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Population-level impacts of natural and anthropogenic causes-of-death for Hawaiian monk seals in the main Hawaiian Islands

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Abstract

Identifying, assessing, and ranking the impact of individual threats is fundamental to the conservation and recovery of rare and endangered species. In this analysis, we quantify not only the frequency of specific causes-of-death (CODs) among Main Hawaiian Island (MHI) monk seals, but also assess the impact of individual CODs on the intrinsic growth rate, λ, of the MHI population. We used gross necropsy results, histopathology, and other evidence to assign probabilities of 11 COD types to each mortality and then used Monte Carlo sampling to evaluate the influence of each COD on λ. By right censoring realizations involving specific CODs, we were able to estimate λ (and its associated uncertainty) when CODs were selectively removed from influencing survival. Applying the analysis to all known and inferred deaths believed to have occurred 2004–2019, the CODs with the largest influence on λ were anthropogenic trauma, anthropogenic drowning, and protozoal disease. In aggregate, anthropogenic CODs had a larger effect on the growth rate than either natural or disease CODs. Possible bias associated with differential carcass detection, recovery, and COD classification are discussed.

KEYWORDS
anthropogenic impacts, cause-of-death (COD), Hawaiian monk seal (*Neomonachus schauinslandi*), lifetable analysis, population growth rate, toxoplasmosis, undetected mortality

1 | INTRODUCTION

Identifying, assessing, and ranking the impact of individual threats is fundamental to the conservation and recovery of rare and endangered species. The International Union for Conservation of Nature (IUCN) guidelines include a threats classification scheme that both identifies threats and assesses "threat impacts" in terms of timing, scope, and severity (https://www.iucnredlist.org/resources/threat-classification-scheme). In the United States, recovery planning guidelines associated with the Endangered Species Act (ESA) recommend that Recovery Plans contain a formal threats assessment that "includes (1) identifying threats and their sources, (2) determining the effects of threats, and (3) ranking each threat based on relative effects." (National Marine Fisheries Service & U.S. Fish and Wildlife Service, 2018). Threats to imperiled species typically manifest by reducing survival. Among the many challenges inherent to the task of ranking threats is the fact that for most species, most deaths are not observed. This hinders the ability to assign causes of death, and ultimately compare the impact of multiple threats.

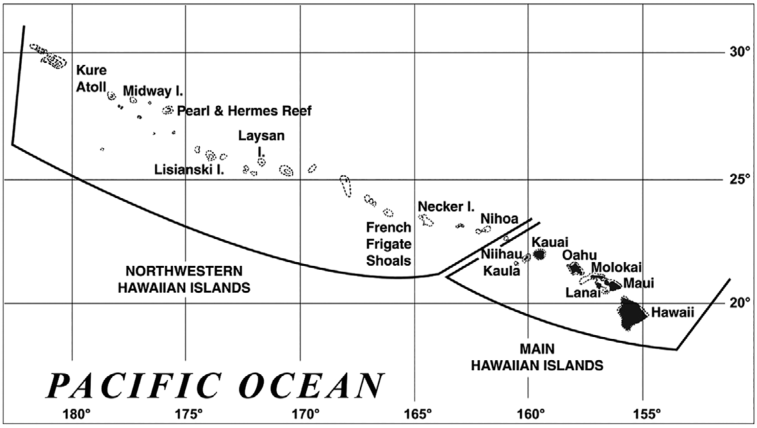
Because robust and quantifiable data on causes of death (COD) are so rare, the IUCN and ESA threat ranking approaches tend to be qualitative or semiquantitative. Conceptual models informed by expert elicitation have been used to improve the rigor of threats assessment where data are lacking (Darst et al., 2013; Donlan, Wingfield, Crowder, & Wilcox, 2010).

Even in populations where data pertaining to cause of death are available, evaluating the importance of each threat requires scaling up from simple tallies of known or estimated deaths owing to each COD (basically a head count of carcasses or known deaths) to a metric more meaningful at the population scale. This requires detailed information about not only the number of animals affected, but also their sex, age (or age class), and the composition and vital rates of the general population. In many threat assessments, the requisite data to undertake this extrapolation are lacking, necessitating an array of assumptions which may be difficult to validate.

The Hawaiian monk seal (*Neomonachus schauinslandi*) population residing in the main Hawaiian Islands (MHI) affords a rare opportunity to conduct a rigorous, quantitative threat assessment. Because many individual seals are identified and monitored throughout their lifetimes, age-specific survival rates can be estimated. Because annual resighting probabilities of individuals are high, the timing of deaths are either known or can be confidently estimated within a tolerable range of uncertainty (Baker, Harting, Wurth, & Johanos, 2011). Further, a large proportion of the carcasses are retrieved and examined postmortem to ascertain the COD. Mortality data of this quality enables us to proceed to a detailed evaluation of the population-level impacts of specific CODs. These results can then inform the separate process of prioritizing conservation measures, which takes account of a suite of other factors, such as the potential for each threat to be mitigated, cost of mitigation, and other social, economic, and logistical factors (Mace & Lande, 1991).

