Critical factors for the recovery of marine mammals

Heike K. Lotze^{(D), 1*} Joanna Mills Flemming,² and Anna M. Magera¹

¹Department of Biology, Dalhousie University, 1355 Oxford Street, P.O. Box 15000, Halifax, NS B3H 4R2, Canada ²Department of Mathematics and Statistics, Dalhousie University, 1355 Oxford Street, P.O. Box 15000, Halifax, NS B3H 4R2, Canada

Abstract: {*en*} Over the past decades, much research bas focused on understanding the critical factors for marine extinctions with the aim of preventing further species losses in the oceans. Although conservation and management strategies are enabling several species and populations to recover, others remain at low abundance levels or continue to decline. To understand these discrepancies, we used a published database on abundance trends of 137 populations of marine mammals worldwide and compiled data on 28 potentially critical factors for recovery. We then applied random forests and additive mixed models to determine which intrinsic and extrinsic factors are critical for the recovery of marine mammals. A mix of life-bistory characteristics, ecological traits, phylogenetic relatedness, population size, geographic range, human impacts, and management efforts explained why populations recovered or not. Consistently, species with lower age at maturity and intermediate babitat area were more likely to recover, which is consistent with life-bistory and ecological theory. Body size, trophic level, social interactions, dominant babitat, ocean basin, and babitat disturbance also explained some differences in recovery patterns. Overall, a variety of intrinsic and extrinsic factors is recovery, pointing to cumulative effects. Our results provide insight for improving conservation and management strategies to enhance recoveries in the future.

Keywords: cumulative effects, geographic range, habitat disturbance, life-history traits, management strategies, population trends, recovery rate, trophic level

Factores Críticos en la Recuperación de los Mamíferos Marinos

Resumen: En las últimas décadas mucha investigación se ha enfocado en el entendimiento de los factores críticos para las extinciones marinas con miras a la prevención de más pérdidas de especies en los océanos. Aunque la conservación y las estrategias de manejo están permitiendo que varias especies y poblaciones se recuperen, otras permanecen en niveles bajos de abundancia o continúan en declinación. Para entender estas discrepancias, utilizamos una base de datos publicada sobre las tendencias de abundancia de 137 poblaciones de mamíferos marinos en todo el mundo y compilamos datos sobre 28 factores potencialmente críticos para la recuperación. Después aplicamos bosques de azar y modelos aditivos mixtos para determinar cuáles factores intrínsecos y extrínsecos son críticos para la recuperación de los mamíferos marinos. Una mezcla de características de bistoria de vida, caracteres ecológicos, relación filogenética, tamaño poblacional, extensión geográfica, impactos humanos, y esfuerzos de manejo explicó por qué las poblaciones se recuperaron o no. Consistentemente, las especies con una menor edad de madurez y menor área intermedia de hábitat tuvieron mayor probabilidad de recuperarse, lo que es consistente con la bistoria de vida y la teoría ecológica. El tamaño corporal, el nivel trófico, las interacciones sociales, el bábitat dominante, la cuenca oceánica, y la perturbación del hábitat también explicaron algunas diferencias en los patrones de recuperación. En general, una variedad de factores intrínsecos y extrínsecos fueron importantes para la recuperación de las especies, lo que apunta a efectos acumulativos. Nuestros resultados proporcionan conocimiento para mejorar las estrategias de conservación y manejo para aumentar las recuperaciones en el futuro.

Palabras Clave: características de historia de vida, efectos acumulativos, estrategias de manejo, extensión geográfica, nivel trófico, perturbación de hábitat, tasa de recuperación, tendencias poblacionales

1

Introduction

After a long history of population depletions and extinctions in the marine realm (Lotze et al. 2006; Harnik et al. 2012), there are now increasing incidences of recoveries of marine species (Neubauer et al. 2013; Roman et al. 2015). Although providing some hope, recent reviews suggest the proportion of formerly depleted species showing signs of recovery is still low, as is the magnitude of recovery relative to historical baselines (Lotze & Worm 2009; Lotze et al. 2011). Even within a species or taxonomic group, some populations show varying signs of recovery, whereas others continue to decline or remain at low levels (Hutchings & Reynolds 2004; Magera et al. 2013). Thus, an important question is which factors are critical for the recovery of depleted species in the ocean? Answers to this question will enhance our knowledge of population dynamics in long-lived marine animals and inform conservation efforts aiming at increasing recoveries.

Until recently, a major focus in conservation science has been to assess the extinction risk of vulnerable species and the critical factors (correlates or drivers) for extinction. This has enhanced our understanding of which organisms are more at risk and why and helped develop conservation strategies (Harnik et al. 2012). In the marine realm, several researchers have synthesized the critical factors related to extinction risk (Hutchings & Reynolds 2004; Davidson et al. 2012), which is still highly relevant for species undergoing substantial population declines, such as many sharks and rays (Dulvy et al. 2014). Among marine mammals, however, many populations of cetaceans and pinnipeds have shown sometimes remarkable population increases following substantial harvestdriven depletions in the past (Gerber & Hilborn 2001; Magera et al. 2013). These are often celebrated as conservation successes, yet not all populations show signs of recovery and many continue to be threatened (Lotze et al. 2011; Magera et al. 2013). Based on this wide range of population trajectories, marine mammals are particularly well suited for the study of factors that explain observed recoveries.

