Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size

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The use of closed areas (marine protected areas, marine reserves, no-take zones) has been suggested as a possible solution to the perceived global fisheries crisis. However, to optimize the design and evaluate the effectiveness of closed areas, we need to understand the interaction between larval dispersal, adult mobility, and fishing mortality. In this paper, a simple, spatially explicit dynamic population model was developed to examine the effects of these interacting factors on optimal closure size and resulting yields. The effect of using one large or several smaller closed areas was also examined. Our model confirmed previous results: closed areas do not improve the yield of populations that are optimally managed or underexploited and, as mobility increases, optimum closure size increases. The model also predicted some interesting counter-intuitive results; for overexploited stocks, the greatest benefit from closed areas can be obtained for stocks with highest mobility, although this may require closure of 85% of the total area. For the tested parameter settings, adult spillover had greater potential to improve yield than larval export, and using several small closed areas rather than a single larger one had the same effect as increasing the mobility of the population.

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Introduction

The use of permanent closed areas [marine protected areas (MPAs), no-take zones, marine reserves] as part of ecosystem-based management has been advocated by many authors (Guénette and Pitcher, 1999; Roberts et al., 2001; Gell and Roberts, 2003; Neubert, 2003; Rodwell and Roberts, 2004; Grafton et al., 2005). However, scepticism remains about how universally effective closed areas would be in all fishery situations, especially for highly mobile stocks. Most of the currently available evidence of the success of closures comes from low-dispersing stocks, such as territorial reef fish (Galal, et al., 2002), or low-mobility invertebrates (Murawski et al., 2000). When closed areas have been implemented for mobile stocks, there has been little obvious success for varying reasons (Murawski et al., 2000; Pastoors et al., 2000; Kelly et al., 2006).

Compared with sedentary stocks, the implications of juvenile and adult mobility (hereinafter simply referred to as adult mobility) on optimal closure size and resulting yields has received comparatively limited attention (Pelletier and Mahévas, 2005). Previous models examining the interaction of mobility and closure effectiveness have looked at a limited range of closure sizes and mobilities (Hilborn et al., 2006), focused on specific stocks (Guénette et al., 2000; Apostolaki, et al., 2002), or are based on low spatial resolution two-patch models (Polacheck, 1990; DeMartini, 1993; Hannesson, 1998; Guénette and Pitcher, 1999), which are unable to represent the concentration of biomass and effort around closure boundaries, a factor that affects predictions of closed-area-fishery systems

(Kellner et al., 2007). The results of these studies indicate that closures are often not considered part of optimal management for mobile populations with mixed age classes. However, they do suggest that closed areas can increase yield if the stock was previously overexploited, although extremely large areas, up to 80% of the total area, may have to be closed. Despite the developments made in the theory of applying closed areas to mobile stocks, there is still a need to develop a more general understanding of the relationship between adult mobility, larval dispersal, and optimal closure size, especially given commitments, such as the 2002 Johannesburg World Summit on Sustainable Development, to the rapid development of MPA networks globally.

In this paper, a deliberately simple, spatially explicit model was developed to provide a general, qualitative analysis of the interaction between adult mobility, larval dispersal, and fishing mortality on optimal closure size, and the response of biomass and yield to the introduction of a closure. The effects of using one large or several small closures, and the implications of the choice of temporal scale at which movement is modelled, were also examined. This work is done to highlight the importance of accurately modelling movement in MPA studies and to provide a simplified, qualitative study of the interaction of mobility, larval dispersal, fishing mortality, and closure size.

Methods

The model was made up of three submodels: a population submodel, a dispersal submodel, and a fishing submodel. The

spatial domain was a one-dimensional linear array of 100 cells with separate age-structured population models running in each cell. The cells were linked by larval dispersal and adult mobility. This model space represents the full range of distribution of the population under consideration, and therefore, dimensions should be considered relative to the range. For each simulation, the model was run for 250 years to reach steady-state.

Population model

To base the model on realistic life-history parameters, it was parameterized for North Sea cod, *Gadus morhua* (Table 1). However, as a consequence of the generalized dispersal model used, our results should not be considered in a quantitative sense or as specific to this species or population. The population model was based on the standard exponential decay model

$$N_{a+1,t+1} = N_{a,t} \cdot \exp(-(F_a + M_a)), \qquad (1)$$

where $N_{a,t}$ is the number of individuals of age a at time t, M_a the age-specific natural mortality rate, and F_a the age-specific fishing mortality (see the section "Fishing model").

The weight-at-age schedule was based on the weight-at-age reported by ICES (2005a), averaged over the period 1964–2001. The maturity and total natural mortality-at-age are from ICES (2005b). The M-at-age data were averaged over the period 1964–2001. The population was made up of 11 age classes, where for model simplicity, all individuals in the eldest age class were assumed to die at the end of each year.

To incorporate the effects of increasing relative fecundity with age, an egg-production–recruitment (E–R) function was used rather than a spawning-stock biomass (SSB)–recruitment function. To calculate population egg production (E_{pop}), the weight–fecundity relationship of Oosthuizen and Daan (1974) was used:

$$\mathrm{Fe}_a = 196 \cdot w_a^{1.09}, \qquad (2)$$

where w_a is the weight in grammes at age a, and Fe_a individual egg production at age a. Population egg production was then calculated as

$$E_{\mathrm{pop}} = \sum_{a=1}^{11} \mathrm{Fe}_a \cdot N_a \cdot \omega_a, \qquad (3)$$

where N_a is numbers at age a, and ω_a the maturity at age a.

