0 48

utredning

Sustainable use of biodiversity

Bror Jonsson
Reidar Andersen
Lars P. Hansen
Ian A. Fleming
Arne Bjørge

NORWAY/UNEP EXPERT CONFERENCE ON
B·I·O·D·I·V·E·R·S·I·T·Y
TRONDHEIM · NORWAY · 24-28 MAY 1993

NINA

NORSK INSTITUTT FOR NATURFORSKNING

Sustainable use of biodiversity

Bror Jonsson
Reidar Andersen
Lars P. Hansen
Ian A. Fleming
Arne Bjørge

NORSK INSTITUTT FOR NATURFORSKNING

NINAs publikasjoner

NINA utgir fem ulike faste publikasjoner:

NINA Forskningsrapport
Her publiseres resultater av NINAs eget forskningsarbeid, i den hensikt å spre forskningsresultater fra institusjonen til et større publikum. Forskningsrapporter utgis som et alternativ til internasjonal publisering, der tidsaspekt, materialets art, målgruppe m.m. gjør dette nødvendig.

NINA Utredning
Serien omfatter problemoversikter, kartlegging av kunnskapsnivået innen et emne, litteraturstudier, sammenstilling av andres materiale og annet som ikke primært er et resultat av NINAs egen forskningsaktivitet.

NINA Oppdragsmelding
Dette er det minimum av rapportering som NINA gir til oppdragsgiver etter fullført forsknings- eller utredningsprosjekt. Opplaget er begrenset.

NINA Temahefter
Disse behandler spesielle tema og utarbeides etter behov for å informere om viktige problemstillinger i samfunnet. Målgruppen er "almenheten" eller særskilte grupper, f.eks. landbruket, fylkesmennenes miljøvernavdelinger, turist- og friluftslivskretser o.l. De gis derfor en mer populærfaglig form og med mer bruk av illustrasjoner enn ovennevnte publikasjoner.

NINA Fakta-ark
Hensikten med disse er å gjøre de viktigste resultatene av NINAs faglige virksomhet, og som er publisert andre steder, tilgjengelig for et større publikum (presse, ideelle organisasjoner, naturforvaltningen på ulike nivåer, politikere og interesserte enkeltpersoner).

I tillegg publiserer NINA-ansatte sine forskningsresultater i internasjonale vitenskapelige journaler, gjennom populærfaglige tidsskrifter og aviser.

Tilgjengelighet: Åpen

Prosjekt nr.: 35230

Ansvarlig sign:

Tor G. Heggberget

Oppdragsgiver:
Direktoratet for Naturforvaltning

Abstract

The diversity of life constitutes a unique resource for the human population. To date, 1.4 million species have been catalogued, which is only a fraction of the 5 to 50 million species thought to exist. Biodiversity consists of organic matter and genetic material, and it is exploited at different levels; population, community and ecosystem. A sustainable use of biodiversity should not interfere severely with the evolution rate of exploited populations. No part of the exploited species should at any moment be depleted, but instead controlled and conserved. Many renewable resources are commonly owned and freely accessible. Such freely accessible biodiversity is often over-exploited. This has likely been responsible, in part, for the present extinction rate of species which is far higher than ever before. To reduce this rate, nature management must be based on detailed knowledge about individuals, populations, communities and ecosystems. At present single-species models may be our best tool for attempting to manage biodiversity. It is important, however, that we continue to work to develop multi-species models that incorporate both exploited species and assemblages to which they belong. Moreover, we need to incorporate appropriate risk or uncertainty terms to the population estimates to account for natural fluctuations in population abundance. From a practical point of view, use of commonly owned biodiversity requires regulation. To do this, social, cultural and economic means often seem more effective than governmental management. Human disagreement, population growth, poverty and selfishness are major impediments. Sustainable use of biodiversity thus represents one of the greatest challenges facing human societies today.

Bror Jonsson, Reidar Andersen, Lars P. Hansen & Ian A. Fleming, Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

Arne Bjørge, Norwegian Institute for Nature Research, Post Office Box 1037 Blindern, 0315 Oslo, Norway.

Referat

Biologisk variasjon er en unik ressurs som vi mennesker kan utnytte. Til nå har ca. 1,4 millioner arter blitt registrert, og dette er bare en del av de mellom 5 og 50 millioner arter som man mener eksisterer. Ved bærekraftig bruk av biodiversitet skal framtidige generasjoner, hvis de vil, få tilgang til de samme ressursene og bruke dem på samme måte som vi gjør i dag. Biodiversiteten består av organisk og genetisk materiale, og den kan utnyttes på individ-, populasjons-, samfunns- og økosystemnivå. I vår tid er utryddelseshastigheten for artene større enn den noen gang har vært, og vår overbeskatning av dem er en av årsakene til dette. Vår bruk av biologiske ressurser bør imidlertid ikke være slik at den innvirker for sterkt på organismenes evolusjonshastighet; i steden for å forbruke dem bør vi kontrollere og sikre deres fortsatte eksistens. Ofte blir fritt tilgjengelige ressurser overbeskattet. Dette kan motvirkes ved en kunnskapsbasert naturforvaltning som bygger på vitenskapelig dokumenterte fakta. Til dette er énartsmodellene i dag vårt beste forvaltningsverktøy. Arbeidet med å videreutvikle flerartsmodeller må imidlertid fortsette. Modellene bør både inkludere de utnyttete artene og det systemet de lever i. Bestandsestimatene må også inneholde tilstrekkelig høye risikoledd for å hindre overbeskatning av bestander som naturlig varierer i antall. Men uansett hvor gode våre forvaltningsmodeller blir, vil det allikevel være vanskelig å begrense bruken av fellesressursene. Dette skyldes at mennesket er selvisk og ønsker å øke egne ressurser. Vårt økonomisystem er også kortsiktig og vanskeliggjør bærekraftig ressursbruk. Videre virker fattigdom og befolkningsvekst som hinder for langsiktig utnyttelse av biodiversitet. Bruken av fellesressurser må derfor reguleres nøye. For å lykkes i dette må man bruke både sosiale, kulturelle og økonomiske virkemidler. Totalt sett er bærekraftig bruk av fellesressurser en av de største utfordringene vi mennesker har i dag.

Bror Jonsson, Reidar Andersen, Lars P. Hansen & Ian A Fleming, Norsk institutt for naturforskning, Tungasletta 2, 7005 Trondheim

Arne Bjørge, Norsk institutt for naturforskning, Postboks 1037 Blindern, 0315 Oslo.

Preface

This review was commissioned by the Directorate for Nature Management for the 'Norway / UNEP Expert Conference on Biodiversity' in Trondheim, May 1993.

At present, species extinction rate is higher than ever before, and there is an urgent need for conservation of biodiversity. The human population is rapidly growing and posing an intense pressure for increased exploitation of nature. In fact, the situation may be such that biodiversity may not be saved unless we can find a sustainable use for it.

Here, we discuss whether or not it is possible to exploit biodiversity sustainably. Do today's biologists have the proper tools to manage exploited species, and if we have, are we willing and able to apply it successfully in nature management?

Trondheim, April 1993

Bror Jonsson
Reidar Andersen
Lars P. Hansen
Ian A. Fleming
Arne Bjørge

Contents

"It is in the nature of man that no one learns from experience. The follies of the fathers are lost on their children; each generation has to commit its own"

Frederick the Great (1712-86)

1 Introduction

The present document focuses upon exploitation of commonly-owned biodiversity in natural populations. We address the following questions: (1) can adequate schemes for the management of wild populations be developed, and if they can, (2) is it possible to apply them in the real world to secure sustainable use of our renewable, commonly-owned resources? We will not discuss uses directly related to industrialization and urbanization which cause changes to global climate as well as to terrestrial, freshwater and marine ecosystems.

The diversity of life on earth constitutes a critical resource for present and future generations. To date, 1.4 million species of organisms have been catalogued. This is only a fraction of the 5 to 50 million species thought to exist (Lubchenko et al. 1991).

Because only a small fraction of the earth is protected in parks and reserves, and the human population is growing, accelerated extinction of species and habitats will continue. Destruction and alteration of habitats leads to reductions in size of breeding populations, loss of genetic variability and potentially the extinction of species and ecological communities. Yet, continued human existence on earth depends on our ability to sustain the biosphere.

During 99% of its time on earth man has exclusively been gatherers and hunters, and even in modern societies, we depend heavily on natural and managed ecosystems for food, shelter and clothing. Man's existence relies on exploitation of populations of plants and animals. It is known that the Bush-people (Koi-san) in the Kalahari desert exploit 85 species of soft and hard fruits, 30 species of consumable roots and 54 species of vertebrates without over-exploiting them (Hubendick 1985). Such exploitation, however, often leads to over-exploitation even among indigenous people. In Australia, the aboriginals exterminated 13 of 17 large mammal species some 25-30 000 years ago (Lee 1982). The Mastodon and other large mammals in America were also exterminated by man.

Human population growth and activities, particularly those resulting in habitat destruction and degradation, are having pro-found effects on biodiversity (**figure 1**). Habitat destruction is the chief cause of the global extinction rate, estimated at 17 500 species per year (Wilson 1990). Habitat losses or modifications, species introductions and management of exploitable systems tend to decrease species richness and heterogeneity. Land-clearing, agriculture, fossil fuel consumption and industrialization add a variety of trace toxic substances, wastes, and pollutants to air, rivers and oceans. For instance, the long distance transportation of pollution resulting in acid rain has major effects on diversity in freshwater ecosystems in southern Scandinavia. During recent years 2 500 Norwegian populations of brown trout have been lost, and another 2 000 are threatened by the acidification (Berger et al. 1992). Acidification has also eradicated Atlantic salmon in 25 rivers in southern Norway. Extinction of locally adapted salmon stocks in this part of Norway represents 100 000-300 000 adult fish or a production of 300-1000 metric tonnes annually (Hesthagen & Hansen 1991).

