Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa

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ABSTRACT

Population trends play a large role in species risk assessments and conservation planning, and species are often considered threatened if their recent rate of decline meets certain thresholds, regardless how large the population is. But how reliable an indicator of extinction risk is a single estimate of population trend? Given the integral role this decline-based approach has played in setting conservation priorities, it is surprising that it has undergone little empirical scrutiny. We compile an extensive global dataset of time series of abundance data for over 1300 vertebrate populations to provide the first major test of the predictability of population growth rates in nature. We divided each time series into assessment and response periods and examined the correlation between growth rates in the two time periods. In birds, population declines tended to be followed by further declines, but mammals, salmon, and other bony fishes showed the opposite pattern: past declines were associated with subsequent population increases, and vice versa. Furthermore, in these taxa subsequent growth rates were higher when initial declines were more severe. These patterns agreed with data simulated under a null model for a dynamically stable population experiencing density dependence. However, this type of result could also occur if conservation actions positively affected the population following initial declines—a scenario that our data were too limited to rigorously evaluate. This ambiguity emphasizes the importance of understanding the underlying causes of population trajectories in drawing inferences about rates of decline in abundance.

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1. Introduction

A central problem in conservation biology is the difficulty of identifying which species are currently at risk of extinction or are likely to be at risk in the near future. The framework developed by the International Union for Conservation of Nature (IUCN) is the most widely used for risk assessments. The IUCN Red List categories and criteria (IUCN, 2001; www.iucnredlist.org) have been used to assess extinction risk of over 70,000 species of animals, plants, and fungi. The five IUCN risk criteria reflect consideration of both the small-population paradigm (Soule and Wilcox, 1980; Frankel and Soule, 1981) and the declining-population paradigm (Caughley, 1994). Under the IUCN framework,

the Red List category (ranging from Least Concern to Extinct) is assigned based on the criterion that produces the highest estimated risk. This means that species can be listed based entirely on a rate of decline (Criterion A), regardless how large the census size (N) is. For example, a taxon that has declined >30% over ten years or three generations (whichever is longer) qualifies as Vulnerable under criterion A2, even if N is very large. According to the IUCN (2014), a 'Vulnerable' classification means that the species is "considered to be facing a high risk of extinction in the wild."

This decline-based approach can be effective for early detection of at-risk species that would not likely be flagged by other methods (Stanton, 2014). Caughley (1994) argued that the declining population paradigm is relevant to most problems in conservation, and few would disagree with the following premise: if a population that has recently declined continues to decline in the future, it will eventually be at risk

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of extinction. Theory shows that if a population has a negative growth rate, then in the absence of density dependence, the expected time to extinction depends more strongly on the rate of decline than on initial N (Lande et al., 2003). In addition, for many species N is more difficult to estimate than rate of decline, which can be based on an index rather than estimates of absolute abundance (Mace et al., 2008). Numerous examples exist of species that were once very numerous ($N > 10^6$) but have since gone extinct (passenger pigeon, *Ectopistes migratorius*; great auk, *Pinguinus impennis*; Galapagos damselfish, *Azurina eupalama*) or nearly so (American bison, *Bison bison*). If conservation actions are not initiated until a population reaches levels that trigger concern because of small population size, recovery options become more costly and less likely to succeed (Wilcove and Chen, 1998; Drechsler et al., 2011; Hutchings et al., 2012). Finally, populations that remain large after being reduced to a fraction of their historical size can be at substantial risk, particularly if their reduction has altered ecosystem functioning in ways that promote negative feedback loops or other Allee effects (Courchamp et al., 1999; Swain and Chouinard, 2008; Swain and Benoit, 2015).

Nevertheless, using rate of decline as an indicator of risk independent of census size remains controversial (Godfrey and Godley, 2008). Trends in abundance are challenging to evaluate in a conservation context for two major reasons. First, trends are typically estimated from a limited number of data points that are subject to measurement error, and this reduces precision and introduces potential biases (Holmes, 2001; Holmes et al., 2007; Connors et al., 2014). Second, a wide range of natural and anthropogenic factors can influence population trajectories, creating the challenge of distinguishing long-term trends from short-term fluctuations. Examples include random demographic stochasticity and environmental fluctuations (such as weather patterns and regime shifts; Coulson et al., 2001; Chavez et al., 2003; Lindenmayer et al., 2010), long-term environmental change related to climate (Anderson et al., 2015), and indirect effects due to changes in community interactions (Borrvall and Ebenman, 2006). A range of anthropogenic factors such as threats from habitat loss, invasive species, and exploitation could accelerate population declines or slow recovery, while implementation of conservation actions could have a positive influence on population trajectories (Hoffmann et al., 2010; Donald et al., 2007, Butchart et al., 2005). The interplay of all of these factors complicates interpretation and makes it more challenging to set priorities for conservation and management.

More fundamentally, to be effective conservation tools, analyses of time-series data must provide useful insights into the likely future status of a species, based on data from an assessment period that provides baseline information on population trends. This raises an important question: How reliable an indicator of conservation status is a single estimate of population trend? If a population has recently declined, is it reasonable to expect that it will continue to decline in the future? Curiously, given the widespread inclusion of population-decline criteria in assessments of extinction risk (IUCN, 2001; Waples et al., 2013), there has been little empirical evaluation of this crucial topic (but see Porszt et al., 2012 for an example for one species of Pacific salmon). That is not to say that evaluations of population trends have been lacking: risk has been assessed using unstructured (Dennis et al., 1991) and structured (Brook et al., 2000) population models, and causes of population change have been inferred based on the pattern of decline (Wolf and Mangel, 2008; Sugihara et al., 2012; Di Fonzo et al., 2013; Shoemaker and Akçakaya, 2015). However, although temporal changes in abundance trends have been examined for some marine fishes (Hutchings et al., 2010), a detailed empirical evaluation of the temporal consistency of trends in natural populations within and among different taxonomic groups has not been undertaken.

In this paper, we make a first attempt to fill this information gap. To better understand the predictability of population trajectories, we compiled an extensive global dataset of time series of abundance data for over 1300 vertebrate populations from four major groups: birds, mammals, salmon, and other bony fishes. We split each time series

into assessment and response periods of equal duration and asked the following questions: (1) Does the per-capita population growth rate (r) in the assessment period predict the growth rate in the response period? (2) Does the relationship between growth rates in the two time periods depend on (a) the taxon, (b) the type of threats affecting the species, or (c) implementation of conservation actions? (3) For populations that declined substantially in the assessment period, does the subsequent trajectory depend on the magnitude of the previous decline? Question 1 allows an empirical evaluation of the assumption that population declines will be followed by continued declines. Question 2 asks whether patterns of population trajectories are taxon-specific or can be related to specific anthropogenic factors. Question 3 asks whether severity of decline can be used as a reliable early-warning sign (a 'red flag') of compromised recovery potential (Hutchings et al., 2012).

To provide context for interpreting results for actual populations, we also simulated time-series data to characterize how temporal patterns of population trajectories change under three simple null models that do not involve any long-term population trend:

1) A true random walk, with population growth rate chosen randomly and independently at each time period;
2) A random walk with temporal autocorrelation, whereby growth rate is affected by the previous time period; and
3) A population with random fluctuations constrained by density dependence.

Null model #1 is unlikely to be realistic for any natural population but provides a useful point of reference. Null model #2 captures some aspects of environmental forcing. Null model #3 reflects the reality that long-term growth rates must be close to 0 for populations that persist for any appreciable length of time (Peterman, 1981).