In the ocean, critical factors for recovery have been studied for overexploited fish (Hutchings & Reynolds 2004; Neubauer et al. 2013) and marine species in general (Lotze et al. 2011) but not for marine mammals. Critical factors in the decline or recovery of populations are usually separated into 2 groups. Intrinsic factors are population or species specific and typically include lifehistory and ecological traits, such as body size, age at maturity, number of offspring, range size, and habitat requirements. Extrinsic factors include natural predation, competition, and environmental change and human impacts such as harvest, habitat disturbance, and management efforts. Intrinsic and extrinsic factors can interact; for example, intrinsic factors can affect a population's response to external factors (de Little et al. 2007; Reynolds et al. 2009).

Our goal was to investigate which factors are critical for the recovery of marine mammal populations worldwide. We used a published database on abundance trends of populations of marine mammals (Magera et al. 2013) and built on previous research on critical factors in terrestrial and marine mammal extinctions and in fish decline and recovery to select intrinsic and extrinsic factors potentially critical for the recovery of marine mammals. We used random forests and additive mixed models (AMMs) to identify those factors most related to observed recoveries. We sought to provide insight into reasons for recovery or lack thereof in formerly depleted species and how conservation and management could be improved to enable more population recoveries in the future.

Methods

Population Trends

The original database contained 198 population abundance time series for 46 marine mammal species worldwide (Magera et al. 2013). These included adult and pup counts and data for small and large spatial areas that could overlap (e.g., Southern Hemisphere, large area; Argentina or Brazil, small areas). It also contained trend estimates for each population based on robust linear and log linear weighted regression, including the coefficient (slope) and its SE, *p* value, 95% confidence interval (CI), and R^2 value as measures of reliability. Because log linear regression provided better trend estimates for most data (Magera et al. 2013), we used those coefficients as estimates of the direction and magnitude of population trends. Thereby, recovery was defined as an increase after a harvest-driven depletion (Supporting Information).

We assessed all 198 populations and excluded 38 for which no trend estimate was available due to insufficient data (Supporting Information). To ensure the independence of all data series, we excluded another 23 populations due to overlap with other populations or areas or duplicate pup and adult counts (Supporting Information). In all cases, we kept the longer time series with more reliable trend estimates (i.e., smaller SE, 95% CI, or higher R^2). The remaining 137 populations (Fig. 1) spanned 44 species; 122 were nonoverlapping small-area populations and 91 were nonoverlapping large-area populations (Supporting Information), which provided 2 distinct sets of populations.

Magera et al. (2013) distinguished between significant and nonsignificant abundance trends based on whether 95% CIs did not or did include zero. Based on their definition, 86 of our 137 populations had significant positive (66) or negative (20) trends. However, we were

Table 1. Potentially critical intrinsic and extrinsic factors influencing recovery in marine mammal populations.^a

Factor	Description (unit of measure, data type)		
Intrinsic factors			
taxonomy	taxonomic level: order, family, genus, and species (category)		
length	female length, mean or median (m, continuous)		
weight	female weight, mean or median (kg, continuous)		
birth mass	mass at birth, mean or median (kg, continuous)		
age at maturity	female age at maturity, mean (years, continuous)		
gestation time	gestation time, mean (months, continuous)		
interbirth interval	interbirth interval, mean (years, continuous)		
litter size	number of offspring per birth (number, continuous)		
life history	integrated rate of mean-mass production (continuous)		
social interactions	importance of social interactions (category: low, medium, or high)		
trophic level	trophic level (continuous)		
habitat type	habitat type (category: nearshore, nearshore and oceanic, or oceanic)		
dominant habitat	dominant habitat type (category: coastal, offshore, or both)		
ocean basin	ocean basin occupied (category: Arctic Ocean, North Atlantic, North Pacific, Eastern Tropical Pacific, Southern Hemisphere, or Antarctica)		
habitat area	habitat area occupied (km ² , continuous)		
abundance	total population size (mean number of individuals, continuous)		
density	population density (mean number of individuals per km^2 , continuous)		
Extrinsic factors			
maximum habitat disturbance	maximum habitat disturbance (index, continuous)		
mean habitat disturbance	mean habitat disturbance (index, continuous)		
direct harvest	direct harvest ongoing (category: yes or no)		
bycatch	incidental bycatch occurring (category: yes or no)		
cumulative threats	cumulative number of threats (numerical: 0-11)		
harvest management	level of harvest management (category: none, partial, or full)		
harvest management time	when harvest management was implemented (category: recent, mid, distant past, or NA)		
habitat management	level of habitat management (category: none, partial, or full)		
habitat management time ^b	when habitat management was implemented (category: recent, mid, distant past, or NA)		
trade management	level of trade management (category: none, partial, or full)		
trade management time ^b	when trade management was implemented (category: recent, mid, distant past, or NA)		

^a For detailed information on critical factors, their sources, and the compiled data, see Supporting Information. ^bFactors had too many NAs (not available) and were therefore excluded from further analysis.

interested in a wider range of population trends that varied in both direction and magnitude. Therefore, we visually examined abundance trends for the 51 populations with nonsignificant trends (fig. S1 in Magera et al. [2013]). In all cases, these showed a clear direction and magnitude yet were only slightly increasing, decreasing, flat, or more variable, which resulted in low R^2 values or 95% CIs that included zero. We included these populations to ensure our data also reflected populations with weak or stable trends (Supporting Information).

