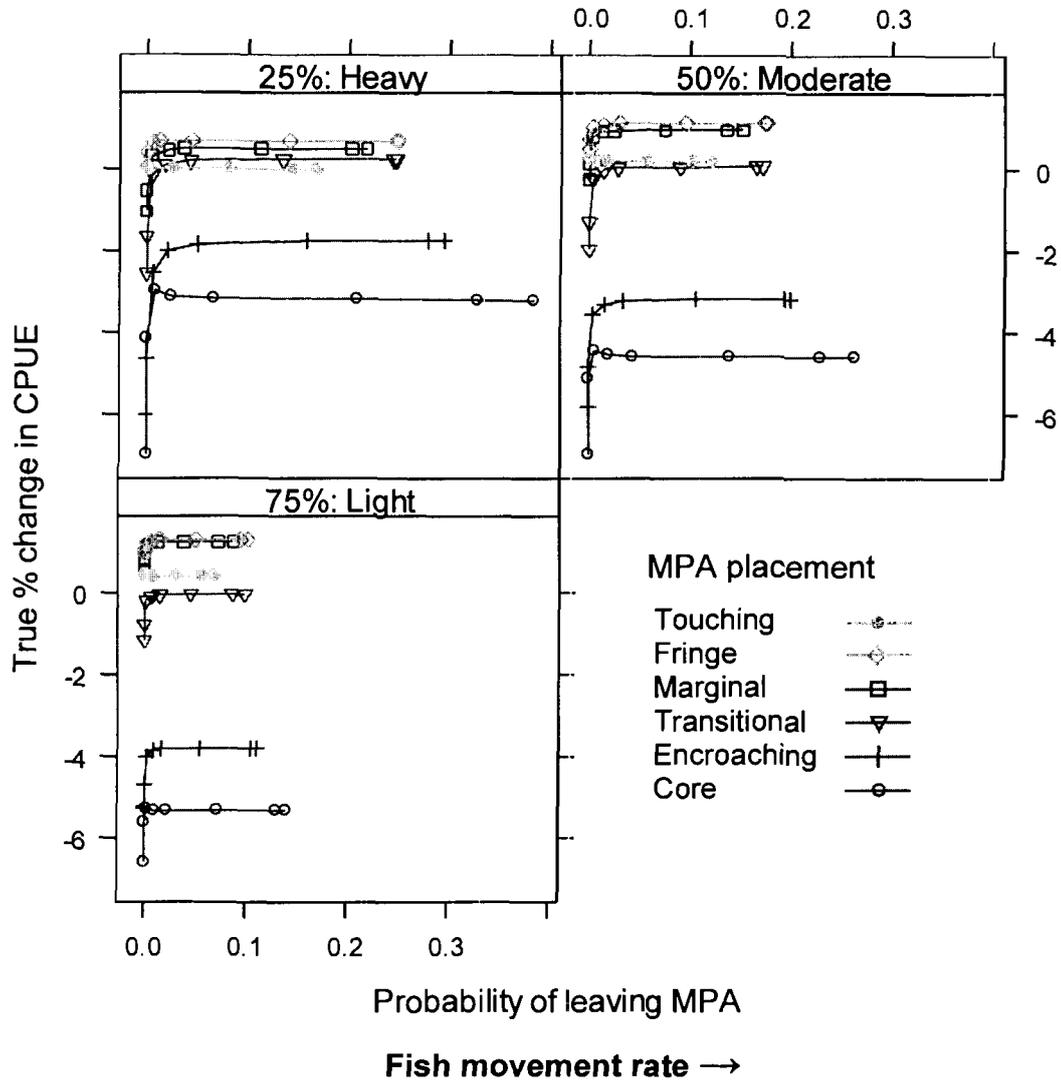
Figure 11. True ΔCPUE for the Core MPA placement (a) and Marginal MPA placement (b), for three levels of depletion.

Fish movement rate →

(a)

Fish movement rate →

(b)
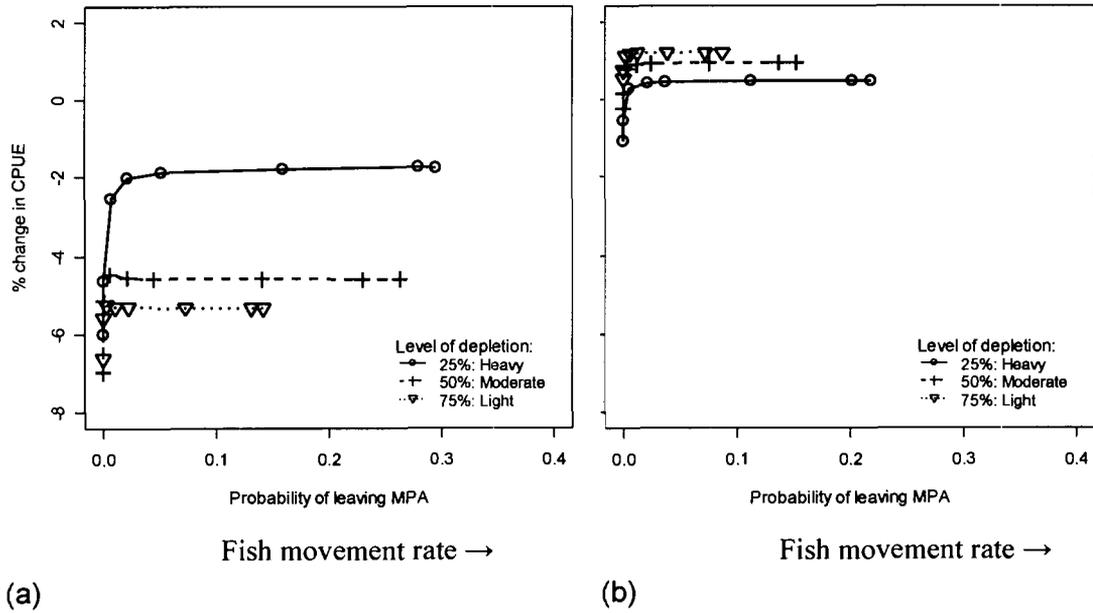
Figure 12. True ΔCPUE versus the proportion of the total catch in each MPA, for three levels of depletion and four rates of fish movement. The proportion of the catch inside the MPA corresponds to the seven MPA placements. The habitat quality of MPAs progresses from left to right within each panel.