Decreased productivity and biological diversity effect all levels within ecosystems, from individuals to species communities. Changes that occur within individuals have cascading effects influencing community structure through altered disturbance regimes and species interactions. These changes will in turn be expressed at the ecosystem level, and may also have deleterious consequences for human well-being.

Human action	Effects
Land-clearing	Deforestation
Water diversion	Desertification
Agriculture	Acid precipitation
Forestry	Eutrophication
Fisheries	Pollution
Hunting	→
Altered species distribution	
Grazing	Extinction
Fossil fuel consumption	Loss of genetic diversity
Industrialization	Loss of habitat diversity
Urbanization	
Introductions and transfers	

Figure 1
Human activities affecting maintenance of biodiversity (modified after Lubchenco et al. 1991).

2 Sustainable use of biodiversity

2.1 Definitions

'Sustainable exploitation' of biodiversity means that future generations will have access to the same resources we have access to, so they, if they want, can exploit them in the same manner as we did. This implies that no part of the exploited species at any moment should be depleted to the extent that random phenomena like genetic drift, inbreeding depression, demographic or environmental stochasticity threaten the viability and survival of populations and species.

Biodiversity consists of genetic diversity, species diversity and ecosystem diversity. Populations are assemblages of interbreeding individuals at given localities, i.e. local representatives of species. Within populations, genes interact in numerous combinations among individuals, called genotypes. Each individual genotype represents only a small proportion of the population's gene pool and it is the entire, effective population that is the incarnation of the gene pool. Therefore, by removing large proportions of the population we are also removing genes and thereby decreasing biodiversity.

No two individuals are identical genetically in sexually reproducing species. This variation contributes to the variation in phenotypic appearance of individuals which results from the interaction between genes and environment. When genes have a discontinuous effect on the phenotype, two or more variants, often denoted as morphs, may arise. This phenomenon, known as polymorphism, is common within species.

Among vertebrates fishes are phenotypically variable both within and among populations (Allendorf et al. 1987). This is, in part, related to the fact that the vast majority of fish exhibit indeterminate and flexible growth. They continue to increase in size throughout life given sufficient food resources. In contrast, most other vertebrates stop growing after attaining sexual maturity. Many fish populations are also divided into morphs exploiting different habitats and food resources (e.g. brown trout and perch (Alm 1959), whitefish (Svärdson 1979, Lindsey 1981), and Arctic charr (Johnson 1980)). As a result, conspecific morphs often differ in life history and morphology (Hindar & Jonsson 1982, Jonsson 1989).

This higher phenotypic variability among fish than other vertebrates is a consequence of greater susceptibility to environment-

al factors, and not due to higher genetic variability. In addition to indeterminate growth, fishes are heterothermic and environmental temperatures directly effect metabolic processes. Moreover, age and size at maturity are highly influenced by growth rate permitting greater flexibility without loss of reproductive success (Alm 1959, Jonsson et al. 1984). In contrast, genetic variability for life history traits is low relative to other vertebrates (Allendorf et al. 1987).

In the literature, genetic considerations have been given less attention in management of fish than bird and mammal populations (Allendorf et al. 1987). This may, in part, be due to the strong environmental influence on fish life histories. It may also result from difficulties in observing fishes, and making even rough estimates of basic genetic parameters.

Human exploitation of biodiversity occurs at three levels; (1) within-population, (2) among populations (community) and (3) within ecosystems. Exploitation at each level will affect nature differently, and our potential to control these effects will decrease the higher the level, and the greater the exploitation.

2.2 Production of organic matter

Within closed, exploited populations, four main processes occur (Russell 1931): (1) Recruitment of new individuals (R), (2) growth of tissue (G), (3) natural mortality (M) and (4) loss caused by anthropogenic use (E) (**figure 2**). Population biomass (B) is therefore: $B=(R+G) - (M+E)$. When gains from recruitment and growth equal losses from natural mortality and anthropogenic causes, population biomass is at equilibrium, whereas it becomes depleted when losses exceed gains.

The three terms: growth, recruitment and mortality are influenced by abiotic environmental variables like weather, as well as biotic variables like richness of resource base, competition, predation, and diseases.

Effects of anthropogenic use of biodiversity depend on the life history stage of the organism being exploited (e.g. growing juveniles, reproducing adults or post-reproducing individuals). In general, organisms initially grow rapidly, but their growth rate usually levels off with age, size and sexual maturity. Furthermore, female reproductive capacity usually limits the reproductive potential of the population, although exceptions are known (e.g. pipefishes (Syngnathiformes) where males are often the limiting sex).

Abiotic conditions Number of parents Fecundity and fertility of parent Competition Predation		Abiotic conditions Resource base Competition Age and size Sex and state of maturity

Recruitment → Biomass ← Growth

Natural mortality → Biomass ← Other loss

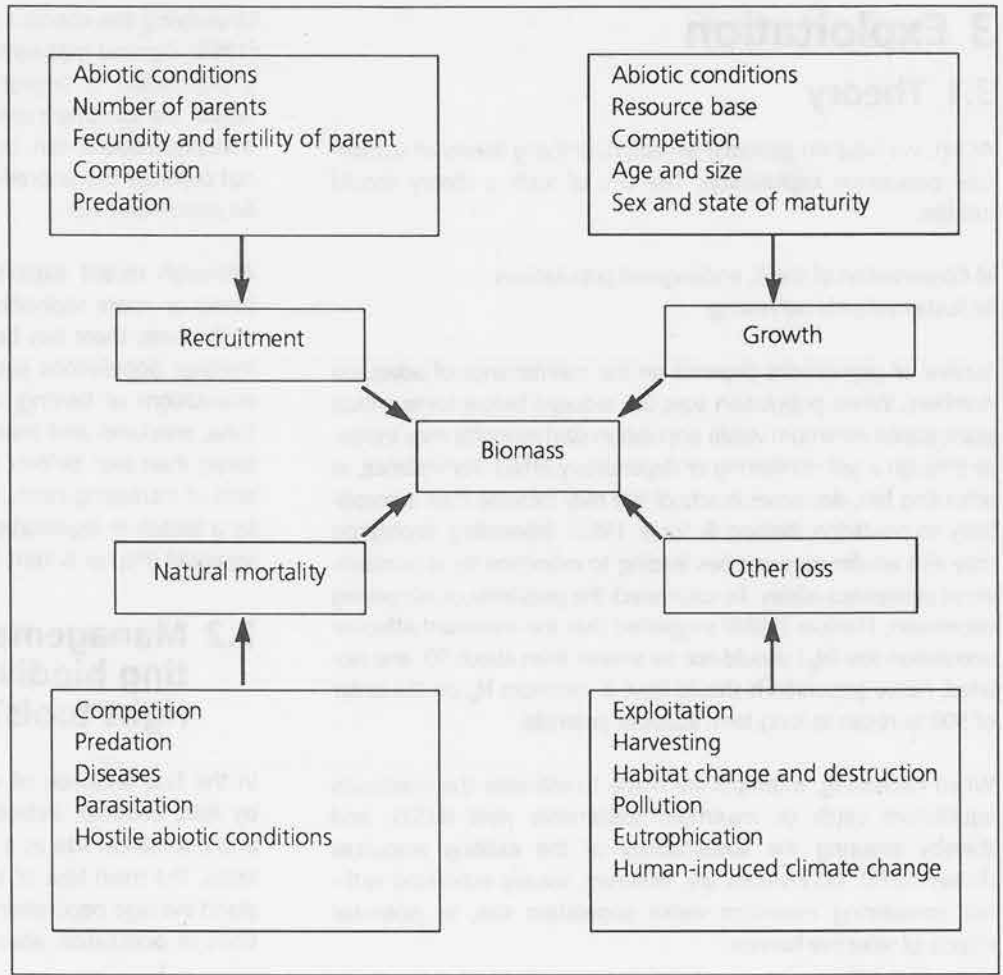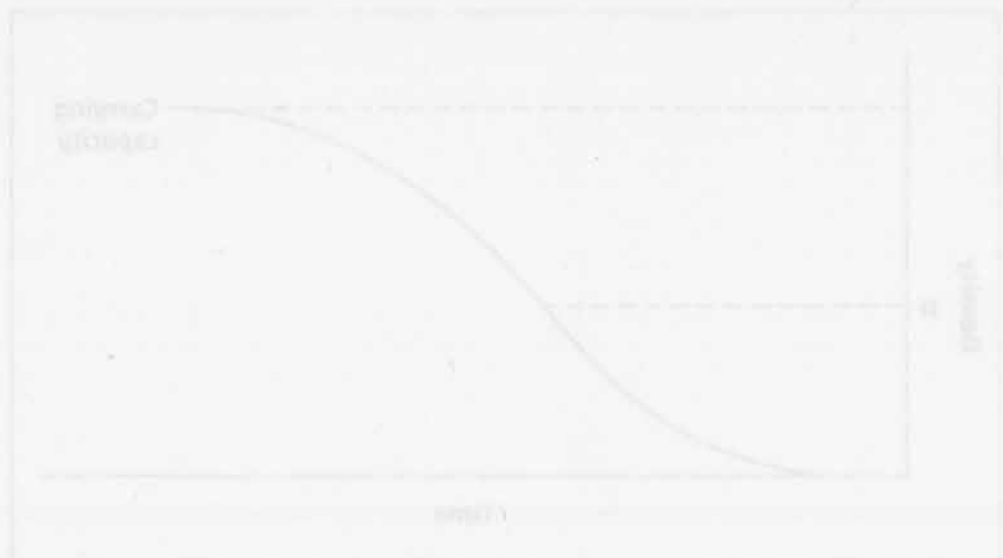| Competition Predation Diseases Parasitation Hostile abiotic conditions	Exploitation Harvesting Habitat change and destruction Pollution Eutrophication Human-induced climate change

Figure 2
Factors influencing biomass of closed populations. For further explanation see text.