A Beverton–Holt-style E–R function was calculated using the formulation

$$R_1 = \frac{E_{\mathrm{pop}} \cdot S_{\max E}}{(1 + k \cdot E_{\mathrm{pop}})}, \qquad (4)$$

where R_1 is the number of recruits at age 1. The parameters for the E–R relationship were calculated from the SSB–recruitment

function from the ICES Study Group on Multispecies Assessment in the North Sea (SGMSNS) 2003 model run (ICES, 2005b). The maximum survival per unit biomass ($S_{\max \mathrm{SSB}}$), based on the SSB–recruitment relationship, was converted to maximum survival per unit egg production ($S_{\max E}$) for the E–R relationship according to

$$S_{\max E} = S_{\max \mathrm{SSB}} \left(\frac{\mathrm{SSB}_0}{E_0} \right), \qquad (5)$$

where SSB_0 and E_0 are the initial population SSB and egg production, calculated by running the model in the absence of fishing mortality, using the maximum recruitment ($R_{\max}$) value from the ICES SGMNS 2003 model run (ICES, 2005b). The k value is then calculated according to the relationship (Quinn and Deriso, 1999):

$$k = \frac{S_{\max E}}{R_{\max}}, \qquad (6)$$

to give $S_{\max E} = 8.05 \times 10^{-6}$ and $k = 1.026 \times 10^{-14}$ for the population egg production to recruitment-to-age-1 relationship.

Two different assumptions about larval dispersal, "mixed larval pool" and "local recruitment", were compared. For the mixed larval pool scenarios, the number of recruits at age 1 was calculated according to the total population egg production across all cells and the recruits were distributed evenly across all cells. For the local recruitment scenarios, individual E–R relationships were set up for each cell, so recruitment to the cell depends on egg production in the cell. The k value per cell was 100th of the scaling factor of the full model space.

The starting population for each simulation was a previously unexploited population, distributed evenly across the whole model space, generated by applying M to a population recruiting at $R_{\max}$.

Fishing model

For each simulation, it was assumed that the total effort remained constant and redistributed as areas were closed to fishing. A simple "gravity model" for fishing effort was used where the effort applied to a cell was proportional to the ratio of available biomass in that cell to the total available biomass (Hilborn and Walters, 1987); this allowed the model to capture effects such as "fishing the line" around closed areas.

Net selectivity was based on selectivity of *grande overture verticale* trawls (not Scotland) calculated by Andrews *et al.* (2006); the length–weight relationship of Daan (1974) was used to convert between the weight-at-age calculated from ICES data and the net selection by length reported by Andrews *et al.* (2006; Table 1).

For each simulation, a starting instantaneous fishing mortality rate (F_{base}) was defined; this is the F applied to fully selected age groups when the whole area was open to fishing. It was

Table 1. The life-history parameters used for the population model (see text for sources).

Age	1	2	3	4	5	6	7	8	9	10	11
Weight (kg)	0.62	0.97	2.13	4.01	6.26	8.34	10.00	11.13	12.51	13.61	14.66
Maturity	0.01	0.05	0.23	0.62	0.86	1	1	1	1	1	1
Natural mortality	0.989	0.555	0.381	0.238	0.231	0.262	0.20	0.20	0.20	0.20	0.20
Selectivity	0.48	0.277	0.366	0.495	0.989	0.995	0.995	1	1	1	1

assumed that 100 units of effort were applied, and the catchability was calculated according to the relationship $F = q \cdot e$ (Beverton and Holt, 1957). As areas that were closed to fishing q were held constant, and e per cell varied according to the gravity model, the resulting fishing mortality per age class per cell was

$$F_{c,a} = S_a \cdot q \cdot e_c, \qquad (7)$$

where $F_{c,a}$ is the instantaneous fishing mortality applied to age a in cell c, and e_c the effort applied to cell c.

Dispersal model

The model space was a 100-cell, one-dimensional linear array. To avoid edge effects, the model space was looped so the ends connected; any individual moving off one end of the model space moved to the appropriate location at the other end of the model space. Adult organisms were assumed to undergo uncorrelated random dispersal with no regard to local density or mortality, based on the standard, one-dimensional diffusion equation (e.g. Okubo and Levin, 2001). For each model time-step, the individuals in a given cell were distributed according to the probability distribution

$$p(x, t) = \frac{1}{\sqrt{4\pi Dt}} e^{-x^2/4Dt}, \qquad (8)$$

where $p(x, t)$ is the probability that an individual from a given cell i will end up in a given cell at time t, and x the location of cells relative to each "source" cell for $-100 < x < 100$. Parameter x was measured as the distance between cell centres. As x was measured as discrete cells, rather than a continuous measurement, the sum of $p(x, t)$ was rescaled to 1 at each time-step. D is the diffusion parameter, and t is the time or number of "position jump" steps that have occurred between observations. For annual time-steps as used in the main simulation model, $t = 365$; to model monthly dispersal, $t = 30$ was used and compared with the results of the main model. The diffusion parameter, D, controls the rate of dispersal. For the purposes of this work, it is only necessary to note that a large D value represents stocks with high mobility and vice versa. The effect of the diffusion parameter (D) values used is illustrated in Figure 1. The D values were chosen to cover a range of mobility from almost sedentary ($D = 0.001$) to rapidly dispersing ($D = 1$).

For the geographic scale of the model, the model space should be seen as covering the full range of a stock or population and the area closed as a fraction of the total distribution of the population. The diffusion parameter, therefore, controls the rate of dispersal relative to the population range. This allows for the analysis of varying the relative rate of dispersal.

Model simulation runs

The model was initially run across a range of F_{base} values, without a closed area to examine the relationship between yield and F for the fully exploited population.

