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The impacts of different management strategies and environmental forcing in ecological communities

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Contents

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Understanding the effects of population management on the community a target species belongs to is of key importance for successful management. It is known that the removal or extinction of a single species in a community may lead to extinctions of other community members. In our study we assess the impacts of population management on competitive communities, studying the response of both locally stable and unstable communities of varying size (between four and ten species) to three different management strategies; harvesting of a target species, harvesting with non-targeted catch, and stocking of the target species. We also studied the consequences of selecting target species with different relative abundances, as well as the effects of varying environmental conditions.

We show here how the effects of management in competitive communities extend far beyond the target population. A crucial role is played by the underlying stability properties of the community under management. In general, locally unstable communities are more vulnerable to perturbation through management. Furthermore, the community response is shown to be sensitive to the relative density of the target species. Of considerable interest is the result that even a small (2.5%) increase in the population size of the target species through stocking may lead to extinction of other community members. These results emphasize the importance of considering and understanding multi-species interactions in population management.

1. INTRODUCTION

Concern over the impact of long-term changes to the environment is growing, particularly in relation to the potential consequences on ecosystems. Recent studies have shown that marine communities can be extremely sensitive to the combined effects of human management and changes in the environment (Frank *et al.* 2005; Hsieh *et al.* 2005). We are interested in assessing the relative effects of these factors in the context of different species management strategies (through harvesting or stocking) within a multi-species network in a fluctuating environment, with communities possessing different forms of underlying stability properties. While much work has focused on harvesting in a single species framework, there remains a lack of research carried out when interspecific interactions are explicitly incorporated (but see Hollowed *et al.* 2002, Bascompte *et al.* 2005, Bruno & O'Connor 2005). Ecological communities are composed of coexisting species with interactions of various forms influencing species-specific population renewal (May 1971). As a starting point we will concentrate on competitive communities.

Community stability (in this study defined as the persistence of all species in the assemblage) and the impact of different disturbances to the community structure have been under investigation for several decades (Elton 1958; May 1971; Goodman 1975; Grimm & Wissel 1997; Lundberg *et al.* 2000; McCann 2000; Fowler 2005). Much discussion had concentrated around the so-called 'stability-diversity debate' (McCann 2000). Depending on the methods of community assembly and the underlying community structure theoretical and empirical studies have shown that increased community diversity either decreases the community stability (May 1971, 1972, 1973; Fox & McGrady-Steed 2002) or increases it (Frank & McNaughton 1991;

Death 1996; Tilman 1996; de Grandpre & Bergeron 1997; Rozdilsky & Stone 2001; Fowler & Lindström 2002). Several authors have shown that extinction (or removal) of a single community member may lead to the extinction of other species in the community, or at worst to extinction cascades (Paine 1966, 1980; Borrvall *et al.* 2000; Lundberg *et al.* 2000; Fowler & Lindström 2002). Recent work has shown that it may be possible to predict which species are likely to be involved in such extinction events (Fowler 2005).

The extensive human intervention on marine environment and resources has lead to worldwide decline of marine resources (Ludwig *et al.* 1993; Hutchings 2000; Hutchings & Reynolds 2004, Reynolds *et al.* 2005). Overexploitation has been identified as the major cause of this decline (Ludwig *et al.* 1993; Casey & Myers 1998). Habitat alteration and destruction are also mainly human-caused disturbances in marine environments.

Natural fluctuations in the environment affect the growth and survival of species, and therefore the assembly and persistence of ecological communities. Some disturbances affect the whole community, such as catastrophic events and habitat destruction, whereas others only involve one or a few species, such as carefully targeted harvesting. The relative strength of a perturbation determines whether the compensatory capacity of species and functional groups in the community is sufficient to balance the disturbance, or whether the system will reorganize and possibly loose some of its original properties (Brown *et al.* 2001). Yet the effects of disturbances may filter through to other community members through both direct and indirect effects (Schoener 1983). These indirect effects are of particular relevance when considering, for example, multi-species fisheries management (Hollowed *et al.*

2002). Examples exist where intensive harvesting of one species has lead to changes in community structure as a consequence of species interactions. For example, the loss of Cod (*Gadus morhua*) in the Baltic Sea has lead to changes in relative abundances of other species: herring (*Clupea harengus*) has decreased while sprat (*Sprattus sprattus*), the main prey of God, has increased in abundance (ICES 1999). Frank *et al.* (2005) have recently shown that through the potential interaction between changing environmental conditions and interspecific interactions across trophic levels, Atlantic cod populations were unable to recover, even following a long-term moratorium on harvesting.