3 Exploitation

3.1 Theory

As yet, we have no generally accepted, unifying theory of sustainable population exploitation. The aim of such a theory should include:

a) *Conservation* of small, endangered populations
b) *Sustained-yield harvesting*

Survival of populations depends on the maintenance of adequate numbers. When population sizes are reduced below some critical point (called minimum viable population size) mortality may increase through a self-reinforcing or depensatory affect. For instance, in schooling fish, decreases in school size may increase their susceptibility to predation (Nelson & Soulé 1987). Inbreeding depression may also accelerate processes leading to extinction by accumulation of deleterious alleles. To counteract the possibility of inbreeding depression, Franklin (1980) suggested that the minimum effective population size (N_e) should not be smaller than about 50, and isolated, native populations should have a minimum N_e on the order of 500 to retain its long-term adaptive potential.

When harvesting, attempts are made to estimate the maximum equilibrium catch or maximum sustainable yield (MSY), and thereby ensuring the sustainability of the existing resources (Ricker 1975). MSY-values are, however, usually estimated without considering minimum viable population size, or potential effects of selective harvest.

Underlying the concept of sustained-yield harvest is Leopold's (1955) sigmoid management principle, that net recruitment to a population is largest at intermediate densities, often far below the carrying capacity (**figure 3**). This principle assumes that populations can be maintained at equilibrium and does not consider the unpredictable nature of environmental factors on population size.

Although recent exploitation of natural resources has been based on more sophisticated and accurate models than those in the past, there has been little improvement in our ability to manage populations sustainably. In fishes, for example, most populations of herring, cod, hake, sardine, anchovy, pilchard, tuna, mackerel and many flat fishes, are all in a worse state today than ever before. In region after region the familiar pattern of increasing catch, stock depletion and collapse, followed by a switch in exploitation to the next population or species is repeated (Pitcher & Hart 1982).

3.2 Management models for exploiting biodiversity: do we have the right tools?

In the first textbook of wildlife management, written in 1933 by Aldo Leopold, individuals were treated as being identical, and population size as a stable average ignoring yearly fluctuations. The main task of early models was to attempt to understand average population size. Only more recently have fluctuations in population abundance and their relationship to envi-
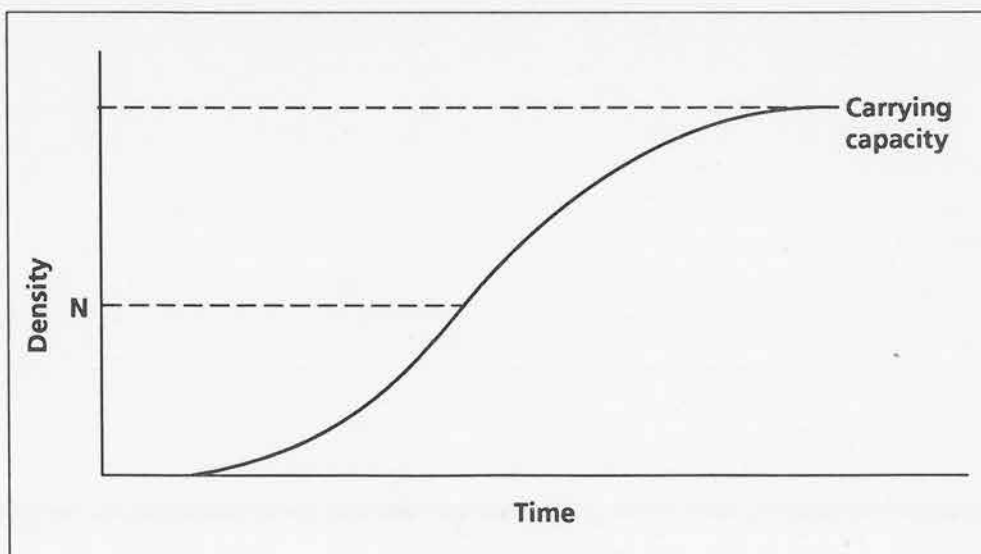
Figure 3
Sigmoid growth curve of populations. Net recruitment is largest at the density N.

ronmental change been investigated. Studies have aimed at expressing the rate of change in population size as a difference between birth rate and death rate with the difference being related to environmental factors (Caughley 1977).

At this stage, individuals were still handled as homogenic averages of populations. This made modelling feasible but ignored the essential fact that in any population there is a great variety of individuals of different ages, sizes, and reproductive capabilities.

At present, approaches have been developed that recognize individual differences in harvested populations. While individual-based models will be of great use in many areas of ecology, their usefulness in sustainable exploitation of biodiversity is questionable. This is not only due to the models' inherent limitations, but also to the lack of fine-tuned management techniques needed to apply the more precise information. A key advantage of individual-based models, however, is their ability to account for rare individuals, as well as rare events or circumstances which can come together in a few individuals (Gross et al. 1992). For some situations, rare individuals of a certain size, physiology or genetic composition have effects on the population far beyond their relative biomass or numbers.

Early management models were based on the ecology of single species. Soon, however, it was recognized that such models had limited use and could not explain ecosystem effects like those following the over-exploitation of the Atlanto-Scandinavian herring (see below). Therefore, ecosystem models began to incorporate some of the varied components of the system, and much work is now concentrated in developing multi-species management models. Such models incorporate not only the species in question and its resource base, but also effects of abiotic factors as well as competitors, predators, parasites etc. The models are very complicated and we should not be too optimistic about their present usefulness in nature management. There are many intra- and interspecific relationships in nature that are unknown, or not fully appreciated. There is also a general lack of long-term data series on interactions among ecosystem components. In addition, animals often exhibit alternative life-histories. For instance, populations may consist of both migratory and resident individuals which differ in resource use, growth rate and age at sexual maturity. We still do not know enough about how environment and genetics together determine whether organisms develop either of the two tactics. At present, the best use of multi-species models seems to be for quantification of species interactions in systems, and pinpointing of relationships where more precise knowledge is needed. For management of most systems, simpler

models that include the harvested species and their resource-base, may presently be the most operationable, though not completely satisfactory. We need to continue to increase our knowledge of systems. Some time in the future, we may develop harvesting models for natural ecosystems which include all important associations related to sustainable exploitation of the species of interest.

When harvesting organisms, it is often assumed that populations can be maintained at equilibrium, without considering the unpredictable nature of environmental factors affecting population size. Furthermore, it is presumed that the optimum harvest rate can be employed year after year without affecting population abundance. However, large fluctuations in abundance of exploited animal populations seems to be the rule rather than the exception. According to Caughley (1976), the reason is found in the paradox that nature management is essentially applied population dynamics, but the principles of population dynamics are seldom applied when natural populations are managed.

Environmental variation, causing much of the variability in population abundance, promotes co-existence among genotypes or species in communities (Lubchenco et al. 1991). Recent theoretical and empirical results have identified conditions that relate environmental variation to long-term community stability or change. These results have directed attention to the specific ways environmental fluctuations affect populations.

So far, models of the extinction of single populations have not included culling or harvesting, and models of harvested populations in fluctuating environments have ignored the possibility of extinction (Lande et al., in prep.). When we harvest populations where demographic parameters are missing, and where uncertainty exists in the estimation of total population size, the optimal strategy must be to lower the risk of over-exploitation, instead of obtaining maximum sustainable yield. We should only harvest at the calculated MSY-level when this is found to be acceptable through learning and adaptive management (Collie & Walters 1991, Hilborn & Walters 1992). In addition to uncertainty in demographic parameters and sampling error, it is of vital importance to take into consideration effects of variation in environmental factors. According to Lande et al. (in prep.) information about variation in demographic parameters for individual animals under different environmental conditions is a prerequisite for a sustainable use of biodiversity.

3.3 Ecosystems

It is often assumed that the rate of production of food is independent of the number of animals using it; animals comsume only a certain proportion and leave the capital intact (Caughley 1977). This, however, is not always the case, as illustrated by the following examples.

Important evidence concerning the nature of changes in vegetational diversity has become available from results of pollen analysis. Peat profiles from different localities yield a picture of forest history, and ratios of non-arboreal to arboreal pollen provide indications of changes in the extent of forest cover. Pollen diagrams from western Europe provide convincing evidence that forest vegetation almost universally preceded heaths.

These heathlands were heavily grazed by sheep, cattle, and wild ungulates in addition to hares, rabbits and different grouse species. In many areas, grazing promoted the replacement of vegetation communities. Gimingham (1972) gave evidence of the replacement of *Calluna*-dominated communities by *Agrostis-Festuca* where grazing pressure by rabbit was high. The latter was sometimes replaced by *Deschampsia flexuosa*, and under intensive grazing pressure the grass turf was destroyed and replaced mainly by lichens. Herbivores clearly influence plant communities.