Critical Factors

For each population, we compiled data on intrinsic and extrinsic factors suggested to be important for the decline, extinction, or recovery of species (Supporting Information). Intrinsic factors included life-history characteristics, importance of social interactions, trophic level, and habitat use (Table 1). Because these were not consistently available for individual populations, we compiled them on a species level. However, population-specific data were compiled for the ocean basin and habitat area occupied and for mean population size and density over the last 3 generations (Table 1 & Supporting Information). We also calculated a composite measure of life-history speed, the rate of mass-specific production: P = (birth mass/adult mass)*litter size*births per year (Hamilton et al. 2011) (Supporting Information).

Extrinsic factors included measures of habitat disturbance based on Halpern et al. (2008), direct harvest, bycatch, and other threats, as well as existence of harvest, habitat, and trade management and their implementation times (Table 1 & Supporting Information). For habitatand trade-management implementation time, there were too many data gaps (e.g., not available); thus, these were excluded from further analysis, leaving us with a total of 25 critical factors plus 4 levels of taxonomy (Table 1).

Statistical Analyses

Our analytical approach was 2-fold. First, we used random forests to evaluate the relative importance of all critical factors in explaining abundance trends (Cutler et al. 2007). We then used AMMs (Wood 2006) with a reduced set of the most important (per random forests),



Figure 1. Global distribution of all marine mammal populations (n = 137) (other includes polar bears, sea otters, and manatees; gray dashed lines, ocean demarcations [Arctic, Eastern Tropical Pacific, and Antarctic]; Roman numerals I-VI, areas of the Antarctic Ocean).

transformed, and uncorrelated critical factors to identify quantitative relationships between critical factors and abundance trends and determine whether these were linear or nonlinear. To account for various levels of phylogenetic relatedness among populations, we included nested random effects for the taxonomic levels order, family, genus, and species (Dulvy et al. 2014). To evaluate the robustness of results, we analyzed the 2 distinct sets of small- (n = 122) and large-area (n = 91) populations separately, as well as only small-area populations with significant abundance trends (n = 73) as identified by Magera et al. (2013). All statistical analyses were performed using the R Package (version 3.3.1).

Following Davidson et al. (2012), we used the random-Forest package to build random forests of 500 regression trees to evaluate which critical factors were important for explaining the estimates of abundance trends. Two measures of variable importance were used (both available in R): percent increase in mean squared error (%IncMSE) and increase in node purity (IncNodePurity). For both measures, larger values indicate greater variable importance. These tools were used with the initial set of 25 critical factors and the 4 taxonomic levels and again with a reduced set of transformed and uncorrelated factors (see below) that were used subsequently within the AMM framework. In both cases, dot charts of variable importance measures were prepared to identify those critical factors that were most likely to be informative for abundance trends.

Data visualizations aided the determination of critical factors in need of transformation. Abundance (19-4,069,000), habitat area (1,380-209,500,000 km²), fe-

male weight (20-105,000 kg), and birth mass (1-7250 kg) all had large ranges and were therefore log (ln) transformed.

Pairwise correlations were obtained using the cor package, and pairs with correlations larger than a predetermined standard cutoff of 0.7 were deemed highly correlated. Starting with the highest correlation, the factor most highly correlated with the largest number of other factors was removed first and this process was repeated as necessary. In cases where neither critical factor was highly correlated with any others, the factor that was less differentiated (i.e., had fewer levels or categories) was removed. This process was continued until all remaining factors had pairwise correlations <0.7.

Additive mixed models (mgcv package in R) (Wood 2006) were then used to formally quantify whether there were any linear or nonlinear relationships between the remaining critical factors and the estimates of abundance trends. For variable selection, both the significance of critical factors at a 90% confidence level, minimizing the Akaike information criterion (AIC), and examination of diagnostic plots were utilized. We aimed for p < 0.05 for all critical factors in the model but also considered those with p < 0.2 if they improved model fit as per any of the above criteria.

Results

Random Forests

For both small- and large-area populations, random forests identified a consistent set of critical factors based on



Figure 2. Results from 500 random forest trees for small-area populations (n = 122) scaling all 25 intrinsic and extrinsic factors critical to recovery plus 4 taxonomic levels by 2 measures of variable importance, the percent increase in mean squared error (%IncMSE), and the increase in node purity (IncNodePurity) (mgt, management; dist, disturbance; *, variables later In-transformed for use in additive mixed models; [, variable removed due to bigb correlation).