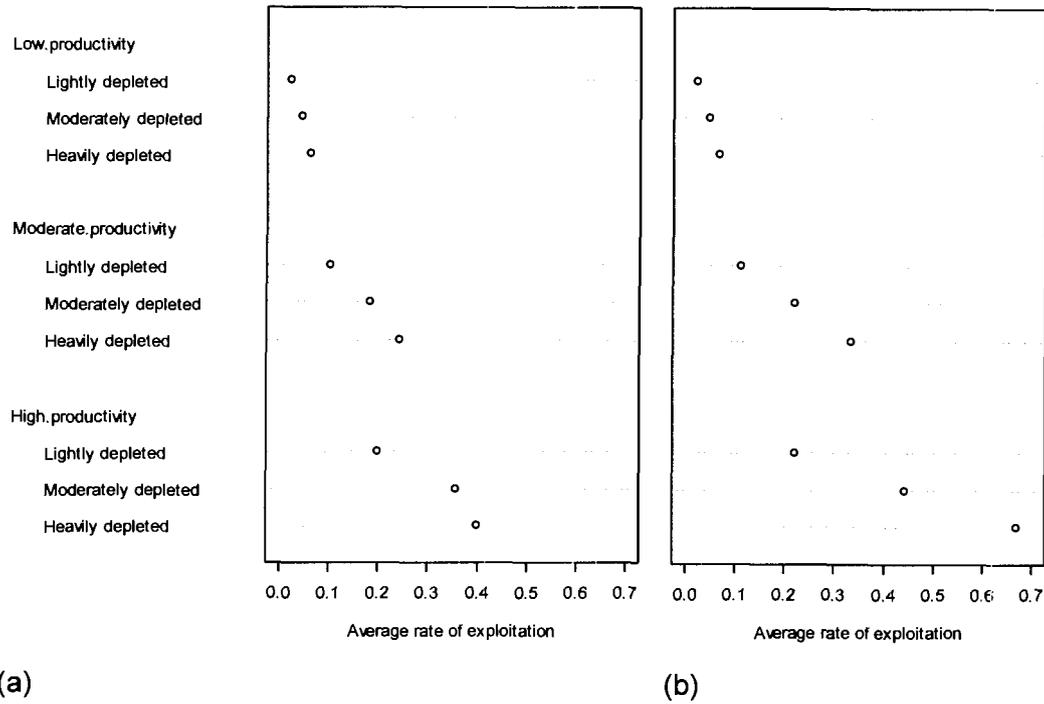**Table 3.** Average proportion of total catch in potential MPA

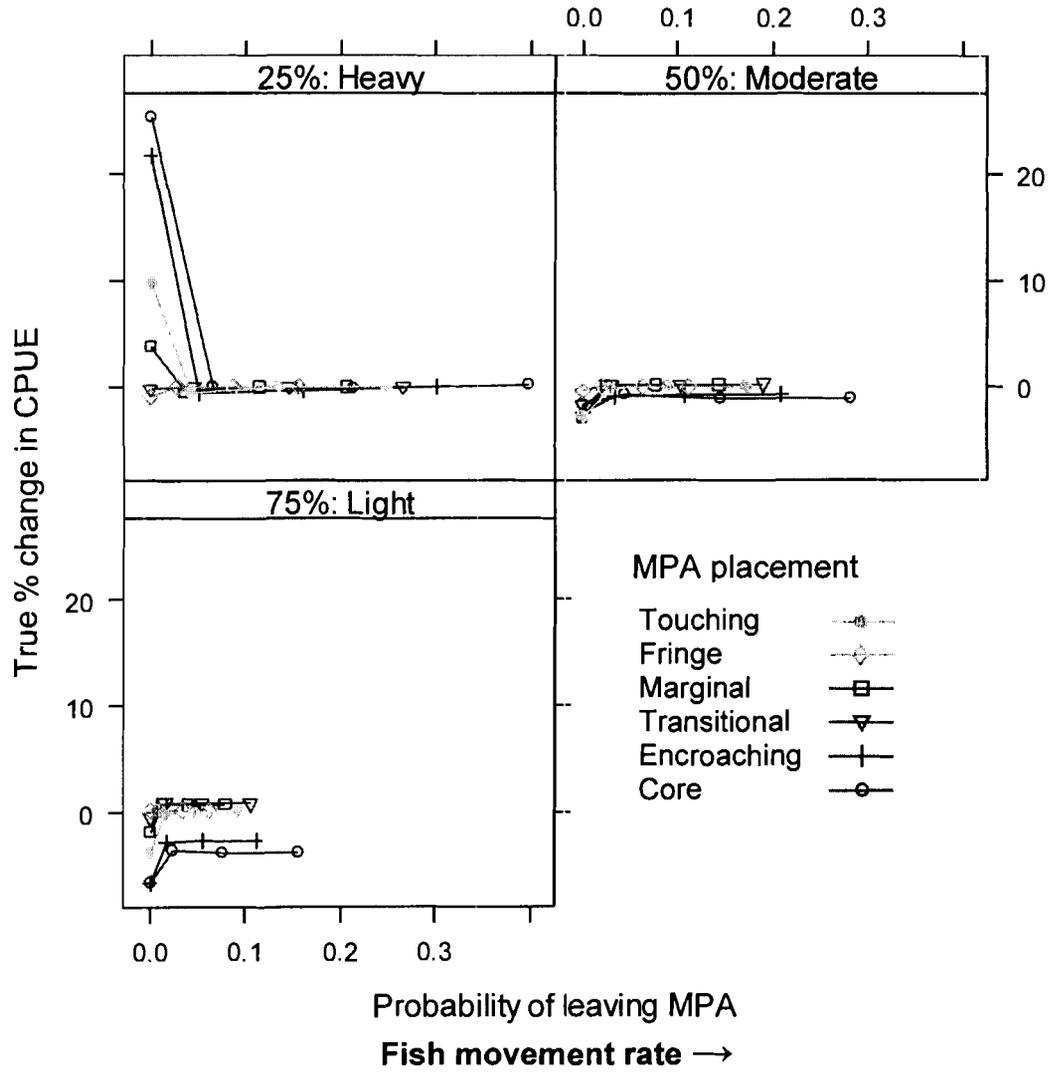| MPA name	Proportion of total catch (%)	
	Plateau	Ridge
Outside	0.0	0.0
Touching	0.1	0.1
Fringe	2.0	1.0
Marginal	7.0	5.0
Transitional	12.0	12.0
Encroaching	22.0	18.0
Core	25.0	24.0

