

DYNAMICAL AND STATISTICAL MODELS FOR EXPLOITED POPULATIONS[†]

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Summary

Human activities have indirectly modified the dynamics of many populations, accelerating considerably the natural rate of species extinction and raising strong concerns about biodiversity. In many such cases, the underlying 'natural' dynamics of the population has been modified by human-induced increases in mortality, even if the populations are not exploited or harvested in the strict sense. Both dynamical and statistical models are needed to investigate the consequences of human-induced mortality on the overall dynamics of a population. This paper reviews existing approaches and the potential of recent developments to help form a conceptual and practical framework for analysing the dynamics of exploited populations. It examines both the simple case of an extra source of mortality instantaneously in time, and the theory involved when both risks compete over a continuous time scale. This basic theory is expanded to structured populations, using matrix population models, with applications to the conservation biology of long-lived vertebrates. The type and degree of compensation expected and approaches to detect it are reviewed, and ways of handling uncertainty are discussed.

Key words: population dynamics; harvested populations; exploited populations; capture–recapture; compensatory mortality.

1. Introduction

For thousands of years, humans have exploited animal and plant populations, by hunting, fishing, harvesting, timber-cutting, etc. More recently, human activities have indirectly modified the dynamics of many populations, accelerating considerably the natural rate of species extinction and raising strong concerns about biodiversity (Soulé, 1987 p.2). In many such cases, the underlying natural dynamics of the population is modified by sources of mortality induced by human activities, whether or not the populations are exploited or harvested in the strict sense.

Study of the interplay of such additional sources of mortality with the natural dynamics is termed 'the dynamics of exploited populations'. Models explore the sustainability of the dynamics and particular interactions between natural mechanisms and 'harvest', in the broad sense. Dynamical models are used to understand the consequences of changes in mortality patterns on the overall dynamics of a population of concern, and statistical models are used to estimate such parameters as harvest level. There is a long tradition of modelling in fisheries (Beverton & Holt, 1957), based on a general faith in a strong density-dependence in recruitment, in which the so-called stock-recruitment curves play a central role (Sale, 1990). Getz &

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Haight (1989) review a wide range of theoretical models. Statistical models have been used for demographic analyses of duck populations in North America (e.g. Anderson & Burnham, 1976; Burnham & Anderson, 1984; Nichols, 1991).

Overall, the dynamics of exploited populations has received less attention than might be expected given the generality of the problem. For instance, only recently has the integration of dynamical and statistical models been considered (Maunder, 2001a,b,c). Altogether, because of the economic and ethical questions associated with the sustainability of exploitation, and because of the intricacies of population dynamics mixing natural and man-induced mechanisms, the dynamics of exploited populations constitutes quite a challenging field for biometricians.

This paper reviews existing approaches, and the potential of recent developments to help form a conceptual and practical framework for analysing the dynamics of exploited populations. A strong personal bias towards bird population dynamics and the associated methods (e.g. Lebreton, 2001) is present throughout, but the concepts should still be broadly useful.

Section 2 introduces the simple case of an extra source of mortality acting before or after natural mortality. Section 3 recalls the theory when both risks compete over a continuous time scale. The material in these two sections is largely based on Nichols, Lancia & Lebreton (2001). Section 4 reviews the basic theory for structured populations, using discrete time projection models (Caswell, 2001) and applications to conservation biology of long-lived vertebrates. A key question for the sustainability of harvest, whether for quarry species, commercially exploited species or endangered or threatened species, is whether the effect of human-induced mortality can be attenuated in some way by some changes in other parameters. Sections 5 and 6 examine some predictions on the type and degree of compensation one can expect and approaches that have been, or can be, used to determine whether compensation is present or not. The recent diversification and generalization of capture–recapture methodology (Lebreton, 1995) opens some new possibilities. Uncertainty in many components of population dynamics, such as population size or harvest level, often appears to be a critical problem. Section 7 discusses various ways of handling this uncertainty, such as by integrated modelling (Maunder 2001a,b,c; Besbeas, Lebreton & Morgan, 2001, 2002), adaptive management (Nichols *et al.*, 2001), and Bayesian approaches (Maunder, Starr & Hilborn, 2000).

