Introduction

Attention has recently focused on the use of marine protected areas (MPAs) in protecting habitats and maintaining ecological functions. MPAs serve as a means of managing exploited populations by imposing bans on fishing in defined areas. They are also referred to as closed areas, no-take zones, or fisheries marine reserves, and have been implemented to help replenish target populations, enhance recruitment, or protect habitats used by critical life-history stages (Jones, 2002). Although MPAs have sometimes been used to supplement management based on catch quota or fishing effort limitation, they have advantages over management strategies that require knowledge of population parameters to determine suitable levels. For example, overestimation of a total allowable catch may exhaust certain populations (Karagiannakos, 1996). However, MPAs can maintain a constant number of individuals by sheltering sedentary populations (Hastings and Botsford, 1999) and can improve the status of mobile populations (Guenette and Pitcher, 1999). MPAs reduce variability in catches in the face of stochastic events such as recruitment failures (Sladek-Nowlis and Roberts, 1999; Rodwell and Roberts, 2004). In this sense, MPAs can be robust to uncertainty in populations and fisheries.

A feedback management procedure (FB) was proposed by Tanaka (1980), by which catch is controlled to achieve a target population size. This process does not require population dynamics models or their parameters and is robust to uncertainties in estimates of population size and fishery impacts. As an extension, Harada et al. (1992) proposed a FB based on controlling fishing effort (Effort-FB) instead of catch.

Kai and Shirakihara (2005) proposed a FB based on controlling the size of an MPA (MPA-FB), increasing the size of the no-take area when the population is below a predetermined target level, and reducing it when it is above that level. They predicted that the FB can sustain the population at the target level without directly controlling the catch quota or fishing effort if the target level is set to equal or exceed the maximum sustainable yield (MSY) and if a drastic change in MPA size is avoided.

One difficulty in adopting the FB proposed by Kai and Shirakihara (2005) is that the absolute population size, which is used in controlling MPA size, is not always known. If the catch per unit effort (cpue), which is available for many populations, can be used as an index of the population size, the FB will be effective. However, the direct relationship between the cpue and the population size cannot always be determined. The worst case for management is that the cpue remains high while the population declines. Clark (1982) suggested a non-linear relationship between them. This is also known as "hyperstability" (Hilborn and Walters, 1992), and evidence of this has been reported in several papers (e.g. Harley et al., 2001). Hyperstability may reduce the effectiveness of the FB using cpue, because it may...
allow high-fishing pressure even when the population is depleted. However, the management effect is unlikely to be the same between the MPA-FB and the Effort-FB in that the former can save individuals in MPAs.

We investigated the effectiveness of the MPA-FB using the cpue and compared it with the corresponding Effort-FB from three perspectives: (i) whether the management procedures using the cpue (hereafter, MPA-FB and Effort-FB refer to the procedures using the cpue) successfully approach a predetermined population target level; (ii) whether the procedures can prevent collapse of depleted populations with stochastic fluctuations; and (iii) what advantages and disadvantages each FB possesses.

Basic models
To examine the effectiveness of the MPA-FB, we use a discrete dynamic model for an exploited population:

\[ N_{t+1} - N_t = G(N_t) - C_t, \]  

(1)

where \( N \) is the absolute population size, \( G \) a function of the population increase, \( C \) the catch, and \( t \) the year. The model used to describe each FB is

\[ S_{t+1} - S_t = -h\left(\frac{U_t}{U_{\text{target}}} - 1\right) \quad \text{for MPA-FB}, \]  

(2)

\[ X_{t+1} - X_t = h\left(\frac{U_t}{U_{\text{target}}} - 1\right) \quad \text{for Effort-FB}, \]  

(3)

where \( S \) is the MPA size, \( X \) the fishing effort, \( h \) a positive constant, \( U \) the cpue, and \( U_{\text{target}} \) a target level cpue. Equation (2) shows an increase in \( S \) when \( U \) is below \( U_{\text{target}} \), and a decrease in \( S \) when \( U \) is higher than \( U_{\text{target}} \). A system for the MPA-FB is given by combining Equations (1) and (2), where \( C \) is a function of \( N \) and \( S \). In this system, \( X \) is not controlled directly. To determine whether population recovery can be attained only by controlling \( S \), effort \( X \) is assumed to be constant. A system for the Effort-FB is given by combining Equations (1) and (3), where \( S \) is equal to \( 0 \) and \( C \) is a function of \( N \) and \( X \).