2. Methods

2.1. Data sources

We compiled time series of abundance data (estimates of absolute abundance or indices of relative abundance) for individual populations from several large global databases (for detailed information about the sources for abundance and metadata, see Supplementary material). We only used populations for which estimates were available for at least 20 years or 6 generations, whichever was greater; this provided sufficient data for analysis of population trends in two consecutive time periods of duration comparable to that relevant to the IUCN Red List criterion A (the longer of 10 years or 3 generations). After applying this filter, we had sufficient data to conduct separate analyses for four different groups of species: birds ($n = 800$), mammals ($n = 51$), salmon ($n = 343$) and other bony fish ($n = 121$) (Table 1). These data were compiled at a variety of geographic scales, from global to local (Table 2). We analyzed data for salmonids and other bony fishes separately because most salmonids are anadromous and semelparous (or nearly so), which means typical measures of abundance include only adults maturing in a single year (as opposed to all adults in iteroparous species).

Table 1
Number of populations for which we obtained sufficiently long time series of abundance data to use in the analyses described in this paper. Data sources are described in Supplementary material. LPI = Living Planet Index (Loh et al., 2005; Collen et al., 2009); SCC = Species of Conservation Concern (Holmes et al., 2007); NABBS = North American Breeding Bird Survey.

Source	Birds	Mammals	Salmon	Other bony fish	Elasmobranchs	Total
LPI	442	48	79	120	4	693
SCC	11	3	–	1	–	15
NABBS	347	–	–	–	–	347
Holmes et al. (2005)	–	–	264	–	–	264
Totals	800	51	343	121	4	1319

Table 2
Geographic scale covered by time-series data for each major taxonomic group. Numbers are fractions of populations that fall into each category.

	Birds	Mammals	Salmon	Other fish
Global	0	0	0	0.008
National/Ocean	0.104	0	0	0.24
Regional	0.854	0.059	0.038	0.339
Smaller unit	0.029	0.882	0.962	0.388
Unknown	0.014	0.059	0	0.025

In addition to abundance data, we collected auxiliary information for each population, including geographic location, generation length, an indicator of conservation status (IUCN Red List category), and whether they were affected by each of three different threats (habitat loss, overexploitation, and interactions with invasive species). For the latter analyses we supplemented the 1315 populations of the four groups mentioned above with data for four populations of elasmobranchs. Table A1 provides summary information for each of the time series we used, including the population growth metrics we calculated as described below.

2.2. Data processing and analysis

2.2.1. Population trajectories

For time series with more data points than needed to produce two time periods of 3 generations or 10 years (3G/10), we used the most recent $2 \times 3G/10$ years of data. This approach ensured equal power to detect trends in both time periods and minimized (within constraints imposed by variable generation length) differences in power across species; it also avoided using the same data both to identify a breakpoint and to analyze trend. Time series with a gap of more than 5 years between assessment and response periods were not used, nor were time series with identical values for 5 or more consecutive time periods. If a large systematic change in frequency of measurement occurred over the course of the time series (e.g., moving from decadal to annual sampling), we subsampled the more frequently sampled period to achieve a consistent measurement interval throughout the time series.

We used an exponential growth model to estimate per-capita population growth rate (r = proportional change per year) during the assessment period (r_{assess}) and response period ($r_{response}$). Let $N_{i,t}$ be abundance of population i in year t, then on the (natural) log scale for an assessment period,

$$\log(N_{i,t}) = \log(N_{i,t-1}) + \log(r_{assess,i}). \tag{1}$$

We estimated r_{assess} using linear regression of $\log(N_{i,t})$ on t, which produced model-fitted abundances at the start (N_1) and end (N_t). The response period started one year after the end of the assessment period; $r_{response}$ was calculated as above, but the intercept was set as the model estimate (N_t) from the last year in the assessment period. This approach assumes that all of the variation around the trend line arises from measurement error (Dennis et al., 1991; Hilborn and Mangel, 1997). To enable calculation on the log scale, zeros were replaced by half the minimum non-zero value. Percent change in N for each time period was estimated as $100(N_t - N_1) / N_1$.

2.2.2. Model analyses

We first examined the relationship between r in the assessment and response periods and how this varied among the four taxonomic groups. We assessed the relationship using the model:

$$r_{response,i} = \alpha \, r_{assess,i} + \beta_{tax} + \gamma(r_{assess}, tax) + \varepsilon_i, \tag{2}$$

where $r_{response,i}$ is the per-capita population growth rate of the ith species in the response period, $\alpha r_{assess,i}$ is the main effect of population growth in the assessment period, β_{tax} is the main effect of taxonomy,

$\gamma(r_{assess}, tax)$ is the interaction between the assessment period population growth rate and taxonomy, and ε_i is the normally distributed error term. We used a weighted regression, with weights set inversely proportional to the standard error of the estimate of r_{assess}. We also ran the model without the interaction term and used an analysis of variance to evaluate significance of the interaction term.

For species that declined during the assessment period, we conducted additional analyses to evaluate whether percent change in abundance in the response period depended on the magnitude of decline. We evaluated four decline thresholds based on those used to determine IUCN threat categories under Criterion A1 for managed populations (IUCN, 2001): ≥90% (Critically Endangered); 70–89.9% (Endangered); 50–69.9% (Vulnerable). No decline threshold is specified for Near Threatened, but following IUCN (2010) we used a 30–49.9% decline for this category. The assessment period was the first 3G/10 period in which the population decline met the specific threshold, and the response period was the 3G/10 year period following this decline. This was only done once for each population (for each threshold). We used a simple one-way ANOVA to test whether $r_{response}$ was significantly different from zero.

We assessed the impact on per-capita population growth rate of threats from invasive species, habitat loss, and over-exploitation using a two-factor ANOVA for each threat:

$$r_i = \alpha_{threat} + \beta_{period} + \gamma(period, threat) + \varepsilon_i, \tag{3}$$

where α_{threat} is the main effect of the threat, β_{period} is the main effect of period (assessment vs response), and $\gamma(period, threat)$ is the interaction between period and threat. Finally, we explored the relationship between IUCN Red List category and population growth rate in the 10-year or 3-generation periods immediately before and after the year the species was categorized on the IUCN Red List as Threatened (Critically Endangered, Endangered or Vulnerable), or Near Threatened. The model was:

$$r_i = \alpha_{listing} + \beta_{period} + \gamma(period, listing) + \varepsilon_i, \tag{4}$$

where $\alpha_{listing}$ is the main effect of listing action and $\gamma(period, listing)$ is the interaction between period and listing.

