

Sustainable exploitation: a review of principles and methods

Author: Sutherland, William J.

Source: Wildlife Biology, 7(3) : 131-140

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2001.017>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Sustainable exploitation: a review of principles and methods

William J. Sutherland

Sutherland, W.J. 2001: Sustainable exploitation: a review of principles and methods. - *Wildl. Biol.* 7: 131-140.

Although the main theoretical framework determining how to exploit populations was derived almost 50 years ago, overexploitation is common. I review 10 major concepts underlying the regulation of exploitation: population increase can be exploited; density dependence is essential; quantifying density dependence is exceedingly difficult; sustainable exploitation involves reducing population size; population growth rate is usually mismeasured; sustainability has many conflicting definitions and the choice depends upon the objectives; it is better to monitor the population than the harvest; quotas are unstable; increasing effort is simple, reducing it is painful; exploit conservatively. I then give a brief account of each of the nine main methods that are used to determine sustainable exploitation and the uses, advantages and limitations of each. The nine techniques are: surplus production models, yield per recruit models, Robinson and Redford model, linking yield to recruitment and mortality, adjusting to population changes, comparing demography across sites, reducing to a fixed fraction of unexploited population size, full population models and adaptive management.

Key words: density dependence, exploitation, harvesting, hunting, sustainable

William J. Sutherland, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK - e-mail: w.sutherland@uea.ac.uk

Almost half a century ago the main concepts underlying sustainable exploitation were devised in a series of remarkable papers (Schaefer 1954, Ricker 1954, Beverton & Holt 1957). These pioneering studies provided the framework for a series of sophisticated models and methods of analyses that make current fisheries management a highly advanced process (e.g. Hilborn & Walters 1992, Quinn & Deriso 1999, Jennings, Kaiser & Reynolds 2001). However, despite this understanding, the last 50 years have seen considerable overexploitation of numerous species (Ludwig, Hilborn & Walters 1993, Casey & Myers 1998). Even many intensively studied populations managed by affluent countries have collapsed, often resulting in local unemployment (e.g. Walters & Maguire 1996).

Against this generally pessimistic landscape of over-

exploitation there are many success stories in which populations are currently reasonably healthy even with intensive exploitation. Examples include the moose *Alces alces*, the South African fur seal *Arctocephalus pusillus* and most goose populations in North America.

There are two objectives in writing this review. In preparing this review I was struck by the fact that the literature is very fragmented: papers on fisheries, mammals, birds and forestry all consider similar issues but each uses a different terminology and seems developed largely in isolation. My first objective has been to identify the essential principles of sustainable exploitation and reviewing the main issues.

My second objective is to outline the main methods used for determining levels of exploitation and describe the benefits, problems and uses of each.

Fundamental principles of exploitation

I suggest that these are the 10 fundamental principles of exploitation.

1. Population increase can be exploited

The essence of sustainable exploitation is the exploitation of the population at the rate at which it increases (Caughley & Gunn 1995). Thus, if the population is increasing by 5% per annum then that 5% may be removed while keeping the population constant. In practice the actual rate will be below this, for example due to the interaction with demographic and environmental stochasticity (Lande, Engen & Sæther 1995).

2. Density dependence is essential

There are very rare circumstances in which population shows a persistent increase over a reasonable period, such as an introduced population or a population whose food supply has continually improved, but the norm is for naturally occurring unexploited populations not to show increases over long periods of time. There is thus not an increase that can be exploited. However, if as a result of density dependence, reducing the population results in increases in breeding output or survival, then the resulting increase may be exploited. It thus follows that density dependence is absolutely central to sustainable exploitation (Ricker 1954, Schaefer 1954) and without density dependence exploitation would be comparable to mining. The ability of so many species to have persisted in the presence of sustained exploitation is good evidence for the ubiquity of density dependence. As an example, McGarvey (1996) noted that populations of Georges Bank sea scallops *Placopecten magellanicus* persisted despite long-term intensive exploitation and in exploited areas the survival rate from eggs to age 3 was 32–63 times larger than in unexploited areas.

3. Quantifying density dependence is exceedingly difficult

Although density dependence is fundamental to sustainable exploitation, it is very hard to measure as a result of sampling errors (Shenk, White & Burnham 1998), the fact that most data sets start relatively recently and so result in short time series (and, less excusably, often change methods without evaluating the consequences) and due to difficulties in isolating density dependence from population fluctuation resulting from habitat change or variation in weather conditions (e.g. Dennis & Otten 2000).