Artificial enhancement of the population density — stocking — is a common fisheries management practice throughout the world. Natural populations of fish have been enhanced since the nineteenth century (Jennings *et al.* 2001). In stocking, the abundance of a natural fish population is increased by releasing cultured fish to the area. Even though this has been practised for over 150 years, stocking is still one of the least well-understood and controversial approaches to fisheries management (Lorenzen 2005). The effectiveness and possible undesirable effects of stocking on wild stocks have been under intense debate for over a century (Hilborn 1999; Smith *et al.* 2002).

We study the relative effects of fluctuating environmental conditions and different population management strategies, i.e., harvesting and stocking, on all community members, and the long-term persistence of the community. Recent work (Hsieh *et al.* 2005) has suggested that a variety of physical environmental variables are likely to have a linear stochastic form in the marine environment, while biological factors are best described as non-linear. Our methods reflect both of these issues, using a non-

linear function for population renewal, and a linear noise generating process. We put a further emphasis on the effect of the initial stability properties of the communities on the consequences of management procedures. This also represents an important topic, as previous human or environmentally induced changes to ecosystems mean we may not be sure of the underlying stability properties of those systems we are interested in.

2. METHODS

Ecological communities can be classified into two groups based on their feasibility: feasible and unfeasible communities. Feasible communities, i.e. those where all members have a positive equilibrium population density, can be further divided based on their local stability properties. These properties are dependent upon the magnitude of the dominant eigen value of the Jacobian matrix, formed using the matrix of interspecific interactions, the population renewal kernel and the equilibrium densities of each species present (May 1973). As we were interested in studying the effect of initial community stability on long-term community persistence we assembled the communities with known local stability conditions in the absence of external perturbations.

To simulate the population dynamics of the species forming the community we used a discrete-time Ricker growth equation (Ricker 1954) with Lotka-Volterra competitive interactions. The population densities (N) of each species i in a S-species community were governed by:

$$N_{i,t+1} = (1-h_i)N_{i,t} \exp\left[r_i \left(\frac{1-\sum_{j=1}^{S}\alpha_{i,j}\left[N_{j,t}\right]}{K_i} \right) \right], \tag{1}$$

where r_i is the species specific population growth rate, K_i is the species specific carrying capacity in the absence of competitors, and the strength and form of interspecific interactions (*i≠j*) are indicated by $\alpha_{i,j}$. Here we consider competitive interactions [$0 < \alpha_{i,j} < 1$], and the intraspecific interaction terms ($\alpha_{i,i}$) were scaled to unity for all species, so that the intraspecific interaction was always stronger that interspecific interactions (Rees *et al.* 1996; Kokkoris *et al.* 2002). The interaction matrix was asymmetric, in accordance with field studies on symmetry of competitive interactions (Schoener 1983). Such asymmetry in interactions may lead to facilitation between species (Emlen 1984). Higher order or indirect interactions may also have important consequences on population dynamics between competitors, e.g. the indirect benefits one damselfish species gains through the effects of a competitor on their shared sea anemone host (Holbrook & Schmitt 2004). For simplicity, all population growth rates and carrying capacities were held at constant values ($r = 1.75$ and $K = 1$). In this way, all population densities are expressed as a proportion of the long-term species equilibrium density in the absence of competitors. The species-specific management ratio is given by h_i, taking positive values for harvesting and negative for stocking.