2.2.3. Simulated data

We simulated three null models of population trajectories to provide context for interpreting observed trends. These simulations included process error but not observation error. The first model was a true random walk, stochastic exponential growth model: each time period, the population growth rate ($r_t = N_{t+1} / N_t$) was randomly drawn from a log-normal distribution, $\log(r_t) \sim N(0, \sigma)$. We modeled scenarios where the process standard deviation (σ) ranged from 0.01 to 0.1, which includes a range typical for vertebrates (Holmes et al., 2007). We simulated populations for 20 years starting at an arbitrary initial value $N_0 = 1000$ and calculated growth rates separately as described above for years 1–10 (assessment period) and 11–20 (response period). The second null model involved a random walk with temporal autocorrelation of annual growth rates, as might occur if population dynamics are positively or negatively influenced by persistent environmental conditions. The strength of autocorrelation was determined by a lag-one autocorrelation parameter ρ; we assumed a stationary time series, so $|\rho| < 1$. The auto-correlated model is $\log(N_t) = \log(N_{t-1}) + \log(r_t)$, where $\log(r_t) \sim N(\rho \, r_{t-1} - \frac{\sigma^2}{2}, \sigma)$ and the $\frac{\sigma^2}{2}$ term adjusts for bias that arises from using log-normal errors (Hilborn and Mangel, 1997). We used the same values for process error ($\sigma = 0.01$–0.1) and evaluated moderate to strong positive autocorrelations ($\rho = 0.5$–0.9).

The third null model used a Beverton–Holt population dynamics function with carrying capacity (K) varying randomly within a specified range. Density dependence at upper and lower values of N created a series of realized population growth rates that varied randomly around a

mean of 0. The recursive model was $N_{t+1} = R_0 N_t / (1 + N_t / M)$, where R_0 is the maximum net reproductive rate (achieved at low density) and $M = K / (R_0 - 1)$. In the scenarios we evaluated, R_0 ranged from 1.1 to 10, and K varied randomly and uniformly in the range 600–1000 or 100–1000.

Results for all simulations were compiled across 10,000 replicate time series of 20 years. All statistical analyses and simulations were conducted in R (R Core Development Team, 2011), using code that is available upon request.

3. Results

3.1. Overview of the data and results

Summary information for each time series is given in Table A1. Mean total length of the data series we used ranged from 21.3 years for mammals to 27.9 years for birds (Table 3). For species with generation lengths >3.3 years, more than 10 years of data were required to accommodate 3 generations of data, and the mean generation length for birds (4.5 years) was higher than that for the other groups (2.2–3.8 years) (Table 3; Fig. A1). The interaction between $r_{response}$ and taxonomy was highly significant (ANOVA, $P \ll 0.001$), so in subsequent analyses we evaluated the relationship between r_{assess} and $r_{response}$ separately for each major taxonomic group. Mean r_{assess} was negative for all groups except salmon; mean $r_{response}$ was positive for birds and mammals and negative for both groups of fishes (Table 3). In all cases, however, growth rates varied widely among populations, so none of the overall mean growth rates differed significantly from zero. Birds showed a much narrower range of growth rates than did the other groups of species (Fig. 1A) and also much less dramatic changes in growth rate (94% of $\Delta r = r_{assess} - r_{response}$ values constrained to the range −0.1 to 0.1, compared to 43% to 53% in the other taxa; Fig. 1B).

With two periods for measuring growth rates, each of which can be positive or negative, we can identify 4 quadrants describing possible relationships between $r_{response}$ and r_{assess}: both positive (Quadrant I), both negative (Quadrant IV), r_{assess} negative but $r_{response}$ positive (Quadrant II), and r_{assess} positive but $r_{response}$ negative (Quadrant III) (Fig. 2). If population growth rates were drawn randomly from a symmetrical distribution with a mean of zero, with no influence by previous growth rates (as would occur if population size were a random walk), then an equal number of data points would be expected to fall in each quadrant. Therefore, the dotted line representing 25% in Fig. 2 provides a useful point of reference for comparing empirical results. It is apparent that birds are overrepresented in Quadrants I and IV (combined), which represent consistent direction of growth rates in the two time periods, while the other groups are underrepresented in these quadrants and overrepresented in Quadrants II and III (combined), which reflect a change in the direction of growth rate between the assessment and response periods.

Results for data simulated under one scenario for each of the null models are also plotted in Fig. 2. The true random walk model produced results that agreed closely with the expectation of equal representation in each quadrant (Fig. 2). The positive temporal autocorrelation model produced results that were qualitatively similar to those of birds (overrepresentation in Quadrants I and IV). Data simulated with density dependence and random variation in carrying capacity produced results that were qualitatively similar to those for mammals and fish (overrepresentation in Quadrants II and III).

3.2. Consistency of population growth rates over time

Each of the major taxonomic groups showed strong evidence for non-random association of population growth rates in the assessment and response periods (all correlations highly significant; Table 4). Two general patterns were evident. For birds, past population trajectory was a good predictor of future trajectory [strongly positive (0.593) correlation between r_{assess} and $r_{response}$ (Fig. 3a and Table 4)]. Bird populations that declined by at least 1% in the assessment period on average also declined in the response period, while birds that increased in the assessment period also had positive mean growth rates in the response period (Table 3). The opposite pattern was found for the other three taxa: a significantly negative (−0.370 to −0.485) correlation between r_{assess} and $r_{response}$ (Fig. 3b–d and Table 4). In mammals and other bony fishes, populations on average had positive growth rates following declines and negative growth rates following increases (Table 3). Salmon also had negative mean growth rates after increases ≥1%, while mean growth rates were nearly flat ($r_{response} = -0.003$) following declines.

These results are consistent with the 4-quadrant patterns shown in Fig. 2. This point is further emphasized by comparing the empirical results with those for the simulated data (Table 4, Table A6). All null model scenarios with density dependence produced negative correlations (as strong as −0.32 with low R_0) between r_{assess} and $r_{response}$, which was qualitatively similar to the pattern found for mammals and both groups of fishes. Conversely, all scenarios with positive temporal autocorrelation produced positive correlations between r_{assess} and $r_{response}$, in agreement with the result found for birds, but large correlations (>0.4) were only found for strong temporal autocorrelation. As expected, the true random walk model produced correlations that deviated only slightly from zero and provided no evidence for a relationship between r_{assess} and $r_{response}$ (Table 4).

3.3. Responses after steep declines

Three of the four taxonomic groups showed a common pattern of response following declines in abundance of at least 30% in the assessment period: mean growth rate of populations that had experienced steeper declines was higher (more positive or less negative) in the response period than it was for populations that had experienced shallower declines (Fig. 4; Table 5). This pattern was monotonic ($r_{response}$[decline ≥90%] > $r_{response}$[70] > $r_{response}$[50] > $r_{response}$[30]) for mammals, salmon, and other bony fishes. Again, birds were outliers: $r_{response}$ was negative following all rates of decline and did not follow a consistent pattern (Fig. 4). Mammals were unusual in showing positive mean growth rates following all rates of decline ≥30%. Both groups of fishes showed a significantly negative mean growth rate after declines less than 50% but growth rates that were not significantly different from 0 or positive when declines in the assessment period were larger (Fig. 4).

Table 3
Summary of time-series data for four major taxonomic groups. Values shown are means (standard deviations). Generation length is in years; T is the total length of the time series in years, including assessment and response periods. The last two rows shows the mean $r_{response}$ for populations that declined or increased by at least 1% in the assessment period.