Figure 13. True ΔCPUE for seven MPA placements for a lightly depleted fish population (to 75% of unfished abundance), with low and high productivity. Panels also show harvest rate (h) for each scenario.
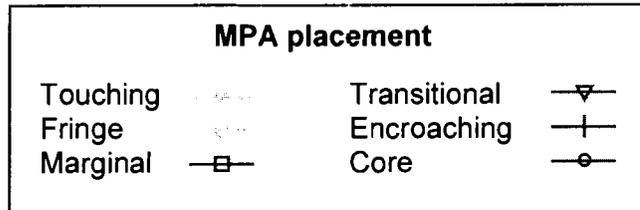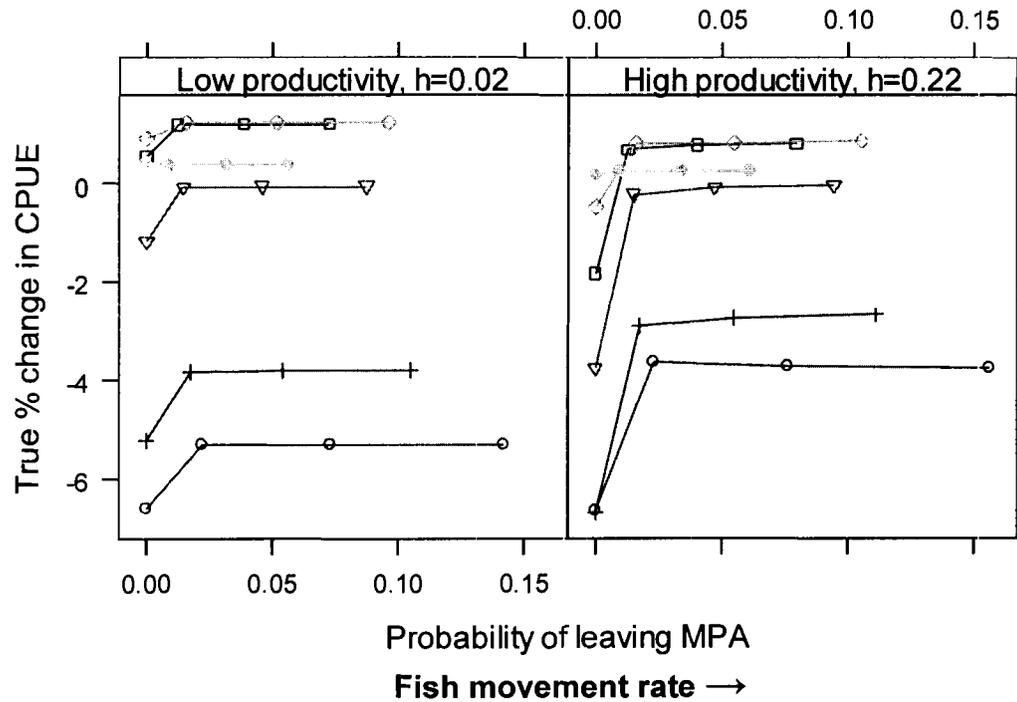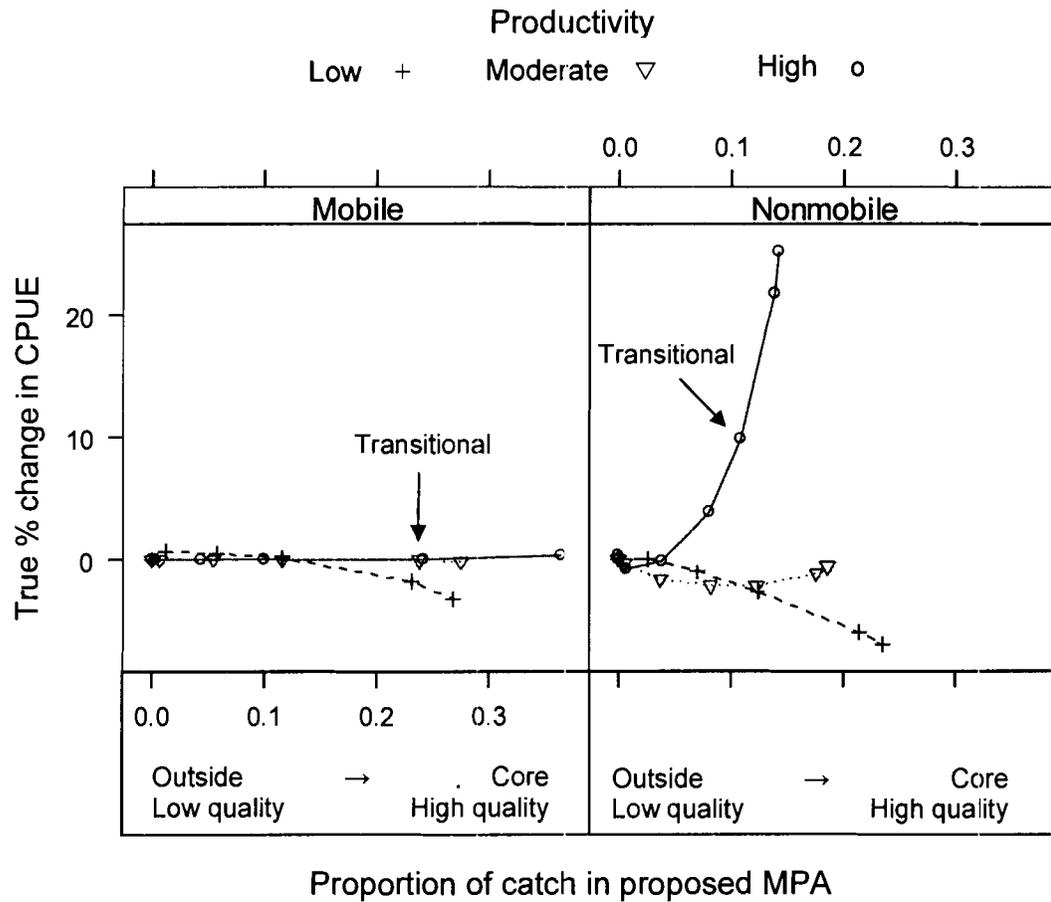
Figure 14. Average exploitation rate (proportion of total biomass captured by fishery) in final year of 10-year simulation, shown by fish population productivity, and the level of depletion from unfished abundance. (a) Nonmobile fish; (b) mobile fish.

Low.productivity

   Lightly depleted

   Moderately depleted

   Heavily depleted

Moderate.productivity

   Lightly depleted

   Moderately depleted

   Heavily depleted

High.productivity

   Lightly depleted

   Moderately depleted

   Heavily depleted

0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7

Average rate of exploitation

(a)

0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7

Average rate of exploitation

(b)

Figure 15. True ΔCPUE for different MPA placements over a high productivity fish population, for three levels of depletion and four fish movement rates.

Figure 16. True ΔCPUE for a heavily depleted fish population, with low, moderate and high productivity. Panels contrast results for mobile and nonmobile fish. Each panel shows ΔCPUE versus the proportion of the total catch within the potential MPA. The habitat quality of MPAs increases from left to right in each panel.



