Sustainable harvesting in variable environments

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Academic dissertation

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Contributions

	I	II	III	IV	V	VI
Original idea	ER	VK	KE, VK	KE, ER	KE, ER	VK, ER
Study design and methods	AG, KE	VK, NJ, KE	KE	KE	KE, MF	VK, ER, KE
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Contents

Summary

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> ***"Despite its crucial importance for the survival of humanity, marine biodiversity is in ever-greater danger, with the depletion of fisheries among biggest problems." - United Nations 2004, in 'Ten stories the world should hear more about'.***

1. Introduction

1.1 Population, community, and fisheries ecology

Exploitation of natural resources has essentially influenced the development of population ecology (Lindström *et al.* 1999). The study of commercial fisheries (Hjort 1914) and fur trade statistics by the Hudson Bay Company (Elton 1924, Elton and Nicholson 1942, Ranta *et al.* 1997) have played an especially important role in improving our understanding of how and why natural populations fluctuate.

Although ecology is a broadly ranging field of science, it basically concentrates on understanding the abundance and distribution of individuals, and how they respond to their biotic and abiotic environment (Krebs 1972). In my thesis, I have integrated key elements of ecology — population, community and spatial ecology — with fisheries ecology, thus addressing the most important features of this diverse field of science. I have dealt with single species population ecology, with (**III**) and without (**II**) age-structure, species interactions in communities (**IV**, **V**), and I have also explored the significance of the spatial dimension in a harvesting framework (**VI**). All this work has had a single focus: to search for means of sustainable harvesting in an uncertain world. In order to underline why this kind of research is essentially important, I begin by describing the current state of world's fisheries. I then introduce the methods of my thesis, the results and discussion of these results, and close with some concluding remarks.

1.2 The current state of fisheries

Human intervention on the marine environment and its resources is massive: the total yield of biomass in marine fisheries is more than 80% of global fish production (Jennings *et al.* 2001). Global fisheries landings are declining by about 500 000 metric tons per year from a peak of 80 to 85 million tons in the late 1980´s (Pauly *et al.* 2003). This worldwide decline of marine resources is a widely established fact (Ludwig *et al.* 1993, Hutchings 2000, Hutchings & Reynolds 2004). The cause for this decline is mostly overexploitation (Ludwig *et al.* 1993, Casey & Myers 1998), but often even ceasing the harvest does not guarantee a recovery of the reduced stock (Rose *et al.* 2000).

Ultimately, overexploitation is mostly caused by economic factors of unregulated competition and by economic discounting of future yields (Clark 1990, Ludwig *et al.* 1993, Lande *et al.* 1994, Ludwig 2001). Nevertheless, uncertainties in the environment and stochastic processes influencing population dynamics have also contributed considerably to overexploitation, particularly in coastal fisheries (Lande *et al.* 2001). Thus, taking account of the stochasticity of harvested populations and their environments is a key concept of sustainable harvesting.

One big problem with contemporary fisheries is that large amount of caught fish is used as fish meal for agriculture (to grow chickens and pigs, and used as fertilizer), and aquaculture. With the words of Pauly and others (2003), this can be considered as 'robbing Peter to pay Paul'. Moreover, the contribution of fishing to the global protein supply is only 5%, yet it is a major factor jeopardizing the oceans' biodiversity (Pimm *et al.* 2001).

The persistent myth that marine species are safe from human induced extinctions — that they could somehow always find shelter in the deep and wide ocean — is catastrophically false (Malakoff 1997). Considering that a wealth of marine organisms have not even been identified yet, it might be that they could pass away without anyone noticing (Malakoff 1997).

1.3 Sustainable harvesting — fact or fiction?

Man has a long history of overexploiting natural resources. Extinctions of many species had already been caused by human activity in ancient times (Mace & Reynolds 2001). Escalating human population growth and increased use of natural resources have resulted in harvesting now being a major threat to many animal species (Mace and Reynolds 2001). For example, the sustainable use of fish resources worldwide has hardly proved itself successful: globally 28% of marine fish stocks are overexploited or depleted, and 50% are fully exploited (Ludwig *et al.* 1993, FAO 2004). And all this in spite of well developed theories on management.

An eminent question is: Is it even possible to harvest in a sustained manner? In his foreword on the 'Conservation of Exploited Species' Lord Robert May takes a Darwinian approach to this question (May 2001). He suggested that: There are three fundamental concepts in the 'Origin of Species'. (i) Heritable variation exists within natural populations. (ii) All natural populations have the capacity for continuous geometric increase if resources are not limiting. (iii) When environmental conditions change, the individuals best adapted to the new conditions are more likely to survive. According to (ii), it should be possible to exploit populations in a sustainable manner, such that we harvest the potential surplus in the population growth. The third point, however, implies that even sustainable exploitation will cause changes in the genetic structure of the harvested population (May 2001).

Currently the role of fisheries management is changing, and in future it will most likely be more concerned with controlling the unwanted effects of harvesting – collapse of the resources, economic inefficiency, increasing unemployment, habitat loss or a decrease in the abundance of rare species. The old principal objective of maximising yield may soon be history. Previously it was thought that marine species are relatively safe from extinctions, but recently this view has given way to a more cautionary approach (Malakoff 1997). There are a number of ecological factors that make certain marine species particularly vulnerable to extirpation: small geographical range, dependency on limited, vulnerable and/or patchily distributed habitats; low fecundity; long and unpredictable intervals between recruitment, low dispersal ability and strong Allee effects (Roberts & Hawkins 1999, Powles *et al.* 2000). Roberts and Hawkins (1999) even claim that the documented extinctions may only be the peak of a marine extinction wave that has been underway since the 19th century.