Seldal et al. (in prep.) present a mechanism to explain the enormous variation in abundance of plant-grazing animals. These fluctuations in population density have been known at least since Biblical times. Seldal et al.'s (in prep.) hypothesis is based on a grazing-induced production of enzyme inhibitors in plants defending their tissue. Although the existence of such wound-induced proteolytic inhibitors has been known for about 20 years, they have thus far not been applied in theory to explain population dynamics of plant-animal interactions.

Production of enzyme inhibitors in grazed plants reduces their allocation of resources to growth and reproduction. This not only effects the population dynamics of the plants, but has wide ecosystem effects. Plant production of enzyme inhibitors will effect mono- and polygastric animals differently. Ruminants have the capacity to decompose these inhibitors in the rumen, whereas the monogastric animals do not. In Norway, the disappearance of the monogastric hares on islands where the polygastric roe deer have been introduced may be explained by this hypothesis.

When exploited ecosystems are managed, presence of pests, pathogens and diseases, and the interface between ecological processes and human social systems must be considered. Sustainability of ecological systems is one of the greatest challenges facing human society, yet it has to date received less attention than sustainability of lower levels. We therefore endorse expanded efforts to develop sustainable harvesting regimes based on ecosystem level considerations.

3.4 Populations

Man has always affected intraspecific diversity by selective harvesting of sex or age groups. For instance, the wapiti in North America was subjected to different harvesting regimes before and after European settlement (**figure 4**). Expected life span decreased, and total population structure changed as a consequence of changes in harvesting policy (Davis 1983).

Similarly, changes in harvesting policy for moose in Scandinavia altered population structure (**figure 5**). Under the present harvesting scheme, where adult females are protected and juveniles harvested selectively, population size has increased. By doing this, neither population size at carrying capacity (K) nor size at highest recruitment rate changed. Age and sex ratios, however,
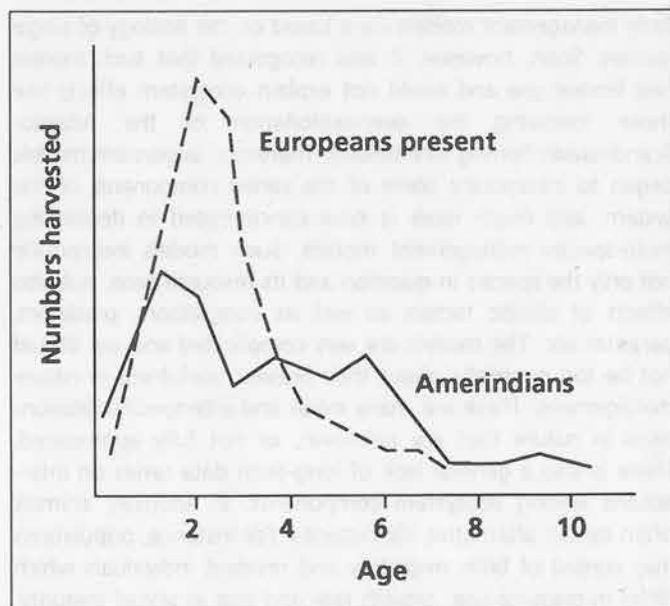

Figure 4
Effect of hunting. Before Europeans invaded North America, Amerindians mainly hunted adult red deer. Europeans harvested younger animals and mean age in the population decreased (after Hubendick 1985).

Figure 5

Changes in moose harvesting policy to protect adult females and chiefly harvest young animals do not effect population density at carrying capacity (K), but meat production increases (change from solid to dotted line). Age and sex distribution, however, do change.
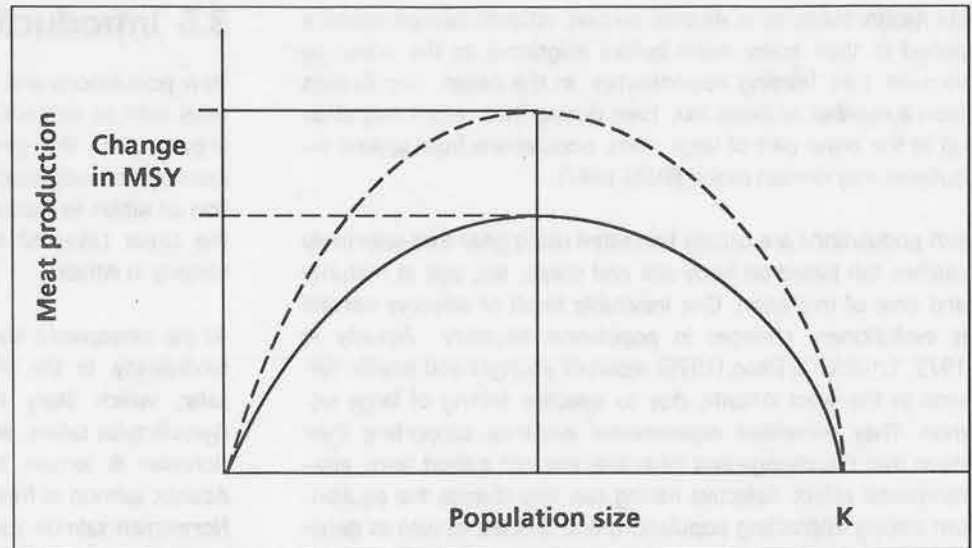
were altered. Furthermore, meat production at maximum sustainable yield increased.

In the Scandinavian moose, only a few percent of males reach an age of 4 years. Consequently, due to lack of mating competition, mostly yearling and 2 1/2 year old males mate with females. This obviously alters the selection regime acting on males, but whether or not the skewed sex and age distributions in any way effect the population negatively is still unknown. However, the effective population size, which is approximately equal to the least numerous sex (Ryman et al. 1981), is decreased. Thus, there may be conflict between increased productivity, through the extensive hunting of males, versus avoidance of inbreeding depression, which in the long run can threaten population viability.

3.5 Successful nature management demands detailed ecological knowledge

Sustainable exploitation and management of animal resources depend on precise knowledge of the dynamics of populations. The less knowledge we have, the more care we need to take when exploiting a renewable resource. Unfortunately, such detailed knowledge is often not available. Moose management in Scandinavia, however, is one example where harvest is based on detailed studies.

A general problem in harvesting models for ungulates is that several aspects of the reproductive biology greatly effect popu-

lation growth rate. Age at maturity, twinning rate and proportion of reproducing cows all effect population growth. These factors vary with body size and age of the animal, and in addition show geographic variation reflecting differences in environmental conditions and adaptations. In moose, there is a negative correlation between age at sexual maturity and life-time reproductive success. Cows which mature earlier begin to produce twins sooner than cows which mature later and as a result have higher reproductive output. Successful management implies that we know the effect of variation in food abundance on individual growth-rate and age at first reproduction and that this can be included in the management model. Based on data from Norwegian moose populations, a realistic population model must include:

- density-dependent effects on fecundity and mortality
- demographic parameters as a function of variation in environmental variables.
- effects of different harvesting policies
- dynamics of interactions between animals and their resource bases.

Many salmonid fishes are examples of less successfully managed species. The species are subdivided in discrete populations adapted to their local environments through natural selection. Genetic differences among populations are exhibited in a number of life history characters, e.g. growth-rate, age at sexual maturity, migration pattern, and disease and parasite resistance (reviewed by Jonsson 1982). Large rivers with several tributaries may even support several populations differing in a number of

life history traits, as in Atlantic salmon. Atlantic salmon spend a period in their home rivers before migrating to the ocean to increase their feeding opportunities. In the ocean, populations from a number of rivers mix. Even during their return migration up to the lower part of large rivers, populations from several tributaries may remain mixed (Ståhl 1987).

Fish populations are usually harvested using gear that selectively catches fish based on body size and shape, sex, age at maturity and time of migration. One inevitable result of selective harvest is evolutionary changes in population structure. Already in 1975, Schaffer & Elson (1975) reported younger and smaller salmon in the west Atlantic due to selective fishing of large salmon. They presented experimental evidence supporting their claim that this change was inherited, and not a short term, environmental effect. Selective fishing can also change the equlibrium among interacting populations and species, as well as genetic structure. Furthermore, over-exploitation of weak populations may be the result of selective harvest of mixed populations (Larkin 1981).

A genetic change due to selective fishing may also have occurred in several species of Pacific salmon (Ricker 1981). Large, fast-growing fish tend to be harvested more than small slow-growers, which may have led to a selective premium on slow growth or earlier sexual maturity. A recent decline in body-size of returning Pacific salmon of comparable year-classes, lends support to this suggestion (Healey 1986).

About 100 years ago, sockeye salmon on the west coast of North America showed a unimodal seasonal timing of return. Long term, heavy exploitation during mid-migration, has probably selected for bimodal timing of return of some populations (Mathisen 1980).

A sustainable harvest of mixed stocks and species can be maintained if the weakest component forms the basis for exploitation policy. To minimize undesirable effects of selective harvesting of fish species, it is important that spawning populations contain the genetic variation of the entire population. If populations have to be maintained by artificial propagation, the broodstock must reflect the genetic variation of the population. One should note, however, that artificial propagation may itself, inevitably lead to genetic change (Fleming 1993). In the management of salmon populations, it is recommended that exploitation be carried out on a population level. When based on biological knowledge, this will help ensure that exploitation is sustainable.

3.6 Introductions and transplantations

New populations and species are often introduced into ecosystems with or without purpose. Such introductions may heavily impact upon the genetic diversity of indigenous organisms. Examples of such introductions are numerous, e.g. the introduction of rabbit to Australia, red deer to New Zealand, lamprey to the Great Lakes of North America, and Nile perch to Lake Victoria in Africa.