We assume that the following relationship between \( U \) and \( N \) (Clark, 1982) holds:

\[ U \propto N^a, \]  

(4)

where \( a \) is constant. This power function can describe various situations. When \( a = 1 \), \( U \) is proportional to \( N \). When \( 0 < a < 1 \), the function reproduces the hyperstability on which we focus. We assume that \( 0 < a \leq 0.99 \) describes not only the hyperstability but also approximately the proportionality. Stability and dynamics of the systems are examined under the constraint of Equation (4).

Equation (4) shows that \( U \) is uniquely determined from \( N \), and may not be applicable to the MPA-FB because the observed value of \( U \) depends on areas in which MPAs are placed: \( U \) is high when all MPAs are placed in areas of low density, and low when in areas of high density. Therefore, the MPA-FB that controls \( S \) with \( U \) requires special attention to \( U \). This is a disadvantage of the MPA-FB relative to the Effort-FB. To cope with this difficulty, we assume that MPAs are temporarily removed for a short time before the fishing season of each year. Fishers can then utilize the whole fishing ground freely. They earn their money from fishing but should report the fishing area, the catch, and the effort. Using the catch and effort from this experimental fishing, \( U \) for the whole ground can be calculated, and areas of high densities where MPAs can be placed are evaluated. We further assume that the experimental catch is small enough so that Equation (1) holds.

Stability of the systems
To determine whether the two systems can direct \( N \) to \( N_{\text{target}} \) (a target level of \( N \)) obtained from \( U_{\text{target}} \) and Equation (4), we examined the local stability, that is, the dynamic properties in the neighbourhood of the equilibrium point: \((N^*, S^*)\) for the MPA-FB system, and \((N^*, X^*)\) for the Effort-FB system. The point is stable, if state variables \((N \text{ and } S \text{ for the MPA-FB system, } N \text{ and } X \text{ for the Effort-FB system})\) return to the point when a small perturbation causes the variables to depart from this point. If the following conditions are fulfilled, the point is locally stable (Bulmer, 1994):

\[ A = \alpha_{11} \alpha_{22} - \alpha_{12} \alpha_{21} < 1 \quad \text{and} \]

\[ B = |\alpha_{11} + \alpha_{22}| - (\alpha_{11} \alpha_{22} - \alpha_{12} \alpha_{21}) < 1. \]

Here, the system we consider is generally described as \( y_{t+1} = f_t(y_t, y_{t-1}) \) and \( y_{t+1} = f_t(y_t, y_{t-2}) \), and \( \alpha \) is the partial derivative at the equilibrium point \( \alpha_i = [\partial f_i/\partial y_i]^* \). Thus, \( y_1 = N \) and \( y_2 = S \) for the MPA-FB system, and \( y_1 = N \) and \( y_2 = X \) for the Effort-FB system.

We assume that the population growth function \( G(N) \) shows \( \partial G/\partial N = 0 \) only at \( N_{\text{MSY}} \) (the population size yielding MSY), which is satisfied by the logistic model or more generalized Pella–Tomlinson-type production model (Pella and Tomlinson, 1969): \( G(N) = rN - rN^p/K \), where \( r \) is the intrinsic growth rate, \( K \) the carrying capacity, and \( \psi \) the shape parameter. We treat the stability only when the target population level is set at \( N_{\text{MSY}} \). We regard the catch \( C \) as having the following properties:

\[ \frac{\partial C}{\partial S} < 0 \quad \text{for MPA-FB}, \]  

(5)

\[ \frac{\partial C}{\partial X} > 0 \quad \text{for Effort-FB}, \]  

(6)

\[ 0 < \left[ \frac{\partial C}{\partial N} \right]^* < 1 \quad \text{for both FBs}. \]  

(7)

Equation (5) shows that an increase in \( S \) in a given year leads to a decrease in \( C \) within that year. Equation (6) shows that an increase in \( X \) in a given year leads to an increase in \( C \) within that year. Equation (7) is derived as follows:

\[ \left[ \frac{\partial C}{\partial N} \right]^* = \left[ \frac{\partial (EN)}{\partial N} \right]^* = \left[ \frac{\partial E}{\partial N} \right]^* N^* + E \equiv E, \]

where \( E (0 < E < 1) \) is the rate of exploitation in a given year. The partial derivative \( [\partial E/\partial N]^* \) is given under a constant level of \( S \) or \( X \), so that the increase in \( N \) does not change \( E \), i.e. \( [\partial E/\partial N]^* = 0. \)
The MPA-FB system can be summarized using Equations (1), (2), and (4):

\[ S_{t+1} - S_t = -h \left( \frac{N_t}{N_{\text{target}}} - 1 \right). \]  

(8)

At equilibrium \( (N_{t+1} = N_t \) and \( S_{t+1} = S_t \),

\[ G(N^*) = C^* \quad \text{and} \quad N^* = N_{\text{target}}, \]

where \( C^* \) is a function of \( N^* \) and \( S^* \). If this system has multiple equilibrium points, \( N \) may change irreversibly (Shirakihara and Tanaka, 1978). Here, we will prove that the number of points is 1 at maximum.