The Hawaiian monk seal is an endangered pinniped endemic to and distributed throughout the Hawaiian Islands, with the majority of the population found in the remote Northwestern Hawaiian Islands (NWHI) (Baker, Harting, Johanos, & Littnan, 2016; Figure 1). When intensive studies were initiated in the early 1980s, monk seals were rare in the Main Hawaiian Islands (MHI) with the exception of Niihau Island, the westernmost island in the MHI, which harbored a population of unknown size. By the early 2000s, monk seal abundance in the MHI was increasing (Baker & Johanos, 2004; Baker et al., 2011) even as numbers in the NWHI underwent a protracted decline, which appears to have moderated or reversed only recently (Baker et al., 2016; Kenyon & Rice, 1959; Ragen & Lavigne, 1999). The total range-wide abundance is now estimated to be slightly greater than 1,400 with roughly 20% of the population inhabiting the MHI (Carretta et al., 2019).

FIGURE 1 The Hawaiian Archipelago showing the entire range of the Hawaiian monk seal. This study examined causes of death in the Main Hawaiian Island segment of the range only.



As monk seal abundance in the MHI has increased, many of the mortality risks they confront are unlike those documented in the NWHI where, although entanglement in marine debris and some other human-related risks do exist, direct anthropogenic threats remain relatively uncommon (Antonelis, Baker, Johanos, Braun, & Harting, 2006; Lowry, Laist, Gilmartin, & Antonelis, 2011; Ragen & Lavigne, 1999). Natural CODs inherent to the species' life history, such as reproductive complications, conspecific trauma, predation, and malnutrition, are clearly operative in both the NWHI and MHI regions. However, other classes of CODs, such as fisheries interactions and disease transmitted by domestic animals, are either unique or far more prevalent in the MHI. These latter risks present novel challenges for research and management, both in understanding their import to the long-term outlook for monk seals in the MHI, and in charting the best means for eliminating or mitigating the various types of threats (National Marine Fisheries Service 2007, 2016).

Our research was motivated by concerns about the relative population-level significance of various mortality factors in the MHI, especially those of anthropogenic origin (e.g., net entanglements and hookings during recreational fishing, intentional killing), along with questions about the potential benefits that could accompany effective mitigation of those threats. We reviewed all known monk seal deaths in the MHI and then extrapolated from the information thus obtained to make inferences about the range of possible impacts associated with different classes of mortality factors. The quantitative methodology hinged on isolating and removing the effects of each COD through a modified survival analysis and observing the magnitude of the change (improvement) in the intrinsic growth rate, λ.

2 | METHODS

2.1 | MHI data collection

The MHI study area consisted of seven large islands (Hawaii, Maui, Lanai, Kahoolawe, Molokai, Oahu, and Kauai) that span most of the MHI chain, although observational effort was relatively low and inconsistent on Lanai and Kahoolawe (Figure 1). There are three remaining islands in the westernmost extent of the MHI (Ni'ihau, Lehua, and Ka'ula) that were not included as part of the study because they were rarely surveyed due to limited access (Baker et al., 2011).

Information on monk seals in the MHI was collected through reporting by a well-established network of volunteer observers, agency partners, and directed observation effort by the National Marine Fisheries Service (NMFS). Individual seals were identified using a combination of natural markings, applied bleach marks, and flipper tags, with identifying characteristics cataloged in an extensive collection of digital photographs (Baker et al., 2011; Harting, Baker, & Becker, 2004). Where necessary, identities were reviewed and verified by NMFS personnel. All sightings were entered into a database, along with pertinent information on location, reproductive or molt status, and other data necessary to monitor the long-term status and condition of the seal. Nursing pairs were closely monitored and pups were tagged and measured as soon as possible after weaning.

All reports of seal strandings[1] were investigated as soon as possible. Depending on accessibility and level of decomposition, carcasses were either examined in the field or transported to a laboratory for necropsy. Findings were described in a gross necropsy report. In fresh dead carcasses, blood, tissue, and organ samples were collected along with conjunctival, oral, nasal, rectal, and genital swabs. Fixed samples were examined by board certified veterinary pathologists according to standard methods. Histopathology results were used to guide ancillary diagnostic tests such as serology, immunohistochemistry, or molecular diagnostics. Deaths directly attributed to protozoal disease were classified according to established case definitions (Barbieri et al., 2016). Ancillary information that may be related to the cause of death, such as presence of nearby natural hazards or man-made infrastructure (buildings, roads, trails or other), suspicious objects that may have been used to inflict harm, or other noteworthy items, were documented. In cases where anthropogenic causes were suspected, seal deaths were referred to agency or local law enforcement for further investigation. Additional details on the standard field and laboratory procedures for investigating monk seal deaths are provided in the Supporting Information.