Proportion of catch in proposed MPA

Figure 17. Average exploitation rate (proportion of total biomass captured by fishery) within each potential MPA placement in the final year of a ten-year simulation, for each spatial configuration: plateau (10-by-10 cell spatial grid), and ridge (7-by-18 spatial grid). Exploitation rates were averaged over all movement rates and levels of depletion, for each configuration.
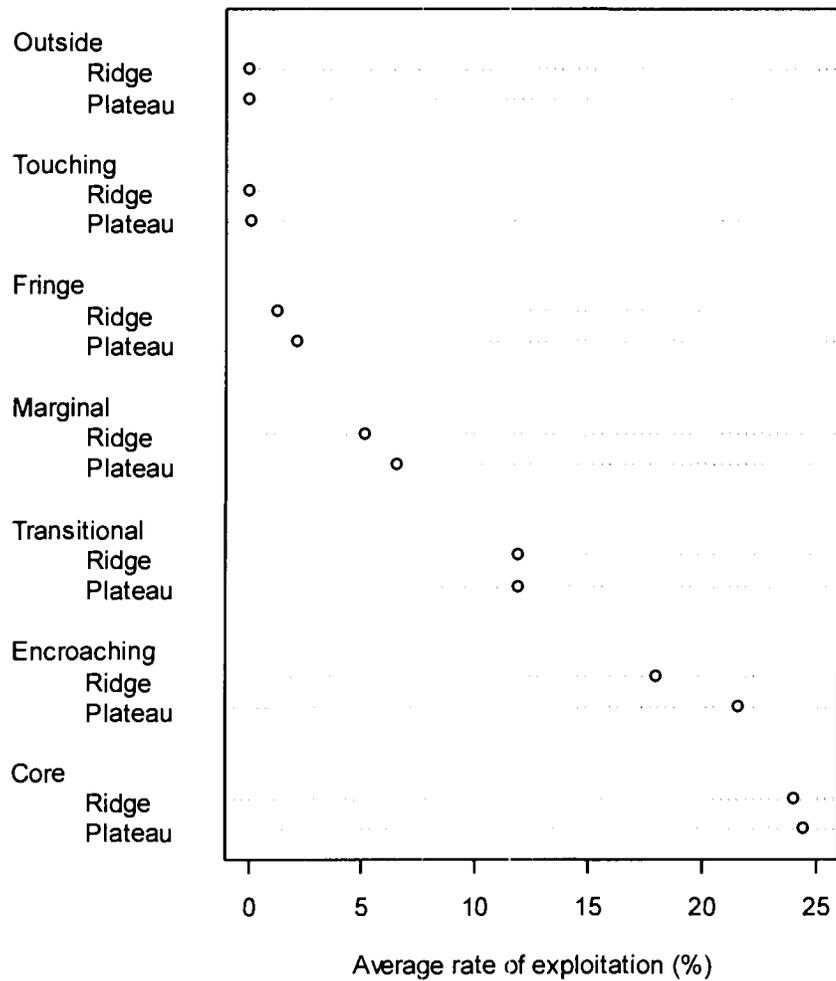
Figure 18. Contrasting change in true ΔCPUE for two spatial configurations of the fish population, for nonmobile fish (upper panels) and mobile fish (lower panels). Left-hand panels show plateau configuration, right-hand panels show ridge configuration. All panels show 3 levels of depletion from unfished abundance. Habitat quality of MPA increases from left to right in each panel.
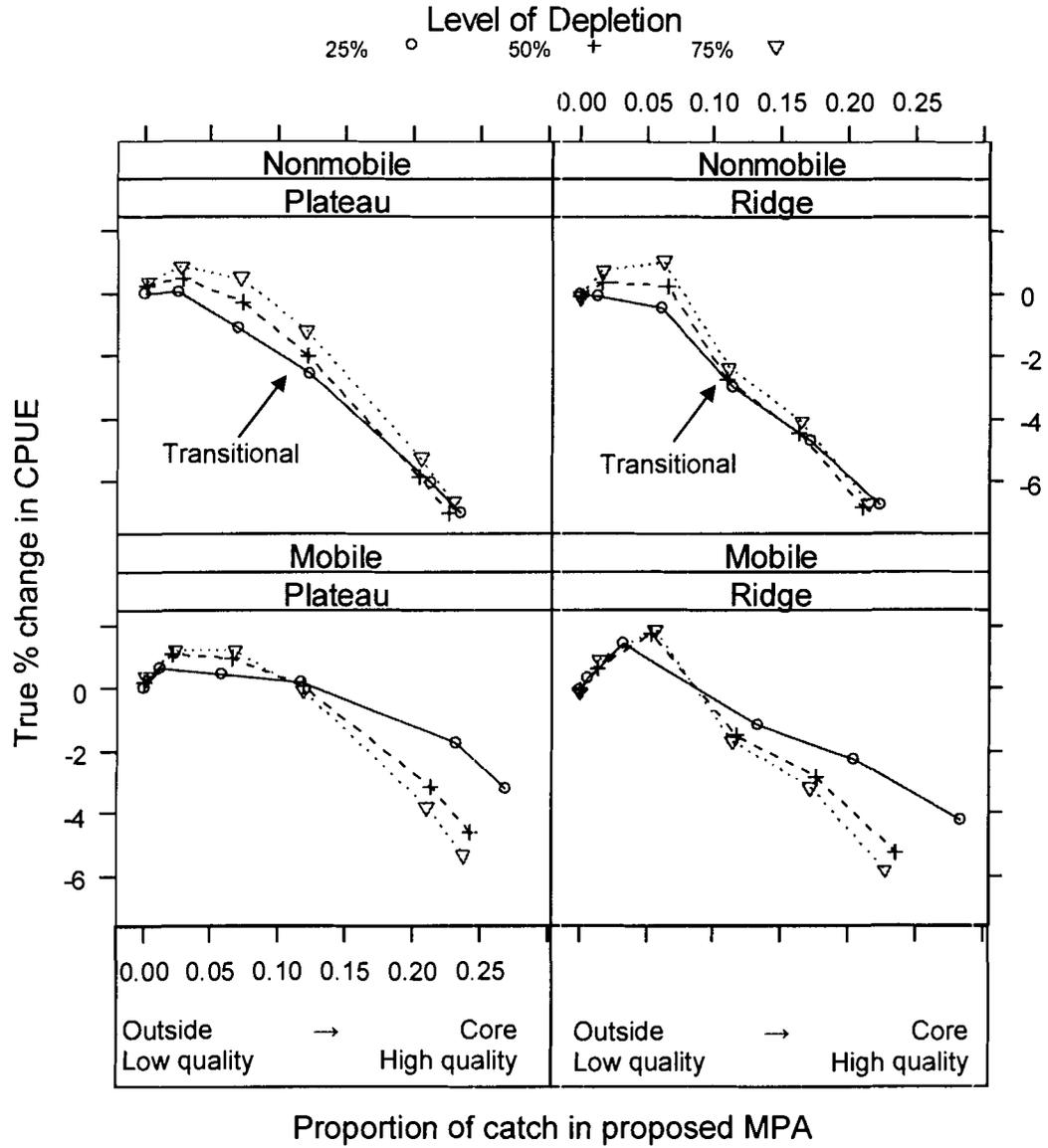
Figure 19. True ΔCPUE for (a) Marginal and (b) Core MPA placements, showing increasing fish movement rate by population state. Results are for a low productivity fish population. The equilibrium population has been moderately depleted to 50% of unfished abundance.
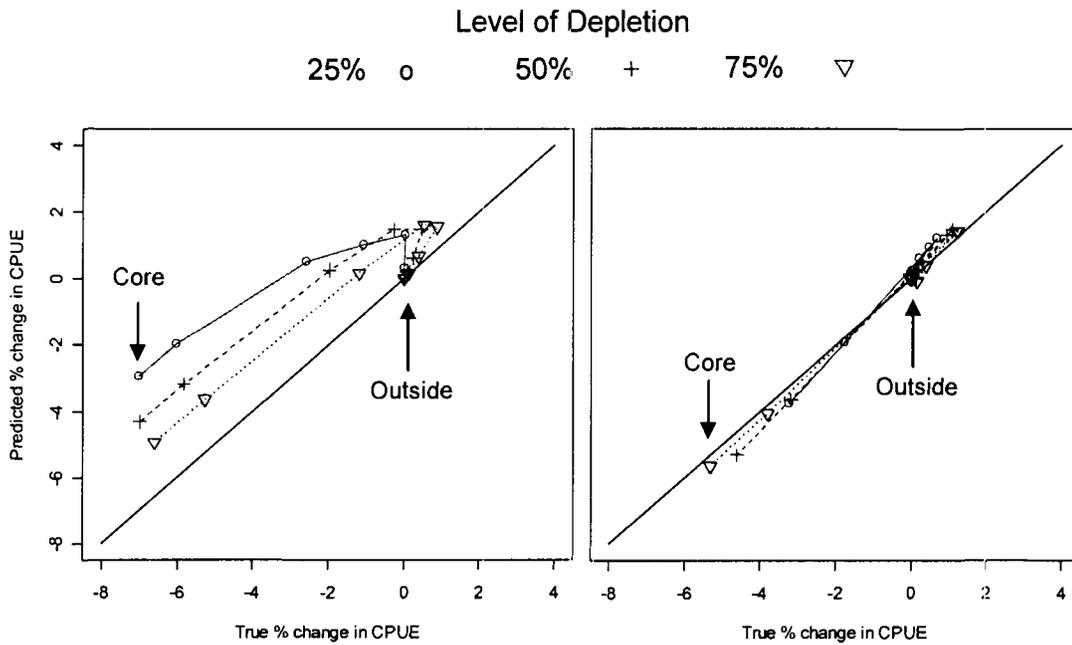