Because \( N^* \) is uniquely determined, \( C^* \) is a function of \( S^* \). \( G(N^*) = C^* \) can be rewritten as follows, considering that its left side is a constant when the function \( G \) is known:

\[ C^*(S^*) = \text{constant}. \]

From Equation (5), the value of \( C \) corresponds to the value of \( S \). Therefore, \( S^* \) is also uniquely determined. The corresponding Effort-FB system can be summarized using Equation (1) and

\[ X_{t+1} - X_t = h \left( \frac{N_t}{N_{\text{target}}} - 1 \right), \]

(9)

also has 1 or 0 equilibrium point. This is proved in a similar way, except that an increase in \( X \) in a given year leads to an increase in \( C \) in that year.

We now examine the local stability of the MPA-FB system [Equations (1) and (8)]. Partial derivatives at an equilibrium point are

\[ \alpha_{11} = - \left[ \frac{\partial C}{\partial N} \right]^*, \quad \alpha_{12} = - \left[ \frac{\partial C}{\partial S} \right]^*, \quad \alpha_{21} = \frac{ah}{N_{\text{target}}}, \quad \alpha_{22} = 1. \]

Then,

\[ A = - \left[ \frac{\partial C}{\partial N} \right]^* + 1 - \left[ \frac{\partial C}{\partial S} \right]^* \left( \frac{ah}{N_{\text{target}}} \right) \quad \text{and} \]

\[ B = 1 + \left[ \frac{\partial C}{\partial S} \right]^* \left( \frac{ah}{N_{\text{target}}} \right). \]

Because \( \left[ \frac{\partial C}{\partial S} \right]^* < 0 \) from Equation (5), \( B \leq 1 \) holds. To show that \( A < 1 \), we add a constraint; we set \( h \) at a sufficiently small value. In other words, we change \( S \) only slightly. As \( h \) becomes smaller, \( A \) becomes smaller. When \( h = 0 \), \( A \) is equal to \( -\left[ \frac{\partial C}{\partial N} \right]^* + 1 \), which from Equation (7) is less than unity. In summary, when \( N_{\text{target}} \) is set at \( N_{\text{MSY}} \) and \( S \) is changed slightly, the equilibrium point is stable.

The local stability of the Effort-FB system [Equations (1) and (9)] can be examined in a similar way. Partial derivatives under \( [dG/dN]^* = 0 \) are

\[ \alpha_{11} = - \left[ \frac{\partial C}{\partial N} \right]^* + 1, \quad \alpha_{12} = - \left[ \frac{\partial C}{\partial S} \right]^*, \quad \text{and} \]

\[ \alpha_{21} = \frac{ah}{N_{\text{target}}}, \quad \alpha_{22} = 1. \]

Then,

\[ A = - \left[ \frac{\partial C}{\partial N} \right]^* + 1 + \left[ \frac{\partial C}{\partial S} \right]^* \left( \frac{ah}{N_{\text{target}}} \right) \quad \text{and} \]

\[ B = 1 - \left[ \frac{\partial C}{\partial S} \right]^* \left( \frac{ah}{N_{\text{target}}} \right). \]

With the aid of \( \left[ \frac{\partial C}{\partial S} \right]^* > 0 \) from Equation (6), it is proved that the equilibrium point is stable.

Note that our local stability analysis never guarantees management success when \( N \) is far from \( N^* \). It is difficult to prove the global stability of the systems analytically, but our numerical analysis (see Appendix) suggests that the systems are globally stable.

### Specific models

We considered deterministic systems that are described by basic models. We proved that the systems are locally stable and suggest that they are globally stable. Therefore, the basic models do not account for population collapse. To examine the performance of the FBs, such as robustness against collapse, we considered stochastic population dynamics using the models specified below.

First, the growth function \( G(N) \) was specified as a stochastic version of the logistic model:

\[ G(N) = rN \left( 1 - \frac{N}{K} \right) e, \]

where \( e \) is the lognormal distribution with mean 1 and variance \( \sigma^2 \).