2. A simple case: harvest not competing with mortality

Consider a population growing exponentially from year to year with multiplication rate a , because demographic parameters are constant, i.e.

$$N(t) = aN(t - 1).$$

Ignore the effects of population structure (in sexes, age classes, sites, etc). Assume that a fixed proportion K (for ‘Kill’) of the individuals is removed at a fixed point in time, just before or after reproduction and natural mortality, i.e. just before or after multiplication by a . Then

$$N(t) = a(1 - K)N(t - 1).$$

Hence the population still changes exponentially, with rate $a(1 - K)$. This result still holds if harvest occurs at periods during which natural mortality does not occur, i.e. if harvest ‘does not compete with’ mortality.

The sustainability of the harvest is then entirely determined by

$$a(1 - K) > 1, \quad \text{i.e. } K < \frac{a - 1}{a}.$$

By this formula, a hypothetical population of roe deer *Capreolus capreolus*, with a maximum rate of increase of 40% ($a = 1.40$) can sustain, at most, a harvest rate of 28.5% (after Nichols *et al.*, 2001).

3. Interaction between sources of mortality

Harvest that operates separately over time from natural population dynamics leads to simple results. How do natural and additional mortality sources interact on a continuous time scale? This question has been the subject of work by Baranov (1918; see Beverton & Holt (1957) and translation of his work by Vilim (1977)) which led to the development of the theory of competing risks of mortality. General and formal presentations of the theory of competing risks are given e.g. by Kalbfleisch & Prentice (1980 pp. 163) and Elandt-Johnson & Johnson (1980 pp. 269).

If instantaneous mortality rates m and k apply simultaneously in time, the number of deaths among $N(t)$ animals over an infinitesimal interval $[t, t + dt]$ is

$$N(t)(m + k) dt .$$

The instantaneous rates add their effects: the two mortality probabilities $m dt$ and $k dt$ are both infinitesimally small and the term $km dt^2$ is an order of magnitude smaller and does not enter the equation. When the process goes on over time, the number of individuals, i.e. the number at risk of death by one of the two causes at any time, changes under the influence of the two causes of death. As a consequence, the proportions dying of each cause over a finite interval $[0, T]$ are not a function of the rate for this single cause and cannot be obtained simply. The survival in the absence of harvest, S_0 , the proportion of the initial number harvested, K , and the overall proportion surviving, S , can be shown to be linked as:

$$1 - \frac{K}{1 - S} = \frac{\log(S_0)}{\log(S)} .$$

We cannot obtain S as an explicit function of K from this equation. However, as shown in Figure 1, for large values of S_0 and moderate values of K , S is well approximated by an analogue of the discrete time-scale result in the previous section:

$$S \approx S_0(1 - K) .$$

If we denote as K_0 the proportion that would be harvested if there were no natural mortality, then we obtain an exact relationship,

$$S = S_0(1 - K_0) .$$

However, since natural mortality cannot be suppressed, K_0 is of little theoretical and practical value. In practice only K can be estimated, and it differs from K_0 because of the change in the numbers at risk over time induced by both the harvest and natural mortality, as explained above. The approximation above can be extended to rates $m(t)$ and $k(t)$ variable over time. Because the instantaneous rates are added to get the overall mortality rate, one speaks of 'additive mortality' (Anderson & Burnham, 1976; Burnham & Anderson, 1984).

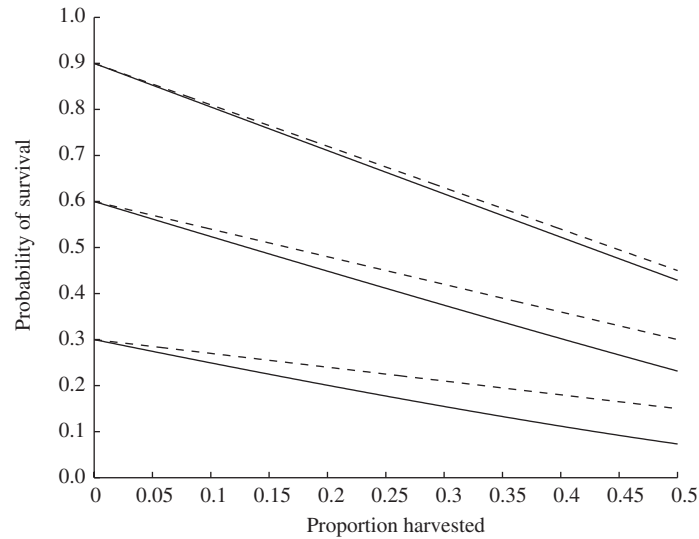


Figure 1. Variation in the probability of survival S as a function of proportion killed, or 'harvested' in the broad sense, K . Exact implicit relationship $1 - K/(1 - S) = \log(S_0)/\log(S)$ (dotted lines); approximate explicit relationship $S = S_0(1 - K)$ (continuous lines).