In order to study the effect of a fluctuating environment, we introduced stochasticity to the population growth function such that the population densities of all the species were multiplicatively modified with a noise term, ε_t, which is produced using a first-order autoregressive process (Ripa & Lundberg 1996):

$$\varepsilon_t = \kappa \varepsilon_{t-1} + s_t \sqrt{1 - \kappa^2} , \qquad (2)$$

7

where κ is the autocorrelation parameter, or the colour of the noise (Kaitala *et al.* 1997). Here we used $\kappa = 0$, which generates white noise, but using other values of κ yield qualitatively similar results. The term s is a normally distributed random variable limited to the range $[1 - w, 1 + w]$, and the square root term scales the variance of the generated time series so that its true variance is independent of κ (Heino *et al.* 2000). In the stochastic model, the target of the management was the most abundant species, with harvesting being carried out in a community of size $S = 7$.

We studied the effect of three different management scenarios; harvesting with a proportional harvest ratio $h_i = 0.2$ (20% of the target population removed annually), harvesting that included both targeted and non–targeted catch, where in addition to harvesting the target population with ratio $h_i = 0.2$, the rest of the community members were harvested with rates $h_j = 0.1$. The third management procedure applied was stocking, where the population density of the target species was increased annually with a ratio of $h_i = -0.025$, i.e., an annual increase of 2.5% in the population density of the target species. Another stocking scenario was also tested, where a fixed density (rather than stocking a proportion of the current density) of the focal species was added to the community each generation. This density was taken to be 2.5% of the equilibrium density of the focal population in the absence of any form of disturbance. However, no qualitative differences were found in the results under this scenario compared to stocking a proportion of the current population density. The target species of the various management procedures where chosen to be either the most abundant or the least abundant community member in order to study the effect of different relative densities of the target species. The parameter values chosen for

harvesting and stocking represent conservative estimates. For example, for Atlantic cod in the North Sea the instantaneous rate of mortality caused by harvesting (for age classes > 2) is around 0.9. A harvest ratio of 0.6 in our study would equate to that. Thus the harvest ratio we use, 0.2, is relatively conservative. Reliable measures of stocking rates in the nature are hard to find, but we believe our chosen value of 2.5% annually is also a conservative estimate.

While it is possible to find an analytical solution to the equilibrium densities for community members, and form and test the Jacobian matrix to show local stability conditions under management strategies such as those used here, for anything above a two species community in this framework this becomes extremely cumbersome mathematically, and still does not allow us to test the impact that different structures of the stochastic noise process may have on the model in combination with the harvest rate.

All of the above management scenarios (harvesting, harvesting with non-targeted catch, stocking) were tested independently, and the same community was tested under each scenario. In order to investigate the influence of these different common management practices, the community stability status and the initial target density, on the long-term community persistence of differently sized communities, we simulated the model communities for 1000 time-steps. The community characteristics collected at $t = 1000$ were: change in community size, probability of target species extinction, probability of non-target extinction, and the mean number of non-target extinction events. The results presented here are taken from either 500 (deterministic model) or 1000 (stochastic model) community replicates, for community sizes ranging from $S = 4$ to $S = 10$. In all of the management scenarios the same communities were used in

order to ensure that the potential differences are caused by the management and not by differences in community properties. A species was regarded as extinct if its population density dropped below a critical threshold, taken here to be equal or below a density of 10^{-6}.

3. RESULTS

We initially disturbed harvested communities ($S = 7$) with environmental forcing (figure 1; table 1), with interesting results. In the locally stable community (from now on we use "stable" and "unstable" community) context (figure 1a, c, e; table 1), variation in the strength of environmental forcing (parameter w) had no significant effect on the probability of target species being lost from the community, while varying the harvest ratio led to a significant increase in target species loss with increasing harvesting pressure (figure 1a). With no harvesting, there were no extinctions in stable communities. The probability of extinction events in unstable communities was always 1 if they were disturbed with either environmental forcing or harvesting (figure 1b, d, f). When both of these disturbances were set to zero, there were no extinctions in stable or unstable communities. The number of species lost in unstable communities was unaffected by changes in range of environmental forcing and harvest ratio combinations (figure 1b). When the most abundant species is the target species (figure 1d), increasing the harvest rate increases the probability of target extinctions. This clearly has an overriding effect on the results of the comparison between different strengths of harvesting and environmental forcing (table 1b).