For the single closed-area simulations, two sets of simulations were run: one set under the assumption of a mixed larval pool and the second under the assumption of local recruitment. For each set, the model was run for all D values displayed in Figure 1, and with F_{base} values of 0.2, 0.4, 0.6, 0.8, and 1.0 year^{-1}. For each combination of F_{base} and D values, the model was run for the full range of area closures from 0 to 100% closure. The closed area was increased in 5% steps.
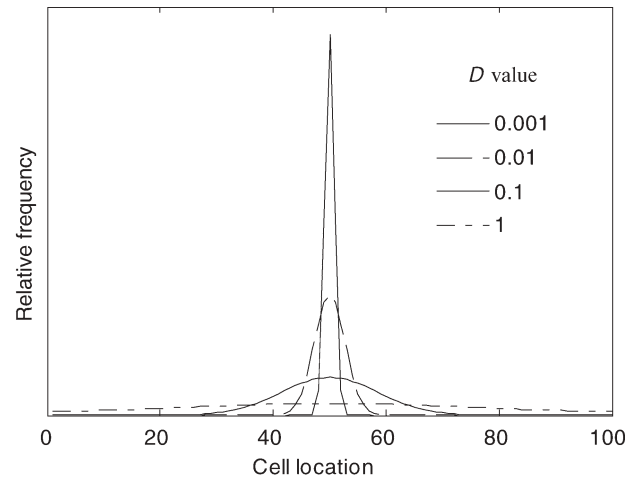
Figure 1. Dispersal pattern of a unit item starting at location 50 after 1 year for the different levels of mobility assessed in this study.

To examine the effects of using one large or several smaller, fragmented closures, a similar set of simulations was run. For these simulations, three closure schemes were compared: a single closure, two equally sized closures, and eight equally sized closures. In each case, the closures were distributed evenly across the model space. These simulations were also conducted with the fully mixed larval dispersal and local recruitment models. To constrain the number of model runs, the simulations were only conducted for D values of 0.001 and 0.1, and for F_{base} values of 0.2, 0.6, and 1.0 year^{-1}. To avoid closing fractions of a cell, the model was run for all closure sizes between 0 and 100% closure, with the closure size increasing in 8% steps for the fragmented MPA simulations.

The main model was run in annual time-steps following the cycle

$$\text{mortality} \rightarrow \text{dispersal} \rightarrow \text{growth} \rightarrow \text{recruitment},$$

where dispersal only occurs once annually after mortality has been applied for the year. This represents movement as a single, annual event with organisms being moved directly to their "end of year" location after the equivalent of a year of smaller movements. This assumption is commonly used in MPA modelling studies (e.g. Guénette and Pitcher, 1999; Hilborn *et al.*, 2006; Pitchford *et al.*, 2007) and allows for quick simulation of the model (but see the section "Model considerations"). However, the assumption simplifies actual movement; in reality, some individuals that are predicted to start and end the year, inside the closure may have moved into the fished area for part of the year, and vice versa. To examine the implications of the temporal scale at which movement is represented to MPA modelling studies, we also ran the model in monthly time-steps and compared the results with the annual model. For the monthly movement model, mortality and dispersal occurred monthly; growth and recruitment still occurred annually.

Results and discussion

Fishing at F_{max}

Without a closure, the maximum sustainable yield of $Y_{max} = 2.84 \times 10^8$ kg year^{-1} was achieved with $F_{max} = 0.25$ year^{-1}.