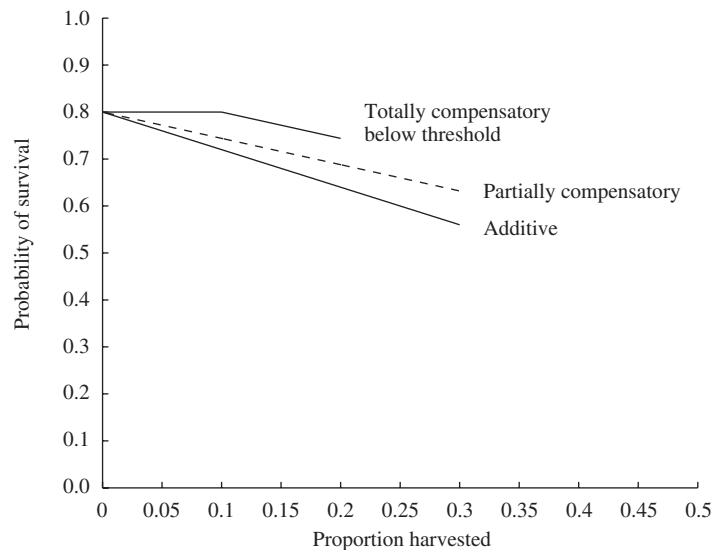


Figure 2. Probability of survival as a function of proportion harvested under different relationships between natural mortality and harvest

When, at a given level of harvest, survival remains higher than in the additive case, i.e. $S > S_0(1 - K)$, the effect of harvest is equivalent to that of an additive harvest of lower level, i.e. $S = S_0(1 - K')$ with $K' < K$. The population behaves as if harvested in an additive fashion at a lower level than the actual one. One speaks then of compensation. Various curves relating the probability of survival to harvest in presence of compensation are given in Figure 2.

One simple form of compensation is

$$S = S_0(1 - bK) \quad \text{with } b < 1.$$

Anderson & Burnham (1976) provide an excellent discussion of the topic.

4. Modelling the effect of harvesting in structured populations

Matrix models are a canonical tool for studying structured populations (Caswell, 2001 p. 3). In presence of harvest, the approximation above can be used for each survival probability entering such a model, i.e.

$$S = S_0(1 - bK).$$

The effect of harvest can thus be viewed in most cases as a decrease in survival from S_0 to $S = S_0(1 - bK)$. We see later the specific problems that arise in the estimation of S_0 , b and K . Provided estimates are available, the assessment of the effect of harvest is directly linked to sensitivity analyses of the matrix models; Darwin & Williams (1964) provide an early application of matrix models to a harvest problem. Consider, for instance, a hypothetical age-structured duck population subjected to hunting, in which the proportions of young and after-first-year birds killed are K_Y and K_A , respectively. Based on $S = S_0(1 - bK)$, the effect of harvest, in the broad sense, can be viewed as the effect of relative changes in survival, of magnitude $-bK$. Then, the approximate change in the asymptotic growth rate of the population directly depends on the elasticities (Caswell, 2001 p. 206 ff) of the first-year and after-first-year survival, which are simple functions of generation time T (Lebreton & Clobert, 1991). We get

$$\Delta\lambda \approx -b\lambda \left(K_Y \frac{1}{T} + K_A \left(1 - \frac{1}{T} \right) \right).$$

This shows the susceptibility of long-lived species (species with large T) to harvesting of adults, repeatedly noted in the literature (e.g. Mertz, 1971). This result is applied to the greater snow goose *Chen c. caerulescens* by Gauthier & Lebreton (in press). The same results hold for spatially subdivided populations, provided the adequate definition of generation time T is used (Lebreton, 1996). When the harvest proportion K is equal for young and adults, one gets an exact relationship, as in a non-structured population:

$$\Delta\lambda = -b\lambda K.$$

Optimal harvesting methods can be developed based on sensitivity analysis, and generalized to spatially structured populations (Brooks & Lebreton, 2001). In a spatial context, there are no simple rules such as the total harvesting of a given age class (that make older age classes disappear in a one-site context), because dispersal can bring older individuals to any site. The dependency of sensitivities on reproductive values (Caswell, 1978, 2001 p. 225) gives reproductive values a central role in optimal harvesting, whether one is aiming to maximize the harvest for a given cost (commercial resource) or minimize the impact of an incidental source of mortality (conservation biology).