Overfishing is a major threat to fish stocks worldwide. This fact underlines the reality that it is necessary to look for more sustainable ways to utilize marine resources. Moreover, the importance of taking into account the natural variation in environmental conditions affecting the renewal and survival of fish resources cannot be overemphasized (Hofmann & Powell 1998, Arnott & Ruxton 2002). Even though it has been claimed that the ultimate fate of all populations is extinction, at least in the light of history (Jablonski 1986), exploitation can severely hasten the process of declining marine resources by pushing the populations to such low levels that demographic or environmental stochasticity will have fatal effects.

1.4 Environmental stochasticity

Random variations in the environment affect the dynamics of populations through changes in individual life histories (Benton *et al.* 2002). Such environmental forcing has been considered as an important process influencing, for example, the structure of ecological communities (Andrewartha & Birch 1954). Even though the "null model" for environmental stochasticity has traditionally been uncorrelated white noise, environmental variables and population fluctuations are often autocorrelated.

For example marine environments (particularly temperature) fluctuate slowly, that is, their dynamics are dominated by low-frequency variation and are positively auto-correlated (Steele 1985, Halley 1996). This means that a good year is more likely followed by another good year, and likewise, runs of bad years are also to be expected. This kind of reddened spectra can also be observed in ecological time series data (Pimm & Redfearn 1988, Ariño & Pimm 1995, **II**). The effect of red shifted environmental forcing on, for example, the extinction risk of population has been under vigorous investigation, yet no consistent pattern has been revealed (Ripa & Lundberg 1996, Johnst & Wissel 1997, Petchey *et al.* 1997, Heino 1998, Cuddington & Yodzis 1999, Halley & Kunin 1999, Heino *et al.* 2000, Heino & Sabadell 2003). The strength of environmental forcing is also supposed to play its own role. Increasing environmental stochasticity should decrease population size (Benton *et al.* 2002) and time to extinction (Lande 1993, Sæther & Engen 2003).

I have studied the role of environmental stochasticity when it affects recruitment (**II**, **III**), survival (**III**), carrying capacity (**IV**), and population growth rate (**V**). The form of stochasticity ε_t is in most cases (**III**, **IV**, **V**) taken after a first-order autoregressive process (Ripa & Lundberg 1996):

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

where κ is the autocorrelation parameter, or the colour of the noise (negative values refer to blue colour with short wave lengths dominating, positive values generate red noise with dominance of long wave lengths, and κ = 0 refers to white noise). The term *s* is a normally distributed random variable with range $[1 - w, 1 + w]$, 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).

1.5 Competitive community stability

Competition is a fundamental structuring process in many ecological theories. Competition requires that the shared resources are limiting, and hence it is closely tied to the carrying capacity of the system for suites of competitors (Hollowed *et al.* 2000). The question about the effect of community diversity on the stability of ecosystems is an issue that has been under consideration for several decades (Elton 1958, Odum 1971, Lawlor 1980, McCann 2000). Theoretical, laboratory, and field experiments have suggested that increased diversity increases the stability (Naeem 1998, Yachi & Loreau 1999, McGrady-Steed *et al.* 1997, Naeem & Li 1997, Tilman *et al.* 1996, 1997, Borrvall *et al.* 2000). Increased stability is supposed to be the result of species in more diverse communities being able to compensate for lost species. In contrast, several studies have also shown that greater diversity and complexity reduce stability (Gardner & Ashby 1970, May 1972, 1973, Moulton & Pimm 1986, Lundberg *et al.* 2000a, Enberg & Kaitala 2003, Ranta *et al.* 2005). Regardless of the extensive effort put on studying the diversity-stability dilemma, not even the basic definitions of diversity and stability are clear-cut. However, in the present thesis diversity is considered as the number of species in the community (sensu MacArthur 1955, Elton 1958, Margalef 1969, Pimm 1984, Lundberg *et al.* 2000a), and stability as the ability of the community to retain all original species in the face of different disturbances.

The equilibrium properties of communities with Lotka-Volterra competitive interactions can be calculated with the following set of equations. Interaction strengths are stored in a square matrix (called the interaction or community matrix) containing all the species interaction terms, $a_{i,j}$. Intraspecific interaction terms $a_{i,i}$ are given on the main diagonal, whereas interspecific interaction terms $a_{i,j}$ are the off-diagonal elements of the community matrix:

$$A = \begin{pmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,s} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,s} \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{s,1} & \alpha_{s,2} & \cdots & \alpha_{s,s} \end{pmatrix} \qquad (2)$$

In **IV** and **V** the intraspecific interaction terms were standardized to 1 for all species, so that the intraspecific interaction was always stronger that interspecific interactions (this assumption is supported by Kokkoris *et al.* 2002 and Rees *et al.* 1996). The interaction matrix was asymmetric as interspecific competition observed in nature is rarely, if ever, symmetric (Schoener 1983). Positive values of *a* indicate negative feedback and vice versa. Should the interaction coefficient be zero, the species have no direct interaction. Even then there may still be indirect interactions, which can be summed up by taking the inverse of the interaction matrix.

Communities can be classified in two groups based on their feasibility: feasible and unfeasible communities. A community is feasible, if the equilibrium densities, N*, of all its members are positive (*e.g.*, May 1973):

$$\mathbf{N^*} = \mathbf{A}^{-1}\mathbf{K} \tag{3}$$

where K is a vector of the species specific carrying capacities, and A^{-1} is the inverse of the community matrix A.