(a)   (b)
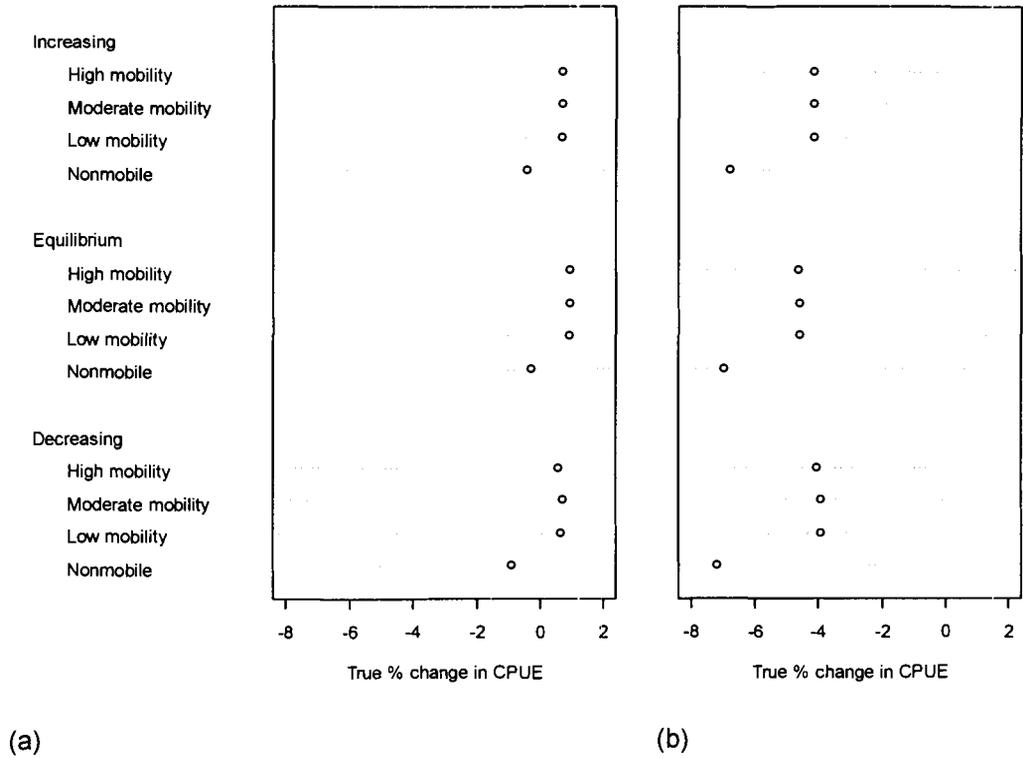
Figure 20. Effects of nonlinear versus linear CPUE. Panels show ΔCPUE for different MPA placements, for a moderately depleted fish population (to 50% of unexploited abundance).
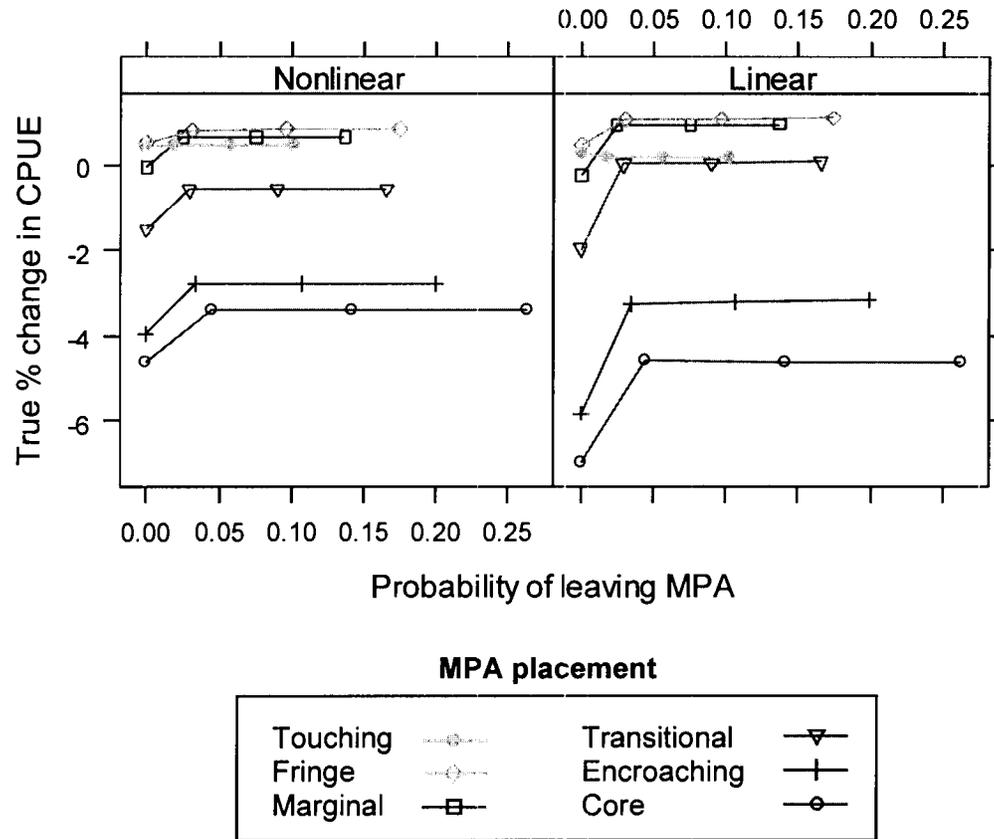
Figure 21. Proportion of total catch within each potential MPA, contrasting nonlinear versus linear CPUE. Upper panels show ΔCPUE for nonmobile fish, lower panels show mobile fish. All panels show three levels of depletion from unfished abundance.