At the intraspecific level, introductions may also seriously affect biodiversity. In the mid-1970's Atlantic (Baltic) salmon *Salmo salar*, which likely carried the parasitic, monogean fluke, *Gyrodactylus salaris*, were transplanted from Sweden to Norway (Johnsen & Jensen 1986). This ecto-parasite infects juvenile Atlantic salmon in freshwater. Due to a lack of resistance young Norwegian salmon usually die, whereas Baltic salmon have an evolved resistance to the parasite (Bakke et al. 1990).

These and many similar examples of biological transfers indicate that movement of species or populations into new environments should be made with utmost care and preferably avoided. Such introductions invariably alter and destroy, instead of increasing the biodiversity.

In some species, releases of artificially cultivated organisms are performed to enhance yield (supportive breeding). A classic example is the artificial propagation of salmon in the Baltic Sea to compensate for the depletion of salmon populations due to hydropower developments. A massive compensatory programme of releasing juvenile salmon started in the 1940s. Today, ca. 90% of the salmon in the Baltic are of reared origin. The releases support a heavy salmon fishery, and the remaining wild salmon are endangered (Ackefors et al. 1991).

In addition to resulting in over-exploitation of wild populations, supportive breeding influences the effective size and genetic structure of the populations it is meant to assist (Ryman 1991). Increases in reproductive success and survival of one segment of the overall population above all others, may reduce the total effective population size far below what it would have been without supportive breeding. There is a trade off between increased production and decreased effective population size and loss of genetic variability. When the absolute size of a wild population is small, supportive breeding can lead to serious depletion of genetic variability. When extinction probabilities are high due to demographic processes, and supportive releases are most warranted, the risk of negative genetic effects increase.

Hence, even in cases where only a single generation boost appears justified to reduce the probability of extinction, it must be carefully evaluated.

Biodiversity is also threatened by accidental releases of cultured organisms, which have often diverged from the wild form (e.g. cultured fishes reviewed by Fleming 1993). For instance, large numbers of the farmed Atlantic salmon escape from sea-pens along the Norwegian coast and migrate into rivers to spawn each year. As a consequence, they threaten natural populations through interference competition, gene flow and spread of parasites and contagious diseases (Egidius et al. 1991, Hindar 1992). Moreover, these salmon are now occurring in large numbers in nature. If not accounted for in stock assessments, wild populations may be seriously overexploited (Hansen et al. 1993).

4 Commonly-owned resources

4.1 Tragedy of the commons

Sustainable harvest of commonly owned biological resources is rarely observed. In fact, it has become a truism that such resources are over-exploited. Hardin (1968) popularized this in the term 'tragedy of the commons'. At an early stage, the exploiter expects a return proportional to the efforts put in (**figure 6**), and hard work produces handsome returns. New exploiters are attracted to the profitable resource in false hopes of similar gains. However, the profit of each exploiter decreases as the number of exploiters increase. Attraction to the resource can be expected to continue as long as rewards are greater than can be gained working elsewhere. By the time exploitation is no longer profitable to the individual, the resource may have been heavily over-exploited and even in danger of extinction (e.g. the passenger pigeon of North America). Of course this may not necessarily happen, but the point is that the process of exploitation of common property is inherently flawed because it automatically proceeds without reference to the biological status of the exploited population. Populations are in greatest danger when opportunity costs are low, as is likely to occur in remote areas with subsistence economies.

Commonly-owned resources are accessible to all members of at least one group of people, but are not owned by any specific member of the group. Thus controlling access to resources of potential users is problematic, and in some cases virtually impossible. Fugitive resources such as migratory fishes and wildlife, pose obvious difficulties to control, as do expansive resources such as ground water, range and forest lands, high seas and atmosphere. Such resources are free to be exploited and sold by the harvester, whose only cost is that of harvesting (e.g. high-seas fishes). The fact that each user is capable of subtracting from the welfare of others, is another characteristic of common-property resources. This characteristic creates a potential divergence between individual and collective economic rationality in joint use.

4.2 Over-exploitation in a monopoly-situation

There are many situations where renewable, natural resources are overexploited in a monopoly (Clark 1973, 1976, 1989). One simple situation occurs when costs of harvesting are low at small population sizes and exploitation efforts are coupled with high prices for small landings of the resource in demand. Under
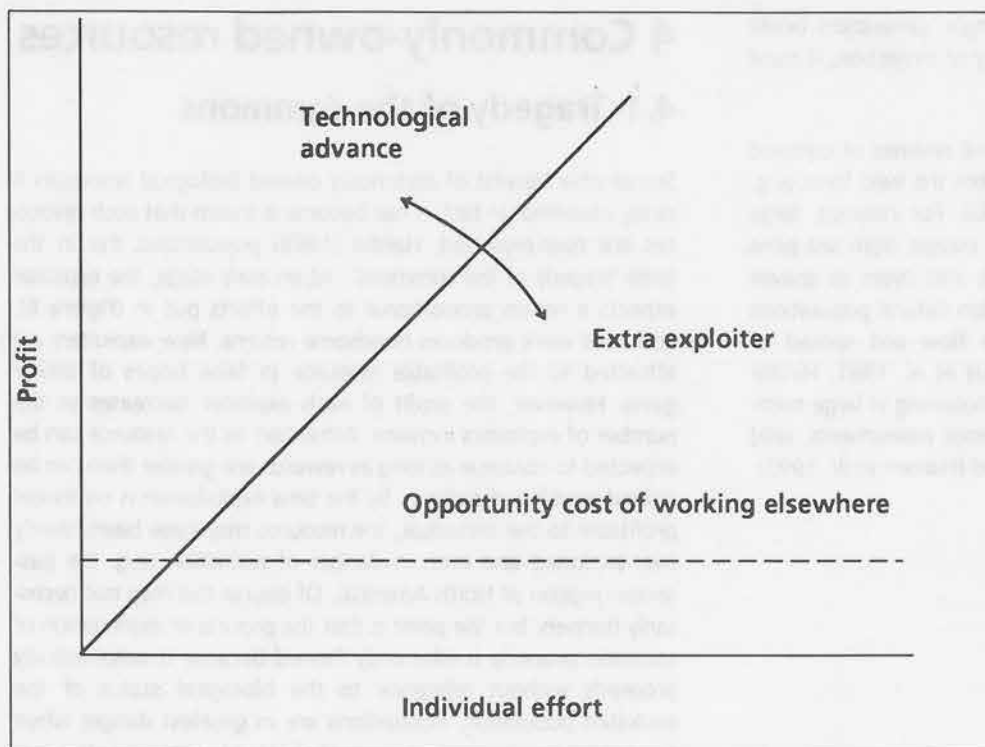
Technological advance

Profit

Extra exploiter

Opportunity cost of working elsewhere

Individual effort

Figure 6
Tragedy of the commons. Profit increases with technological advance, but decreases when extra exploiters are attracted. For further explanation see text (modified after Pitcher and Hart 1982).

such circumstances, it may be profitable even if it means harvesting every last animal. An even more dangerous mechanism is maximizing the present value income gain from exploitation. Simply put, the exploiter may ask whether it would be worth leaving a proportion of the population to provide future income or whether it would be better to catch all individuals now, sell the harvest and invest the money elsewhere? The manager can compare the expected returns of the two strategies in pure economic terms and make decisions based on that. He has to compare present, fairly certain rewards with more or less uncertain, future rewards either to himself and/or to his descendants, where interest rates and discount rates are included in the evaluation. When discount rates are high, it may pay even to harvest the last animal and invest the proceeds into a bank-account or some more profitable enterprise. However, if the manager is poor, there may be no choice but to think of the present (Stenseth 1992).

One example of over-exploitation under monopoly management (i.e. limited access) where biological resources have been depleted is the anchoveta *Engraulis ringens* off the coast of Peru. In most years cool, nutrient rich water wells up along this coast and supports the productive plankton community which provides food for both larva and adult anchoveta. In turn, anchoveta are prey for piscivorous birds including cormorants, boobies and pelicans which establish dense breeding colonies along the coast of Peru. The droppings of these birds form deposits of guano which are mined for fertilizer.

In the late 1960s, the anchoveta fishery was the largest fishery in the world. In 1972, it collapsed, with the catch dropping to one third of peak levels. The collapse was associated with an El Niño event. El Niño is a current which periodically floods the coastal Peruvian waters with warm, nutrient poor waters and persists with some fluctuations for up to 18 months. During El Niño, production of plankton and recruitment of anchoveta are reduced. Guano birds also suffer a decline in abundance as many adults abandoned breeding in response to the decline in their prey. In the absence of a normal fishery, the anchoveta population can recover quickly when normal upwelling conditions resume. The massive collapse in 1972 was probably caused by the intensity of El Niño combined with continued fishing pressure on a reduced population, which prevented a recovery once El Niño had receded (Cushing 1982).

Another recent example is the eco-crises in the Barents Sea. The fisheries there are managed by Norway and Russia, and herring and capelin are the major pelagic species foraging on plankton in the system. These two species therefore transform the rich

plankton production into a form that is available for piscivorous species such as large fish, sea birds and sea mammals. The herring population collapsed due to over-exploitation in the late 1960s. Since the collapse of the herring, the capelin has been a bottle-neck in the food web in the Barents Sea, and a key species in the ecosystem.

Oceanographic conditions and climate in the Barents Sea fluctuate with the influx of Atlantic waters. Periods with low sea temperature alternate with periods with higher temperatures. In 1982-3, there was a change from a cold to a warm period resulting in strong year-classes of herring and cod. Competition from herring and predation from cod on capelin increased, and in 1986, the capelin population collapsed. Significant reduction in quotas were recommended in 1983, and a zero quota was recommended in 1986. However, these recommendations were not implemented immediately and the fishery exasperated the extent of the collapse.