Feasible communities can further be divided into locally stable and locally unstable communities. Local stability of a community depends on the eigen-values of the linearised form of the interaction matrix, and the specific function used to describe population growth over time (May 1973). Throughout this thesis (**IV**, **V**) I have used the discrete time Ricker (1954) function to model population growth, giving the linearised population projection matrix B (Ranta *et al.* 2005):

$$\mathbf{B} = \begin{pmatrix} 1-\frac{r_1}{K_1}N^*{}_1 & -\frac{\alpha_{1,2}r_1}{K_1}N^*{}_1 & \cdots & \frac{\alpha_{1,s}r_1}{K_1}N^*{}_1 \\ -\frac{\alpha_{2,1}r_2}{K2}N^*{}_2 & 1-\frac{r_2}{K_2}N^*{}_2 & & \frac{\alpha_{2,s}r_2}{K_2}N^*{}_2 \\ \vdots & \vdots & \ddots & \vdots \\ -\frac{\alpha_{s,1}r_s}{K_s}N^*{}_s & \frac{\alpha_{s,2}r_s}{K_s}N^*{}_s & \cdots & 1-\frac{r_s}{K_s}N^*{}_s \end{pmatrix} \tag{4}$$

where *r* is the species-specific per capita growth rate. Local stability is achieved when the absolute values of all eigen-values of B are < 1. In locally stable communities population sizes of all the species will tend towards their equilibrium density, whereas if locally unstable communities are not initiated in their equilibrium densities, the community will find an alternative stable state(s) and community members may be lost (Fowler *et al.* 2005, Ranta *et al.* 2005).

2. Methods

The main method throughout this thesis has been mathematical modelling. I have used basic ecological population renewal models to describe the dynamics of populations and communities, and observed the responses of these "virtual animals" to differing environmental conditions, harvesting strategies, and spatial settings. Population dynamics of all of the modelling studies (**II**, **III**, **IV**, **V**, and **VI**) have been governed by Ricker dynamics (Ricker 1954). The reason for using Ricker equation is its simplicity (it has only two parameters, *r* and *K*) yet it can produce complicated dynamics. Moreover its behaviour has been extensively studied (May 1974, 1976, May & Oster 1976) and it has been widely used in the population ecology literature during the past 30 years. The Ricker equation is given as:

$$N_{t+1} = N_t \exp\left[r\left(1-\frac{N_t}{K}\right)\right] \tag{5}$$

where N_t is the population size at time *t*, *r* is the intrinsic rate of increase, and *K* is the carrying capacity of the environment (Fig. 1a, e). In the age-structured form (**III**, Fig. 1b), population ageing is defined by the Ricker function as follows:

$$N_{a+1,t+1} = N_{a,t} \exp\left(-m_a \varepsilon_t\right) \tag{6}$$

where $N_{a,t}$ is the number of individuals in age class *a* in year *t*, m_a is the instantaneous mortality rate at age *a* and ε_t is the environmental stochasticity affecting the survival. In the age-structured model (**III**), the number of recruits is assumed to depend on the spawning stock biomass (SSB) according to a Beverton-Holt recruitment function as follows:

$$N_{0,t} = \frac{aSSB_t}{1+SSB_t/b}\varepsilon_t \tag{7}$$

where *a* and *b* are parameters.

In multispecies studies (**IV**, **V**, Fig. 1c, d), the Ricker equation has been coupled with Lotka-Volterra competitive interactions, such that the dynamics of species *i* in a *S* -species community are as follows:

$$N_{i,t+1} = N_{i,t} \exp\left[r_i\left(1-\frac{\sum_{j=1}^{S}\alpha_{i,j}N_{j,t}}{K_i}\right)\right] \tag{8}$$

where $N_{i,t+1}$ is the population density of species *i*, r_i is the species specific per-capita growth rate, K_i is the species-specific carrying capacity (in the absence of interspecific competition), and $\alpha_{i,j}$ is the interspecific interaction term.

3. Main questions

My thesis aims at answering the following questions:

- Are there observable ecological patterns in population recovery after a crash, possibly due to harvesting, and if there are, what are the implications for management (I)?
- Are threshold strategies, as expected, superior in managing fluctuating populations (**II**)? How does the inclusion of age-structure and age-selective