This was the highest yield obtained from the modelled fishery from all the scenarios tested. This agrees with previous modelling studies that found yields are maximized with effort regulation rather than the introduction of closures (Polacheck, 1990; Hannesson, 1998; Sladek Nowlis and Roberts, 1999; Hilborn *et al.*, 2006). Therefore, under the simplifying assumptions applied in many modelling studies, the best strategy for single-species management is for a fishery to operate at F_{max} (but see below).
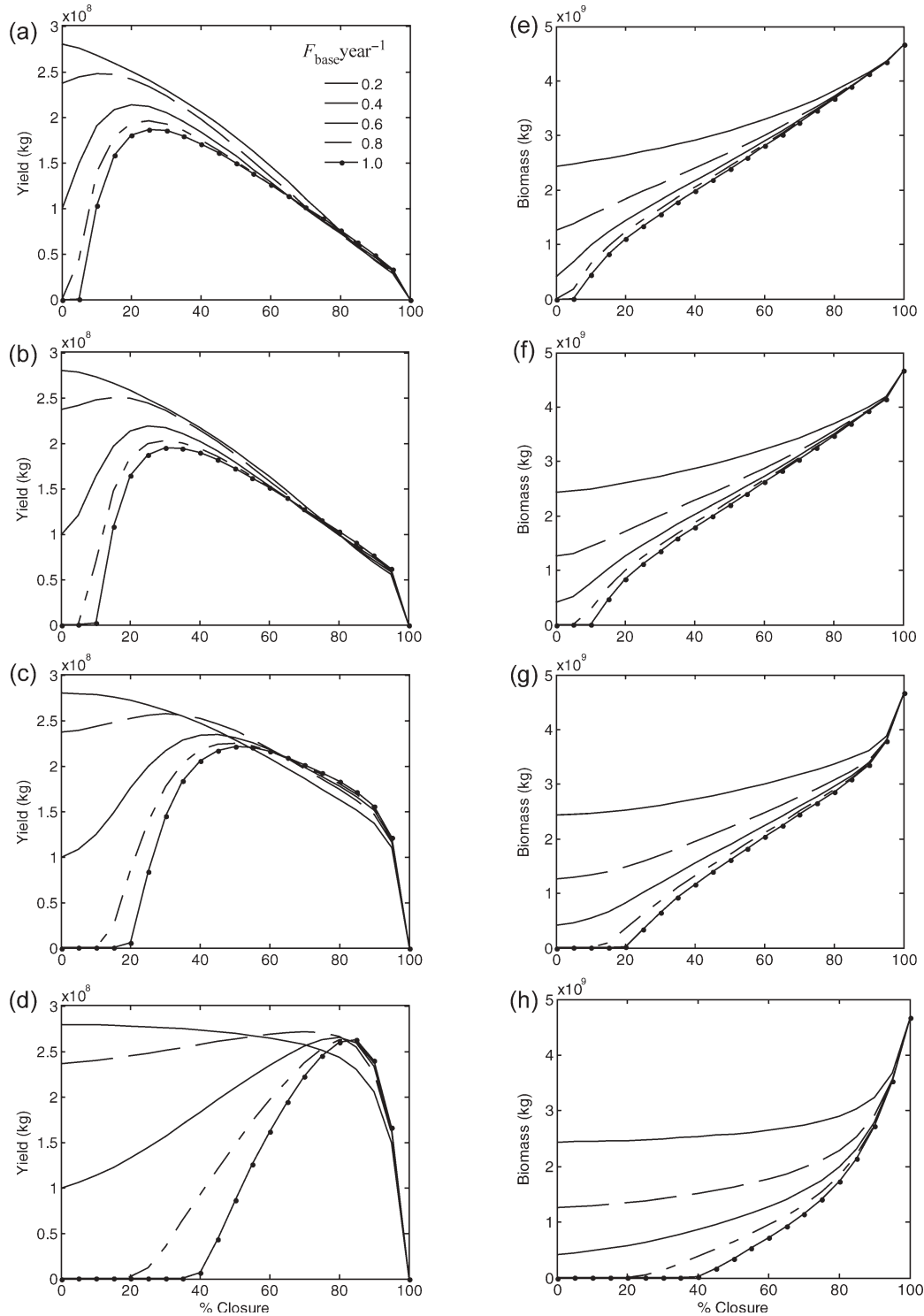
Figure 2. Long-term annual yield and biomass of the population under the assumption of a mixed larval pool at different levels of dispersal: (a–d) yield for fixed levels of F_{base} and varying sizes of closure; (e–h) biomass for fixed levels of F_{base} and varying size of closure. Top row (a and e), $D = 0.001$; second row (b and f), $D = 0.01$; third row (c and g), $D = 0.1$; bottom row (d and h), $D = 1$. Closure size increased in 5% steps.
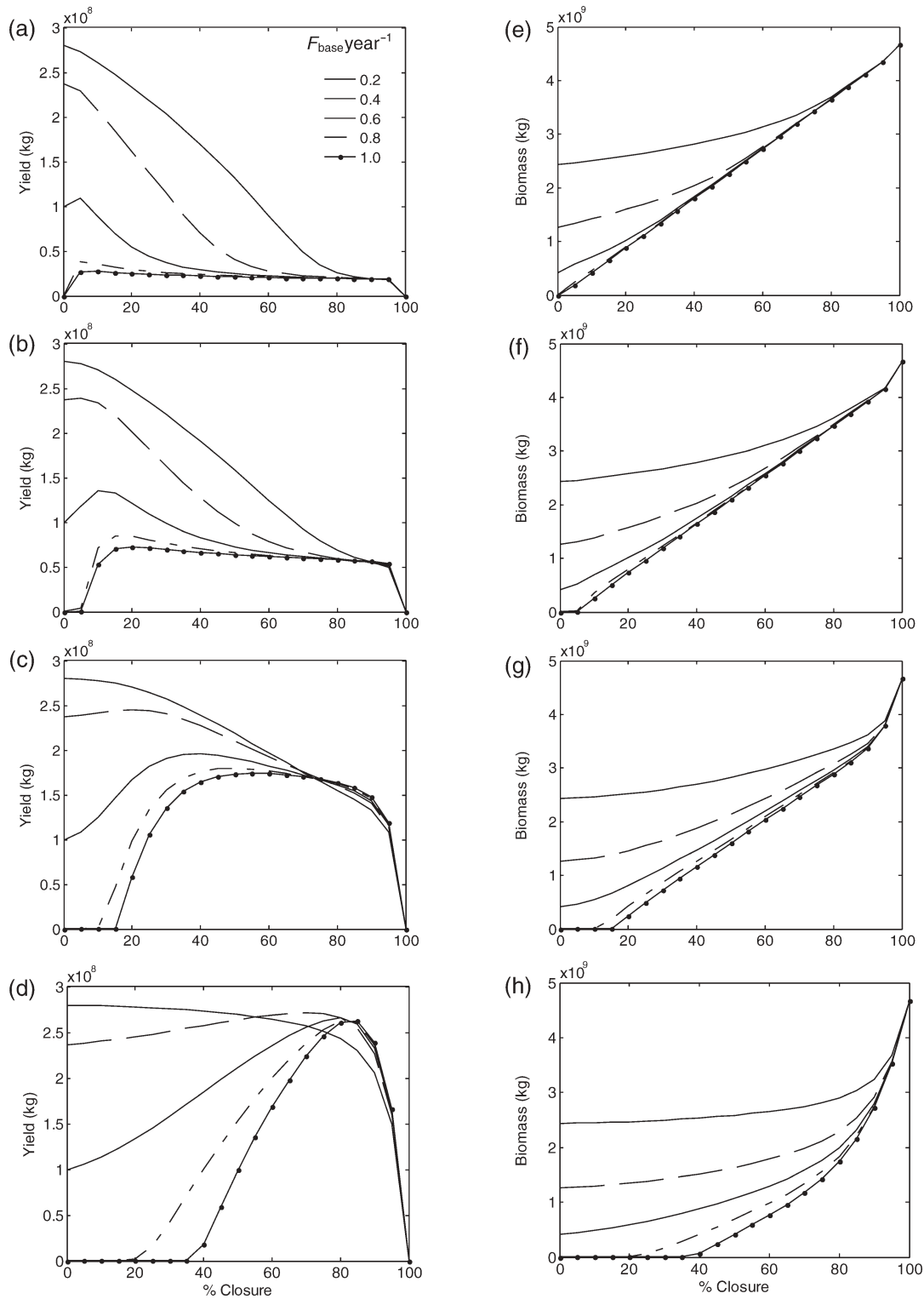
Figure 3. Long-term annual yield and biomass of the population under the assumption of a local recruitment at different levels of dispersal: (a–d) yield for fixed levels of F_{base} and varying sizes of closure; (e–h) biomass for fixed levels of F_{base} and varying size of closure. Top row (a and e), $D = 0.001$; second row (b and f), $D = 0.01$; third row (c and g), $D = 0.1$; bottom row (d and h), $D = 1$. Closure size increased in 5% steps.