2 measures of variable importance. For all small-area populations (n = 122), both measures identified 10 critical factors among the top one-third of highest variable importance (n = 13) (Fig. 2): species, ocean basin, density, habitat area, abundance, length, family, trophic level, age at maturity, and genus. Additional factors within the top 13 included birth mass, life history, dominant habitat for %IncMSE, and mean habitat disturbance, maximum habitat disturbance, and weight for IncNodePurity. For the reduced set of only significant small-area populations (n =73), the selection of the top 13 factors by both measures was very similar (Supporting Information), except that life history and weight were not included. Trade management was identified by both measures and habitat management and harvest management by %IncMSE. For large-area populations (n = 91), the selection varied slightly, but also included habitat area, density, abundance, family, species, age at maturity, and trophic level in the top 13 of both measures plus weight (Supporting Information). Length, trade management, harvest management, bycatch, and interbirth interval were identified by %IncMSE and genus, and mean habitat disturbance, maximum habitat disturbance, ocean basin, and life history were identified by IncNodePurity.

Correlation of Critical Factors

Excluding the 4 taxonomic levels (which were later used as nested random effects within the AMMs), 5 of the 25 critical factors were highly correlated (Supporting Information). These included the In-transformed weight and birth mass (0.96); weight was more highly correlated with other factors (length and life history) and was therefore removed. Birth mass was also highly correlated with length (0.92) and therefore removed. Direct harvest and harvest management were highly correlated (0.84), and direct harvest was removed because it was less differentiated (2 vs. 3 levels). Similarly, age at maturity and interbirth interval were correlated (0.78), and the latter was removed because it was less differentiated (8-16 months) than age at maturity (3-15 years). Finally, life history was highly correlated with several other life-history characteristics (age at maturity and weight) and was therefore removed. This left 20 critical factors for further consideration. This selection process yielded identical results for large-area populations and small-area populations with significant abundance trends.

Rerunning the random forests with this reduced set of critical factors changed results only slightly. For all small-area populations, both measures of variable importance identified 10 critical factors among the top 13 (Supporting Information), all of which were identified previously: species, density, habitat area, trade management, age at maturity, abundance, family, maximum habitat disturbance, length, and ocean basin. Dominant habitat, habitat management, and harvest management were among the top 13 per %IncMSE, and mean habitat disturbance, trophic level, and genus were among the top 13 per IncNodePurity, as identified previously. Thus, in addition to the taxonomic levels, 13 critical factors were included in the initial AMM for small-area populations. For only the significant small-area populations, the selection of the top 13 factors by both measures was the same (Supporting Information). For large-area populations, rerunning the random forests yielded similar results (Supporting Information); 8 factors were identified as important by both measures: abundance, density, habitat area, family, genus, trophic level, age at maturity, and length. Identified only by %IncMSE were trade management, harvest management, social importance, bycatch, and order, and identified only by IncNodePurity were species, ocean basin, mean habitat disturbance, maximum habitat disturbance, and gestation time. Thus, in addition to the taxonomic levels, 14 critical factors were included in the initial AMM for large-area populations.

Additive Mixed Models

For small-area populations, 6 of the 13 critical factors identified as important by random forests were removed in the variable-selection process because they were not significant (mean habitat disturbance, abundance, harvest management, trade management, habitat management, and density). The final AMM with the lowest AIC had an R^2 (adjusted) of 0.28 (Table 2). Age at maturity was the most significant factor and had a nonlinear relationship with abundance trend estimate (Fig. 3a), suggesting highest recovery in populations with a young age at maturity followed by a decrease and a flat relationship at high age at maturity. Habitat area also showed a significant nonlinear relationship (Fig. 3b) with generally highest recovery at intermediate habitat area. All other factors showed linear relationships (Table 2); body size (length) had a significant positive relationship with recovery. Ocean basin was also important (Table 2), in particular; the Arctic Ocean and the Eastern Tropical (ET) Pacific were significantly different from the Antarctic Ocean (with which all others were compared). The positive coefficients associated with these relationships indicated that, given all other factors in the model, populations were more likely to recover in these ocean basins than in the Antarctic. The remaining 3 factors showed weaker relationships with recovery. Of these, trophic level was negatively correlated with recovery (Table 2), suggesting higher recovery at lower trophic levels. Habitat distur-

Table 2. Results from additive mixed models of factors critical to recovery for all small-area populations (n = 122).

Critical factor ^a	Linear relationsbip		Nonlinear relationship	
	coefficient ^b	p	edf ^c	p
Length	0.058	0.001		
Ocean basin:				
-Arctic	0.868	0.006		
-ET Pacific	1.139	0.002		
-N Atlantic	0.588	0.029		
-N Pacific	0.566	0.019		
-S Hemisphere	0.539	0.025		
Dominant				
habitat:				
-nearshore	0.265	0.095		
-oceanic	0.089	0.702		
Mean habitat	0.050	0.058		
disturbance				
Trophic level	-0.339	0.069		
Habitat area (ln			3.113	0.038
transformed)				
Age at maturity			2.226	< 0.001

^aFull descriptions in Table 1.