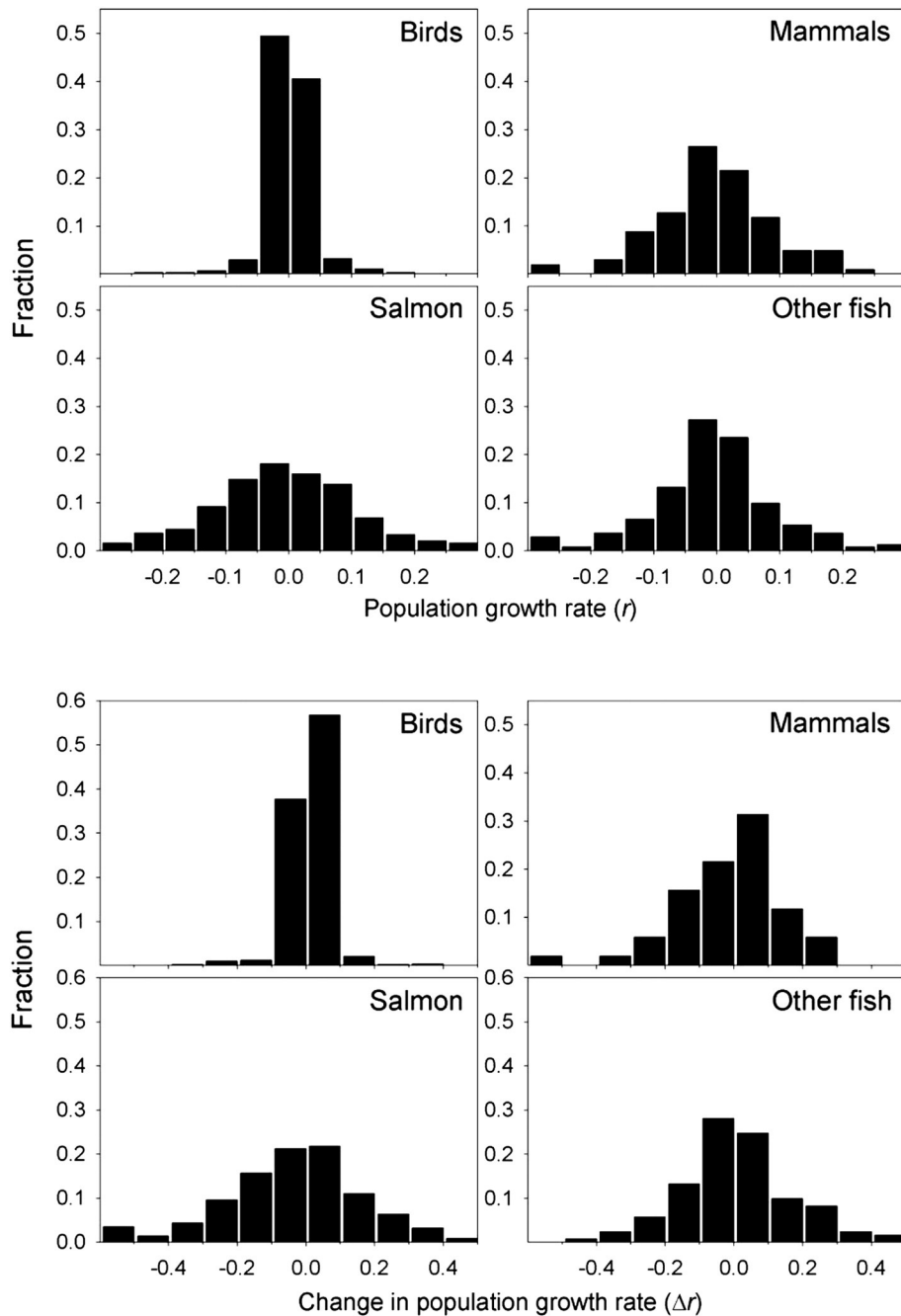|	Birds	Mammals	Salmon	Other bony fish
r_{assess}	−0.004 (0.055)	−0.009 (0.113)	0.009 (0.141)	−0.023 (0.120)
$r_{response}$	0.001 (0.037)	0.008 (0.115)	−0.035 (0.137)	−0.001 (0.096)
Generation	4.5 (1.0)	2.2 (1.3)	3.8 (0.7)	3.2 (1.7)
T	27.9 (6.2)	21.3 (3.2)	24.1 (3.3)	23.6 (8.2)
$r_{response}$ after decline	−0.011 (0.031)	0.049 (0.119)	−0.003 (0.137)	0.036 (0.094)
$r_{response}$ after increase	0.016 (0.053)	−0.052 (0.105)	−0.067 (0.134)	−0.051 (0.075)

Fig. 1. Distribution of estimated population growth rates ($r_{response}$ and r_{assess} combined; top panels) and $\Delta r = r_{response} - r_{assess}$ (bottom panels) across the four major taxonomic groups. The last bins on the left and right include all populations with $|r| > 0.25$ (top panels) and $|\Delta r| > 0.5$ (bottom panels).

Although mammals on average showed significantly positive mean growth rates following declines of at least 50%, and salmon showed significantly positive mean growth rates following declines of at least 90%, on average the subsequent increases were not sufficient to fully offset the declines during the assessment period (all values in Table 5 of PC_T = median percent change over entire data series are negative). Thus, on average within each taxon, abundance of populations that declined by at least 30% during the assessment period was lower at the end of the full time series than it was at the beginning. Individual populations, of course, showed responses that departed from these means. For example, 7 of 16 (44%) mammal time series that declined by 30–49% in the assessment period experienced subsequent increases sufficient to bring final abundance at least to levels that occurred at the start of the time series, and 4 of 21 (19%) mammal time series that

initially declined by 50–69% achieved the same benchmark of full recovery (Table 5). Comparable values were 28% and 18% for salmon and 17% and 17% for other bony fishes. No populations of birds or mammals fully recovered from declines of 70% or more, but 7% of salmon time series fully recovered from declines of 70–89% and 6% of both salmon and other bony fishes fully recovered from declines of 90% or more (Table 5).

Data simulated under one scenario using the null model with density dependence provide a useful perspective for evaluating these results. Of the 50,000 simulated time series for populations experiencing no long-term trends in population size (but random fluctuations in carrying capacity), 8748 (17%) declined by 30–49% and 5113 (10%) declined by 50–69% in the assessment period (Table 5). These simulated populations also showed other general patterns exhibited by mammals, salmon, and other bony fishes: the greater the extent of decline in
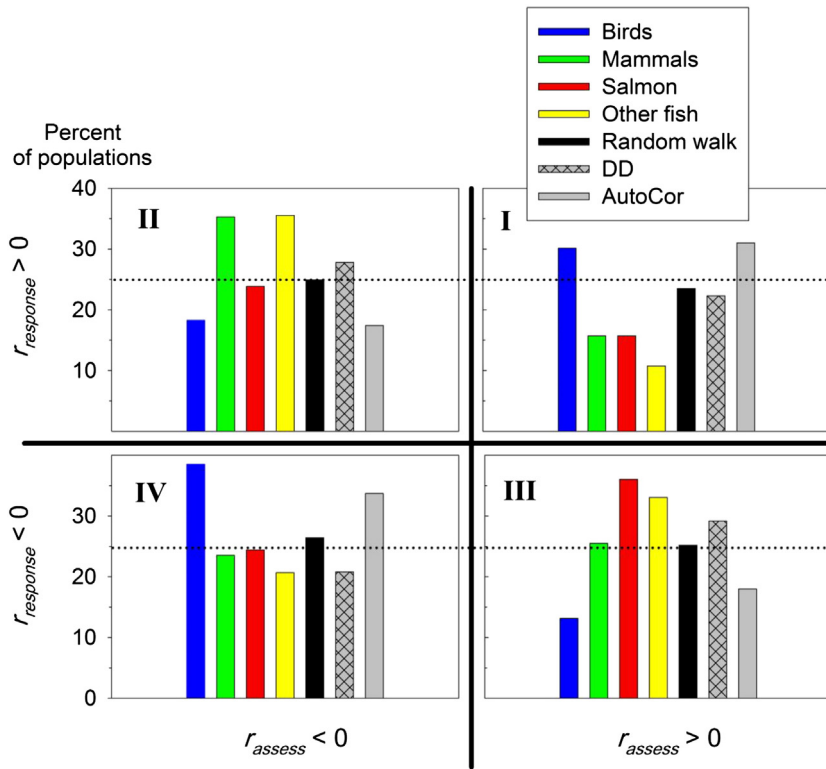
Fig. 2. Percent of populations of each of the major taxonomic groups that fall into each of four quadrants (I–IV), defined by the relationship between $r_{response}$ and r_{assess}. Percentages are calculated over the sample sizes shown in Table 1. The dotted line at 25% is the expected result for populations whose time series of abundance represents a random walk, such that growth rate at time $t + 1$ is independent of growth rate in previous time periods. Black and gray bars show results for data simulated under three different null models, using the following parameters: Random walk ($\sigma = 0.02$), AutoCor (random walk with lag-1 temporal autocorrelation; $\sigma = 0.02$, $\rho = 0.9$), and DD (density dependence with random fluctuations in carrying capacity; $R_0 = 1.5$, K varied randomly in range 600–1000).