There are four main approaches to detecting density dependence and each has considerable problems. The

most widely used approach is to plot the rate of increase over two successive years (i.e. N_{t+1}/N_t) against the number in the first year (N_t) and a negative relationship is evidence for density dependence. However, if there is any measurement error, as there almost always is, then the presence of the same variable on each axis can result in spurious density dependence; thus most estimates of density dependence are flawed (Shenk et al. 1998). Estimating all major components of fitness, such as breeding success and mortality, is a much better method but it is necessary to measure all components to estimate the strength of density dependence and this is rarely practical. The best means is through experimental manipulations (e.g. Cappuccino & Harrison 1996), but this is obviously usually impractical. A final approach is through behaviour-based modelling in which the decisions made by individuals are determined and incorporated into a game theory model (Sutherland 1996, Goss-Custard & Sutherland 1997) but this also requires considerable data and understanding.

There is widespread debate (e.g. Nicols 1991) as to whether exploitation mortality is compensatory or additive to natural mortality. If there is strictly compensatory density dependence then removal of individuals does not affect the numbers remaining (the 'doomed surplus'). If exploitation and natural mortalities are additive then exploitation will reduce the population. Studies of density dependence give no support for the idea of pure compensation (Dusek, Wood & Stewart 1992, Hellgren, Synatzske, Oldenburg & Guthery 1995, Francis, Sauer & Serie 1998, Harris in press) and mortality caused by exploitation is almost always both compensatory and additive. It will generally tend towards being compensatory at high population sizes and tend towards being additive once the population is at a low level (e.g. Bartmann, White & Carpenter 1992).

4. Sustainable exploitation involves reducing population size

A common error amongst conservation biologists is to show that exploitation has reduced a population below its unexploited level and then use this as evidence that the population is overexploited. However, as sustainable exploitation is dependent upon a growing population, and as continuous population growth can only be achieved by reducing populations to take advantage of the density dependent increase in survival or breeding output, then exploited populations must be lower, even when exploited sustainably.

5. Population growth rate is usually mismeasured

Principle 1 is that the population growth can be exploited so it is thus important to assess growth rates. However, there is considerable confusion over what should be measured (Sutherland 2000). There are two common errors. The first is to measure population growth rate for an unexploited population in which case there should be no growth. In practice, as a result of measurement error, the estimated growth rate will often be higher than zero. Such estimates are likely to produce estimates of exploitation that are well below the level that could be sustainable if the population was reduced.

The second common error is to measure the maximum possible growth rate. This may either be the growth rate at which there is no competition (r or λ) or the growth rate under ideal conditions (r_{\max}). In practice r and r_{\max} are used interchangeably and r is also often applied to a range of densities so this subject is horribly confused. The growth rate at very low densities is only useful if the population is to be exploited at the same low densities. It will be an overestimate of the exploitation rate for higher population sizes. The growth rate under ideal conditions, such as zoos, is likely to give inflated results. This error will lead to exaggerated estimates of sustainable exploitation.

The population growth rate is easiest to measure as a deterministic parameter, yet it is, of course, stochastic (Dennis, Munholland & Scott 1991), but measuring the variance in growth rate is thus even harder.

6. Sustainability has many conflicting definitions and the choice depends upon the objectives

There has been considerable debate about the definitions of sustainability (Bennett & Robinson 2000). The main definitions are: (i) that it does not significantly affect the wild population (IUCN/UNEP/WWF 1980). However, principle 4 is that there has to be some reduction for exploitation to occur; (ii) that exploitation balances production. Although some combinations of exploitation rate and population density result in extinction, many combinations are in theory stable and allow regular exploitation with the population persisting at that size. However this could be at very low population sizes (with low yield). A second, less important, problem concerns starting a programme of exploitation during which the population has to be initially reduced to provide growth and thus by this definition is not sustainable in the short term; (iii) that the maximum sustainable yield (MSY) is not exceeded. The concept of MSY has been heavily attacked. One major criticism is that incorporating costs of exploitation into this model shows that

MSY is not the most profitable point. With just one exploiter who has complete control over the level of total exploitation as costs increase with effort it is sensible to exploit at a lower intensity than at MSY. With open access the theoretical expectation is that individuals will increase exploitation levels and further individuals will join until the profits from the yields balance the costs. At this point the population is low, the yield is much lower than it could be and the exploiters make little profit (Hardin 1968). Despite these criticisms of MSY, I believe it is still a very useful concept as it provides an invaluable reference point as an ideal against which current practice can be compared.