^bParametric coefficient.

^cEstimated degrees of freedom.

bance showed a very weak (0.05) positive relationship with recovery, and populations with their dominant habitat nearshore did better than those with oceanic or both habitats (Table 2). When considering only small-area populations with significant abundance trends, the results of the AMMs were similar (Supporting Information) but generally less significant due to the smaller sample size.

For large-area populations, 7 of the 14 critical factors identified as important by random forests were removed in the variable selection process (trade management, harvest management, abundance, gestation time, maximum habitat disturbance, habitat management, and density). The final AMM with the lowest AIC had an R^2 (adjusted) of 0.24 (Table 3). Age at maturity was again the most significant factor, yet this time it showed a linear negative relationship with abundance trend estimate. As for smallarea populations, body size (length) showed a significant linear positive trend (Table 3) and habitat area showed a significant nonlinear relationship with recovery (Supporting Information), following the pattern for small-area populations (Fig. 3b). Trophic level again showed a significant negative relationship with recovery, and habitat disturbance showed a very weak yet significantly positive relationship with recovery (Table 3), like small-area populations. Social interactions were significant, indicating negative effects of low or medium compared with high importance of social interactions on abundance trends. Ocean basin was again important, but this time only the ET Pacific was significantly different from the Antarctic Ocean (Table 3).



Figure 3. Smoothed (s) terms describing the nonlinear relationship between estimates of small-area population (n = 122) abundance trends and (a) age at maturity and (b) habitat area.

Discussion

Our analyses revealed the importance of a range of intrinsic and extrinsic factors for the recovery of marine mammal populations worldwide. Not just one or 2 factors were critical for recovery; rather, a mix of life-history characteristics, ecological traits, phylogenetic relatedness, population size, geographic range, human impacts, and management efforts together explained why populations recovered or not. Similar factors have been identified as important for the recovery of depleted fish stocks (Neubauer et al. 2013) and extinction risk in marine and terrestrial mammals (Cardillo et al. 2008; Davidson et al. 2012). Our results suggest that these multiple factors do not act in isolation. Such cumulative effects are also important for the recovery of estuarine and coastal species (Lotze et al. 2006), depleted fish stocks (Hutchings & Reynolds 2004; Neubauer et al. 2013), and marine species in general (Lotze et al. 2011). This line of research provides important insight for

Table 3. Results from additive mixed models of factors critical to recovery for large-area populations (n = 91).

	Linear relationsbip		Nonlinear relationship	
Critical factor ^a	coefficient ^b	p	edf ^c	p
Trophic level	-0.513	0.038		
Age at maturity	-0.210	< 0.001		
Length	0.079	0.004		
Ocean basin:				
-Arctic	0.734	0.132		
-ET Pacific	1.402	0.012		
-N Atlantic	0.422	0.286		
-N Pacific	0.281	0.441		
-S Hemisphere	0.446	0.234		
Social interactions:				
-low	-1.807	0.009		
-medium	-1.440	0.024		
Mean habitat	0.077	0.024		
disturbance				
Habitat area (ln transformed)			2.894	0.005

^aFull descriptions in Table 1.

^bParametric coefficient.

^cEstimated degrees of freedom.

improving conservation and management strategies to enhance recoveries in the future.

Intrinsic Factors

Life-history characteristics are important correlates for the depletion, extinction, and recovery of marine and terrestrial animals (Cardillo et al. 2008; Lotze et al. 2011; Davidson et al. 2012). Our results consistently showed that age at maturity was highly important for the recovery of marine mammals. Earlier maturation typically means faster population growth, increasing the probability of recovery. Our results generally indicated stronger recovery at lower age at maturity, particularly below 7 years, which includes all pinnipeds, sea otters, polar bears, and sirenia. Thus, faster life history correlated with higher recovery, comparable to terrestrial vertebrates (Collen et al. 2006). In contrast, when age of maturity was over 7 years, which includes most cetaceans, recovery was not much affected by age at maturity. The patterns for female length or body size were the opposite. In general, the greater the length, the stronger the recovery. This suggests that larger marine mammals, such as some great whales, showed stronger recovery than some smaller species. Although not in line with life-history theory, this could be explained by the fact that many large cetaceans have a longer history of management and protection than many smaller ones (Reeves et al. 2003). Such a relationship between body size and type of threat has also been suggested in explaining differences in extinction risk in mammals (González-Suárez et al. 2013). Other life-history factors, such as weight, birth mass, interbirth interval, and life-history speed, were also important according to our random forests, yet they were highly correlated with other life-history traits and therefore excluded from the AMMs.

One important ecological trait in our study was trophic level, which was negatively correlated with abundance trend estimates. This suggests that species on lower trophic levels in the food chain were more likely to recover than higher order predators, such as many dolphin, narwhal, fur seal, sperm, and killer whale populations. This is consistent with terrestrial mammals for which trophic level was positively associated with extinction risk (Purvis et al. 2000).