2.2 | Data review of known monk seal deaths

An expert review of known monk seal deaths in the MHI was conducted to categorize the CODs according to the information available for each case. Members of the review panel were some authors of this paper (A.L.H, M.M.B, J.D.B, T.A.M., T.C.J., & S.J.R.), who were trained in marine mammal biology and/or veterinary medicine and had extensive knowledge of Hawaiian monk seal life history, experience in Hawaiian monk seal stranding response, and monk seal research, including necropsy and sampling techniques and integration of diagnostic data into COD determinations. Data reviewed included sighting, reproductive, and health history prior to death, stranding reports, gross necropsy findings, histopathology findings, and ancillary diagnostic tests (Johanos, 2019a–d; Kashinsky, 2019; Kaufman, 2019). Other circumstances that might reveal the COD, such as geographic location, human presence or structures, and proximity to possible or known hazards, were also taken into consideration.

After preliminary review of these data, 11 COD types were identified (Table 1). For each known death, the review panel then assigned probabilities (p = 0.0–1.0) to each of the 11 CODs. For each individual death reviewed, a "known" COD meant that evidence was sufficient to assign a probability of 1.0 to a specific COD. A COD that could be unequivocally ruled out (e.g., reproductive complications or maternal trauma for an adult male mortality) was assigned p = 0.0. In cases where evidence was not definitive but suggested greater support for certain CODs, intermediate values were assigned to the most likely COD(s) (e.g., 0.25 each to protozoal and other disease) and the remaining probability (0.50 in this case) was distributed equally among the remaining CODs that could not be ruled out.

2.3 | Survival and life table analysis

We assessed the relative impact of individual and grouped CODs (i.e., disease, natural, or anthropogenic) on the growth rate of the MHI population using lifetable and capture-recapture analysis. The analysis quantified the increase in the intrinsic growth rate, (λ), resulting from adjusting the life table survival schedule in a standard Leslie matrix (Leslie, 1945) by removing mortalities associated with each of the CODs. The elements of a Leslie matrix contain the age-specific reproductive rates (first row) and the age-specific survival rates along the subdiagonal. The reproductive rates used in the life table were estimated using methods described in Robinson et al., 2020.

TABLE 1 Identified causes of death (CODs) in Hawaiian monk seals in the main Hawaiian Islands, grouped as disease, natural, or anthropogenic.[a]

Description	Group
Disease: protozoal (including toxoplasmosis)	Disease
Disease: other types (infectious, noninfectious, congenital)	Disease
Malnutrition (including senescent-related)	Natural
Drowning due to natural causes	Natural
Reproductive complications (aborted fetuses, stillborns, abandonment, and neonate deaths for which no other proximate cause is identified)	Natural
Maternal trauma to pup (suffocate, crush or other)	Natural
Trauma due to natural factors (predation, conspecific or other)	Natural
Trauma due to anthropogenic factors (ballistic, blunt force or other)	Anthropogenic
Drowning due to anthropogenic factors (net entanglements or other)	Anthropogenic
Hooking (death due to ingestion or snagging on fishing hooks or similar gear)	Anthropogenic
Research-enhancement activities (unintentional death during handling)	Anthropogenic

[a] Additional details on necropsy protocols and COD definitions are available in the supporting information.

Survival rates were obtained using Jolly-Seber (JS) analysis (Jolly, 1965; Seber, 1982) applied to capture histories of MHI seals with reliable sighting histories within the primary study area. Age-specific rates were estimated for both sexes and all years combined. JS analysis is ideally suited for the survival adjustments needed for our analysis because it incorporates a parameter that simplifies the process for right-censoring data. Without delving into excessive detail about JS methodology, the parameter of interest (referred to here as R_i) tallies the number of individuals "captured and released" at each time step. That terminology, more apropos to traditional trapping studies, may be somewhat misleading in our context. For our purposes, "captured" means simply "observed" at each time step, and "released" means "available for future observation" (i.e., not removed from the sampled population). If a seal is observed but not released, then the seal's observation is not tallied when computing survival to the next time step. Our approach hinges on adjusting parameter R_i according to the number of seals coded as dying due to a specific COD at each age.

To illustrate, a seal observed every year until drowning in a net at age 5 years, would have the following capture history (1 for observed, 0 for not observed) for ages 0–5:

1 1 1 1 1 1 0 0 0 0 0 …

The 1 at age 5 followed by all 0 s would essentially be treated as a mortality at age 5 because the seal was observed at age 5, then died and therefore was not observed at age 6 or later. To evaluate the effect of net drownings on estimated survival, we flag the age 5 observation using a unique code (e.g., –1). The modified capture history would then be:

1 1 1 1 1 –1 0 0 0 0 0 …

Now, the seal is "right-censored" at age 5 so that in the JS survival calculations, it is treated as a survivor to age 5 but it will not be counted in the sample when computing survival beyond age 5. Computationally, the survival rate at age i, ϕ_i, is given by:

$$\phi_i = \frac{M_{i+1}}{M_i - m_i + R_i}$$

where M_{i+1} = number of seals estimated alive at age i + 1, M_i = number of seals estimated alive at age i, m_i = number of seals seen at age i, and R_i = number of seals captured and released at age i.