As an example of assessment of harvesting effects in structured populations, we develop here an example concerning the effect of by-catch of albatross by long-line fisheries (after

Niel & Lebreton, 2005). Various albatross (*Diomedidae*) populations have been subjected over the last decades to such incidental by-catch (Croxall, 1998). In the wandering albatross *Diomedea exulans*, census-based estimated decreases closely matched model-based population projections (Weimerskirch, Brothers & Jouventin, 1997). For some other species, such as the black-footed albatross *Phoebastria nigripes*, no monitoring data were available to determine if the present level of by-catch would induce a decrease in numbers (Cousins & Cooper, 1999). A key quantity in this context is the maximum annual growth rate, denoted as λ_{\max} , since the sustainable incidental mortality cannot exceed $\lambda_{\max} - 1$. In a first approximation λ_{\max} , or, equivalently, $r_{\max} = \log(\lambda_{\max})$, is considered as a characteristic of the species of concern. The maximum annual growth rate (e.g. Charnov, 1993 p. 114 ff) and generation time are linked to body mass (Bonner, 1965; Blueweiss *et al.*, 1978; Millar & Zammuto, 1983) by allometric relationships sharing a common exponent in absolute value, close to 0.25. Hence the maximum growth rate per generation, a dimensionless number (Stahl, 1962), is approximately independent of body mass (Lebreton, 1981; Fowler, 1988; Charnov, 1993 p. 119). By comparative analysis over 13 bird species, Niel & Lebreton (2005) obtain approximately $r_{\max} T \approx 1$ and $R0_{\max} = \lambda_{\max}^T \approx 3$.

For large T , the latter expression implies $\lambda_{\max} - 1 \approx 1/T$. Only an estimate of T is then needed to assess the maximum sustainable rate of incidental mortality. A matrix model with generic albatross demographic parameter estimates leads to $T \approx 25$ years. The stable age structure from that model makes it possible to translate the 60 000 breeding pairs of black-footed albatross into approximately $N = 300\,000$ individuals. The growth excess in numbers can thus be estimated at most to $N/T = 12\,000$ individuals. The annual by-catch, around 12 500 (Melvin, pers. comm.) would certainly be deleterious, in particular because other diffuse sources of mortality (such as ingestion of pieces of plastic) are induced by human activities. Unfortunately, this diagnostic was confirmed by a recent census with 48 000 pairs. Similar conclusions were reached recently by Lewison & Crowder (2003).

In this example, no ecological compensation was considered. Is this a reasonable assumption or not? We attempt to make some predictions in the next section.

5. Additive or compensatory mortality: some predictions

Animals can only detect changes in mortality by the changes induced in the numbers remaining alive. Compensation is thus expected to result from density-dependence, either in survival or in other demographic parameters such as reproductive rate. However, as shown below, heterogeneity among individuals in survival can also change the relationship between survival and harvest in a fashion similar to density-dependent compensation, as already noted by Johnson, Burnham & Schwarz (1986). Although the underlying mechanisms are radically different, the consequences are identical, and one could speak in both cases of compensation, by density-dependence or heterogeneity, respectively.

Predictions of the levels of compensation by these two kinds of mechanisms have to our knowledge never been discussed. Here is an attempt, based on simple calculations.

The effect of density-dependence in survival can be broadly understood from the following calculations. Assume that survival in the absence of harvest depends on population size N as $S_0(1 - aN)$. A slightly different, logistic linear, density-dependent relationship was considered by Johnson *et al.* (1993 p. 580). Assume harvest at rate K occurs entirely before natural mortality, changing population size into $N(1 - K)$. Then the overall survival is:

$$S_0(1 - K)(1 - aN(1 - K)).$$

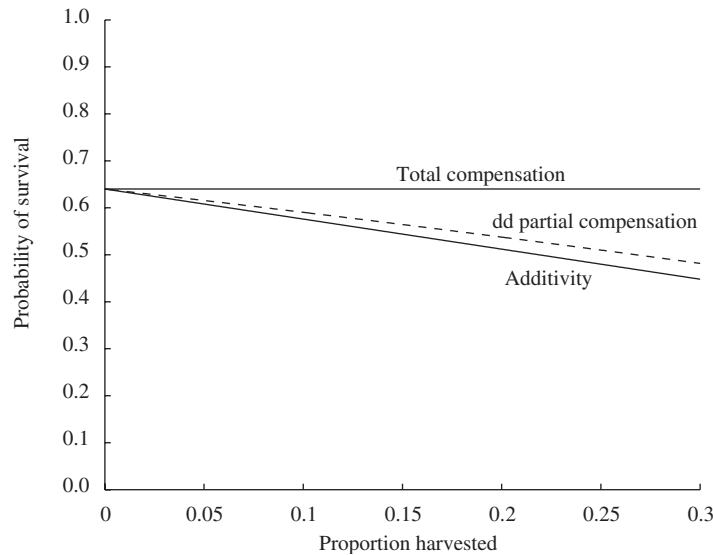


Figure 3. An example of compensation by density-dependence. Survival at density N is 0.64. Density-dependence is strong enough to make survival probability decrease to 0.48 (a 25% decrease) if population size doubles. Despite this strong density-dependence, compensation of harvest is weak, the dotted line being close to $S_0(1 - 0.825K)$.

K is then totally compensated only if $S_0(1 - K)(1 - aN(1 - K)) \geq S_0(1 - aN)$, an inequality met for:

$$0 \leq K \leq 2 - \frac{1}{aN}.$$

If $aN < 0.5$, total compensation even for small K is not achievable. In practice, even with strong density-dependence (i.e. large a) the compensation is weak, as shown in Figure 3, where compensation is weak although a 25% decrease in survival follows a doubling of population size. Such an extreme variation in survival with density has to our knowledge never been reliably documented in any bird population. However, over the years, even weak compensation can play a non-negligible role in the equilibrium level of population (see e.g. Frederiksen, Lebreton & Bregnballe, 2001). Boyce, Sinclair & White (1999) examine compensation in the presence of seasonality.

As an example of apparent compensation resulting from heterogeneity in survival, consider a hypothetical duck population with 1000 individuals at the beginning of the hunting season. Assume the population is made up of 500 'non-vulnerable' individuals with natural survival equal to 0.8, and 500 'vulnerable' individuals with natural survival equal to 0.2. The average natural survival probability is $S_0 = 0.5$, i.e. 500 would survive in the absence of harvesting. Assume that the harvest proportion in the vulnerable segment of the population is 30%, against 10% in the other segment, i.e. $K = 20\%$ on average. Then, the approximate number of survivors after harvest followed by natural mortality is

$$(500 \times (1 - 0.3) \times 0.2) + (500 \times (1 - 0.1) \times 0.8) = 70 + 360 = 430,$$

leading to $S = 0.43$, with 400 animals harvested and 170 dying from natural causes.

An additive mortality scheme neglecting the heterogeneity would predict

$$1000 \times (1 - 0.2) \times 0.5 = 400 ,$$

with 400 animals harvested, and 200 dying from natural causes. Based on the figures above, the resulting survival S in presence of heterogeneity can be expressed as $S = S_0(1 - bK)$ with $b = 0.7$, a moderate compensation despite the very strong heterogeneity in this theoretical example.

Hence, a striking conclusion is that one can rarely expect strong compensation of harvest by either density-dependence or heterogeneity in survival. It is thus not surprising that many attempts to detect compensation from mark–recapture data have led to controversial results (Anderson & Burnham, 1976).

The same mechanisms can act on reproductive parameters. To what degree can a reproductive parameter F compensate for the effect of a harvest proportion K equal across age classes on the growth rate of a population? A simple approximation of the change needed in such a parameter F can be obtained for an age-structured population from the expression of elasticities as simple functions of generation time as:

$$\frac{\Delta F}{F} \approx TK .$$

As is generally agreed, recruitment can thus compensate for harvest in fish populations with a high fecundity. In long-lived species (say $T = 10$), a 50% change in, say, fecundity, is needed to compensate for a 5% harvest rate. On this basis, even if an acceleration in recruitment has been noted in some seabird species after decreases induced by long-line fisheries impact (Weimerskirch *et al.*, 1997), it has only second-order effects on the growth rate. An interesting idea is that recruitment and breeding performance in ducks, species with a fairly short generation time among birds, could be partly compensating for hunting mortality (Kalchreuter, 1996). This still has to be empirically demonstrated.

Altogether, the degree of compensation expected in vertebrates such as birds or mammals appears thus to be weak. Is this theoretical reasoning in contradiction or in accordance with empirical evidence? A review of statistical models and analyses may help answer this question.