The strength of environmental forcing had an influence, solely in terms of environmental noise being either present or absent. When only positive rates of harvesting and environmental forcing were included in the analysis, no significant

10

effect of varying the strength of environmental forcing on the number of extinctions was found, while varying harvest ratio did significantly affect the probability of target extinction (table 1c). Probabilities of extinction in the absence of harvesting and/or environmental forcing can be considered as a background level for extinction. In both stable and unstable communities the underlying probability of target extinctions without harvesting and environmental forcing is 0 (figure 1a, b): The communities will remain intact if they are not disturbed in any way. Unstable communities suffer a background extinction probability of 1 under any type of disturbance, with little variation in the number of species lost from the community. The background probabilities of most and least abundant species are found when either harvest rate or environmental forcing is set to zero.

Because of the lack of effect of varying the strength of environmental forcing, we chose to present the rest of the results using only the deterministic system. This avoids confusion that may arise from interactions between environmental and management processes. The processes influencing the community in the remaining results were therefore (i) harvesting only, (ii) harvesting with non-targeted catch, or (iii) stocking.

The change in community size (relative to the initial community) was strongly influenced by the specific management strategy (figure 2a-c). The underlying stability state of the community also affected the persistence of community members. Unstable communities were (unsurprisingly) considerably more vulnerable to perturbations that stable communities (figure 2). The effect of selecting the target species according to its relative density on the relative change in community size was seen when the community was harvested only (figure 2a), but not under the other management procedures.

The probability of target species extinction varied extensively depending on the community size, management procedure, stability of the community, and also on the target species (figure 3; table 2a). When the least abundant species in a stable community was harvested, the probability of target extinction was high, and increased further with increasing community size. A similar increase occurred when the most abundant species was the target of harvesting in a stable community, even though the probability was substantially lower than in the previous scenario (figure 3a). In unstable communities the result was very different. The probability of target extinction showed a significant decrease with increasing community size, a result that held when either the most or least abundant species was harvested. This was in direct contrast to the result obtained from stable communities (figure 3a). When harvesting also affected non-targeted species there was no clear trend associated with the community size (figure 3b). The lowest probability again occurred when the most abundant species of a locally stable community was the target species, and in both stable and unstable communities, harvesting the least abundant species gave a higher probability of target extinction (figure 3b). Increasing the population density of the target species by stocking in unstable communities also had detrimental effects on the target species (figure 3c). Stocking the least abundant species in unstable communities produced a reasonably high probability of extinction of the target species. Moreover, this probability increased significantly with increasing community size (table 2a). It is worth emphasizing that this is exactly opposite to the effect of community size when unstable communities were harvested rather than stocked (compare figures 3a and c).

For precautionary population and community management it is essential to pay attention to non-target species. The probability of non-target extinctions increased significantly with increasing community size in stable communities regardless of the

12

target of the harvesting, this probability being considerably higher when the most abundant species was the target (figure 4a; table 2b). Harvesting in unstable communities also had a major influence on the non-target species (figure 4a), and when the most abundant species was the target of harvesting, non-target extinctions were almost certain to happen throughout all different community sizes. When the least abundant species was harvested in unstable communities, the probability of non-target extinctions increased significantly with increasing community size. The relative number of species involved in these extinctions increased with increasing community size in spite of the relative abundance of the target species (figure 2). Interesting interactions arose between the rates at which non-target species became extinct when by-catch was or was not included (figure 4b, table 2b). In stable communities with the most abundant species harvested with bycatch, extinctions rose at a slower rate with increasing community size than in communities where no bycatch was taken. When the least abundant species was harvested, harvesting with bycatch lead to an increase in the rate of extinctions with increasing community size. Stocking influenced unstable communities in very similar way to harvesting and non-target harvesting, but produced a lower probability of non-target extinctions in stable communities (figure 4c).

4. DISCUSSION

We have shown that the impacts of certain common management practices have negative effects on ecological communities that often extend far beyond the target population. A crucial role is played by the underlying stability properties of the community under management. In general, locally unstable communities are more vulnerable to perturbation through harvesting and stocking than locally stable

13

communities. Furthermore, the relative density of the target species had marked effects on the studied response variables.