the assessment period, the more strongly positive the growth rate in the response period ($r_{response}[70] > r_{response}[50] > r_{response}[30]$, Table 5; no simulated populations declined by as much as 90% in the assessment period under the parameters used). Probability of full recovery for simulated populations was only 20% for those experiencing declines of 30–49% and only 1% for populations experiencing declines of 70% or more.

3.4. Association between threats and population growth rates

Documented information about the three types of threats we considered was available for only a small subset of the populations ($n = 23$ for invasive species; $n = 52$ for habitat loss; $n = 12$ for exploitation;

Table 4
Weighted correlation coefficients between population growth rates in assessment (r_{assess}) and response ($r_{response}$) periods for empirical and simulated datasets. Weights for each pair of values were inversely proportional to standard errors of the estimated growth rate. Correlations for each of the major taxa are highly significant (mammals; $P < 0.01$) or very highly significant (birds and fishes; $P < 0.001$) based on a two-tailed test. Sample sizes for empirical datasets are given in Table 1. Results for simulated data are for 10,000 replicates; values in brackets are ranges of results for various parameter combinations (see Table A6 for details).

Dataset	Cor(r_{assess}:$r_{response}$)
Empirical data	
Birds	0.593
Mammals	−0.485
Salmon	−0.374
Other bony fish	−0.370
Simulated data	
Random walk	[−0.005, 0.044]
Density dependence	[−0.329, −0.028]
Autocorrelation	[0.023, 0.434]

Fig. 5). [Note: the analysis of exploitation only included birds, because all fishes were considered exploited and exploitation was not considered a primary threat for any of the mammals.] For populations not documented to be facing each type of threat, mean r in both assessment and response periods was close to, and did not differ significantly from, zero (Fig. 5), and Δr also did not differ significantly from zero. Mean growth rate for populations documented to be facing habitat loss was significantly lower than for populations not known to be facing such threats, and this result did not depend on the time period (interaction of habitat loss and period not significant; Table 6, Fig. 5b). Populations known to be facing invasive species threats had negative growth rates, and this was significantly more pronounced in the assessment period ($r_{assess[invasive]} = −0.08$; standard error = 0.015) than in the response period ($r_{response[invasive]} = −0.02$ (−0.01)), leading to a significant interaction between invasive species and period (Table 6 and Fig. 5a). We found no significant relationship between growth rate and whether a population is known to face exploitation threats (Table 6; Fig. 5c). Only a few populations were documented to face more than one of these threats, and all of those were birds, so it was not possible to do a meaningful analysis of interactions among threats.

3.5. Association between IUCN risk category and population growth rates

Because we lacked detailed information about the nature and timing of conservation measures for most species, we used inclusion on the IUCN Red List as a proxy for implementation of conservation action. Only 14 populations (12 birds, 2 non-salmonid bony fishes) were listed as threatened on the IUCN Red List at some point during the time series and had at least three generations or 10 years of data both before and after listing. Results below were robust to exclusion of the 2 fish species. Populations that were not threatened had slightly negative growth rates in both the assessment and response periods ($r_{assess[lowrisk]} = −0.002$
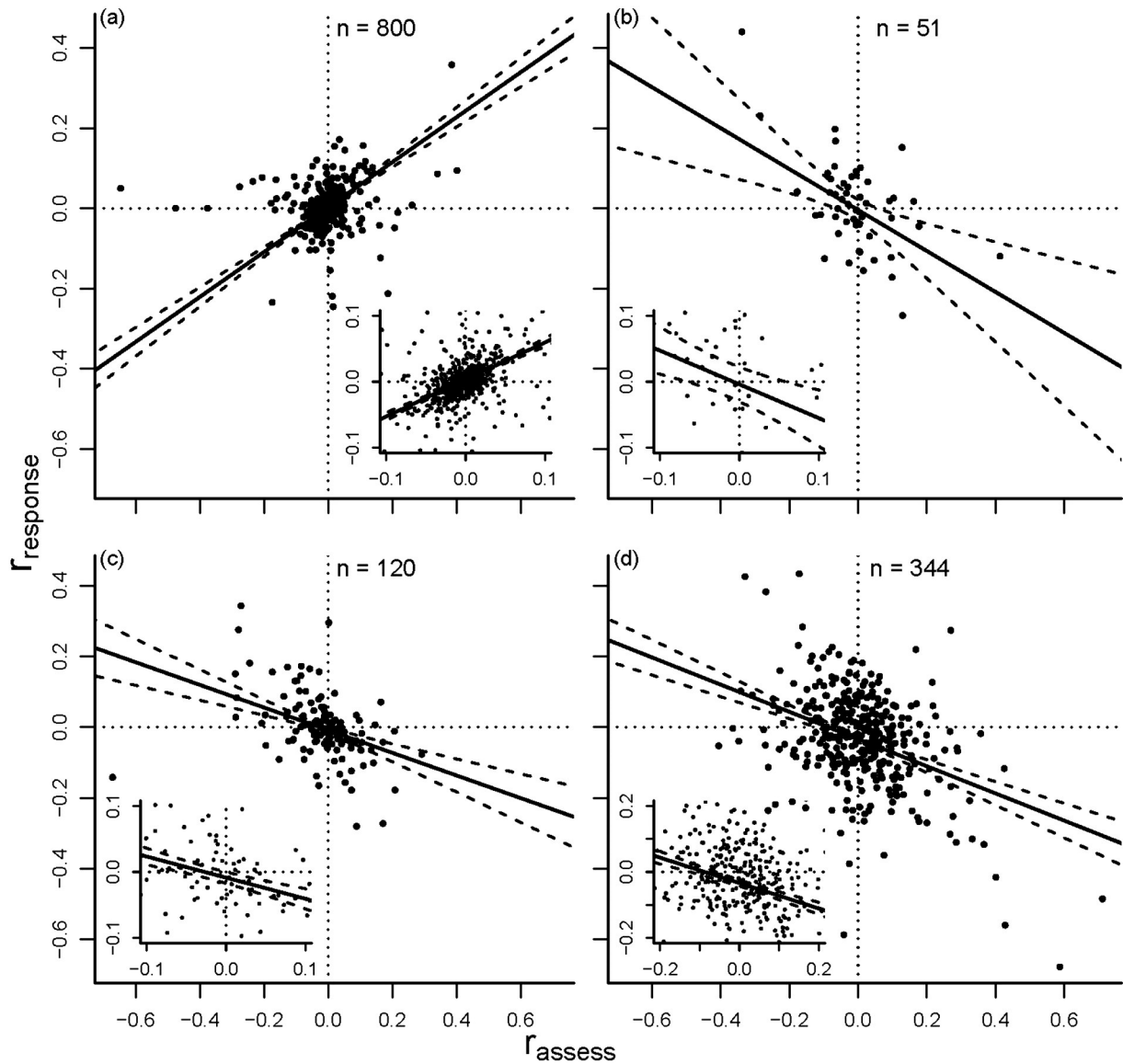
Fig. 3. Relationship between population growth rate in an initial assessment period (r_{assess}) and the growth rate in a subsequent response period ($r_{response}$) of equal duration. (a) Birds; (b) mammals; (c) non-salmonid bony fish; (d) salmon. A total of 1315 populations were included in this analysis, and the sample size of each taxonomic group is shown in each panel. Insets show a magnified view of the central datapoints.