We assume that the population will become extinct without fail once \( N \leq N_{\text{threshold}} \) (the minimum level required for the population to exist). Second, the catch \( C \) was specified:

\[ C_t = \left( N_t^b - \frac{S_t K^b}{T} \right)^{1/b} - \left[ N_t^b - (S_t + X_t) K^b \right]^{1/b} \quad \text{for MPA-FB}, \]

and

\[ C_t = N_t - \left( N_t^b - \frac{X_t K^b}{T} \right)^{1/b} \quad \text{for Effort-FB}, \]

where \( b = 1 - a, T \) is the area that the population can inhabit, and \( X_0 \) is a constant fishing effort evaluated by the area swept by the fishery. Equation (10), which has a complicated form, was used because it can describe the hyperstability (Figure 1) and has some theoretical basis in terms of the relationship between catch and MPA size (see Kai and Shirakihara, 2005, for its derivation). Equation (11) was derived from Equation (10) by making \( S_t = 0 \) and replacing \( X_0 \) with \( X_t \). Third, the expected cpue, \( U_{\text{expected}} \), from experimental fishing in the MPA-FB was specified by assuming that the experimental catch is equal to that calculated from Equation (10) under \( S_t = 0 \) and \( X_t = X_0 \) i.e., \( U_{\text{expected}} = C_t / X_0 \) where \( C_t = N_t - (N_t^b - X_t K^b) / T )^{1/b} \). Note that Equation (10) was
Controlling the size of MPAs through cpue

Figure 1. The relationship between population size and cpue derived from the specified models: $U \propto N^{-1-b}$. When $b = 0.49$ and $b = 0.01$, the models can reproduce hyperstability and proportionality, respectively.

derived under the situation in which fishers always exploit the highest existing concentrations of fish (Kai and Shirakihara, 2005). This situation is plausible when they freely access all fishing grounds. The expected cpue for Effort-FB is provided by Equation (11) and $X_t$. Finally, we considered a stochastic situation of $U_t = U_{expected,t} + \Phi_t$, where $\Phi$ is the normal distribution with mean 0 and constant variance, to investigate the effect of uncertainty in cpue.

In summary, each system is described as follows.

MPA-FB: $S_{t+1} - S_t = -h \left( \frac{U_t}{U_{target}} - 1 \right)$. \hspace{1cm} (12)

where $U_t = [N_t - (N^b_t - X_0 K^b_t/T)^{1/b}] / X_0 + \Phi_t$,

$N_{t+1} - N_t = r N_t \left( 1 - \frac{N_t}{K} \right) \epsilon_t - \left( N^b_t - \frac{S_t K^b_t}{T} \right)^{1/b}$

Effort-FB: $X_{t+1} - X_t = h \left( \frac{U_t}{U_{target}} - 1 \right)$. \hspace{1cm} (14)

where $U_t = [N_t - (N^b_t - X_t K^b_t/T)^{1/b}] / X_t + \Phi_t$,

$N_{t+1} - N_t = r N_t \left( 1 - \frac{N_t}{K} \right) \epsilon_t - N_t + \left( N^b_t - \frac{X_t K^b_t}{T} \right)^{1/b}$. \hspace{1cm} (15)

Simulations using the specific models

Because the models above are specific examples of the basic models, the stability properties derived from the basic models are applicable to the specific models, although stochastic variations in population size are introduced. Therefore, we can expect the population to fluctuate randomly around the target level when enough years have passed since implementation of each FB. Here, we focused on the dynamics of the systems in the short term (5 or 10 years), specifically to assess whether successful recovery of the population and a sufficient level of catch can be achieved by implementing each FB. The performance of each FB was examined using numerical simulations. To reduce the number of parameters, variables were transformed: $n_t = N_t/K$, $s_t = S_t/T$, $x_t = X_t/T$, $c_t = C_t/K$, $u_t = c_t/x_t + \varphi_t$, where $\varphi_t$ is the normal distribution with mean 0 and variance $\xi^2$. These allowed the following equations to be derived:

MPA-FB: $s_{t+1} - s_t = -\left( \frac{u_t}{u_{target}} - 1 \right)$.

$N_{t+1} - N_t = r n_t (1 - n_t) \epsilon_t - \left[ (n^b_t - s_t)^{1/b} - (r^b_t - (s_t + x_0)^{1/b}) \right]$.

Effort-FB: $x_{t+1} - x_t = h \left( \frac{u_t}{u_{target}} - 1 \right)$.

$N_{t+1} - N_t = r n_t (1 - n_t) \epsilon_t - \left[ n_t - (n^b_t - x_t)^{1/b} \right]$.

We assumed that the population keeps an equilibrium state without random fluctuations when $t = 0$, i.e., $n_0$ is a constant. To compare the performance of each FB, we gave a constraint that $n_0$ is the same in the two FBs. By putting $n_{t+1} - n_t = 0$ and $\epsilon_t = 1$ in the last equation, the following relationship was obtained:

$r = \frac{n_0 - (n^b_0 - x_0)^{1/b}}{n_0(1 - n_0)}$.