Single closures

When the model was run with $F_{base} < F_{max}$ ($F_{base} = 0.2$ year^{-1}), the maximum sustainable yield was achieved when the full area

was open, regardless of mobility and the nature of larval dispersal (Figures 2 and 3): introducing a closed area when $F_{base} < F_{max}$ always reduced yield. These results are consistent with results

from previous MPA modelling studies (Guénette and Pitcher, 1999; Hilborn *et al.*, 2006). The rate at which yield declines with increasing closure size lessened as mobility increased.

For all scenarios where $F_{base} > F_{max}$, the yield could be increased with the introduction of a fishery closure (Figures 2 and 3). The only exception was for the low-mobility scenario with local recruitment when the population was only moderately overexploited ($F_{base} = 0.4$ year^{-1}) before introduction of an MPA. Similarly, under all conditions, introducing a closure led to an increase in biomass, although for the medium-high ($D = 0.1$) and high ($D = 1$) mobility scenarios with a high F_{base}, a minimum of 15–25% closure was required to allow significant stock rebuilding.

No single optimum closure size led to maximum yield across all scenarios (Figures 2 and 3). The optimal closure size required to maximize yield varied between 0 and 85% coverage, depending on the level of exploitation (F_{base}) and mobility. For the low ($D = 0.001$) and medium-low ($D = 0.01$) mobility scenarios, the optimum size of a closure for an overfished stock ranged from 5 to 30%. This agrees with the range of closure sizes suggested from modelling studies of low-mobility reef fish (DeMartini, 1993; Sladek Nowlis and Roberts, 1999) and sedentary invertebrates (Quinn *et al.*, 1993; Hastings and Botsford, 1999). For the medium-high ($D = 0.1$) and high ($D = 1$) dispersal scenarios, under high levels of fishing mortality, 40–85% of the area has to be closed to achieve maximum yield. This coincides with the estimated 80% closure required to maximize yield from models based on Baltic cod (Hannesson, 1998) and Newfoundland cod (Guénette *et al.*, 2000).

The nature of larval dispersal was most critical for low-mobility stocks. Under the assumption of a mixed larval pool, when $F = 1.0$ year^{-1}, the maximum yield achieved with an optimum closure was 66 and 69% of Y_{max} for the $D = 0.001$ and 0.01 scenarios, respectively. Maximum yields were only 10 and 26% of Y_{max} under the assumption of local recruitment. As the degree of adult mobility increased, the effect of larval dispersal declined.

The maximum yields obtained with an optimum closure and $F_{base} = 1.0$ year^{-1} were 78 and 93% of Y_{max} under the assumption of a mixed larval pool, and 61 and 93% under the assumption of local recruitment for the $D = 0.1$ and 1.0 scenarios, respectively. For the given model assumptions and settings, this indicated that, for species with limited adult mobility, the main fishery benefits from an area closure are from larval production rather than adult spillover. As adult mobility increased, it made up for the lack of larval dispersal under the assumption of local recruitment. However, greater yields could be derived from an optimal closure as a result of adult spillover at high mobility with local recruitment than for low-mobility stocks with larval dispersal.

Regardless of the assumption made about larval dispersal, if a stock was overexploited, the maximum yield achieved with an optimally sized closure increased as mobility increased. This theoretical result contrasts with other studies that suggest that closures will not be effective for highly mobile populations (Botsford *et al.*, 2003; Gell and Roberts, 2003; Hilborn *et al.*, 2004). Polacheck (1990) and DeMartini (1993) are often cited in support of the assertion that closures do not improve yield for highly mobile populations. However, both Polacheck (1990; Figure 6) and DeMartini (1993; Figure 2) demonstrate that, for a previously overfished stock managed with a closure, the optimal yield-per-recruit increases as mobility increases, while protecting a given level of spawning biomass per recruit. The underlying mechanism that leads to this result has not been elucidated and should be the focus of further study.