Referring again to the example of right-censoring to remove the effects of one drowning death, right-censoring one seal at age *i* reduces the denominator (R_i) by 1 (giving $R_i - 1$) thereby raising the estimated survival rate for that age and, when compared to the original value, providing a metric for the expected increase in survival had the drowning death not occurred.

This approach was derived for capture-recapture studies where animals are trapped and where there is a risk of mortality due to the trapping process. In that context, by omitting the portion of sighting histories subsequent to trapping deaths, natural survival estimates can be obtained that are not influenced by the accidental trapping deaths. In the present analysis this same method effectively omits the influence of specified CODs from the survival analysis. Applying this approach to all capture histories of seals that drowned in nets would raise the estimated survival rate of the affected ages. Then, when those survival estimates are incorporated into a lifetable, the associated intrinsic growth rate would be higher than for a lifetable in which the net drowning cases were not right censored. The same recoding methodology can be used for all 11 COD types or for combinations of CODs.

2.4 | Evaluating the aggregate impact of CODs from confirmed and inferred deaths

We quantified the impacts (and associated uncertainty) of individual and grouped CODs on the MHI intrinsic growth rate using two data sets: (1) Confirmed deaths reviewed and classified by the panel and (2) confirmed deaths plus deaths inferred from circumstantial evidence or capture histories.

Inferred deaths included those not directly observed. Various circumstances were considered compelling evidence that a death had occurred. For example, dependent and recently weaned pups were reliably observable as they spend nearly all their time on the beach or very near shore where they were born (Henderson & Johanos, 1988). If such a pup disappeared, one can safely assume it had died. Alternatively, when any seal ceased to be resighted after being observed with severe and presumably fatal injuries or in debilitated condition, we assumed it had died.

Deaths were also inferred from capture histories when a well identified and frequently observed seal was not observed for two or more consecutive years. For this assumption to hold, capture probabilities (the proportion of well identified seals known to be alive and which are observed each year) must be sufficiently high to ensure that unobserved seals had a very high probability of being dead rather than undetected. Factors that can contribute to low capture probabilities are low effort, heterogeneity in distribution and sampling effort, marks that are difficult to observe, or other factors. In the early years of seal recovery in the MHI (circa pre-2004), survey effort and volunteer reporting were inconsistent as the sighting network and reporting were not well established (Baker et al., 2011). Accordingly, the JS analysis was limited to 2004–2019 data (Johanos, 2019a) and the associated capture probabilities were examined to validate that they fell within an acceptable range to reliably infer when a missing seal had died.

If the actual causes of all deaths were known with certainty, it would only be necessary to perform the above survival analysis once for each COD. However, the COD was not known with certainty for many seals, rather multiple CODs had been assigned as described above. Accordingly, each death was associated with a vector, the 11 elements of which were the assigned probabilities that each COD was the true source of the mortality. For the confirmed death cases, the probabilities assigned by the panel were used. For inferred death cases, a probability vector containing the average COD proportions for the corresponding size class or, for adults, the corresponding size/sex class, was used (i.e., the average over all known deaths of seals belonging to that class).

As noted above, we used Monte Carlo sampling of the probability vectors assigned to each seal to produce probability distributions of the effect of CODs on the intrinsic growth rate. For each trial, a single COD for each confirmed and inferred dead seal was randomly determined according to the multinomial probability elements of each seal's corresponding size class vector. Also, at the start of each iteration, a random starting age was selected for each minimum-aged adult seal. The random age assignment was proportionately allocated to a specific age consistent with the estimated survivorship schedule of MHI seals and was constrained to fall between the minimum age for adult-sized seals (age 5) and a maximum of age 32 at the seal's last sighting. Once all mortalities were assigned a random COD, the effects of each COD type were evaluated by right-censoring as described above. Each Monte Carlo trial generated a unique set of survival rates and a unique growth rate associated with removing each COD. Distributions of growth rates representing the potential effects of each COD, along with their associated uncertainty, were generated by repeating this process 1,000 times.

Seventeen different mortality scenarios were evaluated. The first of these was a baseline scenario in which no right-censoring was conducted. The next 11 scenarios tested the effects of each individual COD (Table 1). Three scenarios pooled the CODs into the following mutually exclusive groups:

- 5 Natural CODs (malnutrition, natural-cause drowning, reproductive complications, maternal trauma, and natural trauma)
- 2 Disease CODs (protozoal disease, other disease)
- 4 Anthropogenic CODs (anthropogenic trauma, anthropogenic drowning, hookings, and research/enhancement).

For these pooled groupings, disease was distinguished from natural and anthropogenic CODs because infectious and noninfectious diseases cannot be universally grouped with one or the other. This distinction also allowed us to better describe the possible impacts of some diseases that are of special interest in the MHI (i.e., protozoal disease).

The final two scenarios pooled certain CODs into groupings of special conservation interest for evaluating mortality risks in the MHI:

- Fisheries-related CODs (anthropogenic drownings and hookings)
- 4 Anthropogenic CODs plus Protozoal Disease.

