Inferring functional extinction based on sighting records

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ABSTRACT

The term functional extinction is used to describe a permanent failure of reproduction or recruitment in a population. Functional extinction results in a truncation of the age distribution, but this can be very difficult to detect in poorly studied populations. Here, we describe a novel statistical method for detecting functional extinction based on a sighting record of individuals of known or estimated ages. The method is based on a simple population dynamics model and simulation results show that it works well even with limited data. The method is illustrated using a sighting record of the ship sturgeon (*Acipenser nudiventris*) in the Danube River. The results indicate that this population is functionally extinct, most likely by 2002. Management implications of this finding are discussed.

Keywords: *Acipenser nudiventris*, extinction risk, recruitment failure, reproductive failure, sighting record

1. INTRODUCTION

For many species, negative population trends pass largely undetected across the critical point beyond which management and conservation measures become ineffective, while the likelihood of extinction approaches certainty. As a result, timely and reliable detection of critical population status is of paramount importance to allow effective countermeasures to be taken in due time.

One of the frequently observed patterns that precede extinction of a species is the process of time-delayed deterministic extinction (Ford et al., 2009), which commonly occurs due to persistent lack of reproduction success or recruitment. Such populations are typically represented by a slowly declining number of adults that are no longer able to successfully reproduce (Evans and Keen, 2013). This phenomenon was recognized as the major extinction threat in populations of many species, such as wolf (*Canis lupus*; Bull et al., 2009), baiji (*Lipotes vexillifer*; Xu et al., 2012), tuatara (*Sphenodon punctatus*; Grayson et al., 2014), giant clam (*Tridacna maxima*; Waters et al., 2013) and different bird species (Donald, 2007), and it was denoted as 'reproductive extinction' (Peterson et al., 2001), 'latent extinction' (Evans and Keen, 2013), 'virtual extinction' (Peterson et al., 2001), and 'living dead'-phenomenon (Janzen, 2001 cit. in Evans and Keen, 2013). However, following Ricciardi et al. (1998), Bull et al. (2009), Waters et al. (2013), and others, we refer to a permanent lack of reproductive or recruitment success as functional extinction. It is important to note that the term functional extinction, as it was used in the present study, should not be confused with other uses of this term in literature (Jarić, 2015).

Functional extinction can be particularly difficult to detect, especially in long-lived species, where the point of no return is often crossed long before the actual extinction occurs. In such populations, older individuals tend to remain present for years after the last successful

reproduction event, thus presenting a false image of population viability. Furthermore, for rare or poorly studied species, sighting records often represent the only available source of data for the quantitative assessment of population status (Solow, 1993, 2005). In such circumstances, development of quantitative methods to allow inferences about functional extinction based on limited data available would be valuable.

In this paper, we describe a novel statistical method for inference about functional extinction based on sighting records. The method is illustrated using a sighting record of the ship sturgeon (*Acipenser nudiventris*) in the Danube River.

2. MODEL AND METHOD

In this section, we describe a statistical model of a sighting record of individuals of known ages and the use of this model for inference about functional extinction and its timing.

We begin by describing a model of the unobserved variations in abundance of the species in question. Consider the observation period $t = 1, 2, \ldots, T$ and let the unobserved abundance in year t of a cohort spawned in year j be:

$$Y_{jt} = Y_j \exp(-\beta(t-j)) \qquad t = j, j+1, \ldots, T \qquad (1)$$

where Y_j is the initial cohort size and β is the annual mortality rate. Let τ_E be the last year before functional extinction, so that $Y_j = 0$ for $j > \tau_E$. Populations typically experience large inter-annual fluctuations in year-class strength, often connected to environmental variations. To capture this, we will assume that, for $j \leq \tau_E$, Y_j is an exponential random variable with probability density function:

$$f(y_j) = \theta \exp(-\theta y_j) \quad (2)$$

where the unknown parameter θ is the reciprocal of mean initial cohort size. Let $Y = (Y_1, Y_2, \ldots , Y_T)$.