Three parameters, $r$, $b$, and $x_0$, could not be changed freely, and $r$ was determined uniquely from $b$ and $x_0$. To make $r$ a real number, $n^b_0 - x_0 \geq 0$ should be satisfied.

In carrying out our simulations, values of the following nine parameters were specified: $n_0$ (transformed initial population size), $h$, $\sigma^2$ (constant variance of $\epsilon_t$), $n_{threshold}$ (threshold level of $n$), $u_{target}$ (target level of $u$), $s_0$, $b$, $x_0$, and $\xi^2$ (constant variance of $\Phi_t$). For the first five parameters ($n_0$ to $u_{target}$) that are expected to have little effect on the performance ratio between the two FBs (explained below), their values were fixed: $n_0 = 0.1$ ($N_0 = K/10$, assuming that the population has been overfished before starting the FBs), $h = 0.005$ (the annual increment of $s$ or $x$ is 0.0025 when $u_t/u_{target} = 0.5$), $\sigma^2 = 0.3$ ($\epsilon_t$ ranges from 0.321 to 2.39 with a probability of 0.95), $n_{threshold} = 0.05$ ($n_{threshold} = K/20$), and $u_{target} = MSY$ (cpue giving $MSY = 0.5$). We had concern about the remaining three parameters, $s_0$, $x_0$, and $b$, where $s_0$ and $x_0$ are expected to affect the system dynamics in the short term and $b$ describes the degree of non-linearity between cpue and the population size. In the MPA-FB, $s_0$ was arbitrarily given within its possible range of $0 \leq s_0 \leq 1$, whereas in the Effort-FB, $s_0$ was fixed at 0. The parameters $b$ and $x_0$ were changed freely within their ranges in both FBs: $0 < b < 0.5$ (proportionality or hyperstability was reproduced in this range) and $0 < x_0 < 0.32$ (this was derived from the condition of $n^b_0 - x_0 \geq 0$ and $n_0 = 0.1$). Figure 2 shows the interrelationship among the three parameters of $r$, $b$, and $x_0$. The parameter $r$ increased as $x_0$ became larger as a result of the constraint of keeping $n_0 = 0.1$. Also, $r$ increased with $b$ except when $x_0$ was high. The degree of the stochastic variations $u_t$ was given by a CV (coefficient of variation) of $\xi_t/u_{expected,t}$ whose possible range was set to be $0$–$200\%$.

A simulation trial was performed to reproduce annual changes in variables ($n$, $s$, and $c$ for the MPA-FB, and $n$, $x$, and $c$ for the Effort-FB) for at least 10 years under a set of parameter values. Such trials were repeated with different series of random numbers. Once $n$ was below $n_{threshold}$ in a given year, the population was regarded as having collapsed. However, the simulation was continued, to trace the variables in subsequent years.
To examine the effectiveness of the FBs, we used three performance indicators:

(i) **Mean population size.** In each FB, the mean population size over the first or the second 5 years was calculated from each simulation trial. The mean and the variance were given from 100 trials. The performance ratio concerning this quantity was defined as $\frac{\bar{n}_{\text{MPA-FB}}}{\bar{n}_{\text{Effort-FB}}}$, where $\bar{n}_{\text{MPA-FB}}$ and $\bar{n}_{\text{Effort-FB}}$ are the means over 100 trials for the MPA-FB and Effort-FB, respectively. Owing to the large sample size of 100, both means can be regarded as following a normal distribution. The difference between the two means was evaluated with a $z$-test: the difference is significant at the 5% level when $z > 1.64$.

(ii) **Mean catch.** The mean catch over the first or the second 5 years was calculated from a simulation trial. The mean and the variance were given from 100 trials. The performance ratio was defined as $\frac{\bar{c}_{\text{MPA-FB}}}{\bar{c}_{\text{Effort-FB}}}$, where $\bar{c}_{\text{MPA-FB}}$ and $\bar{c}_{\text{Effort-FB}}$ are the means over 100 trials in the MPA-FB and Effort-FB, respectively. The difference between the two means was assessed using a $z$-test.

(iii) **Probability of collapse.** The probability of collapse $\pi$ was defined as the number of simulation trials that experienced a population collapse during the first or the second 5 years, divided by the total number of trials. An estimate of $\pi$ was based on 100 estimates from 10 000 trials. The performance ratio was defined as $\frac{\pi_{\text{Effort-FB}}}{\pi_{\text{MPA-FB}}}$, where $\pi_{\text{MPA-FB}}$ and $\pi_{\text{Effort-FB}}$ are the means over 100 estimates in the MPA-FB and Effort-FB, respectively. Unlike $\bar{n}$ or $\bar{c}$, a lower value of $\pi$ was preferable in management. Therefore, the denominator and the numerator were exchanged in this ratio. The difference between the two means was evaluated with a $z$-test.