6. Additive or compensatory: statistical models

The principles of statistical models and empirical analyses of the interplay of sources of mortality were laid down in the landmark paper by Anderson & Burnham (1976). The survival probability S_i in, say, year i , is a function of the probabilities of ‘natural’ mortality V_i and of harvest (or ‘kill’) K_i as

$$S_i = 1 - V_i - K_i .$$

The key point is to consider V_i and K_i as random variables: the interaction between the sources of mortality, ranging from total compensation to additivity, is reflected in the covariance $\text{cov}(V_i, K_i)$ or the correlation $\text{corr}(V_i, K_i)$ between these random variables. Under additivity, the correlation is close to zero and slightly negative in most cases (Schaub & Lebreton, 2004).

The slopes in $E(V_i/K_i) = a + b_{VK}K_i$ and in $E(S_i/K_i) = c + b_{SK}K_i$ can be used equivalently, these quantities being related by

$$b_{VK} = \frac{\text{cov}(V_i, K_i)}{\text{var}(K_i)} = -1 - b_{SK} .$$

The first line of development was based upon statistical models for dead recoveries, i.e. retrieval of marks (such as leg rings) found on dead individuals by the public. The application of these models to quarry species, mainly ducks and geese (order Anseriforms), takes advantage of the fact that recoveries are nearly always birds dead from hunting, which hence give information on harvest. Denote as f_i the probability that a marked bird dies in year i and that its mark is retrieved. Then the expected number of recoveries in year i , among R birds released at time 0 (i.e. at the onset of year 1) with a mark, is

$$RS_1 \dots S_{i-1} f_i.$$

Assuming independence of individuals, maximum likelihood estimates of the parameters are then obtainable provided birds are marked and released every year, with a number of variations in the details of statistical model structure (Brownie *et al.*, 1985).

Anderson & Burnham (1976) related K_i to f_i based on some simple assumptions.

- The proportion killed K_i is equal to $(1 + c)H_i$, where H_i is the proportion killed and retrieved by a hunter, because of further deaths (e.g. of wounded birds) not retrieved by hunters. The parameter c corresponds to the so-called ‘crippling loss’. H_i is usually called the harvest rate.
- Only hunting recoveries are taken into account. In quarry species, recoveries from other causes are generally negligible in number. Then $f_i = rH_i$, where r is the reporting rate, i.e. the probability that the mark of a bird killed by a hunter is sent back to the ringing centre.

Under these assumptions $f_i = (r/(1+c))K_i$. With independent estimates of r and c it is possible to go from the simultaneous estimation of S_i and f_i to that of S_i and K_i . This is a critical step in the process, since any relative bias a in K_i , amounting to the use of $K'_i = (1 + a)K_i$ instead of K_i , biases the estimates of $\text{corr}(V_i, K_i)$ or equivalently of b_{VK} or b_{SK} . Finally the variation in estimates of S_i and K_i over time results from (i) the variation in the underlying random variables S_i and K_i over time, in which we are interested, and (ii) sampling variation. A random effect model has to be applied to the estimates to extract estimates of variances and covariances between the random variables (Anderson & Burnham, 1976).

The reporting rate r can be estimated by comparing the proportion recovered using standard marks to the proportion recovered based on reward marks that are supposed to induce a reporting rate equal to 1, possibly analysing reward and standard marks simultaneously (Pollock, Tsai & Hoenig, 1994). Some concern was expressed about the potential bias of reporting rates estimates (see review by Nichols *et al.*, 1991). These authors concluded, based on marks with different reward values, that reward marks in earlier studies led to a reporting rate smaller than 1. Their bias calculation (p. 125) leads us to conclude that the reporting rate estimate used by Anderson & Burnham could have had a relative bias of -33% . Such a **downward** bias induces a positive bias on K_i and, in turn, a bias of tests of additivity towards the alternative hypothesis, i.e. compensation. Whether this really weakens the conclusion of compensation of hunting mortality in the mallard, *Anas platyrhynchos*, reached by Anderson & Burnham still remains to be evaluated in greater detail. Recent analyses on mallards in North America supported the additive mortality hypothesis (Smith & Reynolds 1992; Williams, Nichols & Conroy, 2002 p. 681).