We consider next a model of sampling from this population. A random sample of m_t individuals is collected in year t (m_t may be 0) and the age of each individual is recorded. Individuals from cohorts outside the observation period are not included in this sample. Let X_{jt} be the number of these individuals that come from cohort j and let $X_t = (X_{1t}, X_{2t}, \ldots , X_{tt})$ be the vector of these numbers. Conditional on the observed value m_t, and on the unobserved vector of initial cohort sizes $y = (y_1, y_2, \ldots , y_t)$, X_t has a multinomial distribution with probability mass function:

$$pr(x_t \mid m_t, y) = \frac{m_t!}{\prod_{j=1}^{t} x_{jt}!} \prod_{j=1}^{t} p_{jt}^{x_{jt}}(y) \quad (3)$$

where:

$$p_{jt}(y) = \frac{y_j \exp(-\beta(t-j))}{\sum_{k=1}^{t} y_k \exp(-\beta(t-k))} \quad (4)$$

The conditioning on the unobserved y can be removed by integrating $pr(x_t \mid m_t, y)$ over the distribution of Y leading to the probability mass function $pr(x_t \mid m_t)$ of X_t conditional on the observed m_t alone. Importantly, because the conditional distribution of X_t given m_t depends only

on the relative cohort abundances in year t, $pr(x_t \mid m_t)$ does not depend on the unknown parameter θ. In practice, this probability mass function can be approximated by:

$$pr\left(x_t \mid m_t\right) \cong \frac{m_t!}{\prod_{j=1}^{t} x_{jt}!} \sum_{b=1}^{B} \prod_{j=1}^{t} \frac{p_{jt}^{x_{jt}}\left(y(b)\right)}{B} \qquad (5)$$

where B is a large number and $y(b) = (y_1(b), y_2(b), \ldots, y_T(b))$ and where $y_j(b)$ is a value simulated from an exponential distribution with mean 1. For later use, the log likelihood function for this model is given by:

$$\log L\left(\tau_E, \beta\right) = \sum_{t=1}^{T} \log pr\left(x_t \mid m_t\right) \qquad (6)$$

where x_t is the vector of observed cohort counts in the sample in year t.

We turn now to statistical inference about τ_E based on the model described above. Interest here centers on testing the null hypothesis H_0: $\tau_E = T$ that functional extinction has not occurred during the observation period against the alternative hypothesis H_1: $\tau_E < T$ that it has and, in the event that H_0 is rejected, in constructing a confidence interval for τ_E. A natural statistic for testing H_0 against H_1 is the year R of the most recent observed cohort, with H_0 being rejected for small values of R.

The significance of the observed value of R can be approximated via the following parametric bootstrap. As above, initial cohort sizes $y_1, y_2, \ldots, y_T$ are simulated from the unit exponential distribution. Using these initial cohort sizes, for $k = 1, 2, \ldots, T$, x_k is simulated from the multinomial distribution with m_k trials and probabilities given in (4) with β equal to its

maximum likelihood (ML) estimate $\hat{\beta}(\tau_E)$ with τ_E fixed at T. The value of R for the simulated

dataset is recorded, and the procedure is repeated a large number of times. The significance level

(or p value) can be approximated by the proportion of simulated values of R that exceed the

observed value plus half of the proportion that are equal to the observed value. This is an

application of the so-called mid-p method (Berry and Armitage, 1995).

The upper bound of a one-sided $1 - \alpha$ confidence interval for τ_E is given by the largest

value of τ_0 for which the null hypothesis H_0: $\tau_E = \tau_0$ cannot be rejected at significance level α

against the alternative hypothesis H_1: $\tau_E < \tau_0$. The parametric bootstrap outlined above can be

used to test H_0 against H_1. In this case, initial cohort size y_k is 0 for $k > \tau_0$ and the value of β used

to form the multinomial probabilities is the ML estimate $\hat{\beta}(\tau_0)$ with τ_E fixed at τ_0.

3. SIMULATION RESULTS

We conducted a simulation study to assess the performance of the test for functional

extinction described in the previous section. This involved repeatedly simulating data from the

underlying model for selected values of the parameters β and τ_E, applying the test to the

simulated data at significance level 0.05, and recording the rate at which the null hypothesis H_0

that functional extinction has not occurred was rejected. In each case, the length of the

observation period was fixed at 50 years and individuals were sampled at ten-year intervals. We

considered 3 possible values of the number of individuals sampled at each of these times: 1, 3,

and 5.

The goal of the first part of the study was to assess the agreement between the nominal

0.05 significance level and the rate at which H_0 is rejected when it is true. The results are

presented in Table 1, with each entry based on 2000 simulated datasets and 1000 parametric

bootstrap samples for each of these. The agreement between the nominal and actual significance levels is generally good with a slight tendency for the test to be conservative when the annual mortality rate β is low.