In the latter group, anthropogenic CODs were pooled with protozoal disease because the protozoal pathogens of greatest concern are introduced into the environment by nonnative terrestrial definitive hosts: felids for *Toxoplasma gondii*, and canids for *Neospora caninum* (Dubey, Schares, & Ortega-Mora, 2007; Hill, Chirukandoth, & Dubey, 2005; McAllister et al., 1998). The hosts responsible for *Sarcocystis* infections in Hawaiian monk seals are unknown (Dubey, 1976; Haman et al., 2013).

The sample of seals used for the survival analysis consisted of all well-marked seals with a MHI sighting (Hawaii Island to Kauai) in their most recent year. Seals with irregular or unconfirmed sighting histories, such as those frequenting poorly surveyed areas, and seals taken into permanent captivity were excluded from the analysis. Pups that died prior to weaning required special handling. Because pups were not tagged until they had weaned, the youngest age class in the JS analysis was weaned pups (approximately 5–7 weeks old). To obtain an estimate for first year survival in the lifetable analysis, the proportion of all MHI pups directly observed to have survived from birth to weaning was multiplied by the JS survival estimate from weaning to age 1 year. Just as with other size classes, pups that died prior to weaning were assigned a probability vector corresponding to their size class, and a COD was randomly selected from that vector at the start of each Monte Carlo iteration. When that COD matched the COD being tested, the number of pups surviving to weaning was incremented up and the proportion surviving from birth to weaning was recalculated.

2.5 | Assumptions accompanying the analysis

The primary assumption underlying our analysis is that the known mortalities reviewed by the panel, along with the CODs assigned to those mortalities, were representative of the overall mortality causes throughout the MHI. A secondary assumption, implicit in the preceding one, is that any differences that exist among individual CODs in terms of detectability, reporting or diagnosis were nominal and did not lead to unacceptable bias in our results and conclusions. That is, we assumed that the COD probabilities assigned to the confirmed death cases also applied to the inferred deaths. Finally, we assumed that although 12 of the confirmed deaths reviewed by the expert panel occurred prior to 2004, the CODs associated with those deaths remained applicable to the 2004–2019 JS survival analysis. That is, we assumed that the COD probabilities were constant throughout the period for which MHI data were available.

3 | RESULTS

The initial database for the review comprised 121 confirmed seal deaths from 1992 to 2019. The information available to determine CODs varied widely, from full gross necropsy with tissue examination by histopathology and ancillary diagnostic assays, to virtually no information other than verbal reports, photographs, or external visual examination in the field. Carcass condition ranged from fresh to advanced decomposition (Geraci & Lounsbury, 2005). Seven of the 121 confirmed deaths were fetuses. These fetal mortalities were assigned CODs but were not used for the part of our Monte Carlo JS analysis in which we extrapolated the results to the overall MHI population. Among the 114 nonfetal mortalities, 17 were confirmed dead but not necropsied, and the exact COD could not be determined for many others. However, in most cases, some CODs could be ruled out and probabilities assigned to the remaining possible CODs based on available information, the size class and sex of the seal, or other considerations.

3.1 | COD assignment

Sixty-seven of 121 (55%) of the confirmed deaths (including the seven fetal deaths) reviewed by the panel were unequivocally assigned to a single COD ($p = 1.00$). Another 17 deaths had a COD assigned $p \geq 0.75$, indicating strong evidence of a particular COD but not enough to rule out others. The COD for the remaining 37 deaths remained less certain, with no single COD assigned a value of ≥0.75. In some cases (e.g., a degraded carcass), the only CODs that could be eliminated were research and enhancement deaths (which are always known) and those that were not applicable to that seal's size or age class.

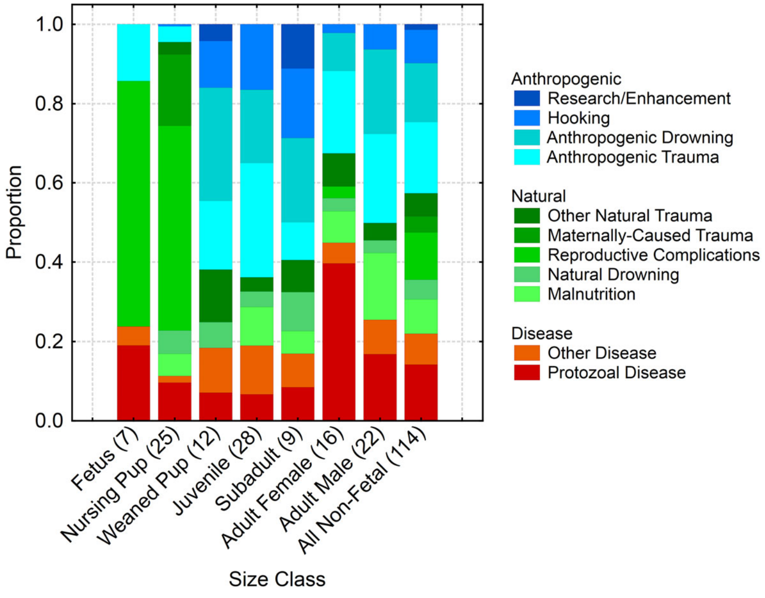


FIGURE 2 Proportion of confirmed mortalities, 1992–2019, assigned to each COD type by seal size class and all nonfetal size classes combined (includes 2 seals of unknown size or sex). Sample sizes for each size class are given in parentheses. CODs are color-coded to indicate COD grouping: Disease CODs: red/orange; Natural CODs: green; Anthropogenic CODs: blue.