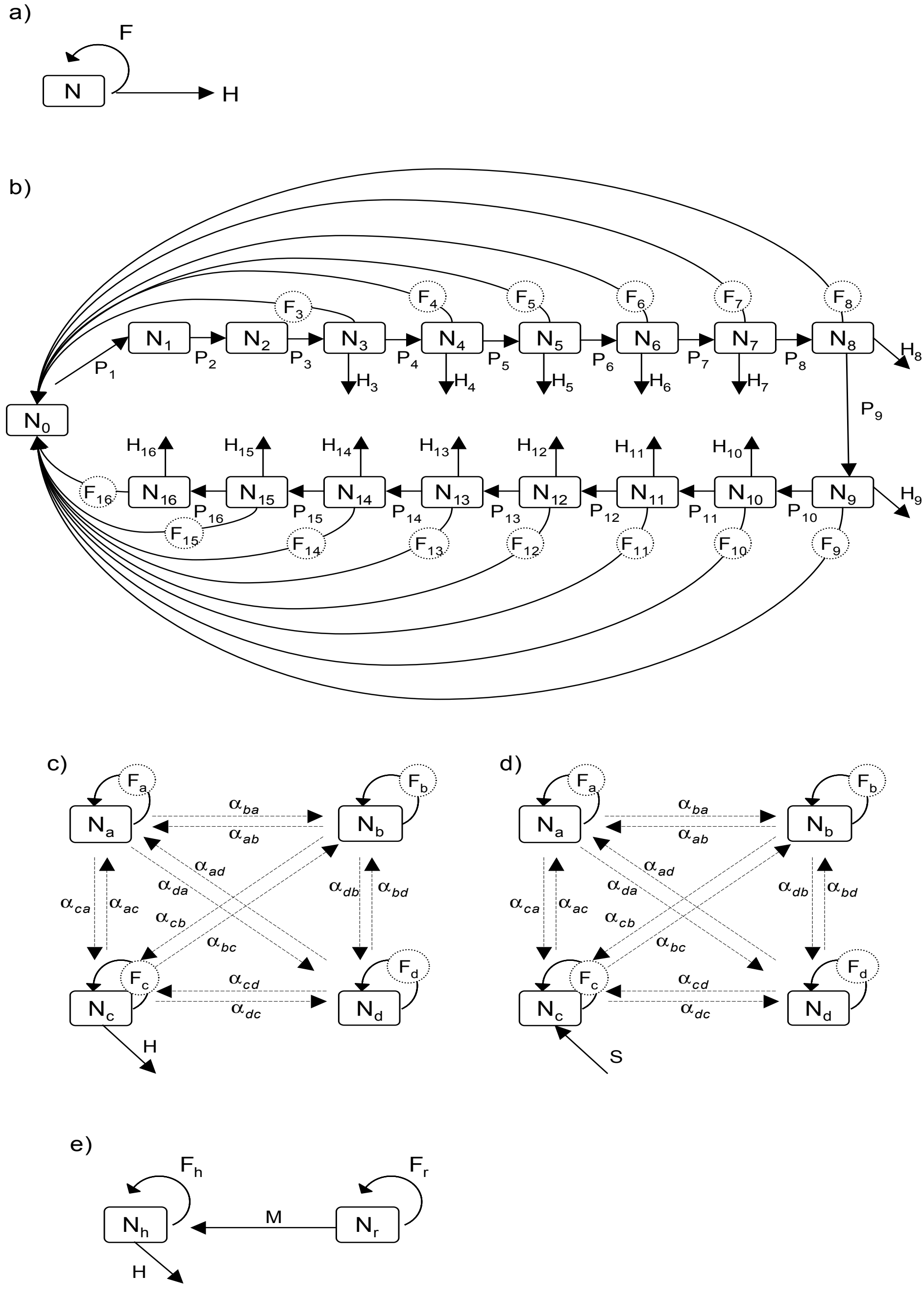

Figure 1. Life cycle graphs from all of the studied systems. H and F refer to harvest and fertility, respectively, and S to stocking. In (a) unstructured single species model (II), (b) age-structured model (III), (c) 4-species community with harvesting on species N_c (IV, V), α's give the interaction strengths between the species, (d) 4-species community with stocking on species N_c (V), and (e) population divided in two sub-areas, harvested (N_h) and reserve area (N_r) (VI). M corresponds to migration from the reserve to the harvested area.

harvesting change the predictions of the more simple models (**III**)?
- How do competitive communities respond to management of a single community member? Does the threshold harvesting strategy perform well in a community context as well (**IV**)? What is the effect of local stability status, community size, and relative abundance of the targeted species (**V**)?
- How do marine reserves work when the IFD theory is incorporated in the model (**VI**)?

4. Results and discussion

4.1 The Ecology of recovery

As a result of the many collapses experienced in harvested stocks, population management is increasingly concerned with population recovery processes. Population crashes are not, as such, unparalleled in natural history — actually quite the contrary. Such collapses in population numbers may be entirely due to natural population fluctuations (caused by unstable inherent dynamics, unstable interactions with other species, or by demographic stochasticity) or due to natural or human-induced environmental changes. However, despite the causes for a collapse, understanding the reasons for success or failure of a recovery would help especially when effort is put on managing recoveries with the help of stocking, breeding programs or habitat restoration (*e.g.* Kareiva 2002).

Under population management framework, it is the management of recoveries that is of particular interest. Naturally, the question of importance is: Is recovery possible? Intuitively it is, we just need to remove the agent that caused the population decline, for example harvesting. However, it is not necessarily easy, even though examples exist. These include ceasing the use of certain pesticides (Borg *et al.* 1969, Newton 1998) as well as establishing a harvesting moratorium (Bjørndal *et al.* 2000). A very famous example of non-recovery despite all actions occurred with the Canadian cod (Gadus morhua) stocks. After five centuries of unlimited fishing (Jennings *et al.* 2001), the cod stocks were fished to commercial extinction in the 1992. The recovery is still to happen.

Fisheries induced changes in food webs and ecosystem structures may significantly influence the probability of recovery (Pauly *et al.* 1997, Jennings & Kaiser 1998, Hutchings 2000). This means that even though the ultimate cause of decline has been removed (such as decreasing the population size by harvesting), there have probably been some changes in the community composition such that the community has reached an alternative equilibrium state.

Ultimately recovery dynamics are equivalent to population dynamics at low densities. What it essential to the success or failure of a recovery, is the rate of population reproduction at low densities (I). If it fails, there is no chance of natural recovery. Phenomena such as positive/inverse density dependence, Allee effects, or depensation (caused for example by difficulties in finding mates at low densities) may cause severe difficulties in recovery. The results of Myers *et al.* (1995) are in this respect comforting. In their study on 128 exploited fish stocks only 3 of them showed significant depensation. Thus recovery should be possible in many stocks, or at least unhindered by inverse density dependence at low densities. Interactions between species may also hinder the recovery process. The recovery of Northwest Atlantic cod, which collapsed round 1990, is considered to have been hampered because of predation of seals (Fu *et al.* 2001, Bundy 2001).

It seems that the ecology of recovery does not really differ from 'basic' ecology. The same phenomena and complications that influence the population dynamics of species at higher densities facilitate or deter recovery, except of course for elements confined to low population sizes, such as the Allee effect. In order to successfully manage recoveries we require adequate knowledge of life history characteristics, population dynamics, and the role of interspecific interactions of the species in question.

4.2 Harvesting strategies

All natural populations show fluctuations in numbers over time. Fluctuations in the population size of natural populations are an intensely studied ecological subject (Jonzén *et al.* 2002). These fluctuations are caused by both endogenous and exogenous (Turchin 1999, Lundberg *et al.* 2000b, Fromentin *et al.* 2001) processes that affect the growth and survival of eggs and larvae, growth and mortality during the adult phase, and behavioural processes such as migration or density dependent habitat use (Jennings *et al.* 2001). Moreover, temporal variability in population numbers is an important factor in determining the extinction probability (Belovsky *et al.* 1999). For successful management of fluctuating populations, a number of articles have emphasized the use of threshold harvesting strategies (Lande *et* *al.* 1994, 1995, 1997, Saether *et al.* 1996, Engen *et al.* 1997, Ludwig 1998). In particular, the inferiority of the proportional harvest strategy, as compared to threshold strategies, has been highlighted.