The goal of the second part of the study was to assess the power of the test- that is, the rate at which H_0 is rejected when it is false. The results of this part of the study are presented in Table 2, with each entry based on 1000 simulated datasets and 1000 bootstrap samples for each. The test has good power in all cases except when β is low and the number of sampled individuals is small.

4. APPLICATION

We illustrate the method application by using a dataset on sightings of ship sturgeon from the Danube River. This species inhabits Black, Caspian and Aral Sea basins, and it is considered as critically endangered throughout its range (Gessner et al., 2010). It was once commonly recorded in the Danube (Hensel and Holčik, 1997) but since the mid-1950s the population has been severely depleted by a combination of factors and there is concern that it has failed to reproduce over a prolonged period (Jarić et al., 2009; Gessner et al., 2010). Due to a lack of systematic monitoring, the ship sturgeon population in the Danube River is known only through a small number of chance sightings and drawing conclusions about its population status is challenging.

The beginning of the observation period was set at 1955. Only 13 sightings of ship sturgeon have been confirmed between 1955 and 2015 (Table 3). Of these, it is possible to estimate the ages of 12 specimens based on a regression of body length and weight (Holčik, 1989), while using the correction factor for age assignment by Bruch et al. (2009; see online

Appendix). Four specimens were omitted from the analysis, since they belonged to cohorts spawned before the beginning of the observation period. Although the number of aged specimens is greater in recent years, the overall sighting rate has remained stable since 1955.

We applied the test for functional extinction to the data in Table 3. The approximate p value based on 10 000 parametric bootstrap samples was around 0.03 and, by conventional standards of significance, we reject the null hypothesis that functional extinction has not yet occurred. The upper bound of an approximate one-sided 0.95 confidence interval for τ_E is 2002. The maximum likelihood estimates of the annual mortality rate β ranged from 0.062 to 0.093 for values of τ_E in this confidence interval. These are generally consistent with values in the literature (Jarić et al., 2010).

Finally, to assess the robustness of the result of the test to errors in the estimated ages, we applied the test to 1000 datasets generated by randomly perturbing each of the age estimates in Table 3 by up to 3 years. Of the 1000 p values generated in this way, 772 were less than 0.05 and none was larger than 0.09.

5. DISCUSSION

This paper presents a novel statistical approach to infer functional extinction. The statistical method described here is based on a very simple model of population dynamics. This level of simplicity is necessitated by the fact that the population and its demography are known only through a very small number of captured individuals. Its data requirements are also low, which facilitates its application for data-deficient situations. Necessary input data are simple sighting records, with the time of sighting and the age estimation of each recorded specimen. With more data, it would be possible to evaluate and, if necessary, elaborate this model.

The method application was illustrated on a sighting record of the Danube River ship sturgeon. The results indicated that this population is indeed functionally extinct, with functional extinction most likely occurring by 2002. With remaining individuals being at least 13-years old, extinction is expected to occur within the next 20 years, based on the expected lifespan of the species. It is likely that functional extinction might be widespread within this group of fish, and that it has already occurred in other sturgeon and paddlefish populations. Lack of successful reproduction or recruitment was reported in a number of sturgeon and paddlefish populations, for example in European sturgeon (*A. sturio*) in the Gironde Estuary in France, where the last confirmed natural reproduction occurred in 1994 (Williot et al., 2009), as well as in Chinese paddlefish (*Psephurus gladius*) in the Yangtze River in China (Zhang et al., 2009), pallid sturgeon (*Scaphirhynchus albus*) in the Mississippi and Missouri Rivers in USA (Webb et al., 2005), and other cases. To what degree the mentioned populations face the risk of functional extinction remains yet to be tested. In some populations, broodstock establishment and supportive stocking were introduced at one point in time to compensate for the lack of reproduction and/or recruitment (Webb et al., 2005; Williot et al., 2009; Zhang et al., 2011). In the case of the Danube ship sturgeon, species rarity and lack of adequate efforts so far prevented establishment of broodstock, despite the fact that this remains recognized as one of the current management priorities (Bloesch et al., 2006).