The introduction of a closed area led to spatial variation in biomass, effort, and yield (Figure 4). Always, the biomass was greatest in the centre of the closure, and effort and yield were concentrated along the closure boundary. This is consistent with evidence of concentrated effort and increased catch rates along the boundaries of large temperate (Murawski *et al.*, 2000) and small tropical (Russ *et al.*, 2003) closures. The spatial pattern of
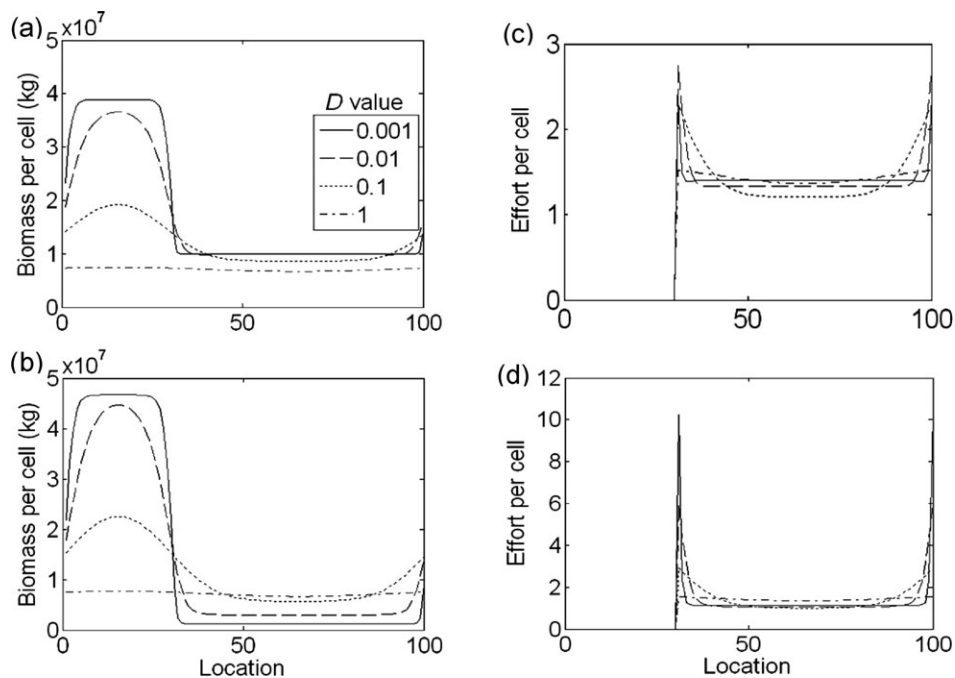
Figure 4. Biomass (a and b) and effort (c and d) per cell, when cells 1–30 are closed to fishing and $F_{base} = 0.6$ year^{-1}, under varying levels of D, under the assumption of mixed larval dispersal (a and c) and local recruitment (b and d).

biomass, effort, and yield were examined across a range of F_{base}, D, and closure values; because there was a consistent pattern to the results, only the plots for $F_{base} = 0.6$ year^{-1} and 30% closure are shown (Figure 4). The gradient in biomass across the closure boundary, and the gradient in effort extending from the closure boundary, was greater at lower levels of dispersal and higher levels of fishing mortality. The gradient in biomass and effort was also greater under the assumption of local recruitment than under the assumption of a mixed larval pool. In this model, the variation in biomass and effort gradients was the result of uncorrelated random movement. Therefore, this pattern did not indicate the action of density-dependent factors, which are

likely to modify further the gradients in biomass and effort across, and extending from, closure boundaries (Abesamis and Russ, 2005).

Multiple closures: the effect of fragmentation

Using several small closures rather than a single large closure increased the number of closure boundaries, which increased the flux of individuals across reserve boundaries for any given level of mobility. Therefore, as noted by Hilborn *et al.* (2006), increasing the number of closures used has the same effect as increasing mobility. Therefore, there are three main effects of using fragmented closures. First, if a population is underexploited ($F_{base} < F_{max}$),
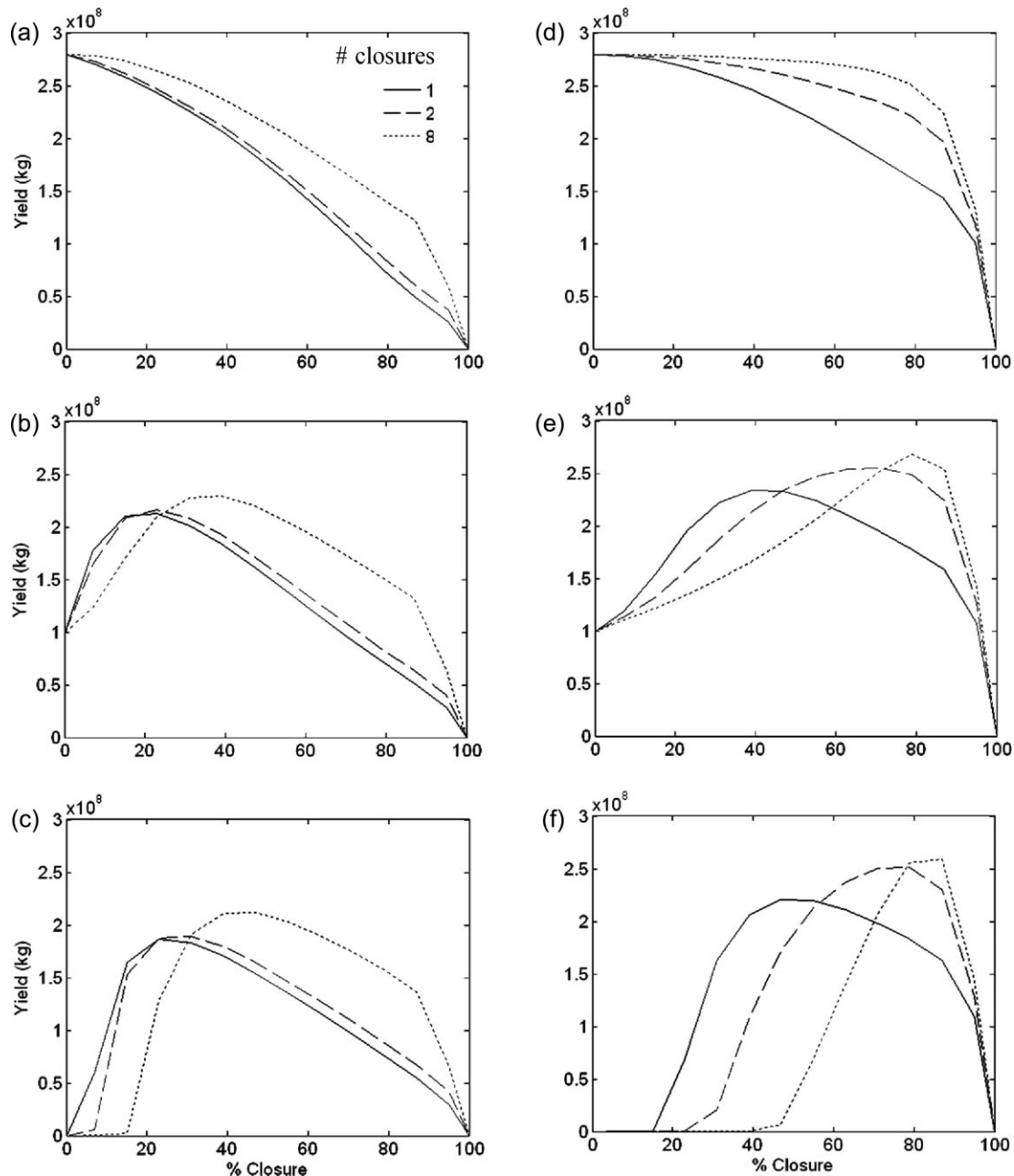
Figure 5. Comparison of annual yield under different D and F_{base} scenarios, when the area closed consists of one, two, or eight evenly spaced closures, under the assumption of mixed larval dispersal. Left column (a, b, and c), $D = 0.001$; right column (d, e, and f), $D = 0.1$. Top row (a and d), $F_{base} = 0.2$ year^{-1}; middle row (b and e), $F_{base}=0.6$ year^{-1}; bottom row (c and f), $F_{base} = 1.0$ year^{-1}. Closure size increased in 8% steps.