Over all 114 nonfetal deaths, anthropogenic trauma ranked highest among the possible CODs (p = 0.18; Figure 2). This COD was also ranked relatively high (≥10%) for all size/sex classes except nursing pups. Anthropogenic drowning had the next highest ranking (p = 0.15), followed closely by protozoal disease (p = 0.14) due largely to its prevalence as the primary cause of adult female deaths (p = 0.40). Reproductive complication (p = 0.12) was the only other COD with probability ≥0.10 for all age/sex classes combined. CODs for seals younger than adults were similar between the sexes and therefore for those size classes, COD results from both sexes were combined. In contrast, COD results for adult seals were separated by sex both because of clear sex-specific differences in COD occurrence and to aid in management application of the results. Overall, the importance of the pooled anthropogenic CODs exceeded that of either disease or natural CODs for all size classes from weaned pups through adult, with the exception of adult females for which disease ranked higher than anthropogenic CODs (p = 0.45 for disease vs. 0.33 for anthropogenic CODs).

3.2 | Effects of CODs on population growth rate

The first analysis only evaluated the effects of confirmed nonfetal deaths that occurred during 2004–2019, which were reviewed and assigned CODs by the panel (N = 413 seals, with 92 deaths). Inferred mortalities were not right-censored for this analysis. The baseline scenario yielded a $\bar{\lambda}$ = 1.043 (center 0.95 quantile 1.041–1.045). Removing the effects of all anthropogenic CODs yielded the largest increase in the mean intrinsic growth rate ($\bar{\lambda}$ = 1.061; 1.058–1.064). Among the single CODs, removing the effects of anthropogenic trauma ($\bar{\lambda}$ = 1.050, 1.048–1.053), protozoal disease ($\bar{\lambda}$ = 1.050, 1.048–1.052), and anthropogenic drowning ($\bar{\lambda}$ = 1.050, 1.047–1.052), resulted in the largest increases in $\bar{\lambda}$. However, there was considerable overlap in the distributions for all 11 of the single CODs (Figure 3).

The second survival analysis applied the Monte Carlo methodology to all deaths, both confirmed and inferred (N = 413 seals with 202 deaths). Of the 202 nonfetal deaths confirmed or believed to have occurred during 2004–2019, 99 (49%) were confirmed (including 7 known deaths that were not reviewed by the panel) and 103 (51%) were inferred deaths. We found no significant difference in the size/sex composition for seals in the inferred deaths and confirmed deaths (χ^2 = 3.98, df = 4, N = 178,[2] p = 0.408). All but 10 of the inferred deaths had

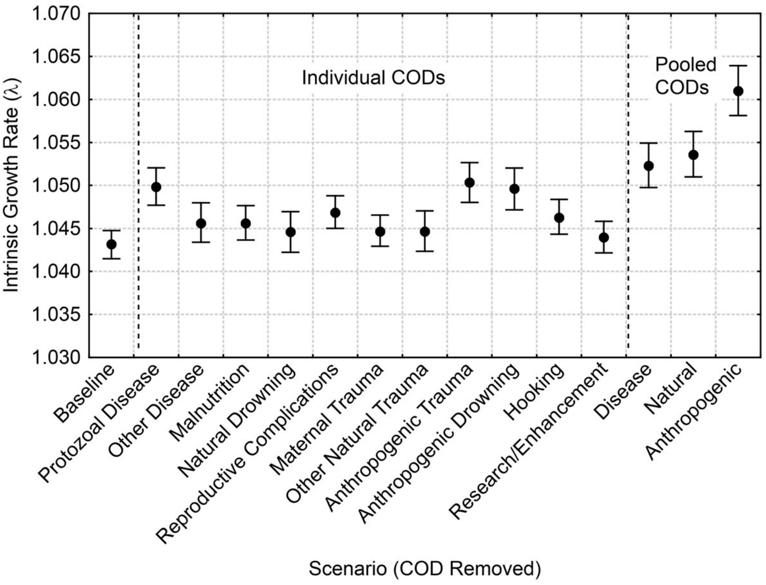


FIGURE 3 Effects of individual and grouped CODs on the intrinsic growth rate (λ) when only the 92 confirmed nonfetal deaths (2004–2019) reviewed by the panel were included in the Monte Carlo Jolly-Seber survival and life table analysis (no inferred mortalities). Means (circles) and center 0.95 quantile of λ obtained with the influence of CODs selectively removed are shown.