The common cause of functional extinction is the persistent reproductive failure, which can occur due to different factors and mechanisms such as the lack of habitat, sterility or embryo mortality induced by genetic erosion, mutations, inbreeding or pollution, catastrophic events, phenological shifts caused by climate change, parasitism, diseases, invasive species, sex-ratio bias, and population fragmentation (Loehle and Li, 1996; Janssen and Jude, 2001; Smithers et

al., 2003; Brodie et al., 2006; Taylor et al., 2006; Engelstädter and Hurst, 2009; Finger et al., 2011; Kudo and Ida, 2013; Grayson et al., 2014). Alternatively, persistent lack of recruitment, due to continuous elevated mortality of early life phases, represents another cause of functional extinction (Webb et al., 2005). The above mentioned mechanisms are more likely to occur in small or declining populations, where various factors can contribute to reproductive failure synergistically, such as inbreeding, Allee effect, reproductive asynchrony or demographic stochasticity (McCarthy, 1997; Peterson et al., 2001; Calabrese and Fagan, 2004; Waters et al., 2013). Besides fish, reproductive failure has been reported in many other species groups, including mammals (Brodie et al., 2006; Bull et al., 2009), birds (Smithers et al., 2003; Bolger et al., 2005), reptiles (Grayson et al., 2014), amphibians (Taylor et al., 2006), molluscs (Peterson et al., 2001; Waters et al., 2013) and plants (Loehle and Li, 1996; Warburton et al., 2000; Finger et al., 2011; Evans and Keen, 2013).

One of the key problems regarding functional extinction is that it can represent a slow and long-lasting process. This may make it difficult to identify before the population approaches actual extinction, since the process of adult mortality may extend over more than a century (Evans and Keen, 2013). The American chestnut (*Castanea dentata*) population has managed to persist as stump sprouts for decades, in spite of a loss of reproductive ability (Loehle and Li, 1996). In addition, some forms of functional extinction may be less detectable. For instance, in sexually monomorphic species, functional extinction resulting from a population comprised of specimens of only one sex may be difficult to distinguish (Donald, 2007).

Based upon the results of the test developed, the likelihood of functional extinction can be assessed based on the sightings of individuals and their age. The method is able to indicate whether natural recovery of the population under natural conditions will be impossible, and

provide early warning signs that countermeasures need to be taken to prevent such situation. The method also makes it possible to assess the risk of functional extinction, which may allow managers to come to a timely decision whether it is necessary to invest into *ex situ* measures, or the *in situ* conservation measures would suffice to prevent the species in question from extinction. As a result, the test has potential as a decision support tool in conservation management, and might be of value for the scientific community, wildlife managers, decision makers and other stakeholders involved in the conservation management of rare or endangered species.

6. ACKNOWLEDGEMENTS

7. REFERENCES

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Table 1. Estimated true probability of false rejection of H_0 for the test for functional extinction with nominal significance level 0.05 for selected values of beta and sighting frequency; H_0 - the species is not functionally extinct at time T; results are based on simulating 2000 samples.

N^*	$\beta = 0.05$	$\beta = 0.15$
1	0.031	0.051
3	0.021	0.048
5	0.036	0.048

* Number of sightings in each year with sightings

Table 2. Estimated power of the test for functional extinction (i.e. probability of true rejection of the H_0) for different scenarios, applied at the 0.05 significance level; H_0 - the species is not functionally extinct at time T; results are based on simulating 1000 samples, with the total duration of 50 years.

Year of functional extinction	N^*	$\beta = 0.05$	$\beta = 0.15$
30	1	0.068	0.990
	3	0.719	1.000
	5	0.994	1.000
15	1	0.381	0.999
	3	0.971	1.000
	5	0.996	1.000

* Number of sightings in each year with sightings

Table 3. Sightings of ship sturgeon (*Acipenser nudiventris*) in the Danube River since 1955, with the estimated birthyears.

Sighting year	References	Mean estimated birthyear
1956[1]	Vásárhely, 1957	1941
1957[1]	Vásárhely, 1957	1953
1957[1]	Vásárhely, 1957	1949
1957	Vásárhely, 1957	1957
1961[1]	Kálmán, 1961	1944
1975	Hensel and Holčik, 1997	1972
1989	Hensel and Holčik, 1997	1973
1992	Guti, 2006	1982
1998[2]	Harka pers. comm.	/
2003	Sallai pers. comm.	1971
2003	Simonović et al., 2005	1974
2005	Guti, 2006	1975
2009	Suciu, 2009	1990

[1] Omitted from the analysis since the spawning date occurred before the sighting period

[2] Two adult specimens with no size data (>5 kg) caught in 1998 in the Tisza River (Harka pers. comm.)