the rate at which yield declines with increasing total closure size is reduced as the number of closures used increases (Figures 5 and 6). Second, if the population is overexploited ($F_{base} > F_{max}$), a greater proportion of the total area has to be closed to achieve a given yield when fragmented closures are used. Third, the maximum sustainable yield obtainable with optimum closures increases as the number of closures increases (Figures 5 and 6).

The fishery benefits of fragmented MPAs were particularly pronounced for local recruitment and limited adult mobility. In this situation, the yield was not limited by population reproductive output, but rather by the net flux across closure boundaries; introducing a fragmented closure reduced this diffusive bottleneck.

Under the assumption of local recruitment with $D = 0.001$ and $F_{base} = 1.0$ year^{-1}, there was a 430% increase in the maximum yield that could be achieved with optimum closure coverage when eight small closures were used, compared with a single closure (Figure 6c).

Model considerations

The model used a simplistic, diffusion-based representation of movement, combined with the assumption of a homogenous environment. This approach was chosen as a simplified, first-case approximation of the movement of a mobile species that allows comparison of how MPA effects change with increasing levels
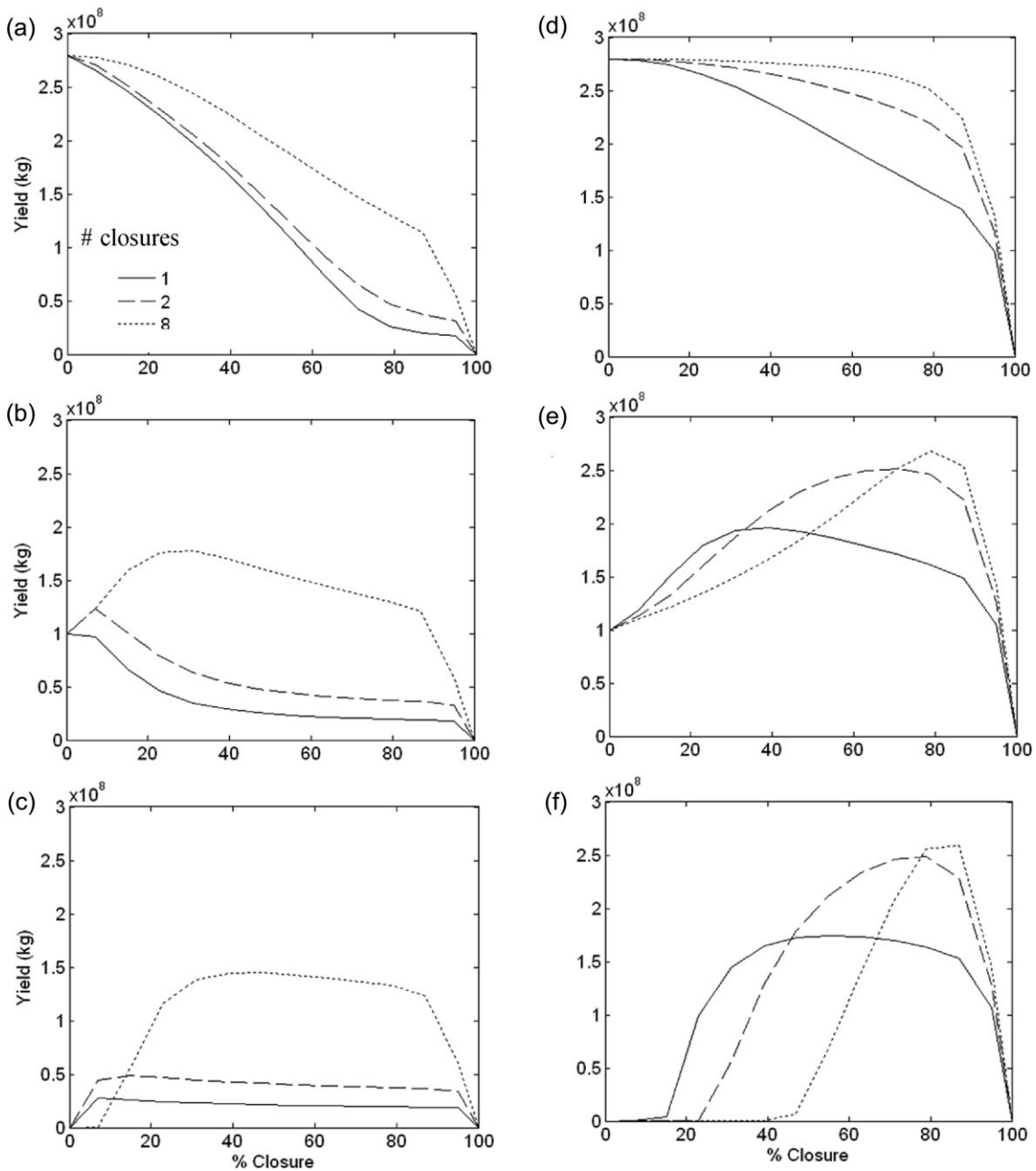
Figure 6. Comparison of annual yield under different D and F_{base} scenarios, when the area closed consists of one, two, or eight evenly spaced closures, under the assumption of local recruitment. Left column (a, b, and c), $D = 0.001$; right column (d, e, and f), $D = 0.1$. Top row (a and d), $F_{base} = 0.2$ year^{-1}; middle row (b and e), $F_{base} = 0.6$ year^{-1}; bottom row (c and f), $F_{base} = 1.0$ year^{-1}. Closure size increased in 8% steps.