Proportion of catch in proposed MPA
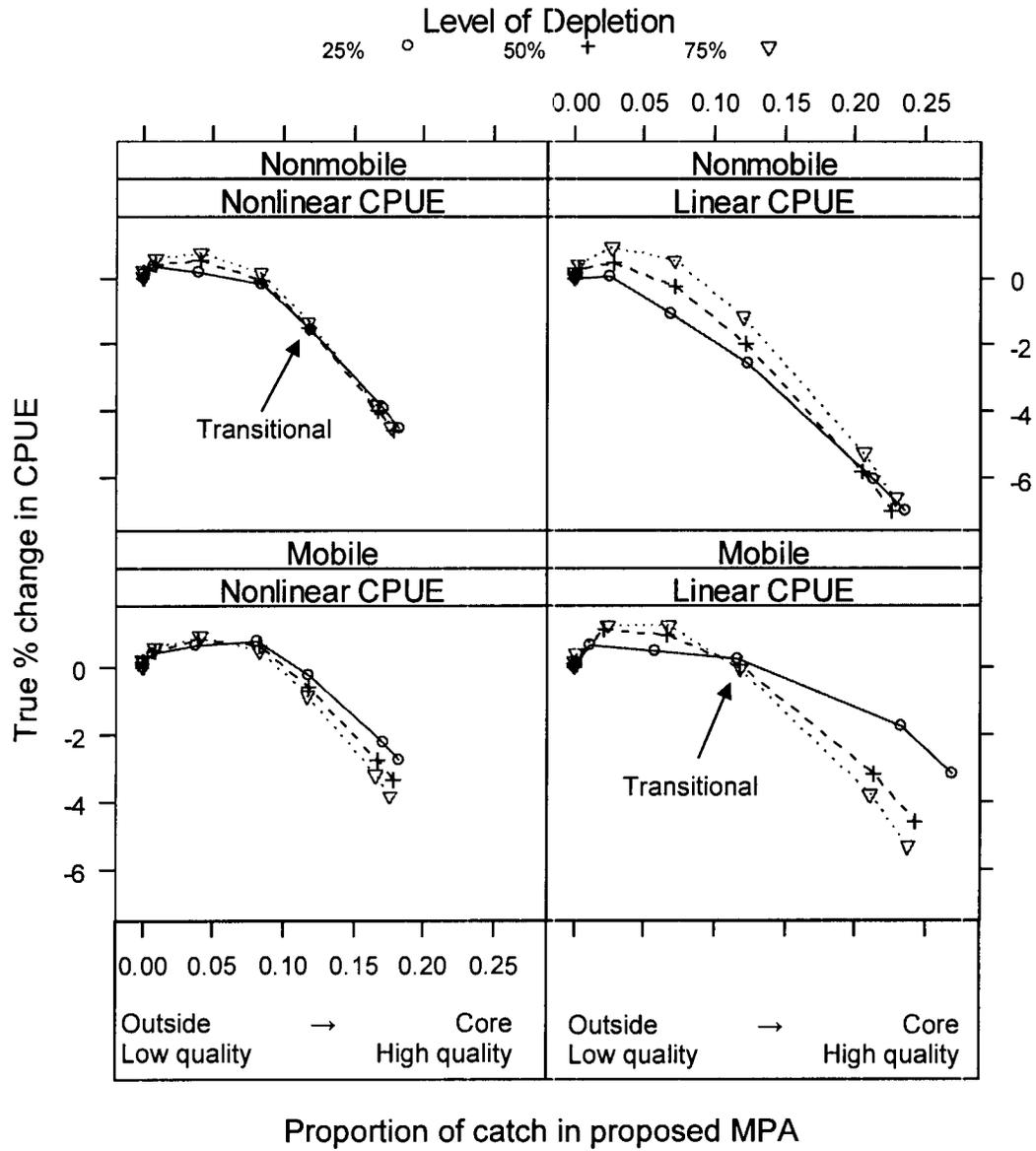
Figure 22. Predicted ΔCPUE against true ΔCPUE, for each MPA placement over a **low productivity** fish population: (a) Nonmobile fish, (b) all mobile fish. Plots show predicted ΔCPUE for three levels of depletion from unfished abundance. High quality MPAs are on left side of plots, with the proportion of the total catch inside the potential MPA decreasing from left to right.

Level of Depletion

25%   o   50%   +   75%   ▽

Predicted % change in CPUE

Core

Outside

True % change in CPUE

Core

Outside

True % change in CPUE

(a)   (b)

Figure 23. Predicted ΔCPUE against true ΔCPUE, for **nonmobile** fish. Panels show each MPA placement over (a) moderately productive and (b) highly productive fish population, for three levels of depletion from unfished abundance. Note differences between locations of Core MPAs in each plot; also x- and y-axes differ between panels.

(a)   (b)

Figure 24. Predicted ΔCPUE against true ΔCPUE, for **mobile** fish. Panels show each MPA placement over (a) moderately productive and (b) highly productive fish population, for three levels of depletion from unfished abundance.

(a)   (b)
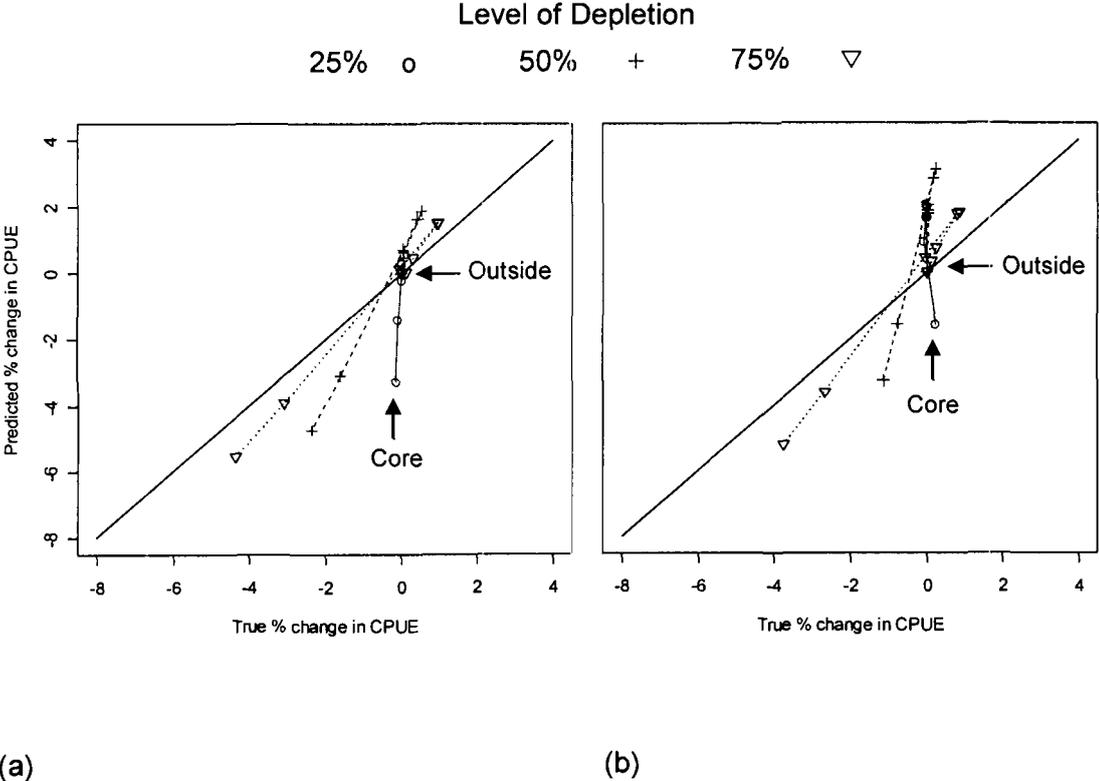
Figure 25. Predicted ΔCPUE against true ΔCPUE for (a) nonmobile and (b) mobile fish. Panels show each MPA placement for three population states. Equilibrium population was depleted to 50% of unexploited abundance (moderate). High quality MPAs are on left side of each panel, with the proportion of the total catch inside the potential MPA decreasing from left to right.