On a population level, habitat area and population size (abundance and density) both affected marine mammal recovery. Generally, the more abundant a population and the larger its geographic area or range size, the lower its extinction risk (Cardillo et al. 2008, Harnik et al. 2012). This is generally supported by our result, although we found significant nonlinear effects in our AMMs with strongest recovery at intermediate habitat areas. Very large habitat areas, such as the entire ocean, may be problematic if populations are spread too thin, which can hamper finding mates or implementing effective management. So far, habitat area has been less of a concern for marine than terrestrial species because of the lack of habitat fragmentation and the migratory nature of many marine species (Dulvy et al. 2003). Yet, our results suggest that habitat area is important for the recovery of marine mammals. In comparison, population abundance and density were consistently important in our random forest but were removed in the AMM selection process.

In terms of habitat use, populations in nearshore waters were doing better than those in offshore waters or both habitats. This may point to challenges for species in offshore waters or those crossing multiple political and biogeographical boundaries. It may also reflect the history of marine mammal management and conservation, which started earlier in nearshore populations that could be more easily seen compared to oceanic, more cryptic ones (Magera et al. 2013). Our results also suggested that the ocean basin in which a population occurred was important. Generally, and given all other factors in our models, populations in the Arctic, North Atlantic, North Pacific, ET Pacific, and Southern Hemisphere were doing better than those in the Antarctic Ocean. This may reflect the longer history of management and protection in the Northern Hemisphere and many national waters relative to the more recent history of whaling, sealing, and fisheries harvest in Antarctic waters.

Social interactions were important in some of our analyses. Social interactions can contribute to declines and recoveries of highly social organisms such as many cetaceans (Jackson et al. 2008; Davidson et al. 2012). For example, the disruption of mother-calf bonds may explain the lack of recovery in spotted (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) in the ET Pacific, where high incidental mortality occurs due to the tuna fishery (Wade et al. 2007). Our results suggest that populations with low or medium social interactions show less recovery than those with high social interactions, yet our data set contained only a few populations of killer and sperm whales with high social interactions. This suggests that more research is needed on the importance of social interactions and culture in marine mammals and on how they influence population dynamics and recovery.

Our random forests identified several taxonomic levels as important, particularly species and family level. Generally, phylogenetic relatedness is important when comparing population dynamics (Purvis et al. 2000; Cardillo et al. 2008; Davidson et al. 2012) because populations of the same or closely related species share an evolutionary history that has shaped their intrinsic traits (Fisher & Owens 2006). In our AMM framework, this phylogenetic relatedness of population-level abundance trends was incorporated by including nested random effects for several taxonomic levels. Notwithstanding, there were instances where populations of similar species did not respond in similar ways. Thus, although intrinsic factors (which were compiled on a species level) greatly affected recovery, a population's response could be influenced by extrinsic factors (which were compiled on a population level). For example, among minke whale populations, those in the northeastern Atlantic (Balaenoptera acutorostrata) showed strong recovery, whereas all 6 populations in the Antarctic Ocean (Balaenoptera bonaerensis) were declining, possibly due to the more recent and continued history of harvest (Christensen 2006). Among pantropical spinner dolphin populations, coastal stocks in the ET Pacific were increasing, whereas offshore stocks and those in Japanese waters were declining, likely due to more bycatch or less-stringent management (Wade et al. 2007).

Extrinsic Factors

Habitat loss and degradation are major threats to many marine species worldwide (Lotze et al. 2006; Schipper et al. 2008; Harnik et al. 2012). Growing human populations influence coastal waters through development, fishing, mining, aquaculture, and pollution, generally resulting in more disturbed coastal than offshore areas (Halpern et al. 2008). There are many examples of negative effects of habitat disturbance on marine mammals (Lotze et al. 2011), such as human disturbance on beaches and depletion of resting and pupping habitats hampering recovery of Hawaiian monk seals (*Monachus schauinslandi*) (Carretta et al. 2008). In our random forests, habitat disturbance was consistently selected as a critical factor. However, some of our AMMs point to a slightly higher likelihood of recovery in more disturbed areas, although this was a very weak effect. Higher levels of habitat disturbance are not intuitively linked with population recovery but can be explained. Many marine mammals require coastal habitats for feeding, breeding, or haul-out sites; thus, their habitat usage overlaps with more disturbed areas. Moreover, relatively higher visibility of nearshore populations has often resulted in earlier and more conservation efforts, making many coastal habitats safer havens for marine mammals despite higher disturbance. In contrast, many offshore, highly migratory, transboundary, or cryptic species have often received less management attention (Magera et al. 2013) and may not recover despite living in less-disturbed areas.

Other human impacts, such as direct harvest, bycatch, and cumulative number of threats, were less important. For most marine mammals today, commercial harvest is largely banned, except for some limited whaling, sealing, and subsistence hunting (Hovelsrud et al. 2008). However, indirect harvest, such as incidental bycatch and entanglement, affects many species, including many dolphins (Wade et al. 2007), small cetaceans (Young & Iudicello 2007), and some seals and sea lions (Carretta et al. 2008; Chilvers 2008). In contrast, for many harbor and grey seals, bycatch has apparently little effect on population abundance (Belden et al. 2006). Thus, whether a population can sustain bycatch or other disturbances may strongly depend on population size or life history.