of mobility. This approach demonstrated the important effect that assumptions about movement have on the outcome of MPA modelling studies and indicates the need for MPA research to focus on movement as one of the key determinants of the effects, and optimal design, of MPAs. Furthermore, this highlights the importance of accurate dispersal models for operational assessments of MPA effects.

The model was based on processes (e.g. dispersal, mortality, growth) occurring in a sequential manner, although in reality, these processes are synchronous. The implications of this assumption were partially tested by comparing models set up for movement and mortality to occur on an annual or monthly basis. In general, regardless of the assumption of larval dispersal, running the model with monthly simulation of dispersal and mortality decreased the yield achieved with an optimal closure, and increased the size of an optimal closure. Under the assumption of a mixed larval pool, the maximum sustainable yield that could be achieved from an optimally sized closure was never reduced by more than 6%, when dispersal was calculated monthly rather than annually. However, under the assumption of local recruitment, when dispersal was low ($D = 0.001$) and fishing mortality was high ($F_{base} = 1.0 \, year^{-1}$), calculating dispersal monthly led to a 99% reduction in the yield achieved, following the introduction of an optimal MPA compared with the annual simulations. This effect is less pronounced as dispersal increases. This demonstrates that the temporal resolution of a model can affect the quantitative results and that quantitatively targeted studies need to consider the appropriate temporal resolution for analysis.

To concentrate the analysis on the effects of varying the dispersal parameter, the model was run with a single, simple set of life-history parameters. Specifically, the shape of the egg–recruitment relationship determines the stock size at which population collapse occurs, so in this study, the minimum MPA coverage required to avoid stock collapse will be partly controlled by the choice of egg–recruitment relationship. Further work can be done on the effects of varying the life-history and egg–recruitment relationship parameters on the response of a population to the introduction of an MPA.

The model used is deterministic. In contrast, the real environment is highly variable, and variability and uncertainty can be introduced to the system through annual recruitment (Myers, 2001; Patterson *et al.*, 2001; Needle, 2002). To incorporate this stochasticity, simulations were also conducted with random noise added to recruitment. However, this had little quantitative effect on the results, and hence, the details and results are omitted. Our model assumes a fishery based on effort, so the fishing model automatically buffers the stock against recruitment failure. This is in contrast to a total allowable catch (TAC)-based system, where this buffering does not occur, and the introduction of a closure can provide insurance against uncertainty and reduce the probability of stock extinction (Pitchford *et al.*, 2007).

Management implications

The model suggests that, when effort cannot be controlled, the yield from overfished populations can be increased with the introduction of an optimally sized closure. Optimal closure size ranged from 5 to 97%, depending on the parameter values and size of time-step used. However, for low-mobility stocks with local recruitment, only limited fishery benefits could be gained from the introduction of a single, optimally sized MPA.

Where closures are used for conservation rather than fishery management, the enhancement of biomass, rather than yield, is more important. In all simulations, the introduction of a closure led to an increase in biomass. For the low-mobility scenarios, there was an almost linear relationship between the area closed and the biomass under moderate to high fishing mortality. However, for more mobile stocks ($D = 0.1$ or 1) exposed to high fishing mortality, up to 40% of the total area had to be closed before there was any noticeable stock rebuilding.

Although the model demonstrates that, under the assumptions used, effort regulation would provide the optimum yield, other studies incorporating additional assumptions about life history and the effect of fisheries have noted that, under certain circumstances, closures can become an essential part of optimal management (Apostolaki *et al.*, 2002; Le Quesne *et al.*, 2007). Furthermore, it is very difficult for a fishery to operate at F_{max} (Larkin, 1977; Mace, 2001). Therefore, closures might be considered part of an optimal management strategy, because they can act as a buffer against stochastic events and uncertainty in stock, TAC, or effort calculations (Mangel, 2000; Sladek Nowlis, 2000; Rodwell and Roberts, 2004; Pitchford *et al.*, 2007).

Our model only examined management on a single-species basis. However, it can be seen from this model that, in a multispecies fishery, it would be possible to introduce small closures to protect low-mobility species with high conservation value, without having a notable impact on overlying fisheries for more mobile species. Notwithstanding, it would not be possible to use closures to protect highly mobile species without having a significant impact on all other fisheries in the area.

Acknowledgements

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