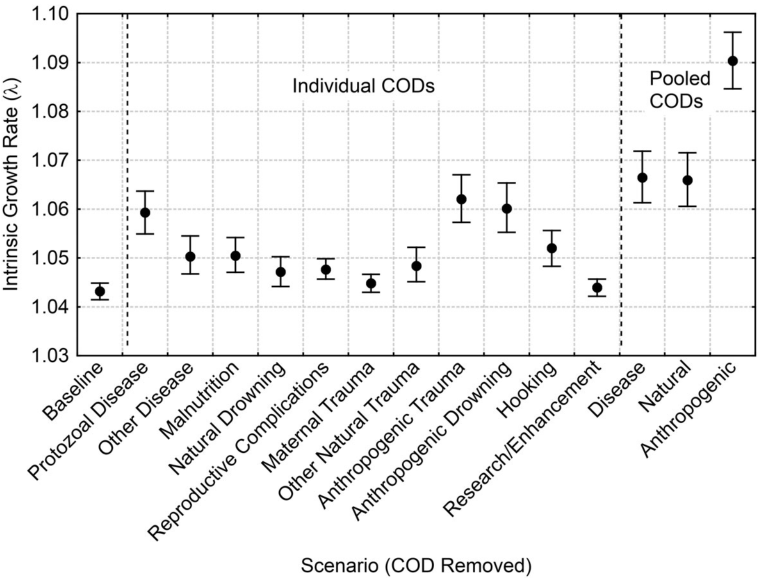


FIGURE 4 Effects of individual and grouped CODs on the intrinsic growth rate (λ) when confirmed and inferred nonfetal deaths were included in the Monte Carlo Jolly-Seber survival and lifetable analysis. Means (circles) and center 0.95 quantile of λ obtained with the influence of CODs selectively removed are shown.

more than two consecutive no-observation years (*M* = 7.3 years), reinforcing the conclusion that the seals were truly dead. The mean capture probability for each size class was (1.00 for pups, 0.98 for ages 1–4, and 0.95 for adults ages ≥5, supporting the conclusion that the inferred deaths were actual deaths rather than undetected seals.

In this more inclusive analysis, the impacts on the growth rate obtained by the removal of CODs were substantially greater than when only the confirmed mortalities were included (Figure 4). The baseline intrinsic growth rate remained the same as in the previous set of runs ($\bar{\lambda}$ = 1.043). The largest increase resulted from removing the effect of all anthropogenic mortality, which raised $\bar{\lambda}$ to 1.090 (1.085–1.096). Among the individual anthropogenic factors, trauma and drownings were the most important CODs, with their removal yielding mean $\bar{\lambda}$ = 1.062 (1.057–1.067) and 1.060 (1.055–1.065), respectively. Considering only the two CODs associated with fisheries (hookings and drowning mortalities; not shown in Figure 4), $\bar{\lambda}$ increased to 1.069 (1.064–1.075). Finally, if protozoal disease is treated as another anthropogenic COD, $\bar{\lambda}$ increased to 1.107 (1.101–1.113).

Removing the effects of all disease raised $\bar{\lambda}$ to 1.066 (1.061–1.072) due primarily to the influence of protozoal disease, which alone raised mean $\bar{\lambda}$ to 1.059 (1.055–1.064). Removing the effects of all natural CODs had less effect than that of the anthropogenic or disease CODs but still yielded an adjusted growth rate well above the baseline ($\bar{\lambda}$ = 1.066, range: 1.061–1.072). For the natural CODs, malnutrition ($\bar{\lambda}$ = 1.050; 1.047–1.054), reproductive complications ($\bar{\lambda}$ = 1.048; 1.046–1.050), and other natural trauma ($\bar{\lambda}$ = 1.048; 1.045–1.052) had the largest effects.

To explore how observed sex differences in COD occurrence for adult seals (Figure 2) might influence our results, we completed a separate analysis using only female adults. Omitting adult males from the analysis reduced the total number of deaths in the sample to 188 (confirmed and inferred). There was little difference in the ranking of single or pooled COD effects when adult males were omitted, with the exception that protozoal disease superseded anthropogenic trauma as the single most influential COD ($\bar{\lambda}$ increased by 1.9% and 1.6%, respectively).

4 | DISCUSSION

Since the mid-1990s, monk seal abundance in the MHI has grown from a few individuals to nearly 300 seals, and now comprises approximately 20% of the total species abundance (Baker & Johanos, 2004; Baker et al. 2011;

Caretta et al. 2019). While researchers had at their disposal a rich body of data derived from decades of intensive research in the NWHI, much of that accumulated knowledge was not directly transferable to the MHI population because many aspects of seal habitat and ecology in the MHI differ from that in the NWHI. Foremost among those differences are an array of mortality risks and associated management challenges that accompany the juxtaposition of seals with over 1.4 million humans that reside in the MHI (U.S. Census Bureau, 2018). This paper represents the first attempt to formally quantify the frequency and population-level impact of those risks on the expanding MHI population.