(0.003) and $r_{response[lowrisk]} = -0.009 \, (0.002)$; Fig. 6). In contrast, threatened populations had more strongly (but not significantly) negative growth rates in the assessment period [$r_{assess[10hreatened]} = -0.023 \, (0.025)$] and significantly positive growth rates in the response period ($r_{response[threatened]} = 0.049 \, (0.023)$; Fig. 6, Table 6). This pattern produced a significant interaction between listing and time period (Table 6).

4. Discussion

4.1. Consistency of population growth rates

Of the four major taxonomic groups analyzed, only birds showed consistency in population growth rates over time. Birds showed a strong positive correlation between r_{assess} and $r_{response}$, and the proportions of declining populations that continued to decline (and increasing populations that continued to increase) were both higher than the random expectation (Fig. 2; overrepresentation in Quadrants I and IV). This latter pattern was more pronounced for populations that had declined in the assessment period, which is the pattern that would be of greatest

conservation concern. No bird populations fully recovered (final $N \geq$ initial N) from declines of 50% or higher, and only 6% of those that declined by 30–49% in the assessment period did so (Table 5).

Empirical data for mammals, salmon, and other bony fishes showed the opposite pattern: past declines generally were associated with subsequent population increases, and vice versa (Table 3; Figs. 2 and 3). Correlations between r_{assess} and $r_{response}$ for these species were all strongly negative (Table 4), and growth rates in the response period were higher (more positive or less negative) when declines were more severe in the assessment period (Fig. 4 and Table 5). All of these patterns agreed closely with data simulated under a null model that incorporated density dependence and random fluctuations in carrying capacity (Tables 4 and 5; Fig. 2). It is worth noting that variations of this general null model are used to analyze population dynamic processes and estimate extinction risk in natural populations of a wide range of species (Dennis et al., 1991; Holmes et al., 2007; Ives et al., 2010; Ward et al., 2014).

It should be stressed, however, that this result does not establish a causal relationship between random fluctuations under density dependence and the empirical patterns for mammals and fish; we have
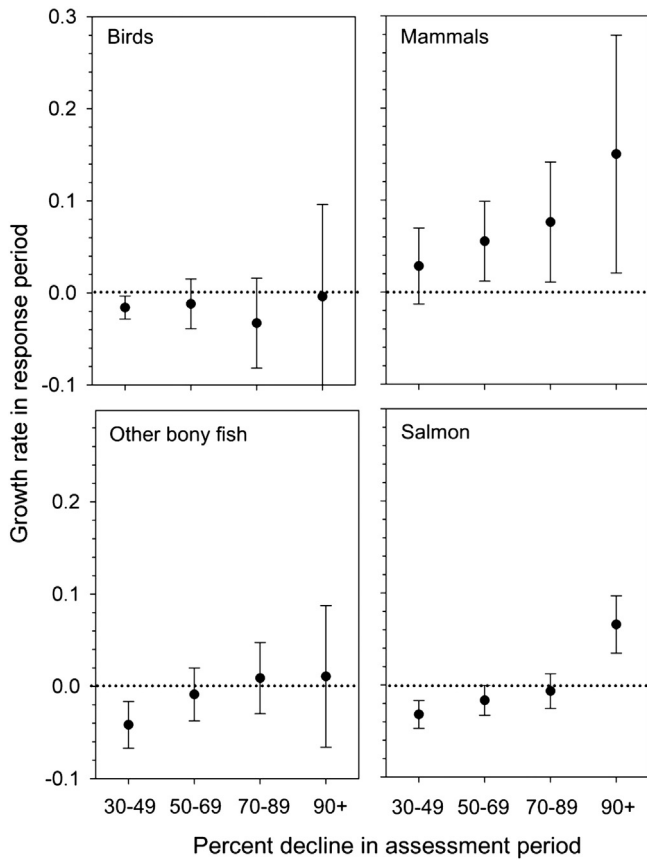
Fig. 4. Population growth rate in the response period ($r_{response}$) following declines in the assessment period of 30–49%; 50–69%; 70–89%; and ≥90%. Filled circles are mean estimates from the linear model, and bars show 2 standard errors in each direction around the mean.
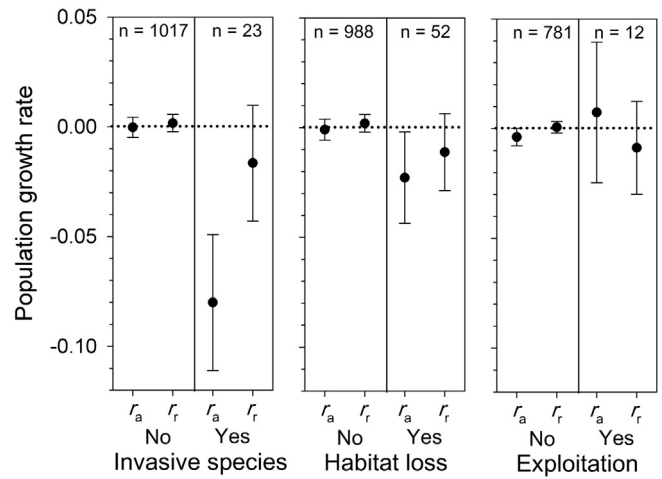

Fig. 5. Mean population growth rates in the response (r_r) and assessment (r_a) periods for populations documented to be threatened by invasive species, habitat loss, and exploitation, compared with those that are not known to be affected by these threats. Bars show 2 standard errors around the means; numbers in parentheses are sample sizes.

merely shown that the available data on trends in these species are largely compatible with such a null model. Other factors can produce a similar result; in particular, a negative association between initial and subsequent growth rates is the expected outcome if effective conservation actions are implemented following an initial decline. Unfortunately, our analyses of the association between existence of threats and temporal patterns in population trends were hindered by small sample sizes of putatively-affected species, so our data do not provide a robust test of this alternative hypothesis. In addition, we lacked information about the nature and timing of specific conservation actions taken in response to threats, as well as likely lag times between intervention and population response. Furthermore, in each threats assessment, most of the data were for birds, so additional information is needed to determine whether results hold for other groups.