Population State

Increasing o   Decreasing +   Equilibrium ▽

(a)   (b)
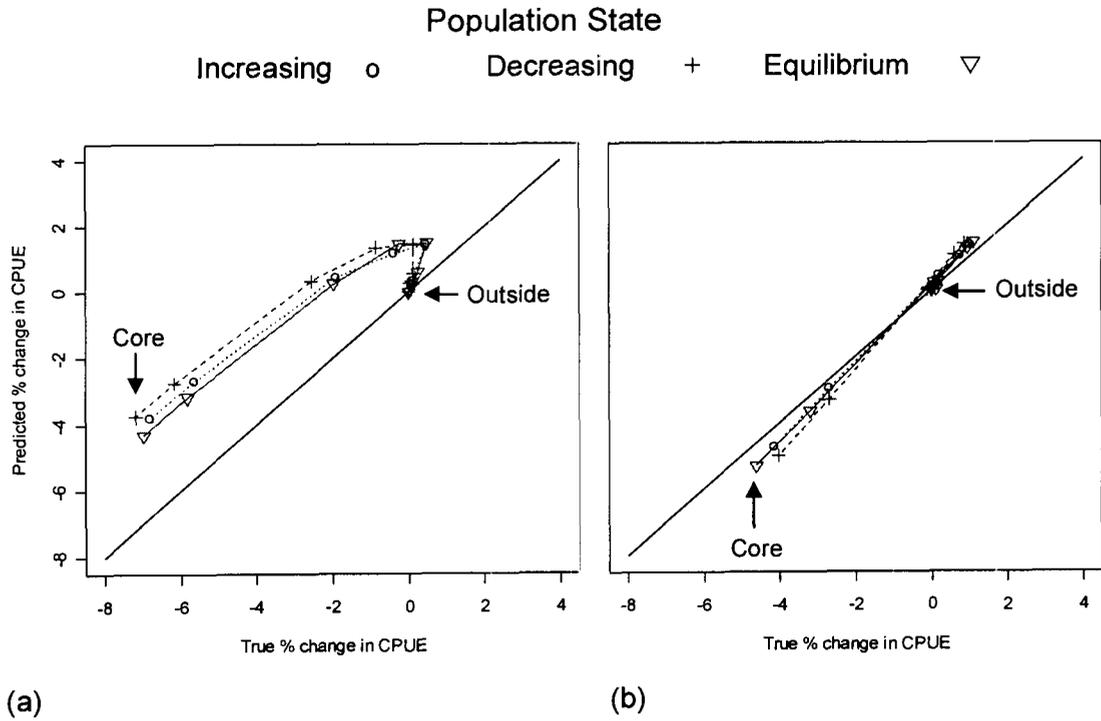
Table 4. Percentage of total sum of squares from analysis of variance (ANOVA), for productivity and geometry of the fish population

Dependent variable: Δ "true" CPUE

| **Productivity:**	Low	Low	High
Geometry:	Plateau	Ridge	Plateau
		% TOTAL SS:	
Single factor regression:			
Predicted ΔCPUE	84.31	89.85	29.18
MPA catch	70.03	75.87	0.715
Stepwise regression:			
Predicted ΔCPUE	84.31	89.85	29.18
+ Fish mobility	0.909	0.252	0.052
+ Level of depletion	0.457	0.809	3.333
Residuals	14.32	9.088	67.42