7. It is better to monitor the population than the harvest

Although it is usually easier to measure changes in the numbers exploited, this measure combines changes in population size and changes in exploitation methodology. Changes in methodology may be subtle, such as new paths cut through a forest, better transport or better exchange of information between exploiters. Thus if the number removed per day is constant it either means the population is being exploited sustainably or it is decreasing but this is compensated for by increased efficiency. Furthermore, if illicit exploitation is taking place, then this will be excluded from the estimates of exploitation. Determining changes in population size is better for adjusting the exploitation level (Walters 1986, Lande, Sæther & Engen 1997) as it is the population size that really matters.

8. Quotas are unstable

Removing a fixed number of individuals is theoretically acceptable if the level is set correctly and the population is stable. However in reality, populations fluctuate (for example due to varying weather conditions), estimates of a sustainable quota are faulty or the quota is illicitly exceeded. If a population declines, then a given quota will become an increasing proportion of those remaining which can drive the population further downwards (Walters 1986, Quinn & Deriso 1999, Hilborn & Walters 1992). Of course careful monitoring can prevent such overexploitation but in reality monitoring is usually difficult, there is a natural variation in the population size and it is often difficult to reduce agreed quotas. A repeated story is for there to be a resistance to reducing quotas such that once a lower quota is eventually agreed on the stock has collapsed so much that even the reduced quota cannot be caught.

9. Increasing effort is simple, reducing it is painful

The history of exploitation shows that populations often continue to be overexploited even when reducing effort would result in a greater long-term yield (Ludwig et al. 1993). Humans are usually risk adverse and the reason for this is that the utility (the perception of values) decreases with each additional sum of money owned. Thus for most people, losing money is much more painful than gaining the same sum is pleasurable. Hence although individuals are very happy to take advantage of higher catches they are often deeply unhappy about reducing the catch.

Individuals often have an economic, social or political commitment to the current levels. As an example currently in the news, the number of fishermen on the Galapagos Islands has doubled from 1999 to 2000 so that the lobster quota was filled in four months. In response the fishermen have threatened tourists, blocked roads, burnt a research station, issued death threats, destroyed the islands telephone antenna and even held a giant tortoise hostage (Anon 2000). As a result the lobster quota has been increased from 50 to 80 tonnes, although no one considers this to be sustainable.

10. Exploit conservatively

For a wide variety of reasons including the uncertainties of the biology, difficulties in estimating parameters, population fluctuations (Beddington & May 1977, Sæther, Engen & Lande 1996) and the difficulties of reducing harvest levels (principle 9), setting exploitation at the level which is calculated to be sustainable is likely to result in population collapses. Caughley & Sinclair (1994) suggest a 25% safety margin and higher with variable populations, poor data or irregular monitoring.

A number of means have been suggested that reduce the likelihood of driving populations towards extinction. These include only restricting effort rather than quotas, only exploiting populations when they exceed a threshold size (Lande et al. 1997), rotational management in which areas are exploited for a period and then left (Myers, Fuller & Kehler 2000), and exclusion zones in which fishing is not allowed (McCollough 1996).

Main methods for exploiting populations

There are nine main methods of exploiting populations (Table 1). I will provide a brief summary of each with comments on their actual and potential application.

Surplus production models

The surplus production models (also known as surplus yield models) come in a wide range of versions but are all based on the original idea of Schaefer (1954). The most simple version consists of collecting information on the numbers or biomass exploited each year and the effort, and then plotting the catch per unit effort against effort to determine the level of effort which produces the maximum yield.

There are serious problems with the simplest versions. The simplest versions assume the population is at equilibrium. Hence a high effort is likely in the short term to result in a reasonable catch per unit effort but this may well be unsustainable. It can be difficult to determine the decline in catch per unit effort unless the stock has been heavily overexploited (Hilborn & Walters 1992) in which case it is difficult to reverse the overexploitation.

The other major problem with this approach is that it is very difficult to standardise effort. Thus for hunting there might be improvements in information, roads, vehicles, guns, ammunition or field techniques, but it is impossible to correct for all of these.

The simplest version of the surplus production model is rarely used. More sophisticated versions are widely used in fisheries (e.g. Quinn & Deriso 1999), but have applications elsewhere, for example one has been used to analyse moose exploitation (Courtois & Jolicoeur 1993).

Yield per recruit models

Larger individuals are usually more valuable, either because they have more biomass or because of their greater trophy value. Beverton & Holt (1957) developed yield per recruit models, also known as dynamic pool models, to determine how to exploit cohorts when incorporating growth and natural mortality. Exploiting when young produces the most individuals but delaying exploitation results in more valuable individuals. The optimal solution balancing these conflicting phenomena can be calculated by determining the yield (as either weight or value) for each recruit.