The fact that the strength of the environmental forcing had such a minor impact in the competitive community contexts is quite unexpected. While environmental forcing did have an effect *per se*, there was no interaction between harvesting and the strength of environmental noise. In some respects, this may seem surprising, particularly as we modelled the scenario which matched predictions of a recent study concerning the linear structure of environmental fluctuations coupled with non-linear biological processes (Hsieh *et al.* 2005). Increasing environmental stochasticity should decrease population size (Benton *et al.* 2002) and the time to extinction (Lande 1993; Sæther & Engen 2003). In the present system it appears as if neither the structure nor the magnitude of the environmental disturbance played such an important role. In other words, harvesting alone is such a strong disturbance that it is considerably more important than the effects of environmental forcing. When the relatively conservative harvesting ratio we used here is also taken into account, the consequences of mismanagement become even more apparent.

Increasing community size (*S*) in locally stable communities had contradictory effects on the relative change in community size following management: In stable communities, when the most abundant species was targeted, the relative reduction in community size increased with increasing community size. In contrast, if the least abundant species in the community was the target of harvesting, the opposite was observed (see also Enberg 2005). Fowler (2005) addressed the effects of removing species completely from a community, according to their relative abundance. That work showed that strong predictions can be made concerning which further species

are likely to be lost from the system if the relative density of the removed species is known. The current findings represent an investigation into management practices that have traditionally been thought of as less severe than removal events, but we emphasize that even these forms of disturbance can lead to further extinction events, in many cases cascading beyond the target species. While we have focused on competitive interactions here for simplicity, cascading effects have also recently been shown across trophic levels for a marine ecosystem once dominated by Atlantic cod (*Gadus morhua*) populations (Frank *et al.* 2005).

The frequency of non-target extinctions is a result that should generate concern. Direct and indirect species interactions often combine leading to unexpected, often catastrophic outcomes. This is especially interesting, as in this study we focus on competitive communities, where intuitively one might expect the other members of a community to gain from a reduction in population density of one community member.

Traditionally the negative effects of stocking have been thought to be related to genetic contamination (Swain & Riddell 1990; Gross 1998; Youngson & Verspoor 1998) and maladaptive behaviour of farmed individuals (Fleming *et al.* 1996; Johnsson *et al.* 2002). Our study highlights that even small changes in the population density of the target species may lead to community-wide disturbances. In unstable communities, the stocked species itself is also endangered. It is worth noting that even though in this study by enhancing the population density of a single community member we are referring to stocking, this is essentially equivalent to an increase in the growth rate of a single community member. Thus changes in the biotic or abiotic environment favouring only one community member could also lead to dramatic changes in community composition.

One might question the value of testing locally unstable communities here, but humans have already had a massive impact on many ecosystems (Pimm *et al.* 1995; Vitousek *et al.* 1997) and marine environments have by no means been safe from this anthropogenic influence (FAO 1994). It is therefore reasonable to assume that by now the composition of several communities has changed from their original characteristics. Previously stable communities may thus have changed into unstable communities, more sensitive to disturbances.

We have strictly concentrated on within trophic level interactions in our models. Inclusion of predator-prey relationships into our models would lead to an undesirable level of complexity in terms of understanding the direct and indirect relationships between species in large communities. However, the importance of considering between trophic level interactions should not be forgotten. Recent empirical evidence has shown that variation in predator diversity in experimental marine food webs can cascade to lower trophic levels (Bruno and O'Connor 2005). Shepherd and Myers (2005) show that predation release can increase numbers of sharks. This effect arises due to the reduced predation from large shark predators that are bycatch in shrimp fisheries. The distribution of interaction strengths within and among trophic levels in a Caribbean marine food web has been shown to have characteristic properties that are likely to buffer the effects of overfishing top predators (Bascompte et al. 2005). However, this study also highlights the dangers across the whole community of selective fishing. If we are to successfully manage marine resources in the future to allow sustainable "domestication" of the seas (Marra 2005), our results emphasize the importance of understanding and accounting for both direct and indirect interspecific interactions in population and community management. Depending on the stability

state of the community and the species targeted by the management the impacts of

limited, yet sustained management can have far reaching consequences.