**Results**

Figure 3 provides examples of annual changes in the population size $n$ and catch $c$ in the MPA-FB. The mean of both population

![Figure 2](https://example.com/figure2.png)

**Figure 2.** Contours of $r$ (intrinsic growth rate) derived from interrelationships among the three parameters $r$, $b$ (degree of non-linearity between the cpue and population size), and $x_0$ (initial fishing effort), when $n_0$ (initial population size) = 0.1. The shaded area represents a range in which an equilibrium point of the MPA-FB system or Effort-FB system does not exist. Emboldened numerals show combinations of $b$ and $x_0$ that were used in some simulations.

![Figure 3](https://example.com/figure3.png)

**Figure 3.** Examples of simulated yearly changes in the population size $n$ and catch $c$ from ten MPA-FB simulation trials under different values of the initial MPA size $s_0$. Means and standard errors in parenthesis for the first and the second 5 years were calculated from all 100 trials, and are shown above the corresponding years. An asterisk (*) indicates that the mean for the second 5 years is larger than that for the first 5 years ($p < 0.05$). A dotted line shows a threshold for the population size ($n_{\text{threshold}} = 0.05$). No stochastic variations in cpue were considered in these examples.
size and catch was higher for the second 5 years than for the first 5 years. However, in simulation trials (Figures 3a and c) and in trials with $n < n_{\text{threshold}}$ when $s_0 = 0$ (when starting the MPA-FB without MPAs), a decreasing trend was observed in $n$ or $c$. Such phenomena were not observed in Figures 3b and d, when starting the MPA-FB with the MPA size equal to 10% of the whole area ($s_0 = 0.1$; Figures 3b and d). Annual changes in $n$ and $c$ were sensitive to the initial MPA size $s_0$. These were trials with $n > n_{\text{target}} (=0.5)$ in Figure 3b. This was caused by the oscillatory property of the equilibrium point. We confirmed the random fluctuations in $n$ around $n_{\text{target}}$ based on simulations for more than 50 years.

Figure 4 shows the relationship between $s_0$ and performance statistics ($\bar{n}$, $\bar{c}$, and $\pi$) in the MPA-FB. As expected from closing at least a part of the fishing grounds, $\bar{n}$ increased with $s_0$, and $\bar{n}$ was higher for the second 5 years than for the first 5 years (Figures 4a and b). The $\bar{c} - s_0$ curves either monotonously decreased or were dome-shaped (Figures 4c and d). The latter shows that $\bar{c}$ increased when $s_0$ increased from 0 to the level giving the maximum value of $\bar{c}$. This level and $\bar{c}$ were higher for the second 5 years. The probability of collapse $\pi$ decreased sharply to almost 0 as $s_0$ increased (Figures 4e and f), showing that an adequate level of $s_0$ prevented a population from collapsing. The level was lower for the second 5 years.

Figure 5 shows the relationship between the CV (degree of stochastic variations in cpue) and the performance statistics for the first 5 years in the MPA-FB under two levels of $s_0$. The mean of both population size $\bar{n}$ and catch $\bar{c}$ was not sensitive to changes in the CV (Figure 5a−d). The probability of collapse $\pi$ increased slightly with the CV when $s_0 = 0$ (Figure 5e), but $\pi$ was almost 0 over the CV range of 0–200% when $s_0 = 0.1$ (Figure 5f).

Figures 6−8 show performance ratios between the MPA-FB and Effort-FB systems under two different levels of $s_0$. Domains of $\bar{n}_{\text{MPA-FB}} > \bar{n}_{\text{Effort-FB}}$ or $\bar{n}_{\text{MPA-FB}} < \bar{n}_{\text{Effort-FB}}$ appeared when $s_0 = 0$ (Figure 6a and c), but domains of $\bar{n}_{\text{MPA-FB}} > \bar{n}_{\text{Effort-FB}}$ were overwhelmingly dominant when $s_0 = 0.1$ (Figure 6b and d), showing that population recovery was accelerated more from the MPA-FB than from the Effort-FB. Figure 7 had domains of $\bar{c}_{\text{MPA-FB}} > \bar{c}_{\text{Effort-FB}}$ or $\bar{c}_{\text{MPA-FB}} < \bar{c}_{\text{Effort-FB}}$. As the relationship...
between \( s_0 \) changed depending on the parameter values (Figures 4c and d), an inconsistent relationship was observed between the ratio \( \frac{\text{MPA-FB}}{\text{Effort-FB}} \) and \( s_0 \). Domains of \( \text{MPA-FB} < \text{Effort-FB} \) or \( \text{MPA-FB} > \text{Effort-FB} \) appeared when \( s_0 = 0 \) (Figures 8a and c), but only \( \text{MPA-FB} < \text{Effort-FB} \) when \( s_0 = 0.1 \) (Figures 8b and d), showing that the MPA-FB was more effective than the Effort-FB in preventing the population from collapsing.