This approach can be simply tackled using a spreadsheet and data on age-specific natural mortality and age-specific value and exploring the yield from different exploitation strategies. However, there are sophisticated models and software for analysing populations with these methods. Developments include virtual population analysis (VPA) and cohort analysis (Pope 1972) in which the age structure of the catch is used to back calculate the natural and exploited mortality. Such an approach requires considerable data but is widely used

Table 1. Main methods used for assessing exploitation with brief details of how the technique is carried out, the data required, the strengths, the weaknesses and the main uses

Method	Outline of method	Data required	Strengths	Weaknesses	Uses
Surplus production	Determines how catch varies with effort and then determines consequences of different strategies.	Simplest version requires data on numbers or biomass exploited per year and effort.	Can be carried out with very little data (e.g. catch and weight data). More sophisticated versions available. Software available to apply to fish populations.	Overexploiting is the easiest way of assessing MSY. Simple versions assume equilibrium. Effort needs to be standardised, but rarely is.	Mainly fisheries but also others e.g. moose.
Yield per recruit	Based on age specific growth and natural mortality determines strategy that results in highest value yield. Incorporates recruitment to determine long term sustainable strategy.	Age-specific natural mortality and age-specific value. One version uses annual variation in age-specific catch. Either size of recruitment or relationship between stock and recruitment.	Sophisticated. Full consideration of increase in value with age. Software available to apply to fish populations.	Requires considerable data on mortality and recruitment.	Main methods for fisheries and forestry.
Robinson and Redford	Calculates maximum growth rate. Calculates yield if population is at 0.6 of expected population size.	Age at first reproduction, annual birth rate, age at last reproduction	Often the only method. Can apply when there are no historical data.	Growth rate often measured at wrong density. Unlikely to be precise. Not necessarily sustainable if yield < MSY.	Tropical forest mammals and birds.
Linking yield to recruitment and mortality	Exploits below rate at which recruitment exceeds mortality.	Recruitment rate. Mortality rate.	No data needed for trends or effort.	Estimates likely to arise from errors in demographic estimates. Does not apply to population in equilibrium. Only applies to populations at sustainable population sizes.	Used occasionally for mammals
Adjusting to population changes	Loosens/tightens regulations in relation to population changes.	Population changes. Ideally magnitude and consequences of environmental changes.	Probably the most successful method. Requires very little data on demography. Concentrates on population sizes.	Difficult to respond to environmental changes.	Widely used for game exploitation

Table 1 continued

Method	Outline of method	Data required	Strengths	Weaknesses	Uses
Comparing demography across sites	Relates exploitation intensity to density or population change.	Exploitation level and density (or population change) at a range of sites.	Focuses on the population. Can be carried out in the short term without carrying out detailed ecological studies.	Need to ensure analysis not confounded by artefacts resulting from exploitation levels being correlated with environmental factors.	A less rigorous version results in a rule of thumb concerning exploitation levels.
Reducing to a fixed fraction of unexploited population size	Maintains population at a proportion (e.g. 60%) of unexploited population.	Likely unexploited population size. Current population size. Environmental data if possible.	Relatively easy. Concentrates on population size. Can be used with very little data.	Requires estimate of unexploited population. Difficult to use for variable population.	Rarely used but often part of other models. Useful for data deficient populations.
Full population model	Creates full model of major components of the population and examines consequences of different harvest levels.	Full data on strength of all density dependent processes.	Probably the best method. Can be used to examine the consequences of other changes.	Almost impossible.	Grey partridge
Adaptive management	Uses models to determine where doubts occur and consequences of these doubts. Runs experiments to reduce uncertainty. Continues forever improving knowledge and management.	Data from experiments.	Continually improves knowledge of system.	Politically difficult to explain. Difficult to carry out.	Used too infrequently. Should be part of any exploitation programme.

by fisheries biologists in countries with an extensive fisheries science programme. A similar approach is used in forestry in which growth and mortality is assessed in plantation blocks or by following groups of marked trees within natural forests.

This approach is based on a given sized cohort. A standard approach has been to assume that the recruitment will be constant, even once the adult population has been markedly reduced. This assumption has lead to some dramatic examples of fish population crashes. One sensible but expensive solution is to carry out surveys of the number of young individuals so that the exploitation can be adjusted according to the size of the recent cohorts.

Thus fisheries managers often carry out surveys of young fish. Another approach is to determine how the recruitment varies with the adult population (stock-recruitment relationships) in order that the population can be managed to reduce the problems of affecting the recruitment. Thus Cook, Sinclair & Stefánsson (1997) showed that as North Sea cod *Gadus morhua* have declined the recruitment has also declined leading to the potential of accelerating declines.