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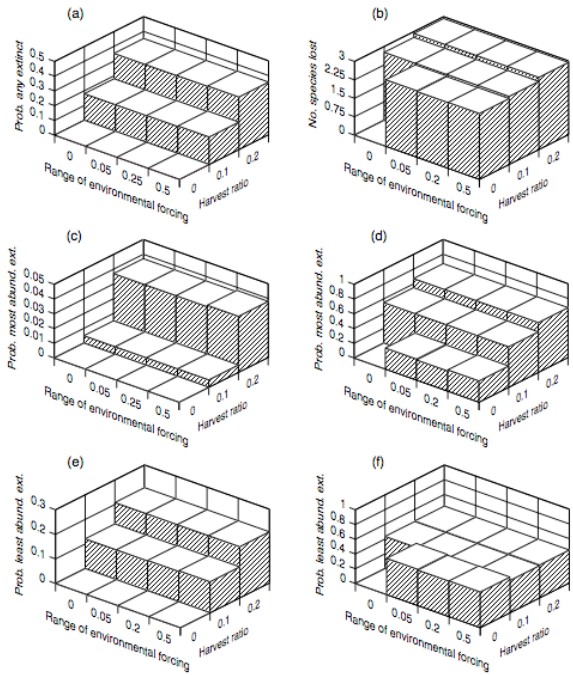Steele J.H. (1985) A comparison of terrestrial and marine ecosystems. *Nature*, 313, 355-358

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Table 1. (a) Generalised linear model (GLM) result for the effects of environmental variation and harvest rate on the probability of any species extinctions (modelled following a binomial distribution). The statistics are shown based on 1000 locally stable seven-species communities (d.f. = degrees of freedom, for large deviance values the figures are rounded). (b) GLM with binomial response result for the effects of environmental variation and harvest rate on the probability of target (most abundant) species extinctions. (c) GLM with binomial response result for the effects of environmental variation and harvest rate on the probability of target (most abundant) species extinctions. Zero harvest and environmental forcing values are removed.

| Source	d.f.	Deviance	Residual d.f.	Residual deviance	$P\ (>c^2)$
a)					
Null model	-	-	11	2265	-
Environmental forcing	3	0.15	8	2264	0.99
Harvest rate	2	2264	6	0.03	<0.01
(b)					
Null model	-	-	11	2487	-
Environmental forcing	3	81	8	2406	<0.01
Harvest rate	2	1942	6	463	<0.01
(c)					
Null model	-	-	5	99	-
Environmental forcing	2	0.001	3	99	0.999
Harvest rate	1	99	2	0.004	<0.01

25

Table 2: Logistic regression results from the effect of increasing community size on the probability of (a) target species extinctions and (b) non-target species extinction according to different management scenarios. Each case was removed independently from the regression model to test for redundancy (b = slope, a = intercept, G^2 statistics with corresponding P value are shown; degrees of freedom = 1 throughout except for effects between all treatments = 11).

| Management practice	Community type	Target abundance	b	a	G^2	P
(a)						
Harvesting only	Stable	Least	0.44	0.06	63.0	<0.01
		Most	0.39	0.11	16.0	<0.01
	Unstable	Least	-0.20	0.08	7.1	<0.01
		Most	-0.20	0.04	22.1	<0.01
Harvesting with bycatch	Stable	Least	9.19	0.05	18.3	<0.01
		Most	0.35	0.20	3.3	0.07
	Unstable	Least	0.04	0.04	1.1	0.29
		Most	-0.01	0.04	0.1	0.77
Stocking	Stable	Least	0.26	0.54	0.3	0.61
		Most	0.00	0.00	0.0	1.00
	Unstable	Least	0.51	0.06	92.6	<0.01
		Most	0.74	0.15	41.2	<0.01
Effects between all treatments					511.6	<0.01
(b)						
Harvesting only	Stable	Least	0.44	0.10	22.2	<0.01
		Most	0.53	0.05	140.9	<0.01
	Unstable	Least	0.69	0.08	117.9	<0.01
		Most	0.33	0.25	1.9	0.17
Harvesting with bycatch	Stable	Least	0.42	0.06	51.9	<0.01
		Most	0.35	0.05	67.3	<0.01
	Unstable	Least	0.64	0.13	38.1	<0.01
		Most	0.13	0.21	0.4	0.54
Stocking	Stable	Least	0.46	0.21	5.9	0.02
		Most	0.28	0.08	13.0	<0.01
	Unstable	Least	-0.30	0.18	3.2	0.07
		Most	-0.31	0.20	2.7	0.10
Effects between all treatments					255.4	<0.01