Another way of relating survival to harvest is to use a regression of mortality over an independent estimate of the proportion killed, built into a survival model. The proportion killed

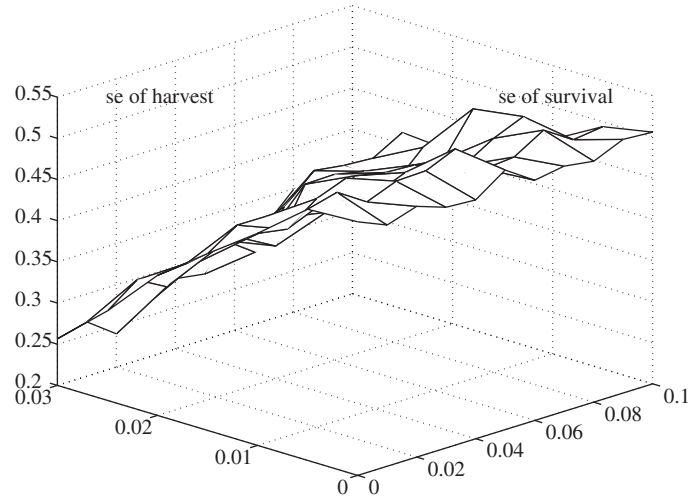


Figure 4. Mean P -value of a test of $H_0: b = 1$ in a logistic model, $\text{logit}(S_i) = a - K_i + e_i + \text{binomial error}$, as a function of the standard error of K_i and e_i ('survival'). A mean P -value close to 0.5 corresponds to an unbiased test since the P -value is then a uniform random variable over $[0, 1]$. This is the case whatever the se of survival (i.e. when S varies with K_i as well as with other unknown sources of variation). However, the P -value decreases when the se of K_i increases, indicating a test more and more often significant when the uncertainty on K_i increases. The uncertainty on harvest proportion being unavoidable, this shows that tests of additivity of natural mortality and harvest in regression models of survival over harvest built in capture–recapture models are non-conservative, i.e. they often lean towards compensation.

K is inevitably estimated with some sampling error and often with some bias. As a consequence the slope estimate in the regression that serves to assess the degree of compensation is biased to an unknown degree. Sampling error on K biases the slope downwards, as shown by simulations using logistic regression, a statistical model close to capture–recapture models with covariates (Figure 4). As usual, 'the effect of the errors is thus to diminish the slope of the regression lines' (Kendall & Stuart, 1961 Vol. 2 p.413). Gauthier *et al.* (2001) provide such an analysis of hunting mortality in the greater snow goose, based on large numbers of live recaptures in autumn and spring that make it possible to look precisely to winter (hunting season) survival. Nevertheless, there is no sign of compensation, a conclusion that could be expected in a fairly long-lived species (S_0 is around 0.93). Since the test could be biased by uncertainty in harvest estimate only in favour of the compensation hypothesis, this seems a reliable conclusion.

The two approaches above have to rely on information independent from the capture–recapture data, and potential bias or uncertainty in this information tends to bias the additivity test towards the alternative hypothesis. This is not a desirable property for a statistical test!

Recently Schaub & Lebreton (2004) proposed a radically different approach for species where recoveries from several causes are available. First, Schaub & Pradel (2004) wrote a capture/recovery model with death from two causes, as a particular case of a multistate capture–recapture model. Although survival is directly related to the probabilities of death as $S = 1 - V - K$, only the products of the death rates with the reporting rates Vr_V and Kr_K are estimable when the parameters are constant over time. However, following the proposition of

Morgan & Freeman (1989) for first-year survival in ring-recovery models, and using formal tools (Catchpole & Morgan, 1997) adapted to multistate models (Gimenez, Choquet & Lebreton, 2003), Schaub & Pradel (2004) showed that S_i , V_i and K_i are separately identifiable when time-dependent, provided the reporting rates are assumed constant. Schaub & Lebreton (2004) estimated then the correlation between the random variables V_i and K_i by fitting by maximum likelihood a random effect model to the estimates of the logit-transformed parameters. Their results suggest that death from collision with power lines and death from other causes are additive both for young birds and adults.

The straightforward conclusion of the last two sections is pessimistic in the sense that the compensation to be expected in mortality is at most weak, and the tools to detect it are subject to inherent biases that are difficult to control.

7. Discussion

Interest in the dynamics of exploited populations is strong and general, in particular if the broad sense of 'exploited' is taken to encompass populations subject to any source of mortality resulting from human activities. The effort made to analyse empirical data and improve our understanding of the dynamics of exploited populations seems, by comparison, somewhat limited.