Robinson and Redford model

Exploitation often takes place on species about which almost nothing is known (Johannes 1998) and this is par-

ticularly true for rain forest species. There is a need to have techniques that can be applied to such species and this method has been widely used (e.g. Fa, Juste, Perez & Satroviejo 1995, Fitzgibbon, Mogaka & Fanshaw 1995, Wilkie & Carpenter 1999). The essence of the Robinson & Redford (1991) model is to calculate the rate of growth from basic data on reproduction. From knowledge of age at first reproduction, age at last reproduction and breeding per year it is possible to determine the maximum possible reproductive rate. To take into consideration the mortality this maximum reproductive rate is then multiplied by 0.2 for long-lived species (age at last reproduction is over 10 years), 0.4 for short-lived species (age at last reproduction 5-10 years) or 0.6 for very short-lived species (age at last reproduction five years). An obvious problem here is the population size at which the population growth rate is being calculated. The estimate is often derived from captive animals or from the field. The values will thus rarely be valid for the population at the density at which it will be exploited. This seems a trivial point but actually it is critical. The growth rate under ideal condition may be high, which would imply high levels of exploitation and so result in overexploitation. Growth rate measured for field populations at equilibrium will usually produce an estimate of negligible population growth and so underestimate the level of sustainable exploitation.

The next stage is to estimate the expected density from other studies. Then assume that the population will be exploited at 0.6 of this level. Multiply by the growth rate to give the number that can be exploited. This is then compared with actual numbers removed to see if the exploitation is sustainable. There are a number of problems with this approach. One is that the estimates of density from other sites will often be very inaccurate because of the variation across sites, for example in soil type (Peres 1993).

Another major problem is that the sustainable yield only applies to a given population density, yet this is rarely measured. For example, the sustainable yield might be calculated at 110 individuals for a population size of 1,500 individuals. However, if the population drops to 110, then removing all 110 is clearly not sustainable. As this simple example shows, in the absence of any idea of population size it is not possible to distinguish sustainable exploitation from eradication.

Linking yield to recruitment and mortality

The recruitment rate and mortality rate can be calculated and one approach has been to use the difference between them to determine the rate of growth. In theory the calculated growth rate can be removed without chang-

ing the population size. In practice, this method has serious problems. Estimating birth and death rates with sufficient precision is likely to be extremely difficult.

Adjusting to population changes

The basic idea is to adjust the exploitation in relation to population changes. Thus the regulations are tightened if the population is declining and relaxed if it is increasing. Environmental changes will also confound the analysis and the better these are understood the better the analysis will be. Thus a population decline may be either due to overexploitation (illustrating long-term reduction in exploitation) or due to environmental changes (showing that there might be a need for a short-term reduction to allow the population to recover but no need for a long-term reduction).

This can be very simple yet is extremely effective and is the basis for most sports exploitation of birds, fish and mammals. It has the huge advantage that it concentrates on the population size and has a good track record for sensible management.

Comparing demography across sites

Comparing sites that differ in the intensity of exploitation is a good method for assessing sustainable levels (Hilborn, Walters & Ludwig 1995). Thus Peres (2000) showed for a range of neotropical primate species that population size was related to hunting intensity (none, light, moderate and heavy). Similarly, comparing Canada goose *Branta canadensis* populations showed that those in decline had shooting mortalities averaging 27% while stable populations had lower exploitation averaging 17% (Hestbeck 1994). It is necessary to consider whether results are confounded by interactions, for example because areas with high hunting levels tend to differ in other ways.

Reducing to a fixed fraction of unexploited population size

In theory the MSY is at half the unexploited population size. This depends critically upon the shape of the relationship between population growth rate and population size, and from what we know about interference, depletion territoriality and social behaviour (Sutherland 1996) there are good reasons for thinking that this might be convex (Sutherland & Gill 2000). It may thus be more realistic to assume that MSY occurs at 0.6 or 0.7 of the unexploited population size; 0.6 seems to be the widely accepted figure.

This is perhaps the simplest of all the methods, which is both its strength and weakness. It only needs data on the current level and the expected unexploited popula-

tion size. One criticism is that the proportional reduction is almost unknown (i.e. should it be 0.5 or 0.8), but this is a minor problem compared to other opportunities for overexploitation. A greater problem is that the unexploited population will often be unknown and extrapolating from other sites may be difficult. Furthermore, if the habitat deteriorates (or improves), then this will change the expected unexploited level and thus also the exploited population size. It would require considerable ecological knowledge to predict these changes. Despite these problems it is likely that attempting to understand natural densities and relating it to current densities is probably the best ways of studying exploitation when there is almost no ecological data, such as for forest species.