Figure 1. Extinctions in harvested communities that are either initially stable (a, c, e)
or unstable (b, d, f). In 1000 seven species communities, the most
abundant species was harvested under different levels of environmental
variation, and extinction events within 1000 time steps were recorded. In
unstable communities, extinctions always occurred under any form of
disturbance, the mean number of species lost from the community is
recorded in 1b. The probability of the most (c-d) or least (e-f) abundant
species becoming extinct is sensitive to the harvest ratio, but not to any
differences in the range of environmental forcing, when present.
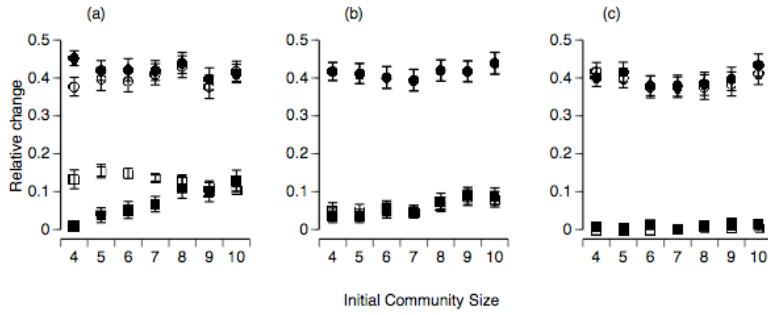
Enberg et al. Fig. 2

Figure 2. Mean relative change in size of managed communities (*c.f.* original community size, ± 95% C.I.). (a) harvesting, (b) harvesting with non-targeted catch, and (c) stocking. Open symbols are the least abundant species harvested, black symbols are the most abundant. Squares are stable communities, circles are unstable communities.
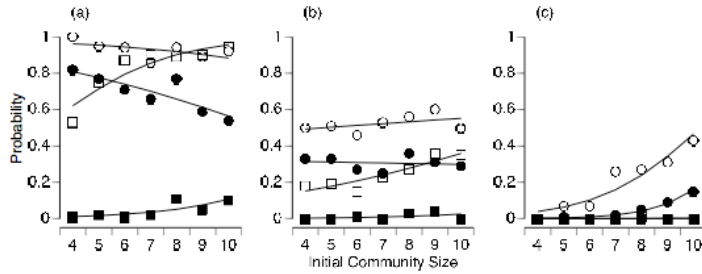
Enberg et al. Fig. 3

Figure 3. Probability of target species extinction as a result of population
       management. (a) harvesting, (b) harvesting with non-targeted catch, and
       (c) stocking. Logistic regression lines are shown for each case. Open
       symbols are the least abundant species harvested, black symbols are the
       most abundant. Squares are stable communities, circles are unstable
       communities.
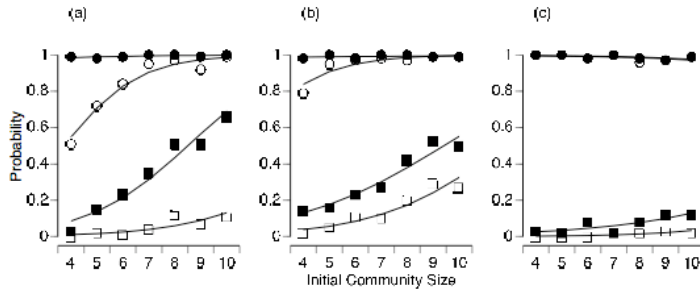
Enberg et al. Fig. 4

Figure 4. Probability of non-target species extinctions as a result of population management. (a) harvesting, (b) harvesting with non-targeted catch, and (c) stocking. Logistic regression lines are shown for each different case. Open symbols are the least abundant species harvested, black symbols are the most abundant. Squares refer to stable communities, circles to unstable communities.