Nevertheless, we found some evidence for an association between anthropogenic factors and population growth rates. Populations known to be affected by invasive species had negative and significantly lower growth rates than those not known to be affected; furthermore, growth rates for affected species were significantly higher (less negative) in the response period than in the assessment period (Fig. 5). This latter result could reflect benefits of conservation measures, but it could also reflect adjustments by the local species to presence of the invader. Populations known to be affected by habitat loss had significantly lower growth rates than unaffected populations, with no significant difference between assessment and response periods for affected species (Fig. 5). Overall growth rates for populations that were classified as threatened at some point during the assessment period did not differ significantly from those that were not, but the interaction with period was significant (growth rates in response periods were significantly

Table 5
Growth rate in the response period for populations that experienced percent declines of 30–49%, 50–69%, 70–89%, or 90% or more in the assessment period. Asterisks indicate mean r_r values that differed significantly from zero (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). PC_a, PC_r, and PC_T are median percent changes in the assessment period, the response period, and in the total data series, respectively. For each taxonomic group, n is the number of populations with specified decline rates, and $Prob_{Rec}$ is the percentage of those that achieved full recovery by the end of the response period (final abundance ≥ initial abundance). Results under DD are for 50,000 replicate time series simulated under the density dependent null model with random variation in carrying capacity ($K = 100$–1000; $R_0 = 2$).

Taxon	Decline range (%)	n	PC_a	Mean $r_{response}$	PC_r	PC_T	$Prob_{Rec}$
Birds	30–49	173	−34	−0.016**	−18	−47	5
	50–69	54	−59	−0.012	−32	−71	7
	70–89	25	−75	−0.033	−37	−86	4
	90+	10	−96	−0.004	14	−95	0
Mammals	30–49	16	−41	0.028	12	−30	44
	50–69	21	−57	0.055**	42	−40	19
	70–89	14	−80	0.076*	90	−62	7
	90+	6	−93	0.150*	348	−76	0
Salmon	30–49	120	−37	−0.032***	−17	−47	28
	50–69	149	−59	−0.017*	−11	−61	18
	70–89	168	−79	−0.005	10	−79	7
	90+	103	−93	0.070***	54	−90	6
Other bony fishes	30–49	42	−38	−0.042***	−25	−54	17
	50–69	48	−55	−0.009	−11	−60	17
	70–89	40	−77	0.002	16	−71	15
	90+	17	−93	0.011	9	−91	6
DD	30–49	8748	−40	0.008	7	−36	20
	50–69	5113	−57	0.017	14	−52	7
	70–89	617	−73	0.029	30	−66	1
	90+	0	–	–	–	–	–

Table 6
Results for models that evaluate the effect of various anthropogenic factors on population growth rate. "Period" represents the effect of the time period (assessment vs response) and "Interaction" represents the interaction between the Factor and Period. The top row shows the number of populations that experience the factor (yes) and are not known to experience the factor (no), and the remainder of the table shows P values from analysis of variance. Significant effects are in bold. See Tables A2–A5 for more details.

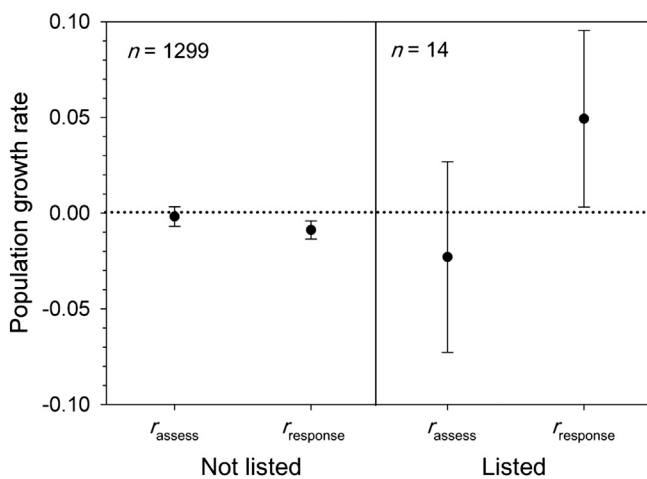|	Invasive species	Habitat loss	Exploitation	IUCN status
n (yes, no)	(23, 1017)	(52, 988)	(12, 781)	(14, 1299)
Factor	**<0.001**	**0.01**	0.92	0.43
Period	0.28	0.28	0.08	0.07
Interaction	**0.003**	0.53	0.28	**0.03**

Fig. 6. Estimated growth rate for populations before and after being classified as threatened on the IUCN Red List. Bars show 2 standard errors around the means; n is the sample size.

higher than in assessment periods). This could reflect positive effects of listing as threatened on population growth rates (presumably mediated by conservation responses), but the sample size was very small (14 total, of which 12 were birds), so this relationship is tentative at best.

4.2. Responses after steep declines

Although populations of mammals and fish showed a tendency to exhibit the most strongly positive growth rates in periods following sharp declines, on average the changes during the response period were not sufficient to fully offset declines of 30% or more (Table 5). In general, therefore, final abundance of these populations was lower at the end of the full data series than at the start. Is this a reason for conservation concern? Perhaps so, in the sense that any population that has declined substantially is likely to be at increased risk during the period when it is depressed in size. However, as illustrated by the simulation results, this type of pattern is not unexpected for populations that are dynamically stable, with random fluctuations in abundance but no long-term trend. Under that scenario, density-dependent compensation will tend to push populations that have declined sharply back up to higher levels, leading to a negative temporal correlation in population growth rates, as observed for mammals and fish. In these analyses, we compared random responses to declines that were selected to represent the most extreme values. Therefore, it is not surprising that populations did not fully recover from the most extreme declines within a single response period, even though they had a flat long-term growth rate. That was the case with the simulated data under the density-dependent scenario: larger declines on average produced larger positive growth rates in the response period, but the subsequent increases were sufficient to provide full recovery for only 20% of the simulated populations following declines of 30–49%, and smaller percentages for populations that experienced more extreme declines (Table 5). Timing of the start of the data series could also influence results like this. If by chance data are first collected when the population is near carrying capacity (especially near an unusually large carrying capacity, if *K* varies over time), then larger subsequent declines are more likely and full recovery less likely. Our results for simulated data are qualitatively similar to the empirical results for mammals and fish but not birds, few populations of which achieved full recovery following any declines of 30% or larger (Table 5).

4.3. Relationship to previous studies

Our results are broadly consistent with those of previous empirical and numerical evaluations of population trends, but provide some novel insights. Hutchings (2000) found that few marine fish populations that

had experienced steep (>45%) declines achieved full recovery within 15 years. We found comparable results in our empirical data for all taxa. In non-salmonid bony fishes, for example, we find that declines in excess of 50% are associated with per-capita growth rates in the response period that are not significantly different from zero (Table 5). We also showed that this pattern can occur in dynamically stable populations with no long-term trend. Connors et al. (2014) simulated data for stable and declining populations and tuned the input parameters based on empirical estimates of observation error and process error for over 600 time series from diverse taxa in the Global Population Dynamics database (http://www3.imperial.ac.uk/cpb/databases/gpdd). They found up to 40% false positives (a conclusion of risk for a stable population) using a 30% decline criterion with short (3G/10) time series and no density dependence, but the error rate was sharply reduced for steeper decline criteria, longer time series, and populations modeled with density dependence. For comparison, in the scenario simulated in Table 5, 29% of the populations with no net trend and randomly varying carrying capacity would have (falsely) been ranked as at least Vulnerable using IUCN Criterion A. Two recent papers have focused more closely on one species (sockeye salmon, *Oncorhynchus nerka*), using simulated data tuned to the sockeye life cycle (d'Eon-Eggertson et al., 2015) and empirical time-series data for 18 populations (Porszt et al., 2012). d'Eon-Eggertson et al. (2015) found that high levels of noise (especially process variation) could cause unreliable identification of population status, and both papers found that indicators that accounted for magnitude of decline performed better than those using only rate of decline.