**Discussion**

Our stability analyses suggest that both the MPA-FB and Effort-FB can approach a predetermined target level for a population when cpue is used instead of population size, and when the non-linear relationship appears between cpue and population size. The necessary conditions are that (i) the target cpue is set at a level corresponding to the population size that provides MSY, and (ii) drastic changes in the MPA size or fishing effort are avoided. Condition (ii) may require many years for a depleted population to approach a target level. A simple solution to cope with this difficulty is that all fishing grounds be closed until the population recovers. However, this may not be accepted by fishers, especially when they exploit a population with a low growth rate. The other solution, which will be examined in future, is to develop a control system for changing the MPA size or fishing effort more rapidly. In the present system, the changes are regulated by a constant \( h \) that must be set at a very low value to make the system stable. If we could assign a high \( h \) (to approach the target level rapidly) when the difference between the target and observed cpue is large, and a low \( h \) (to approach the target level slowly, without overshooting the level) when the difference is small, recovery of a depleted population could be accelerated.

Both FBs can contribute to preventing a depleted population from collapsing if stochastic population fluctuations are independent of population size. Because both FBs can increase the population size, collapse probability is less when the population size is larger, although collapses did appear in some simulation trials incorporating stochastic population fluctuations.

Our simulations, which focused on the system dynamics over the short term after management implementation, showed that the performance of each FB depends on \( s_0 \) (initial MPA size), \( x_0 \) (initial fishing effort), and \( b \) (the degree of non-linearity between cpue and population size). We cannot make a general comment on whether one FB is always better than the other. When \( s_0 = 0 \) (starting the MPA-FB from 0 MPAs), management effect is never remarkable because the MPA size increases only slowly because of a very low \( h \). However, as suggested from simulations with \( s_0 = 0.1 \), when \( s_0 \) is set at an intermediate value, the performance of the MPA-FB may improve. The MPA-FB can save individuals in MPAs, whereas the Effort-FB allows fishers to
use all fishing grounds. Simulations confirmed that the MPA-FB has the advantage over the Effort-FB in preventing a depleted population from collapsing. A trade-off may exist between rapid population recovery and a high level of short-term catch. However, the trade-off will disappear when the MPA-FB succeeds in allowing the population to recover. A high catch can be expected from a fully recovered population even when fishing effort is unchanged (fishing effort \( x_0 \) in the MPA-FB was fixed at \( x_0 = 0 \) in simulations).

The cpue may be variable even when the population size is constant. This will limit the advantages of the MPA-FB. However, simulations incorporating stochastic variations in cpue showed that a population rarely collapses when \( s_0 = 0.1 \).

Adopting the MPA-FB with a high level of \( s_0 \) is a recipe for variability in cpue. Although we cannot specify the level of \( s_0 \) based on the present study, \( s_0 = 1 \) (starting the MPA-FB from the closure of all fishing grounds) is an option for a heavily depleted population, especially when the control system for accelerating population recovery will be applicable. For a lightly exploited population with low variability in cpue, \( s_0 = 0 \) is an option, although no simulation studies for such a population were performed here. It is advisable that a given level of \( s_0 \) be put in place before implementing this FB.

In our simulations, only the population characteristics \( r \) (intrinsic growth rate) and \( b \) were considered to affect the performance of the two FBs. To compare their performance, we

![Figure 6. Contours of \( \bar{n}_{\text{MPA-FB}}/\bar{n}_{\text{Effort-FB}} \) (ratio of mean population sizes) in the plane of \( b \) (degree of non-linearity between the cpue and population size) and \( x_0 \) (initial fishing effort). Numbers in rectangles represent values of \( \bar{n}_{\text{MPA-FB}}/\bar{n}_{\text{Effort-FB}} \). Figure 2 is overlaid. A legend of \( \bar{n}_{\text{MPA-FB}} > \bar{n}_{\text{Effort-FB}} \) \( (p < 0.05) \) indicates that \( \bar{n}_{\text{MPA-FB}} \) was larger than \( \bar{n}_{\text{Effort-FB}} \) at the 5% level of significance. No stochastic variations in cpue were considered in these simulation trials.](image-url)
could not change the values of these parameters independently. Instead, we changed combinations of \( r \) and \( b \), where \( r \) was determined uniquely from a combination of \( b \) and \( x_0 \) (see Figures 6–8). However, irrespective of \( b \), i.e. even when \( b \) was high and hyperstability appeared, we saw a better performance of the MPA-FB than the Effort-FB when \( r \) was high. In the present control system, with a constant and low \( h \), the MPA-FB would be effective for a population that can recover quickly by itself because it has a high \( r \).