Independent of the population dynamics or biological optimisation criteria, the harvesting strategy should include a population threshold. Should the population size of the targeted population decline below this threshold, harvesting should then be forbidden. In addition to increasing the expected long-term yields, threshold strategies are supposed to decrease the risk of resource depletion (Lande *et al.* 1997). Such results have been obtained using both stochastic diffusion models (Lande *et al.* 1994, 1995, 1997, Saether *et al.* 1996, Engen *et al.* 1997) and simulation studies (Ludwig, 1980, 1998, Quinn *et al.* 1990, Mace 1994). Moreover, threshold strategies supposedly function well in varying circumstances including critical depensation, catastrophes (stock collapses), and with strongly fluctuating net reproduction (Ludwig 1998).

The five different harvesting strategies used and compared throughout **II**, **III**, **IV**, **V** and **VI** are as follows (Y_t = yield at time t, h = harvest ratio, and N_t = population size at time t):

- Proportional harvesting (**II**, **III**, **IV**, **V**, **VI**). A constant proportion of the total harvestable biomass is removed annually, such that $Y_t = hN_t$.
- Threshold harvesting (**II**, **III**). A constant proportion of the total harvestable biomass will be removed when the biomass is above a threshold, T. Thus $Y_t = h\,N_t$ when $N_t > T$, otherwise $Y_t = 0$.
- Proportional threshold harvesting (**II**, III, **IV**). A constant proportion of the excess in the total harvestable biomass will be removed when the biomass is above a threshold, T. Thus $Y_t = h\,(N_t - T)$ when $N_t > T$, otherwise $Y_t = 0$.
- Precautionary threshold harvesting (**III**). A constant proportion of the total harvestable biomass will be removed when the biomass is above a reference threshold, T_{ref}, that is, $Y_t = h\,N_t$, else if biomass is $> T$, $Y_t = 0.5h\,(N_t - T)$. If biomass $\leq T$, $Y_t = 0$.
- Precautionary proportional threshold harvesting (**III**). A constant proportion of the excess in the total harvestable biomass above a threshold is removed; that is, when biomass $> T_{ref}$, $Y_t = h\,(N_t - T)$, else if biomass $> T$, $Y_t = 0.5h\,(N_t - T)$. If biomass $\leq T$, $Y_t = 0$.

4.2.1 Optimal harvesting strategy for "red" fish stocks?

Population dynamics of many natural populations, especially in marine environments, are dominated by low frequency variability, *i.e.*, the time series of their dynamics are positively auto-correlated (Steele 1985, II). Hence, they are said to show red dynamics (for a review, see Kaitala *et al.* 1997). This discovery has inspired a number of scientists to study the effect of autocorrelated environmental variability on the performance of different harvesting strategies (Koslow 1989, Walters & Parma 1995, Spencer 1997). The results seem to be dependent of the methodology used (such as the objective function). In II the question of harvesting inherently red resources was addressed with the help of data from the Norwegian spring-spawning herring (Clupea harengus) population. A feature characterizing this stock is the high variability in annual recruitment, which makes successful management of this stock a challenging task. The model used in II grasps the most important feature of the stock dynamics for this study: the inherent positive autocorrelation structure. Three different harvesting strategies (proportional, threshold, and proportional threshold harvesting strategy) were contrasted in terms of risk of quasi-extinction, mean annual yield, and the coefficient of variation (CV) of the yield.

The maximum yields given by the three strategies were comparable, and the quasi-extinction risks associated with these maximum yields were negligible. The CV of the yield was at maximum highest in the threshold harvesting strategy, even though in proportional threshold harvesting the CV corresponding to maximum yield was highest. Adding observation error to the population estimates had only a minor influence on the performance of the proportional harvesting strategy, but in the threshold and proportional threshold harvesting strategies, the quasi-extinction risk increases and average yield decreases. However, this happens only with higher than optimal harvest rates. The proportional threshold strategy was characterized by low risk levels independent of harvest rate, yet simultaneously the yields were satisfactory. Also with the observation error the proportional threshold strategy was the most risk averse strategy. However, no substantial advantages were associated with any of the strategies. Nevertheless, when the threshold level is increased, it allows for higher yields and substantially lower risk level. On the other hand, if observation error is again included, the yield decreases.

The results obtained in II may explain why fisheries scientist advocate using a decreased harvest rate so strongly — if overharvesting can be avoided, the choice of harvesting strategy is of less importance. However, with the current state of fisheries worldwide, where 28% of the harvested stocks are already overharvested or depleted and half of the stocks are fully exploited (FAO 2004) it seems rather unlikely that we could neglect different harvesting strategies. Nevertheless, II also implies that increasing the threshold has positive impact on the yields. But, II also points out another very important feature of fisheries management: the effect of observation uncertainty. In threshold strategies, a reasonable estimation of the stock size is necessary for making a decision on whether or not harvesting is allowed, and consequent setting of the quota. Perfect observation probably does not exist, except perhaps under laboratory conditions. However, counting all the fish in the sea, or even in the stock, is clearly an impossible task, and some observation error will therefore always arise.