The near disappearance of capelin had dramatic impacts on higher trophic levels, individual growth-rate of cod decreased and cannibalism increased. The predicted increase in the commercially important cod population was severely hampered. Seabirds, particulary the highly specialized fish feeding common guillemot, suffered a severe decline. In 1987, all colonies of common guillemont surveyed had declined 15-25 % from 1985 (Vader et al. 1990). Several thousands of guillemonts washed ashore on the coast of Finnmark during winter 1986/7; they had probably starved to death.

When harp seals frequent coastal waters of Finnmark during their winter migration, they are vulerable to incidental captures by coastal gill net fisheries (Bjørge et al. 1981). The number of harp seals incidentally caught in Norwegian coastal fisheries varied between 500 and 2000 seals from 1981 to 1985. In 1986, the number of incidentally caught seals increased to more than 10 000, and in 1987 and 1988 totals of 56 000 and 26 000 killed seals were recorded (Haug et al. 1991). In 1985 the pup production of the Barents Sea was estimated to 140 000 pups. A dramatic reduction in production occurred in 1987, when only 85 000 pups were produced (Anon. 1989). The whole ecosystem in the Barents Sea had come out of balance due to over-exploitation of herring and capelin. This example shows how species interact in ecosystems, and depletion of some stocks may have vast effects on others.

4.3 Over-exploitation of commonly-owned biodiversity

Examples of over-exploitation of commonly owned resources are numerous. For instance, the recent development of fisheries in Antarctic waters has depleted many of the exploited populations (Kock 1992). In the Southern Ocean, 30 populations have recently been subjected to regular commercial exploitation. Status assessments of 13 of the exploited populations show that almost all are depleted. This has occurred despite regulation of the fishery around the Kerguelen Islands since 1978, and the Convention on the Conservation of Antarctic Marine Living Resources which came into effect in 1982.

Another example of over-exploitation of commonly owned biodiversity is the baleen whale. At the turn of our century, whaling started in Antarctica. At that time whale resources had no legislative protetction and exploitation was open to all nations. Antarctic whaling, which started with the easiest catchable humpback whale, was soon extended to the more profitable blue whales; thereafter shifted to fin whales and sei whales. When these more profitable species became depleted, the smaller minke whales were exploited (**figure 7**).

Regulations based on agreement between the participating nations were introduced in the 1930s. But the Blue whale Unit, introduced to regulate the supply of oil to the world market encouraged exploitation of depleted stocks. Following an attempt to regulate whaling in 1937, the International Convention for the Regulation of Whaling was signed in Washington in December 1946. At that time, participating nations wanted to protect all whale species. The history of whaling had been overfishing of area after area and species after species.

One important paragraph in the Convention was the institution of the International Whaling Commission (IWC). At first, however, IWC failed to regulate whale stocks and blue whales did not obtain protection until 1966. Moreover, in 1972 the IWC introduced species by species quota, the first step towards management based on scientific knowledge of the status of populations under exploitation.

In the 1970s, there was a clear demand for scientific advice about whaling, and in 1975, the IWC adopted the New Management Procedures (NMP). The NMP assumed that Maximum Sustainable Yield (MSY) of whale populations was 60% of the initial (pre-exploited) population size. Quotas were set for populations above the MSY-level, but it could not exceed
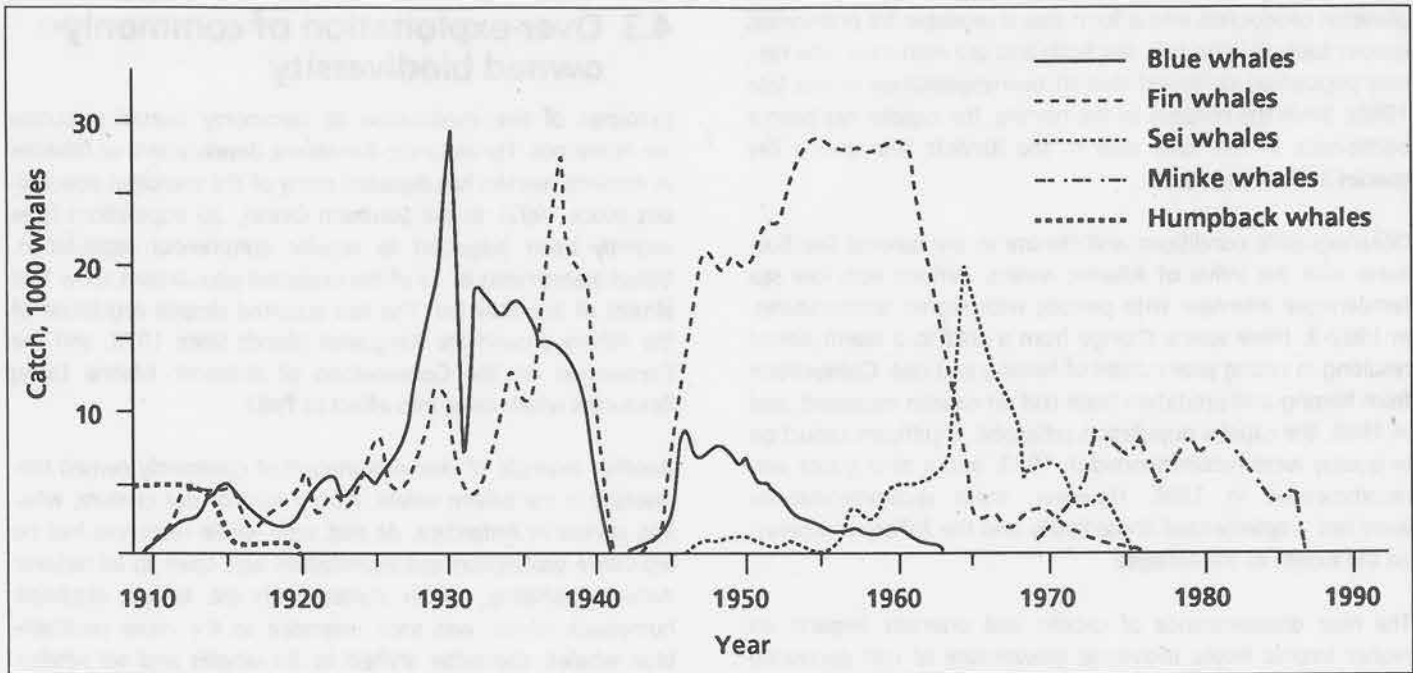
Figure 7
The shift to smaller, less profitable whale species as the larger whales became depleted by Arctic whaling.

90% of the MSY. For populations 10 % below the MSY-level, the quotas were gradually decreased until zero (IWC 1992a).

The NMP was a significant step forward, but quotas tended to fluctuate as estimates of initial and current population sizes changed from one year to the next. As a result, the mechanisms for gradually retarding exploitation with declining population size failed and exploited populations soon became depleted. When the IWC called for a moratorium on all commercial whaling in 1982 (enforced from 1986), it underlined the unsuccessful attempt at sustainable harvest of commonly-owned biodiversity. The IWC instructed its scientific Committee during the moratorium to conduct a Comprehensive Assessment of whale populations. This included an in-depth evaluation of status of whale populations and development of a Revised Management Procedure (RMP).

There appears to be only two solutions for the protection of freely accessible resources from overexploitation. (1) If the population is in superabundance compared to the greatest possible exploitation pressure, it may be safe even though commonly owned. This may have been the case with North American Pacific salmon before European settlement. (2) Many subsisten-

ce-level exploitations may be preserved by the sheer hazard and hardship of exploitation under tough conditions with simple equipment. Expected gain will be counterbalanced by the assessment of risk and danger. The situation will be stable only as long as the level of technology remains undeveloped. An example is Inuit traditional harvest of marine mammals, such as white whales, bearded seals and walrus in some areas (Burns 1981, Fay 1981, IWC 1992b).

4.4 Sustainable use of commonly-owned biodiversity: is it possible?

The development and implementation of the IWC Revised Management Procedure (RMP) for whaling may indicate whether or not sustainable harvest of whales is possible. The objectives for RMP are:

- Stability of catch limits, which would be desireable for the orderly development of the whaling industry;
- Acceptable risk levels so populations avoid depletion below a certain limit;
- Maximizing continued yield from the population.

Large baleen whales migrate over vast oceanic areas. Within these areas, they may or may not be divided into isolated sub-populations. To avoid depleting sub-populations IWC recommend that catch limits should be set for small areas only, and that the hunt should be in proportion to the number of whales sighted in the respective area (Young 1992). Whaling as recommended by IWC is based on the status of stocks and aimed at sustainable harvest to preserve populations and biodiversity.

Today, there is also a strong international opposition against whaling on ethical grounds. There is a growing comprehension of whales as intelligent mammals. Animals with advanced social structures, complex languages for communication and well developed intelegence that enables them to have conceptual memory, as well as experience pain, bereavement and sorrow. This new comprehension of the whales has brought ethical arguments into the whaling debate. The ethical arguments against whaling are enhanced by the tragic history of whaling and mismanagement of the whaling industry. It is possible that this debate will limit future whale hunting to a sustainable harvest (e.g. Holt & Papastavrou 1993).

From elsewhere, there are cases where commonly-owned resources seem to be exploited sustainably even though they are not superabundant relative to the exploiters' harvesting capacity. In these cases, however, the common resource is not a freely accessible resource, but instead limited by strong regulations. Berkes et al. (1989), reported four cases where common resource use did not result in overexploitation, at least on a short time scale.