Full population model

In some rare cases there will be considerable ecological studies and the major sources of density dependence are understood and can be quantified. It is then possible to produce a full population model. The best example of this is the extensive studies of the grey partridge *Perdix perdix* (Potts 1986, Potts & Aebischer 1995). Long-term studies in a range of sites have revealed the density dependent processes and especially the role of density-dependent nest predation. These data can be used to predict the yield and population size resulting from different percentages shot. This was also used to show how yield and population size would be affected by altering the predator control or agricultural practice.

Adaptive management

There is usually a distinction between scientists and exploiters. The essence of adaptive management (Walters 1986) is to carry out the analysis using one or more of the previous approaches, use the best parameter estimates and then rerun the analysis using different assumptions and values to discover where gaps in the understanding are. All exploitation should involve some components of adaptive management. There are, however, problems with this approach. A major problem is that exploiters often are particularly sensitive to different rules in different areas, as these are often perceived as unjust. The long-term gains in understanding have to be balanced against the likely short-term loss from not harvesting in the manner thought to be most efficient (Sainsbury 1991). Adaptive management is more likely to be practical where there are numerous replicated such as lakes or forests (Hilborn et al. 1995) than for large dispersed populations such as most marine fish.

Discussion

A core problem of applying such models is the difficulty in determining the basic components of demography. These are severely hindered by stochasticity and sampling. For example, estimating harvesting strategies for the brown bear *Ursus arctos* in Norway is greatly hindered by the uncertainty in the main demographic parameters (Sæther, Engen, Swenson, Bakke & Sandegren 1998, Tufto, Sæther, Engen, Swenson & Sandegren 1999). Exploitation is largely about density dependence, yet this is very difficult to quantify. Similarly the population growth rate is a key measure for calculating the level that can be exploited, yet this is measured in ways that will markedly overestimate yield (e.g. calculating it for captive animals or animal under ideal conditions) or underestimate yield (the very common method of estimating this for stable populations in which the population is not growing).

Ironically, although the science underpinning sustainable exploitation is highly sophisticated, many of the most successful schemes are based on limited science and data. The explanation is probably that intensive commercial exploitation results in the social and financial pressures that leads both to detailed research and also to exploitation.

There is a case for arguing that for very many species the simplest methods are often the most practical. Assessing effort or demographic components such as density dependence or population growth rates are often too difficult to provide estimates that are sufficient to provide a basis for sufficiently accurate exploitation. The simple means, especially monitoring populations and adjusting regulations according to long-term population changes, is probably often the best method. In applying this method it is very useful to be able to estimate the likely population in the absence of exploitation. Studies on factors affecting the unexploited population size are thus particularly useful.

Adaptive management (Walters 1986) is clearly a highly underused tool. There are obvious political problems in altering the regulations purely to learn more about the system yet the benefits are so clear that there must be far more occasions in which it is practical to adopt this powerful technique.

Global climatic change resulting from global warming is likely to fundamentally affect all of the methods described in this paper (Walters & Parma 1996). The past data may no longer provide a guide to levels of sustainable exploitation. One method is to continually reassess parameters but this may often be impractical.

For many groups, monitoring both exploited and unexploited populations seems the most straightforward means of responding to such changes.

Acknowledgements - I thank Bernt-Erik Sæther for inviting me to such a thought provoking and enjoyable conference and for commenting on the manuscript. I also thank Carlos Peres and John Reynolds for numerous stimulating discussions.