4.2.2 Threshold strategies coupled with size-selective harvesting

All exploitation is selective, be it for moose harvesting where large antlers might be favoured (Solberg *et al.* 2000) or deer hunting for individuals with high quality antlers (Scribner *et al.* 1989). Size selective processes generally characterize fishing: the mesh size of the nets and traps defines the size, and thus age of the individuals caught (Myers & Hoenig 1997, Jennings *et al.* 2001). Myers & Mertz (1998) suggest that fish should be allowed to spawn at least once before becoming vulnerable to harvesting. They also point out that if the age-selection regime is shifted, previously sustainable harvesting can become unsustainable (Myers & Mertz 1998). There are also possible downsides to size-selective harvesting, in particular, the evolutionary effects associated with them have raised discussion (Jackson *et al.* 2001, Ratner & Lande 2001, Conover & Munch 2002, Stergiou 2002, Ernande *et al.* 2003). In the worst case, size-selective harvesting may lead to evolutionary changes by favouring slow growing, early maturing fish. This could be avoided by introducing a maximum size limit in addition to a minimum size limit (Conover & Munch 2002). Moreover, a reasonable rate of harvesting can increase the individual size via density dependent somatic growth (Lorenzen & Enberg 2002). After the collapse in the 1960's, the Norwegian spring-spawning herring matured earlier but at bigger size than before the collapse. This was due to growth-related phenotypic plasticity rather than an evolutionary response to harvesting (Engelhard & Heino 2004). Conover & Munch (2002) show in their experiment that in only four generations the size of the Atlantic silverside (*Menidia menidia*) evolved according to their harvesting regime, *i.e.*, harvesting either small (slow growing) or large (fast growing) individuals resulted in larger or smaller average size, respectively. In my opinion however, their results are slightly biased because their study species has a generation time of one year. If we contrast it with, for example, the Norwegian spring-spawning herring, where only 15% of the individuals at the year class 4 are mature and only age class 6 is fully mature, the selection processes are hardly comparable. Harvesting small herring, *i.e.*, immature individuals, more than anything substantially robs the future growth potential. However, in my studies I have neither directly studied the possible evolutionary nor the phenotypic effects of size-selective harvesting, only their effect on population dynamics and the resulting harvests and other related variables.

In chapter **III**, my aim was to explore the performance of different harvesting strategies in an age-structured, heavily fluctuating population. In addition I included an analysis on the effect of the age/size of fish entering the harvestable stock (note that age selective harvesting can be considered alike to size selective harvesting, Halliday & Pinhorn 2002). My investigation revealed that for management of age-structured populations, the proportional threshold strategy seems to be optimal in terms of mean annual spawning stock size and yield, maximum yield, biological (quasi-extinction) risk, and the CV of yield (**III**). When considering the length and frequency of harvest moratoria caused by threshold strategies, the two precautionary harvesting strategies I developed in **III** performed even better. Based on a comparison with the results of II, it is noteworthy that increasing structure (*i.e.*, age-structure) in the model affects the predictions obtained. Increasing the age at which individuals enter the fishery was substantially correlated with positive effects such as increased yields, decreased CV of yield and biological risk.

The positive effects of increased first harvest age are particularly interesting considering that one component of the collapse of the Norwegian spring-spawning herring in the 1960's is believed to be the overexploitation of not only adult, but also juvenile herring (Toresen & Jakobsson 2002). The displeasing feature of threshold harvesting strategies, the obligatory years with no harvesting, could be tackled with the precautionary strategies developed in **III**. Both the average length and frequency of these no-take periods were reduced with the usage of these bi-stepped precautionary strategies.

4.3 Managing communities

"Given this bewildering complexity in food-web interactions, can ecologists hope to predict the outcome of perturbations on natural systems?" — Smith (1997)

In addition to the effects of harvesting to the target species, harvesting a species belonging to an ecological community can have direct and indirect consequences for non-target species as well. Worldwide, marine fisheries discard 27 million tons of non-target animals annually, an amount equal to 1/3 of the total annual landings (Alverson *et al.* 1994). Moreover, not only harvesting techniques, but direct and indirect interspecific interactions may also cause the non-targeted species to suffer from the harvesting. This may lead to effects cascading through the ecosystems and to dramatic changes in the composition and structure of communities. The number and type of multispecies fisheries models has increased dramatically over the last couple of decades. In multispecies management, complications arise with the formulation of strategies and objectives. At present, multispecies fisheries management commonly deals with specific problems, such as reducing the effect of trawling on benthic diversity (Jennings *et al.* 2001). Thus contemporary multispecies management is not holistic: instead it means incorporating somewhat more within the management consideration than just the single species (Jennings *et al.* 2001). Unfortunately, for a realistic assessment of indirect fisheries effects the scientific understanding of interspecific interactions is still too weak (Jennings *et al.* 2001). In **IV** and **V** a special emphasis is put on these indirect effects.

The early multispecies considerations focused on predator-prey relationships (*e.g.*, May *et al.* 1979). In most multispecies fisheries models, competition is applied in a weaker sense, requiring that any change in abundance of one species be compensated in the trophic structure, by reciprocal changes in abundance of species with overlapping diets (Hollowed *et al.* 2000).

In **IV** and **V** the focus is on communities consisting entirely of competitors and the only source of variation between the species is in their species-specific interaction strengths.

4.3.1 Performance of a threshold strategy

In chapter **IV** I studied the applicability of a threshold strategy in the competitive community context. I confined the study to locally stable communities with the number of species *S* ranging from 4 to 10. The results showed that even though threshold strategies may perform very well in single species management, under a multispecies management framework they do not necessarily do so. The effect of increasing diversity in the proportional harvesting strategy seemed to be dependent on the species targeted by the harvesting: if the most abundant species was the target of the harvesting, increasing community size increased the relative reduction in community size, whereas when the least abundant species was harvested, increasing community size decreased the relative reduction in community size. Previous studies have shown that extinction or removal of a community member may lead to cascading extinctions of other community members (Paine 1966, Estes & Palmisano 1974, Mittelbach *et al.* 1995, Lundberg *et al.* 2000a), while Fowler (*in press)* has shown that predictions can be made about which species are likely to be involved in these extinction events if the relative density of community members is known. I show (**IV**) that a mere reduction in the population density of a single community member may lead to cascades of extinctions. Particularly noteworthy is that even though the proportional threshold harvesting strategy safeguards the targeted species, the amount of non-target extinctions is even higher than with the proportional strategy. In the proportional threshold strategy the target species remains extant, while with the proportional strategy the target species goes extinct more easily. This possibly results in prolonged disturbance of the community that seems to cause more changes in the community composition than mere removal/extinction of a community member. The effect of increased harvest rate was parallel in all the response variables, clearly showing the negative effects of an elevated level of disturbance.