The first example was from James Bay, northeastern Canada (Berkes et al. 1989). There, community-based beaver hunting occurs sustainably due to a territory system, with senior hunters and their families acting as stewards of specific territories, which at present ensures sustainable use.

The second example deals with lobster on the coast of the United States. It shows that communal territories exist even in societies that subscribe to the ideal of freedom of the commons. The lobster resource is vulnerable to overharvesting, but lobster stocks in Maine have remained sustainable. To go lobster fishing, one has to be accepted by the local community. Once accepted, a lobsterman is only allowed to fish in the territory held by the community. Interlopers are usually discouraged by surrepetitious violence.

The third case provides an alternative community-based solution to the common dilemma. In the trawl fishery for whiting in the New York Bight region, USA, fishermen belong to a cooperative. They have ready access to the best whiting grounds in the region, and often dominate the regional whiting market in winter months. The cooperative maintains relatively high prices for members through supply management; it limits entry into the local fishery and establishes catch quotas among members. Limited entry is achieved through a closed membership policy and control of docking space, effectively excluding non-members from whiting grounds and markets. Quotas are based on estimates of what the cooperative can sell to the regional market, and are achieved in ways that reward individual initiative but also discourage 'free-riding'.

Forests in Thailand comprise the fourth case. Traditionally exploitation of high-value timber was regulated by local governments, whereas use of low-value timber was essentially unregulated. Rapid commercial exploitation of teak in Thailand in the late nineteenth century led to the nationalization of all forests. State ownership failed to provide consistent enforcement, and also served to deny users the authority to manage local forests. Illegal logging, followed by further land clearing for cultivation became widespread. Although much of this land is still suitable for cultivation, there are few safeguards for conserving environmentally sensitive areas.

Lack of enforcement of state-forest property rights leading to accelerated degradation is not unique to Thailand. The nationalization of forests in Nepal (1957) and Niger (1935) produced similar outcomes. In Nepal, the situation is being ameliorated by the recreation of communal management at the local level. Without effective control by government, nationalization has often converted traditional communal property into *de facto* open-access resources which are then overexploited.

Hardin's (1968) model leading to the tragedy of the commons provides insight into the divergence between individual and collective rationality. It assumes that users are unable to limit access or institute rules to regulate use. Therefore, he finds over-exploitation to be inevitable unless privatization or governmental controls are imposed.

Recognition that users in some cases, as discussed above, have the potential, motives and means to act collectively opens up other policy alternatives and provides questions about why some communal management systems fail and others succeed. Success or failure of common-property resource management, at least in part, has to do with the exclusion and regulation of joint use. In the cases where sustainable use of biodiversity has occurred, common-property resources are not open for general

access. Property rights are by all means present. Moreover, property users are compelled by strong social pressures to conform to carefully prescribed and enforced rules of conduct. Thus, voluntary collective action is feasible, although rare. However, we do not know for how long such systems will be stable. But even if such regulations are successful only in the short term, they do slow down the loss of biodiversity and constitute a step in the right direction.

5 Conclusion: towards a more effective management strategy for sustainable use commonly-owned biodiversity

Commonly-owned biodiversity can only be used sustainably if individual freedom in exploiting it is limited by rules and regulations. If not, extinction of species will remain unacceptably high. To regulate resource use, social, cultural and economic means often seem more effective than governmental management. As we have seen, there are cases of good, long-term management of commonly-owned resources. In modern societies, old traditions often dissolve and long-term perspectives on resource use disappear. This may be, at least partly, a consequence of higher mobility and looser social bounds.

Nature management should involve populations, and where possible, include higher levels of ecological organization. Populations may be managed as separate units (single-population approach) where an appropriate risk or uncertainty term is added to population estimates in order to prevent over-exploitation. Under the alternative 'multi-species approach', one treats the exploited species and its assemblage as a whole, in terms of energy flow, harvest and production.

The single-population approach is more easily applied. When used, however, one should draw more attention to reducing risks than to maximizing harvest. Under the multi-species approach where ecosystem dynamics are included, the exploitation rate may parallel a variable production of the harvested species. Multi-species-models might also help understanding dynamics and interactions between components at various trophic levels. However, with our present state of knowledge, multi-species-models are difficult to turn into effective management tools even for simple systems, due to lack of knowledge about mechanisms structuring ecosystems and of suitable long-term data series. However, multi-species considerations should, at least, be used to improve our single-species management.

Knowing all this, will it be easy to apply the principle of sustainable use of biodiversity? The answer is no for at least four reasons. First, no matter what rules we make, and no matter who is responsible for setting them, some people will not agree to them (Stenseth 1992). Second, with a rapidly growing human population we may not be able to stop over-exploitation, even if

we want to do so (Ehrlich et al. 1973). Third, large parts of global biodiversity are located in countries where the GNP is low and poor economy may limit the possibility of having a long-term perspective in managing biodiversity (Janzen 1992). Fourth, human nature is selfish (e.g. Dawkins 1976), and the benefits of managing biodiversity sustainably and the ability to cooperate to do so have to be developed, for they do not come naturally. All four dilemmas must be overcome to save biodiversity for future generations.

Sustainability is a human-centred concept and as a result, divisions in thinking exist between concern for sustainable economic output versus concern for ecologically sustainable economic activities. Since resource exploitation is governed by the perceived self-interest of individuals or groups, sustainability of resources requires approaches that alter people's perceptions. There is thus a need, in part, for economic incentives to promote sustainable use of biodiversity.

One means of promoting sustainable use of biodiversity is economic subsidies to encourage sustainable use, rather than over-exploitation. There is the danger, however, that inappropriately applied subsidies will themselves lead to over-exploitation. For example, when subsidies provide incentive for the harvest of resources even if they are no longer economically profitable, as occurred in many marine fisheries (Larkin 1977). Subsidies may also keep prices low and thereby, decrease the value of biological resources and threaten sustainability.

Some biodiversity may be protected if its economic value is increased (Janzen 1992). An increase in price is an effective incentive, especially in countries where the GNP is low.

Laws and regulations that govern resource use and rights may also be effective means of maintaining sustainable use of biodiversity. They can guide the economy, while markets would efficiently help society achieve its goals. For instance, Costanza & Daly (1992) suggested a policy toward sustainable exploitation based on heavily taxing use of ecological resources, especially energy. It would promote technological advances to increase efficiency, while discouraging thoughtless, shortsighted resource use, one of the main impediments to the conservation of resources for the future. The concept is simple and contains a key element for success, market incentive. However, such a policy would only work with national and international cooperation. It would require international agreements or at least national ecological tariffs to prevent some countries from flooding markets with untaxed natural resources or products made from them.

Thus, even if biologists are able to make management schemes for sustainable use of biodiversity, our often "short-sighted" economic system makes the application of this knowledge difficult. Our selfish human nature has to be restricted to reach our common goal of sustainable use of biodiversity.

6 Summary

* Diversity of life constitutes a unique resource for the human population. It consists of genetic, species and ecosystem diversity.

* Sustainable exploitation of biodiversity means that future generations will have access to the same resources we have access to, so they, if they want, can exploit them in the same manner as we did.

* Commonly-owned biodiversity can only be used sustainably if individual freedom in exploiting them is regulated by social, cultural and economic means.

* To reduce the present extinction rate of species, nature management should be based on detailed knowledge about individuals, populations, communities and ecosystems.

* Although single-species models at present are our best management tool, we should continue our efforts in developing multispecies models for exploited ecosystems.

* Appropriate risk or uncertainty terms should be incorporated in population estimates to account for fluctuations in abundance during exploitation.

* Sustainable use of biodiversity is difficult to apply because of human disagreement, population growth, poverty and selfishness.

* Economic subsidies can help users in exploiting biodiversity sustainably, but inappropriately used, it can also lead to overexploitation.

* Sustainable use of biodiversity is one of the greatest challenges facing human societies today.

7 Literature

Ackefors, H., Johansson, N. & Wahlberg, B. 1991. The Swedish compensatory programme for salmon in the Baltic: an action plan with biological and economic implications. - ICES mar. Sci. Symp. 192: 109-119.

Allendorf, F.W., Ryman, N. & Utter, F. 1987. Genetics and fishery management: Past, present and future. - In Ryman, N. & Utter, F., eds. Population genetics and fishery management. Washington Sea Grant Publications/ University of Washington Press, Seattle. pp. 1-19.

Alm, G. 1959. The connection between maturity, size and age in fishes. - Rep. Inst. Freshwater Res. Drottningholm 40: 6-145.

Anon. 1989. Ressursoversikt for 1989 og havmiljørapport for 1988. - Fisken og Havet 1989 (Særnummer 1): 1-99.

Bakke, T.A., Jansen, P.A. & Hansen, L.P. 1990. Differences in the host resistance of Atlantic salmon (Salmo salar) stocks to the monogean Gyrodactylus salaris Malmberg, 1957. - J. Fish. Biol. 37: 577-587.

Berkes, F., Feeny, D., McCay, B.J. & Acheson, J.M. 1989. The benefits of the commons. - Nature (London) 340: 91-93.

Berger, H.M., Hesthagen, T.H., Sevaldrud, I.H. & Kvenild, L. 1992. Mapping of fish community status in relation to acidification in Norwegian lakes. - NINA Forskningsrapport 32: 1-12.

Bjørge, A., Christensen, I. & Øritsland, T. 1981. Current problems and research related to interactions between marine mammals and fisheries in Norwegian coastal and adjacent waters. - ICES, C.M. 1981/N:18: 1-10.