References

- Anonymous 2000: Fishermen's Friends. - *The Economist*, 25 November, p. 154.
- Bartmann, R.M., White, G.C. & Carpenter, L.H. 1992: Compensatory mortality in a Colorado mule deer population. - *Wildlife Monographs* 121: 1-39.
- Beddington, J.R. & May, R.M. 1977: Fluctuating natural populations in a naturally fluctuating environment. - *Science* 197: 463-465.
- Bennett, E.L. & Robinson, J.G. 2000: Hunting for the snark. - In: Robinson, J.G. & Bennett, E.L. (Eds.); *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York, pp. 1-9.
- Beverton, R.J.H. & Holt, S.J. 1957: *On the Dynamics of Exploited Fish Populations*. - London, Her Majesty's Stationary Office, 576 pp.
- Cappuccino, N. & Harrison, S. 1996: Density-perturbation experiments for understanding population regulation. - In: Floyd, R.B., Sheppard, A.W. & De Barro, P.J. (Eds.); *Frontiers of population ecology*. CSIRO Publishing, Melbourne, pp. 53-64.
- Casey, J.M. & Myers, R.A. 1998: Near extinction of a large, widely distributed fish. - *Science* 281: 690-692.
- Caughley, G. & Gunn, A. 1995: *Conservation Biology in Theory and Practice*. - Blackwell Scientific, Oxford, 459 pp.
- Caughley, G. & Sinclair, A.R.E. 1994: *Wildlife Ecology and Management*. - Blackwell Science, Oxford, 334 pp.
- Cook, R.M., Sinclair, A. & Stefánsson, G. 1997: Potential collapse of North Sea cod stocks. - *Nature* 385: 521-522.
- Courtois, R. & Jolicoeur, H. 1993: The use of Schaefer's and Fox's surplus-yield models to estimate optimal moose harvest and hunting effort. - *Alces* 29: 149-162.
- Dennis, B., Munholland, P.L. & Scott, J.M. 1991: Estimation of growth and extinction parameters for endangered species. - *Ecological Monographs* 61: 115-143.
- Dennis, B. & Otten, M.R.M. 2000: Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. - *Journal of Wildlife Management* 64: 388-400.
- Dusek, G.L., Wood, A.K. & Stewart, S.T. 1992: Spatial and temporal patterns of mortality among female white-tailed deer. - *Journal of Wildlife Management* 56: 645-650.
- Fa, J., Juste, E.J., Perez, del Val, J. & Satroviejo, J. 1995: Impact of market hunting on mammal species in Equatorial Guinea. - *Conservation Biology* 9: 1107-1115.
- Fitzgibbon, C.D., Mogaka, H. & Fanshaw, J.H. 1995: Subsistence hunting in Arabuko-Sokoke forest, Kenya, and its effects on mammal reproduction. - *Conservation Biology* 9: 1116-1126.
- Francis, C.M., Sauer, J.R. & Serie, J.R. 1998: Effect of restrictive harvest regulations on survival and recovery rates of American black ducks. - *Journal of Wildlife Management* 62: 1544-1557.
- Goss-Custard, J.D. & Sutherland, W.J. 1997: Individual behaviour, populations and conservation. - In: Krebs, J.R. & Davies, N.B. (Eds.); *Behavioural Ecology: an Evolutionary Approach*. Blackwell Science, Oxford, pp. 373-395.
- Hardin, G. 1968: The tragedy of the commons. - *Science* 162: 1243-1248.
- Harris, R.B. in press: Biological issues in hunting vertebrate populations. - Safari Club International, Herdon Virginia.
- Hellgren, E.C., Synatzske, D.R., Oldenburg, P.W. & Guthery, F.S. 1995: Demography of a collared peccary population in South Texas. - *Journal of Wildlife Management* 59: 153-163.
- Hestbeck, J.B. 1994: Survival of Canada geese banded in winter in the Atlantic flyway. - *Journal of Wildlife Management* 58: 748-756.
- Hilborn, R. & Walters, C.J. 1992: *Quantitative Stock Assessment: choice, dynamics and uncertainty*. - London, Chapman and Hall, 570 pp.
- Hilborn, R., Walters, C.J. & Ludwig, D. 1995: Sustainable exploitation of renewable resources. - *Annual Review of Ecology and Systematics* 26: 45-67.
- IUCN / UNEP / WWF 1980: *World Conservation Strategy*. - IUGN Gland, 200 pp.
- Jennings, S., Kaiser, M.J. & Reynolds, J.D. 2001: *Marine Fisheries Ecology*. - Blackwell Sciences, Oxford, 432 pp.
- Johannes, R.E. 1998: The case for data-less marine resource management: examples from tropical nearshore fin fisheries. - *Trends in Ecology and Evolution* 13: 243-246.
- Lande, R., Engen, S. & Sæther, B-E. 1995: Optimal harvesting of fluctuating populations with a risk of extinction. - *American Naturalist* 145: 728-745.
- Lande, R., Sæther, B-E. & Engen, S. 1997: Threshold harvesting for sustainability of fluctuating resources. - *Ecology* 78: 1341-1350.
- Ludwig, D., Hilborn, R. & Walters, C. 1993: Uncertainty, resource exploitation and conservation: lessons from history. - *Science* 260: 17-18.
- McCullough, D.R. 1996: Spatially structured populations and harvest theory. - *Journal of Wildlife Management* 60: 1-9.
- McGarvey, R. 1996: Is long term persistence of harvest populations evidence of density dependence? - In: Floyd, R.B., Sheppard, A.W. & De Barro, P.J. (Eds.); *Frontiers of population ecology*. CSIRO Publishing Melbourne, pp. 65-77.
- Myers, R.A., Fuller, S.D. & Kehler, D.G. 2000: A fisheries management strategy robust to ignorance: rotational harvest in the presence of indirect fishing mortality. - *Canadian Journal of Fisheries and Aquatic Sciences* 57: 2357-2362.
- Nicols, J.D. 1991: Response of North American duck populations to exploitation. - In: Perrins, C.M., Lebreton, J.D.