4.3.2 The effect of local stability state

Local stability properties can be expected to influence a community's response to disturbances. In **V** the effects of population management on competitive communities was investigated. The response of locally stable and locally unstable communities of varying size (between *S* = 4 and *S* = 10) to three different management procedures;

harvesting, harvesting with non-target catch, and stocking were examined.

The effects of management in competitive communities extend far beyond the target population. An essential role is played by the stability properties of the community under management. In general, locally unstable communities are more vulnerable to perturbation. The relative density of the target species has its marked effects on some of the studied response variables. Most remarkable is that even a small (2.5% annually) increase in the population size of the target species may cause the extinction of other community members. These results emphasize the importance of considering multispecies interactions in population management.

Petchey *et al.* (2004) criticize the use of community models consisting of only one trophic level in predicting the effects of species loss. However, using multi-trophic models in by no means simple: first, models for more complex communities are harder to formulate and analyze, indirect effects make predicting the effects of disturbance difficult (even though this happens also in **IV** and **V**) (Yodzis 1988). Also the order at which the species go extinct has a major influence on a multilevel system (Petchey *et al.* 2004). Considering all this, and the fact that consequences of species loss are by no means clear in the single trophic level model either, it seems that keeping to a model with only competitors provides enough of a challenge for understanding the indirect effects of harvesting.

4.4 Marine reserves

4.4.1 Using marine reserves to ensure sustainable harvesting

Marine reserves are a relatively new and emerging concept for conservation and management of exploited marine resources (Diamond & May 1976, Game 1980, Demartini 1993, Botsford *et al.* 1997, Roberts 1997, 1998, Mangel 1998, Hastings & Botsford 1999, Lundberg & Jonzén 1999, Mangel 2000, Lockwood *et al.* 2002, Acosta 2002, Lubchenko *et al.* 2003). Marine reserves are defined as "areas of the ocean completely protected from all extractive and destructive activities" (Lubchenko *et al.* 2003), and can also be called "no-take areas" or "ecological reserves". Marine reserves have the potential for multiple positive influences, including protection of habitat, conservation of biodiversity, recovery of depleted or heavily exploited species, export of individuals to fished areas, and an 'insurance' against environmental or management uncertainty (Ludwig *et al.* 1993, Allison *et al.* 1998, NRC 2000). Environmental groups, nongovernmental organizations (NGOs), and conservation biologists are all pushing for significant increases in protected marine habitat (Sanchirico & Wilen 2001). For example, 400 prominent marine scientists endorsed in a proclamation at the First Symposium on Marine Conservation Biology to "increase the number and effectiveness of marine protected areas so that 20% of Exclusive Economic Zones and High Seas are protected from threats by the year 2020" (Carr & Raimondi 2001, as cited by Sanchirico & Wilen 2001). This is a notable and ambitious goal considering the current conditions where only 0.5% of the marine environment is protected (Roberts 1997). Negative effects of marine reserves concern fishermen in particular. They are afraid of decreases in yields as the harvestable area decreases.

Marine reserves are supposed to reduce fishing mortality, and for this reason they have been suggested for use in the recovery of depleted stocks. The success of population recovery using marine reserves depends on the level of reduction in fishing mortality. This is dependent on the relationship between patterns of movement, migration, and density-dependent habitat use in relation to the size, shape and location of the reserve (Jennings 2000).

The characteristics of the population dynamics of all the protected species will play a major role in the success of a population recovery through the establishment of a marine reserve. Sometimes the rate of population recovery following reserve establishment may be slow, or, if population size is too small, impossible (Jennings 2000).

Marine protected areas that aim to protect rare and vulnerable habitats can have a particularly important role in protecting, for example, breeding or nursery grounds or some other critical habitat in species' life history (Jones 2002).

4.4.2 Reserve design and the theory of Ideal Free Distributiion

A central concept in ecology of spatially distributed resources is the 'Ideal Free Distribution' (IFD), which is based on optimal foraging and competition between individuals (Fretwell & Lucas 1970, Fretwell 1972). IFD models anticipate that individuals distribute themselves in an environment such that per capita fitness will become equal regardless of the spatial unit in which an individual resides. Resources will be distributed among individuals in a way that makes moving elsewhere worthless in terms of fitness gains. The model is ideal as all individuals know the distribution and value of the accessible resources and the individuals are free to move to any sub-area and utilise its resources. The resulting distribution of individuals, via a fitness equalising process, is called the ideal free distribution (Fretwell & Lucas 1970).

The Ideal free distribution is directly related to the fitness of individuals. For this reason, authors have assumed in their models that the fitness in different environments will be balanced under IFD assumptions (Kaitala & Getz 1995, Lundberg & Jonzén 1999). Lundberg & Jonzén (1999) presented one of the rare studies of combining harvest protection areas with the ecological theory of IFD. They divided the area occupied by a population into two sub-areas, each having a different size, and assume that the driving force behind the redistribution of the individuals is the fitness gained in protected or harvested areas. Thus, I refer to their theory as fitness equalizing IFD. Their results show that the size and quality of marine reserve affect the possibility of protecting a large proportion of the population from exploitation, and that the harvest rate resulting in Maximum Sustainable Yield (MSY) does not change with size or quality of the reserve. The important assumption that is made with the fitness equalizing IFD is that the target of the harvest, *e.g.* fish, are aware of the harvesting and account for that in their fitness calculations. However in **VI** the problem was treated somewhat differently. Individuals were distributed according to resource availability. In such a case, it is common to talk about resource matching. In **VI** we studied the effects of the protected areas when the ecological mechanism behind the dispersal of individuals is based on the IFD that equalizes resources used by the individuals. The dependence of the yield on the harvest effort with resource matching IFD was strongly affected by the proportion of the total area that was protected. Moreover, the harvest effort maximizing the yield was dependent on the fraction protected. The maximum yield may be independent of the fraction of the protected area unless that fraction is large. In that case, the yield may deplete rapidly with an increase in the protected area. The most important and controversial finding was that the protected areas could be established without any loss of maximum yield.