Figure 26. The percentage of the total sum of squares from ANOVA tables, explained by the factors "MPA.catch", proportion of total catch in potential MPA, or "Pred.CPUE", predicted ΔCPUE, for model scenarios A to G. Factors are fitted singly to simple regression of true ΔCPUE. Scenarios A & B contrast two possible spatial configurations of the fish population. Scenarios C – G represent different parameter combinations for the plateau configuration.
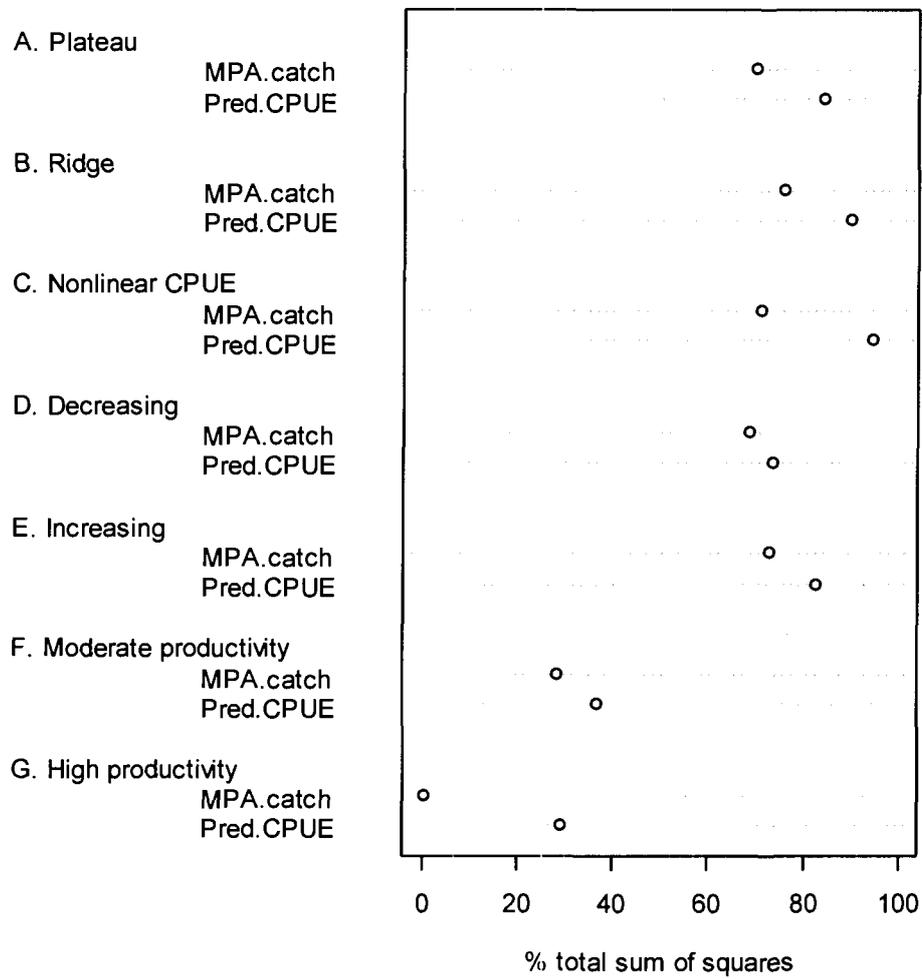
Figure 27. The percent of the total sum of squares (TSS) from analysis of variance tables explained by each group of factors (X1-X3) for model scenarios A to G. Factors in each group were fitted stepwise to a regression of predicted ΔCPUE against true ΔCPUE. Scenarios A through E were for a low productivity fish population. X1: predicted ΔCPUE. X2: predicted ΔCPUE + proportion of total catch within MPA. X3: predicted ΔCPUE + proportion of total catch within MPA + fish movement rate + level of depletion. **Scenarios D and E did not have level of depletion as a factor.
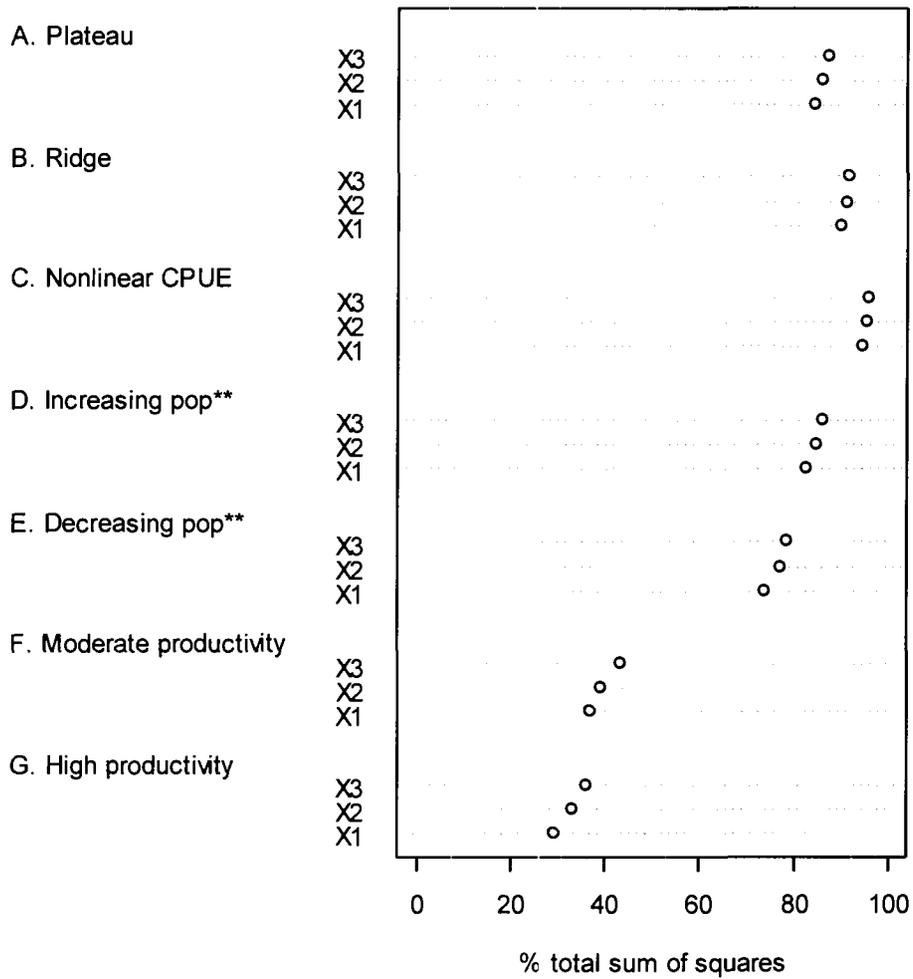
Figure 28. True ΔCPUE with Core MPA placement after 10-year and 100-year simulation periods (low productivity, plateau fish population), for three levels of depletion: (a) nonmobile fish (b) mobile fish.

(a)

(b)
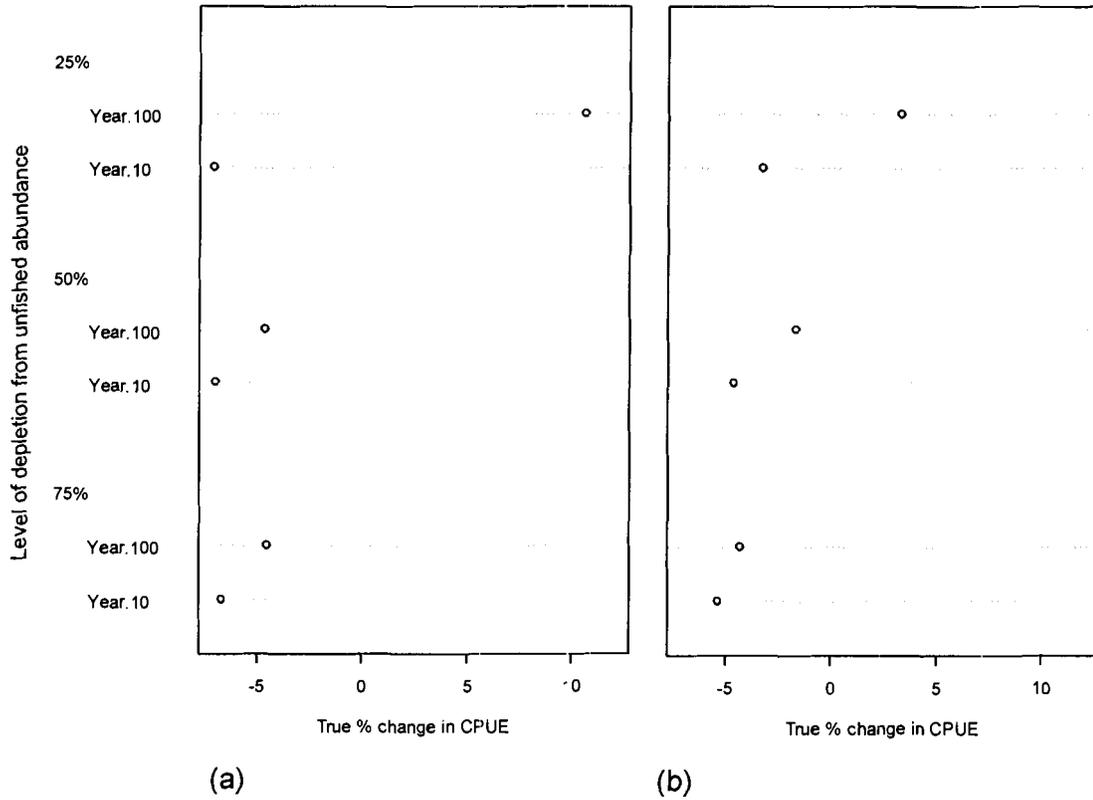
Figure 29. True ΔCPUE with Marginal MPA placement after 10-year and 100-year simulation periods (low productivity, plateau fish population), for three levels of depletion: (a) Nonmobile fish (b) mobile fish.

(a)   (b)