Little effort has been put into attempting to predict the amount of ecological compensation. It seems, from the basic calculations proposed here, that compensation by natural mortality should be, at most, weak, and that compensation by recruitment/reproductive parameters can only be low for species with low productivity and long generation time.

This may explain the success of modelling in conservation biology (e.g. Lahaye, Gutiérrez & Akçakaya, 1994; Hitchcock & Gratto-Trevor, 1997) where compensation is not taken into account, for at least two good reasons: the lack of empirical evidence, and a logical emphasis in this context on the precautionary principle. A bridge has been developed between the fishery world and the conservation biology world, with a variety of modelling studies looking at human-induced mortality among marine mammals and seabirds (e.g. Wade, 1998). For hunted species, there is a near absence of validation by modelling of otherwise good empirical analyses (e.g. Sedinger & Rexstad, 1994), and more generally only a limited amount of discussion in relation to biology. The needs are particularly pressing in Europe where the exploitation rates of duck populations are greater than in North America (Nichols, Lancia & Lebreton, 2001). On such grounds, the debate over the extent and intensity of compensation of hunting mortality remains open.

With respect to statistical models, there is an absence of innovation after the landmark papers by Anderson & Burnham (1976) and Burnham & Anderson (1984). The generalization and standardization of capture–recapture models (Lebreton, 1995) and the possibilities of multistate models for mixtures of information (Lebreton, Almeras & Pradel, 1999) offer nevertheless a variety of new possibilities. The example cited here about the greater snow goose shows how live recaptures and/or combinations of recaptures and recoveries can be used to address the interplay of several sources of mortality. We hope they stimulate more imaginative analyses.

With a limited use of models, except in conservation biology, and a slow evolution of statistical models, it is thus not surprising that existing bridges between the two types of tools have still been hardly used (for fisheries, see Maunder, 2001a,b,c). All empirical approaches

have to rely in one way or another on independent estimates to be able to estimate the proportion harvested. The log-likelihood for estimating, from data denoted as X , a statistic for testing for compensation, say, b , is $\log L(b, X/\hat{a})$.

In this expression \hat{a} is an estimate, based on data Y , of another parameter a , from the log-likelihood $\log L(a, Y)$. The combined log-likelihood $\log L(b, X/\hat{a}) + \log L(a, Y)$ provides a sound basis for the simultaneous estimation of a and b , and can be extended to a Bayesian framework to incorporate *a priori* information on any parameter. More widely, the uncertainty in the harvest proportion is always present: methods should explicitly take this uncertainty into account. Adaptive management has great potential, as shown by Johnson *et al.* (1993, 1997). Another integration method with strong potential consists of linking a projection model and a statistical model for demographic parameters, for instance by the Kalman filter. Besbeas *et al.* (2001) showed that the normal distribution of demographic estimates leads to a good approximation to the log-likelihood of the statistical model and makes this implementation possible. The Kalman filter uses a state equation such as a matrix model and an observation equation. In many cases, the observations consist only of a census of the total population. In the context of exploited populations, if the number harvested was considered as part of the observations, it would be possible to account for its uncertainty in a straightforward way. Below we give an example of integration of a matrix model (state equation) and of observation of population size and number harvested (observation equation). The matrix model considers a single age class (N) together with two states for dead individuals (N_V : natural deaths; N_K : death from harvest).

$$\text{State equation:} \quad \begin{bmatrix} N \\ N_V \\ N_K \end{bmatrix}_{t+1} = \begin{bmatrix} f + S & 0 & 0 \\ V & 0 & 0 \\ K & 0 & 0 \end{bmatrix} \begin{bmatrix} N \\ N_M \\ N_H \end{bmatrix}_t + \varepsilon_t.$$

$$\text{Observation equation:} \quad Y_t = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} N \\ N_V \\ N_K \end{bmatrix}_t + \eta_t.$$

The likelihood for this model can be integrated with the likelihood of a statistical model for estimating the parameters in the matrix of the state equation (see Besbeas *et al.*, 2001, 2002).

Altogether it seems thus that with more biology, a systematic use of models, more sophisticated statistical approaches and integration with projection models, there is a strong potential to address with increased precision the questions raised by the dynamics of exploited populations. This may particularly shed light on the question of compensation in vertebrate populations such as bird and mammal populations. From the biological point of view, and in relation to the precautionary principle, it seems reasonable to work under the assumption of additive mortality risks unless there are good reasons not to do so.

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