There are multiple benefits associated with the establishment of marine reserves — they allow for a natural age structure of target species, maintain genetic variability, and prevent evolutionary changes caused by selective harvesting (Roberts *et al.* 2005). If all these conservation advantages can be achieved without reductions in yield (**VI**), it seems that establishment of marine reserves is a sensible management decision to make.

5. Conclusions

In this thesis my intention has not been to give specific instructions on how to manage certain populations—even though in some studies (II, **III**) data from a natural population has been used. Rather I have tried to provide insight into the relevant processes in sustainable resource management.

Recovery processes, which population management is concerned with to an ever-increasing degree, require close examination of the ultimate causes of the decline and the factors keeping the population size low. There may be multiple factors hindering the recovery, and direct and indirect interspecific interactions may further complicate the identification of factors keeping the populations at low density. However, the best approach is to invest effort into developing more sustainable ways of using natural resources — that way there should not be any need for recovery management. Unfortunately the current state of marine fisheries, for example, is such that attempts to manage recoveries are unavoidable. In these attempts the best possible knowledge of the life history characteristics (*e.g.* reproduction, resource use, dispersal) and biotic and abiotic interactions should promote the success of a recovery.

The performance of threshold strategies does not seem to be as unambiguous as one could hope for. In general, they work well when the harvest rate is rather high, or in other words, higher that the optimum (II). However, if there is uncertainty in the stock assessment (a highly likely situation), the yields will decrease and the biological risk increases. Still, the threshold strategies perform sufficiently. The inclusion of another, upper threshold value, as in the precautionary strategies developed in **III**, helps with a problematic feature of the threshold strategies, periods of no harvesting (moratoria). This means that reacting in a precautionary manner to the decline in stock size before the whole fishery is closed, will substantially reduce the length and frequency of moratoria. Moreover, the precautionary threshold strategies in **III** produced comparable yields with the threshold strategies, yet the biological risk estimations were lower in the precautionary strategies. Still, even if the problems of threshold strategies can be tackled in single-species management, applying them to management in a multispecies community produces new problems. Even though in the community setting using a threshold strategy reduces the chance of target species extinction, it causes an even higher probability of non-target extinctions than the proportional harvesting strategies. This result is an excellent example of how different predictions can be obtained using single- or multispecies approach.

Age- or size-selective harvesting is an issue that raises controversy. On one hand, capturing too young individuals (which consequently are also smaller) decreases the stock size and yields, because individuals are not allowed to breed. On the other hand, selective harvesting may cause genetic (or plastic) changes in the stock by favouring slow growing, early maturing fish. This too might result in decreased stock size and yields. I will thus only conclude that age-selective harvesting has a great potential in fisheries management assuming that its negative effects can be kept under control (by, for example, introducing upper size limits).

The human influence on Earth is massive, to the extent that it is fair to say that our planet is human dominated (Vitousek *et al.* 1997). Marine environments have by no means been safe from the human influence. As of 2003, 78% of recognized marine fisheries were fully- or overexploited or already depleted (FAO 2004). This enormous effect of man has already changed many communities and ecosystems, and it is fair to assume that, by now, the composition of several communities has changed from what it was before the exploitation started. In **V** the effect of disturbances on stable and unstable communities was studied, and based on that it seems that regardless of the initial stability state of a community, disturbances such as management may lead to drastic changes in the community composition. Moreover, as many natural communities have already been changed, it may be that the state they are at the moment is not a stable one, but more extinctions are to occur before a new stability state is established.

Based on the present thesis and numerous other studies, the use of marine reserves in the management of marine resources seems to be the most conservative and safest option. Marine reserves are potentially capable of reversing the general decline in marine resources, together with ensuring the future catches. At the same time, they protect the genetic diversity and also the habitat as such. Unfortunately the amount of evidence from natural environments is still scarce. However, marine reserves combined with more conventional management strategies outside the protected areas are very likely to be the best option for achieving long-term sustainability in marine fisheries.

Using simple models to tackle complicated issues may work well in providing guidelines for managing populations (Lande *et al.* 2001). From the various examples in fisheries management, one aspect in particular has crystallized: No matter how much effort is put on the theoretical and empirical development of means for sustainable use of natural resource, the ultimate goal is to manage human behaviour. At the base of this, fisheries management always has and always will be closely related to socio-economic and political considerations. Currently worldwide subsidies, *i.e.*, the amount of money spent on supporting fisheries, exceed the profits of fisheries (Jennings *et al.* 2001). The costs of fishing, supported by government subsidies, have exceeded direct income by more than $US50 billion each year in the recent past. How is this possible? The reasons that have lead to this situation are manifold, and it is clear that breaking down this system is by no means an easy or fast process. However, if we wish to fish in the future as well, it seems to be the only 'common sense' alternative. It is obvious, that changes this big will not happen overnight, but every beginning is small.

At times writing this summary has filled my mind with disbelief and sorrow — is the situation of aquatic resources really this bad? The "comforting" words of Frank and Brickman (2001) are anything but: "Fisheries Ecologists should not take this news [intense exploitation causes collapses in marine fish populations] too hard as other animal groups are faring no better for somewhat similar reasons. For example, among avian taxa currently endangered by extinction, 82% are associated with habitat loss, 44% by exploitation, 35% by introductions, and another 12% by pollution or natural events (Boyce 1992)". It seems unbelievable, that a task intuitively this simple — do not harvest too much — appears to be outright impossible. I certainly hope it is not.

Elegant theories and strategies will not help to conserve the exploited resources if not put into use. It seems that world may still not be ready for the sustainable use of natural resources—we just have to hope at the time it is, there still exists something to exploit.

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