- & Hiron, G. (Eds.); Bird Population Studies: Their relevance to conservation and management. Oxford University Press, Oxford, pp. 498-525.
- Peres, C.A. 1993: Structure and spatial organisation of an Amazonian terra firme forest primate community. - *Journal of Tropical Ecology* 9: 259-276.
- Peres, C.A. 2000: Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. - In: Robinson, J.G. & Bennett, E.L. (Eds.); *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York, pp. 31-56.
- Pope, J.G. 1972: An investigation of the accuracy of virtual population analysis. - *ICNAF Research Bulletin* 9: 65-74.
- Potts, G.R. 1986: The Partridge: Pesticides, Predation and Conservation. - Collins, London, 274 pp.
- Potts, G.R. & Aebischer, N.J. 1995: Population dynamics of the grey partridge *Perdix perdix* 1793-1993: monitoring, modelling and management. - *Ibis* 137: S16-S28.
- Quinn III, T.J. & Deriso, R.B. 1999: *Quantitative Fish Dynamics*. - Oxford University Press, Oxford, 542 pp.
- Ricker, W.E. 1954: Stock and Recruitment. - *Journal of Fisheries Research Canada* 11: 559-623.
- Robinson, J.G. & Redford, K.H. 1991: Sustainable harvest for neotropical forest mammals. - In: Robinson, J.G. & Redford, K.H. (Eds.); *Neotropical Wildlife Use and Conservation*. University of Chicago Press, Chicago, pp. 415-429.
- Sæther, B-E., Engen, S. & Lande, R. 1996: Density-dependence and optimal harvesting of fluctuating populations. - *Oikos* 76: 40-46.
- Sæther, B-E., Engen, S., Swenson, J.E., Bakke, Ø. & Sandegren, F. 1998: Assessing the viability of Scandinavian brown bear *Ursus arctos* populations: the effects of uncertain parameter estimates. - *Oikos* 83: 403-416.
- Sainsbury, K.J. 1991: Application of an experimental approach to management of a tropical multispecies fishery with highly uncertain dynamics. - *Sainsbury International Council for the Exploration of the Sea, Marine Science Symposium* 193: 301-320.
- Schaefer, M.B. 1954: Some aspects of the dynamics of populations important to the management of commercial marine fisheries. - *Inter-American Tropical Tuna Commission Bulletin* 1: 27-56.
- Shenk, T.M., White, G.C. & Burnham, K.P. 1998: Sampling-variance effects on detecting density dependence from temporal trends in natural populations. - *Ecological Monographs* 68: 445-463.
- Sutherland, W.J. 1996: *From Individual Behaviour to Population Ecology*. - Oxford University Press, Oxford, 213 pp.
- Sutherland, W.J. & Gill, J.A. 2000: Predicting the consequences of human disturbance from behavioural decisions. - In: Gosling, L.M. & Sutherland, W.J. (Eds.); *Behaviour and Conservation*. Cambridge University Press, Cambridge, pp. 51-64.
- Sutherland, W.J. 2000: *The Conservation Handbook*. - Blackwell Scientific, Oxford, 278 pp.
- Tufto, J., Sæther, B-E., Engen, S., Swenson, J.E. & Sandegren, F. 1999: Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway. - *Proceedings of the Royal Society, London Series B*. 266: 961-967.
- Walters, C.J. 1986: *Adaptive Management of Renewable Resources*. - MacMillan, London, 604 pp.
- Walters, C. & Maguire, J-J. 1996: Lessons from stock assessment from the northern cod collapse. - *Reviews in Fish Biology and Fisheries* 6: 125-137.
- Walters, C. & Parma, A.M. 1996: Fixed exploitation strategies for coping with effects of climatic change. - *Canadian Journal of Fisheries and Aquatic Sciences* 53: 148-158.
- Wilkie, D.S. & Carpenter, J.F. 1999: Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. - *Biodiversity and Conservation* 8: 927-955.