Burns, J.J. 1981. Bearded seal - Erignathus barbatus Erxleben, 1777. - In Ridgway, S.H. & Harrison, R.J., eds. Handbook of marine mammals, vol. 2: Seals. Academic Press, London, pp. 145-170.

Caughley, G. 1976. Wildlife Management and the dynamics of ungulate populations. - In T.H. Coaker, ed. Applied Biology, pp. 183-246.

Caughley, G. 1977. Analysis of vertebrate populations. - John Wiley & sons. 232 pp.

Clark, C.W. 1973. The economics of overexploitation. - Science 181: 630-634.

Clark, C.W. 1976. Matematical bioeconomics: the optimal management of renewable resources. - Wiley Interscience, New York.

Clark, C.W. 1989. Bioeconomic modelling and resource management. - In S. A. Levin, T.G. Hallam & L.J. Gross, eds. Applied Mathematical ecology. Springer-Verlag, Berlin. pp. 11-57.

Collie, J.S. & Walters, C.J. 1991. Adaptive management of spatially replicated groundfish populations. - Can. J. Fish. Aquat. Sci. 48: 1273-1284.

Constanza, R. & Daly, H.E. 1992. Natural capital and sustainable development. - Conserv. Biol. 6: 27-46.

Cushing, D.H. 1982. Climate and fisheries. - Academic Press, London.

Davis, S. 1983. By their garbage shall they be known. - New Sci. 17/11: 506-515.

Dawkins, R. 1976. The selfish gene. - Oxford University Press, Oxford.

Egidius, E., Hansen, L.P., Jonsson, B. & Nævdal, G. 1991. Mutual impact of wild and cultured Atlantic salmon in Norway. - J. Cons. int. Explor. Mer. 47: 404-410.

Ehrlich, P.R., Ehrlich, A.H. & Holdren, J.P. 1973. Human ecology. - Freeman, San Francisco.

Fay, F.H. 1981. Walrus - Odobenus rasmarus (Linnaeus, 1758). - In S.H. Ridgeway & R.J. Harrison, eds. Handbook of marine mammals. Vol. 1: The walrus, sea lions, fur seals and sea otter. Academic Press, London. pp. 1-23.

Fleming, I.A. 1993. Reproductive success and the genetic threat of cultured fish to wild populations. - Am. Fish. Soc. Symp., in press.

Franklin, I.R. 1980. Evolutionary change in small populations.- In M.E. Soulé & B.A. Wilcox, eds. Conservation biology: An evolutionary-ecological perspective. Sunderland, Massachusetts: Sinauer Associates. pp. 135-150.

Gimingham, C.H. 1972. Ecology of heathlands. - Chapman and Hall, London.

Gross, L.J., Rose, K.A., Rykiel, E.J., Van Winkle, W. Jr. & Werner, E.E. 1992. Individual-based modelling: summary of a workshop. - In D.L. DeAngelis & L.J. Gross, eds. Individual-based models and approaches in ecology. Chapman and Hall, New York, London. pp. 511-522.

Hansen, L.P., Jakobsen, J.A. & Lund, R.A. 1993. High numbers of farmed Atlantic salmon, Salmo salar L., observed in oceanic waters north of the Faroe Islands. - Aquacult. Fish. Managem. 24: 00-00.

Hardin, G. 1968. The tragedy of the commons. - Science 162: 1243-1248.

Haug, T. Krøyer, A.B., Nilssen, K.T. Ugland, K.I. & Aspholm, P.E. 1991. Harp seal (Phoca groenlandica) invasions in Norwegian coastal waters: age composition and feeding habits. - ICES J. mar. Sci. 48: 363-371.

Healey, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size selective fisheries. In: D.J. Meerburg ed. Can. Spec. Publ. Fish. Aquat. Sci. 89, pp. 39-52.

Hesthagen, T. & Hansen, L.P. 1991. Estimates of the annual loss of Atlantic salmon, Salmo salar L., in Norway due to acidification. - Aquacult. Fish. Managem. 22: 85-91.

Hilborn, R. & Walters C.J. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. - Chapman and Hall, New York.

Hindar, K. 1992. Conservation and sustainable use of Atlantic salmon. - In: O.T. Sandlund, K. Hindar & A.D. Brown, eds. Conservation and Biodiversity for Sustainable Development, Scandinavian University Press, Oslo. pp. 168-185.

Hindar, K. & Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. - Can. J. Fish. Aquat. Sci. 39: 1030-1045.

Holt, S.J. & Papastavrou, V. 1993. Harvesting of whales. - Nature (London) 361: 391.

Hubendick, B. 1985. Människoekologi. - Gidlunds, Stockholm.

IWC 1992a. International Convention for the Regulation of Whaling, 1946. Schedule. As ammended by the Commission at the 44th Annual Meeting, June-July 1992, and replacing that dated October 1991. - Int. Whal. Comm., Cambridge, England.

IWC 1992b. Report of the Scientific Committee. - Rep. Int. Whal. Comm. 42.

Janzen, D.H. 1992. A south-north prespective on science in the management, use, and economic development of biodiversity. - In O.T. Sandlund, K. Hindar & A.D. Brown, eds. Conservation of biodiversity for sustainable development. Scandinavian University Press, Oslo. pp. 27-52.

Johnsen, B.O. & Jensen, A.J. 1986. Infestation of Atlantic salmon, Salmo salar, by Gyrodactylus salaris in Norwegian rivers. - J. Fish Biol. 29: 233-241.

Johnson, L. 1980. The Arctic charr, Salvelinus alpinus. - In E.K. Balon, Charrs, salmonid fishes of the genus Salvelinus. Dr. W. Junk Publ., The Hague. pp fishes. 15-98.

Jonsson, B. 1982. Population genetics in salmonids. - Fauna (Oslo) 35: 97-105.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout. - Freshwat. Biol. 21: 71-86.

Jonsson, B., Hindar, K. & Northcote, T.G. 1984. Optimal age at sexual maturity in sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. - Oecologia (Berlin) 61: 319-325.

Kock, K.H. 1992. Antarctic fish and fisheries. - Cambridge University Press, Cambridge.

Larkin, P.A. 1977. An epitaph for the concept of MSY. - Trans. Am. Fish. Soc. 107: 1-11.

Larkin, P.A. 1981. A perspective on population genetics and salmon management. - Can. J. Fish. Aquat. Sci. 38: 1469-1475.

Lee, B. 1982. Why did Australian animals die out? - New Sci. 27/5: 573.

Leopold, A. 1933. Game management. - Charles Schribner's Sons, New York.

Leopold, A.S. 1955. Too many deer. - Sci. Am. 193: 101-108.

Lindsey, C.C. 1981. Stocks are chameleons: Plasticity in gill rakers of coregonid fishes. - Can. J. Fish. Aquat. Sci. 38: 1497-1506.

Lubcheno, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.P. & Risser, P.G. 1991. The sustainable biosphere initiative: an ecological research agenda. - Ecology 72: 371-412.

Mathisen, O.A. 1980. Adaptation of the anchoveta (Engraulis ringens) to the Peruvian upwelling system. - Proceedings of the symposium on the bioproductivity of upwelling ecosystems, Moscow, USSR, 1979.

Nelson, K. & Soulé, M. 1987. Genetical conservation of exploited fishes. - In N. Ryman & F. Utter, eds. Population genetics and fishery management. Washington Sea Grant Program, University of Washington Press, Seattle. pp. 345-368.

Pitcher, T.J. & Hart, P.J. 1982. Fisheries ecology. - Croom Helm, London.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. - Fish. Res. Board Can. Bull. 191: 1-382.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. - Can. J. Fish. Aquat. Sci. 38: 1636-1656.

Russell, E.S. 1931. Some theoretical consideration on the overfishing problem. - J. Conc. Int. Explor. Mer 6: 3-20.

Ryman, N. 1991. Conservation genetics considerations in fishery management. - J. Fish Biol. 39 (Suppl. A): 211-224.

Ryman, N., Baccus, R., Reuterwall, C. & Smith, M.H. 1981. Effective population size, generation interval, and potential loss of genetic variability in game species under different hunting regimes. - Oikos 36: 257-266.

Schaffer, W.M & P.F. Elson. 1975. The adaptive significance of variation in life history among local populations of Atlantic salmon in North America. - Ecology 56: 577-590.

Ståhl, G. 1987. Genetic population structure of Atlantic salmon. - In N. Ryman & F. Utter, eds. Population genetics and fishery management. Washington Sea Grant Program/ University of Washington Press, Seattle. pp. 121-140.

Stenseth, N.C. 1992. Models for predicting ecological change. - In O.T. Sandlund, K. Hindar & A.D. Brown, eds. Conservation of biodiversity for sustainable development. Scandinavian University Press, Oslo. pp. 137-154.

Svärdson, G. 1979. Speciation of Scandinavian Coregonus. -

Rep. Inst. Freshwater Res. Drottningholm 57: 1-95.

Vader, W., Anker-Nilssen, T., Bakken, V., Barrett, R. & Strann, K.B. 1990. Regional and temporal differences in breeding success and population development of fisheating seabirds in Norway after collapses of herring and capelin stocks. - Trans. 19th IUGB Congress, Trondheim 1989: 143-150.

Wilson, E.O. 1990. Threats to biodiversity. In Managing planet Earth: reading from Scientific American. W.H. Freeman, New York. pp. 49-60.

Young, N.M. ed. 1992. Understanding the Revised Management Procedure. - Center for Marine Conservation, Washington, USA.

0 48

nina
utredning