For technical reasons, the specific models cannot deal with hyperdepletion (Hilborn and Walters, 1992), corresponding to \( a > 1 \) in \( U_{expected} \propto N^a \). However, the basic models can handle it. Stability analyses using them suggest that the dynamic systems are globally stable even when \( a > 1 \). Therefore, our feedback management procedure can recover a depleted population even in a case of hyperdepletion.

Management effectiveness using MPAs depends on the mobility of the target species (Polachek, 1990; DeMartini, 1993; Sladek-Nowlis and Bollermann, 2002; Botsford et al., 2003; Moustakas et al., 2006). As suggested from the specific models used for our simulations, we allowed for the relationship between MPA size and the catch expected from a density-dependent spatial distribution pattern (Kai and Shirakihara, 2005), but we did not consider mobility explicitly. Therefore, we cannot examine differences in the effect between highly migratory species and sedentary species. However, temporal removal of MPAs is unlikely to be feasible for highly mobile species because larger areas are needed for the MPA to achieve benefit as the

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**Figure 7.** Contours of \( \bar{c}_{MPA-FB}/\bar{c}_{Effort-FB} \) in the \( b-x_0 \) plane. Numbers in rectangles represent values of \( \bar{c}_{MPA-FB}/\bar{c}_{Effort-FB} \). Figure 2 is overlaid. A legend of \( \bar{c}_{MPA-FB} > \bar{c}_{Effort-FB} \) \( (p < 0.05) \) indicates that \( \bar{c}_{MPA-FB} \) was larger than \( \bar{c}_{Effort-FB} \) at the 5% level of significance. No stochastic variations in cpue were considered in these simulation trials.
rates of movement increase (Polachek, 1990; Sladek-Nowlis and Bollermann, 2002).

A difficulty in the MPA-FB based on cpue is that the cpue evaluated from commercial catch–effort statistics has no information on abundance within MPAs, so may not reflect the abundance of the whole population. Ad hoc measures, such as temporal removal of MPAs before the fishing season of each year (i.e. preseason), could be applied. Preseason fishing should be implemented carefully to avert serious damage to the depleted population.

The usefulness of the MPA-FB should be evaluated with caution. In a real world, variations in population size may be more complex than simple stochastic variations independent of size. The relationship between size and cpue may be time-dependent. Continuous changes in the MPA size are never feasible for real populations. In future, we will focus on coastal sedentary species, which are suitable for implementation of the MPA-FB in that (i) spatial distributions and annual fluctuations are more readily grasped than migratory species, (ii) the movement cost for the preseason fishing is relatively low, and (iii) low mobility yields advantages to protect individuals in the MPA. We hope to develop a practical rule for these species, by varying the MPA size with annual changes in cpue.

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Appendix

Numerical analysis of global stability

We checked numerically the global stability of the MPA-FB system using the specified models of Equations (12) and (13):

\[ s_{t+1} - s_t = -h \left( \frac{u_t}{u_{\text{target}}} - 1 \right), \]

\[ n_{t+1} - n_t = r_n (1 - n_t) - \left[ \left( \frac{r}{n_t} - s_t \right)^{1/h} - \left( \frac{r}{n_t + (s + x_0)} \right)^{1/h} \right]. \]

In both equations, stochastic terms were excluded. The values of the parameters were: \( r = 0.6, \ x_0 = 0.15, \ u_{\text{target}} = 1.18, \) and \( h = 0.1. \) Figure A1 shows two isoclines (curves satisfying \( s_t = s_{t+1} \) or \( n_t = n_{t+1} \) in the plane of \( s \) and \( n \)). In all, 100 combinations of \( s_0 \) and \( n_0 \) were given to cover the entire plane. Convergence on the equilibrium point was observed with all combinations, as a trajectory from a combination illustrates (Figure A1).

Figure A1. Isoclines (curves satisfying \( s_t = s_{t+1} \) or \( n_t = n_{t+1} \)) and a simulated trajectory \( s_t \) and \( n_t. \) An open circle is the equilibrium point at which the isoclines intersect. Arrows represent the movement direction of \( s_t \) and \( n_t \) in each of the four subplanes, divided by the isoclines. \( n_0 = n_{t=0} = 0.2. \)