4.4. Why are birds different?

Why do birds show different patterns than the other taxa in the temporal patterns of population growth rates? One possible factor is the geographic scale of assessment (Table 2). 96% of the avian time series were collected at the Regional or National/Oceanic scale, whereas 88% of the mammal and 96% of the salmon data were collected at smaller geographic scales, often from local populations. The larger scale of assessment could at least partially explain why birds: a) showed growth rates that clustered much more closely around 0 than did the other taxonomic groups (Fig. 1) and b) had positively correlated growth rates in the two time periods. Including larger areas in the assessment should also help buffer random local fluctuations in abundance through the portfolio effect (Schindler et al., 2010; Anderson et al., 2015), which in turn could produce more temporal stability in estimated growth rates. Further, local populations (like those of mammals and fish) are less likely to be closed, so population growth following declines could, in part, reflect immigration from other areas. Such rescue effects are less likely when trends are evaluated over large scales, as is the case for most birds in our study. However, geographic scale cannot explain all of the differences among taxa, as 24% of other bony fishes were assessed at the National/Oceanic scale, but their temporal patterns in growth rates were similar to those for mammals and salmon that were assessed at more local scales. Nevertheless, our results support the caution by the IUCN (2012) that their risk criteria were designed to be applied globally, and careful consideration is required for applications to smaller geographic scales.

Another likely factor is that birds are commonly monitored by techniques that capture large suites of species, regardless of their conservation status, with the result being that available time series are dominated by common species that are easier to detect and monitor. Conversely, in some other taxa (especially mammals), data are primarily collected separately for each species or population and hence tend to focus on units of management or conservation concern.

4.5. Caveats

Although we analyzed time series for over 1300 populations, sample sizes varied widely from 51 (mammals) to 800 (birds), so robustness of

our results varies by taxon. Because most of the data series are for relatively common species, we were also limited in our ability to evaluate effects of being categorized as threatened by the IUCN (our proxy for initiation of conservation measures).

The decision to split each data series exactly in half was arbitrary but seemed the most objective way of evaluating temporal consistency. Because our results are broadly consistent with those of other recent studies that have used somewhat different methods (see above), we don't believe the choice of splitting point has unduly influenced our results. However, the requirement to have two consecutive time periods amenable to trend analysis meant that we had to focus on trends calculated over relatively short durations (10 years/3 generations). Our results, therefore, are most relevant to evaluations of data sets of comparable duration, as longer time series are less influenced by random fluctuations (Connors et al., 2014).

We used numerical methods to generate hypothetical data under three population-dynamics scenarios, but these represent only a small fraction of possible scenarios that could be evaluated. We didn't explicitly model observation error, which has been estimated to be substantial in many time series (Connors et al., 2014). We modeled a positive temporal autocorrelation of population growth rates, which produced results comparable to the empirical data for birds and to general expectations under the declining population paradigm. However, an autocorrelation model that allows shifting between persistent environmental/ecological "regimes," as has been documented in both the North Pacific and North Atlantic ecosystems (Mantua and Hare, 2002; Hurrell, 1995), could produce negative correlations similar to those found for mammals and fish, depending on how sampling in the assessment and response periods matched the phases of the regimes.

4.6. Implications for conservation

Although IUCN Red List criteria are designed to provide simple rules that can be broadly applied and are not intended to replace more in-depth evaluations of individual species and populations (Mace et al., 2008), in practice these criteria have a large influence on how risks are perceived and conservation priorities are set. Two related studies have recently demonstrated that the IUCN criteria in general can provide substantial warning time for populations headed to extinction, based on a reconstructed past extinction due to harvest and habitat loss (Stanton, 2014), and projected future extinctions due to climate change (Stanton et al., 2015). Our empirical data for birds (but not other vertebrates) support the premise that recent declines predict future declines. In contrast, for mammals, salmon, and other bony fishes, declines tended to be followed by increases, and steeper declines by stronger increases, and these patterns were similar to those for modeled populations with random fluctuations in abundance but no long-term trends in population size.

If past trends do not reliably predict future trends in mammals and fish, how should single estimates of population growth rate be interpreted in a conservation context? With simulated data, true population parameters are known, so it is easy to quantify the frequency of both Type I (overprotection) and Type II (under-protection) errors. Results presented here and in other recent papers show that under some modeled scenarios, application of IUCN Criterion A could lead to significant numbers of Type I errors. These errors are more difficult to evaluate with natural populations because the underlying population dynamics (and true risk status) are often poorly understood; for this reason, we did not attempt to estimate either Type I or Type II error rates from our empirical data. A change in trend following a decline that would have produced a threatened classification under IUCN Criterion A might reflect a Type I error, or it might indicate success of conservation efforts implemented in a timely manner. This uncertainty highlights the importance of supplementing estimates of population trend with additional information about cause and effect. Although our analysis did not focus on causes of declines, other research has

highlighted the importance of information about underlying causes for both accurately assessing risk of extinction and for correctly interpreting the effectiveness of conservation measures.

This underscores the need for monitoring efforts that collect other temporally and spatially specific information, such as age structure, exploitation rates, specific threats and conservation actions, etc. Concerted efforts to link quantification of threats and subsequent conservation actions with estimated trends will improve our understanding of which conservation measures are working and how best to conserve species at risk. We also encourage evaluation of other population metrics (e.g., area occupied, survival of most sensitive or elastic age classes, genetic indices) that might be as sensitive, or more sensitive, to declines (Hutchings et al., 2012; Tallmon et al., 2010).

In the meantime, given that conservation implications of single estimates of population trends can be ambiguous, especially when the data are limited or highly uncertain, managers must decide how best to balance risks and costs of over-protection and under-protection to arrive at a conservation strategy. The IUCN Red List explicitly allows incorporation of attitudes about risk and uncertainty into assessments (IUCN, 2001, 2014) and takes an inherently precautionary approach to evaluation of population trends, in part because waiting too long to intervene can make recovery less likely and more costly (Mace et al., 2008). Although the IUCN recognizes that natural fluctuations can produce temporary declines in stable populations, it maintains that observed trends should be considered real unless proven otherwise (Isaac and Mace, 1998; IUCN, 2014). This approach, therefore, places high importance on avoiding errors of under-protection and is more tolerant of errors of overprotection. This might be an appropriate strategy to achieve IUCN goals, but managers or conservation practitioners might choose to balance the risks of over- and under-protection differently for other applications of risk analysis (Connors et al., 2014). We hope that the information presented here will: a) help managers make informed decisions about the tradeoffs inherent in assessing species' risk of extinction; b) highlight the need to measure and track more than just trends in abundance over time, as changes in demographic, environmental, and ecosystem parameters, as well as conservation measures and threats, can all be crucial to determining the best course of action for a given population; and c) reinforce the need for long-term studies of the effects of different ancillary variables on populations.

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