The effectiveness and timing of management action can also influence recovery. Earlier and more extensive management of harvest, habitat alterations, and trade management have been linked to greater recoveries in some species (Hutchings & Reynolds 2004; Lotze et al. 2011). However, some highly managed marine mammals, such as North Atlantic right whales (Eubalaena glacialis) and Hawaiian monk seals, still show very minimal or lack of recovery (Reynolds et al. 2009). Our random forest results suggested that trade and harvest management were somewhat important, and these factors ranked higher than habitat management. Because most marine mammals have either partial or full trade management and are either fully protected from harvest or strictly managed, these factors may simply not differentiate enough among populations. Similarly, habitat management was not very important, despite evidence that habitat protection has shown strong positive effects on some populations of seals, sea otters, and whales (Lotze et al. 2011). Yet, on a global scale, only 3.5% of the ocean is protected and only 1.6% is in strict marine protected areas (Lubchenco & Grorud-Colvert 2015). Thus, in our data set, only 2 populations (harbor seals in the Wadden Sea and grey seals in the Netherlands) had full habitat protection in their habitat area. Moreover, cryptic, highly migratory, or open-ocean species pose difficulties for habitat protection. Thus, identifying and protecting high-use habitat areas has been proposed as a partial solution to this problem (Bailey & Thompson 2009).

In terms of management implementation time, for many marine mammals, this happened at a similar time, which may explain the lack of a strong effect. Although some species were protected early on (e.g., fur seals and sea otters since the Fur Seal Treaty in 1911; the great whales since the League of Nation in 1936), most marine mammals received some protection only from the 1970s onward, including trade bans under the Convention on International Trade in Endangered Species in 1973, the International Whaling Commission's moratorium on commercial whaling in 1986, and many national conservation measures (Lotze et al. 2011; Roman et al. 2015). These management measures have allowed many marine mammal populations to recover or at least prevented further decline (Magera et al. 2013).

Caveats and the Way Forward

The database we used contained the best abundance data available yet still resulted in a small sample size and taxonomic and geographic data gaps (Magera et al. 2013). Thus, many cryptic or data-poor species were not represented. In many cases, they are exploited for bait or food (many dolphins and manatees), have virtually no management (most beaked whales and river dolphins), and occupy habitats that are highly disturbed (Reijnders 1993; Reeves et al. 2003; Reynolds et al. 2009). As more abundance data become available, our analyses could easily be refined.

We did not cover all possible critical factors, and some could be further refined. Specifically, we did not include the effects of environmental variables (El Niño, climate change), loss of genetic diversity, or species interactions (competition, predation), which may be important for recovery (Gerber & Hilborn 2001; Hutchings & Reynolds 2004; Carretta et al. 2008). The importance of economic drivers could also be considered, such as market demand, capture costs, and availability of alternative products, which likely had an earlier and stronger protective effect on cetaceans than management measures (Schneider & Pearce 2004). Our broad categorical factors for habitat, trade, and harvest management could possibly be refined by quantifying the proportion of a population or its habitat that is being protected, although such information may not be available.

It would be interesting to analyze the variability of abundance trends in addition to overall trend estimates. Higher variability enhances the risk of stochastic population collapse but also may boost abundance levels. Thus, variability could both positively and negatively affect recovery.

The patterns and drivers of recovery in formerly exploited marine populations are of increasing interest to science, conservation, and management. Understanding the dynamics of marine mammal populations is important for cultural, economic, and ecological reasons. They are noteworthy symbols in traditional and contemporary cultures, are hunted commercially and for subsistence, and are increasingly valuable for tourism (Hovelsrud et al. 2008). They shape marine ecosystems from the bottom up via grazing, sediment disturbance, whale falls on the ocean floor, and nutrient cycling and from the top down through predation (Roman et al. 2014). Our results should help deepen understanding of the critical factors for the recovery of marine mammals, and marine species in general, and have implications for marine management, conservation, and future research.

Acknowledgments

We thank H. Whitehead and J. Hutchings for comments and discussion and R. McIver for help with mapping in ArcGIS. Financial support was provided by the Census of Marine Life's Future of Marine Animal Population Project and the Natural Sciences and Engineering Research Council of Canada.

Supporting Information

Additional information on the selection of marine mammal populations and critical factors (Appendix S1) and all population and critical factor data (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Bailey H, Thompson PM. 2009. Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. Marine Ecology Progress Series 378:279–287.
- Belden DL, Orphanides CD, Rossman MC, Palka DL. 2006. Estimates of cetacean and seal bycatch in the 2004 Northeast sink gillnet and Mid-Atlantic coastal gillnet fisheries. Reference document 06–13. Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries Service, Woods Hole, Massachusetts.
- Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proceedings of the Royal Society B **275:**1441– 1448.
- Carretta JV, et al. 2008. U.S. Pacific marine mammal stock assessments: 2007. Technical memorandum. National Oceanic and Atmospheric Administration, Washington, D.C.
- Chilvers BL. 2008. New Zealand sea lions *Phocarctos hookeri* and squid trawl fisheries: bycatch problems and management options. Endangered Species Research **5:**193–204.
- Christensen LB. 2006. Marine mammal populations: Reconstructing historical abundance at the global scale. Fisheries Centre Research Report. University of British Columbia, Vancouver, British Columbia.

- Collen B, Bykova E, Ling S, Milner-Gulland EJ, Purvis A. 2006. Extinction risk: a comparative analysis of Central Asian vertebrates. Biodiversity and Conservation 15:1859–1871.
- Cutler DR, et al. 2007. Random forests for classification in ecology. Ecology **88**:2783-2792.
- Davidson AD, et al. 2012. Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences of the United States of America **109**:3395–3400.
- de Little SC, Bradshaw CJA, McMahon CR, Hindell MA. 2007. Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. BioMed Central Ecology 7:3.
- Dulvy NK, Sadovy Y, Reynolds JD. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25-64.
- Dulvy NK, et al. 2014. Extinction risk and conservation of the world's sharks and rays. eLife **3:**e00590.
- Fisher DO, Owens IP. 2004. The comparative method in conservation biology. Trends in Ecology and Evolution **19:**391–398.
- Gerber LR, Hilborn R. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. Mammal Review **31**:131–150.
- González-Suárez M, Gómez A, Revilla E. 2013. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. Ecosphere 4: https://doi.org/10.1890/ES12-00380.1.
- Halpern BS, et al. 2008. A global map of human impact on marine ecosystems. Science **319:**948–952.
- Hamilton MJ, Davidson AD, Sibly RM, Brown JH. 2011. Universal scaling of production rates across mammalian lineages. Proceedings of the Royal Society B 278:560–566.
- Harnik PG, et al. 2012. Extinctions in ancient and modern seas. Trends in Ecology & Evolution 27:608–617.
- Hovelsrud GK, McKenna M, Huntington HP. 2008. Marine mammal harvests and other interactions with humans. Ecological Applications 18(2 supplement):S135-S147.
- Hutchings JA, Reynolds JD. 2004. Marine fish population collapses: consequences for recovery and extinction risk. BioScience 54:297– 309.
- Jackson JA, Patenaude NJ, Carroll EL, Baker CS. 2008. How few whales were there after whaling? Inference from contemporary mtDNA diversity. Molecular Ecology 17:236–251.
- Lotze HK, Coll M, Magera AM, Ward-Paige C, Airoldi L. 2011. Recovery of marine animal populations and ecosystems. Trends in Ecology & Evolution 26:595–605.
- Lotze HK, Worm B. 2009. Historical baselines for large marine animals. Trends in Ecology & Evolution 24:254–262.
- Lotze HK, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science **312**:1806–1809.
- Lubchenco J, Grorud-Colvert K. 2015. Making waves: the science and politics of ocean protection. Science 350:382–383.
- Magera AM, Mills Flemming JE, Kaschner K, Christensen LB, Lotze HK. 2013. Recovery trends in marine mammal populations. PLOS ONE 8 (e77908) https://doi/org/10.1371/journal.pone.0077908.
- Neubauer P, Jensen OP, Hutchings JA, Baum JK. 2013. Resilience and recovery of overexploited marine populations. Science 340:347– 349.
- Purvis A, Gittleman JL, Cowlishaw GL, Mace GM. 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society B 267:1947-1952.
- Reeves RR, Smith BD, Crespo EA, Notarbartolo diSciara G. 2003. Dolphins, whales and porpoises: 2002–2010 conservation action plan for the world's cetaceans. International Union for Conservation of Nature, Gland, Switzerland.
- Reijnders P. 1993. Seals, fur seals, sea lions and walrus: status survey and conservation action plan. International Union for Conservation of Nature, Gland, Switzerland.
- Reynolds J, Marsh H, Ragen TJ. 2009. Marine mammal conservation. Endangered Species Research 7:23–28.

- Roman J, Dunphy-Daly MM, Johnston DW, Read AJ. 2015. Lifting baselines to address the consequences of conservation success. Trends in Ecology & Evolution 30:299–302.
- Roman J, et al. 2014. Whales as marine ecosystem engineers. Frontiers in Ecology and the Environment **12:**377–385.
- Schipper J, et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science **322:**225–230.
- Schneider V, Pearce D. 2004. What saved the whales? An economic analysis of 20th century whaling. Biodiversity and Conservation 13:543-562.
- Wade PR, Watters GM, Gerrodette T, Reilly SB. 2007. Depletion of spotted and spinner dolphins in the eastern tropical Pacific: modeling hypotheses for their lack of recovery. Marine Ecology Progress Series 343:1–14.
- Wood SN. 2006. Generalized additive models—an introduction with R. Chapman & Hall, CRC Texts in Statistical Science, Boca Raton, Florida.
- Young NM, Iudicello S. 2007. Worldwide bycatch of cetaceans. Technical memorandum, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Silver Spring, Maryland.