Our objective was to go beyond simply tallying the number of observed deaths attributable to each type of threat, by translating those raw tallies into a metric that was more meaningful for characterizing the expected impacts of each COD on MHI recovery and management. Changes in the intrinsic growth rate are ideally suited for this purpose because it is sensitive to not just the number of losses that occur but also to which age and sex classes are diminished by the deaths. The importance of this is evident by observing the extent to which the proportions assigned to each COD varied across age classes (Figure 2). For example, in aggregate, anthropogenic factors affected weaned pups, juveniles, and subadults most strongly. Because the intrinsic growth rate is most sensitive to changes in survival of young seals, those CODs exerted an especially strong influence on this metric.

Overall, the relative importance of CODs on seals of each size/sex class can be quickly assessed by looking for the tallest bars in the assigned proportions displayed in Figure 2. Two CODs stand out. First, and not surprisingly, for nonweaned pups (both fetuses and nursing pups) over 50% of the mortality probability was assigned to reproductive complications. The other noteworthy peak is 0.40 for protozoal disease in adult females (Figure 2). This differs from the other CODs under consideration in that it does not fit unequivocally into either the natural or anthropogenic groupings. It could be argued that protozoal disease rightfully belongs in the anthropogenic group because it primarily includes toxoplasmosis, for which cats are the only definitive host and introduced feral/domestic cats are responsible for land-to-sea contamination of islands within the MHI with infectious oocysts (Barbieri et al., 2016). However, protozoal disease includes other pathogens besides *Toxoplasma gondii* (e.g., *Sarcocystis* spp. and other), and the influence of co-infections with multiple protozoan species in Hawaiian monk seals requires further study. Given that most instances of protozoal disease in monk seals were toxoplasmosis, if we elect to treat protozoal disease as a fifth anthropogenic COD, the overall effect of anthropogenic factors on $\bar{\lambda}$ increases to 1.107 (1.101–1.113), placing it well above any other individual or pooled COD category. That may still underestimate the total impact of this disease on the population because we did not include any of the seven fetal deaths, one of which was definitively attributed to protozoal disease, in our survival analysis.

We are concerned with estimating both the number and probable causes of unobserved deaths. We estimate that of the 202 deaths that occurred 2004–2019, 92 (46%) were necropsied or, at a minimum, investigated in the field. Another seven (3%) were deemed dead based on circumstantial evidence, and the remaining 103 (51%) deaths were inferred from seal sighting histories. Our recovery rate of 46% is well above that normally reported in cetacean recovery studies, which varies widely but is typically below 10% and only exceeds 20% in a few well-studied populations (Barbieri, Raverty, Hanson, Venn-Watson, Ford, & Gaydos, 2013; Caretta et al., 2016; Wells et al., 2015; Williams et al., 2011).

A strong assumption underlying our analysis is that the confirmed deaths constituted a representative subset of all MHI deaths, such that our extrapolation of the probabilities of COD among the known deaths to the inferred deaths did not introduce major biases due to differences in detectability or diagnosis of the various CODs. We acknowledge that the likelihood of detecting carcasses and correctly diagnosing the COD do differ somewhat depending on the COD, however, we have no supportable basis for judging what those likelihoods might be. Having directly examined a high proportion (46%) of likely mortalities to assign COD probabilities reduces, but does not wholly obviate, concerns about such bias.

Our more restrictive survival analysis, which included only confirmed deaths, was designed, in part, to address any concerns about the methodological validity associated with the extrapolation of COD probabilities from the confirmed deaths to the inferred deaths. Results from the confirmed death only analysis (Figure 3) largely accorded with those of the broader analysis (Figure 4), with respect to the relative influence of each COD and the overall importance of anthropogenic CODs to population growth (mean λ raised from 1.043 to 1.061). While considerably less than the change realized in the broader analysis, this 1.7% increase is nonetheless impressive. Further, among the 114 nonfetal deaths reviewed by the panel, 60% of the total probability allocated to anthropogenic CODs was associated with 29 seals for which an anthropogenic COD was deemed certain (i.e., probability of 1.0 for one of the anthropogenic CODs). This indicates that the strong influence of anthropogenic CODs was not an artifact of deaths for which an anthropogenic COD could not be ruled out, but instead was due largely to unequivocal diagnostic evidence for a large number of deaths. Viewed yet another way, 25% (29/114) of the confirmed deaths were classified as certain anthropogenic deaths. In this light, it is difficult to discount the importance of anthropogenic CODs to MHI seals, even without further extrapolation of the findings to the many inferred deaths.

Understanding, and quantifying, the magnitude of undetected, mortality, along with the many factors that influence the rate of carcass deposition and detection is an important issue in marine mammal stranding studies (Wells et al. 2015). The manner in which this undetected mortality is handled has major implications when assessing the importance of the various threats affecting population welfare. The most direct approach for assessing the types and severity of CODs occurring within the undetected mortality component of the total mortality is to assume that the mortality factors responsible for the unobserved deaths are of the same types and occur in the same relative proportions as that observed for the known deaths. Alternatively, researchers can posit that, because of differences in detectability or other factors, certain CODs are disproportionately represented within the subset of deaths that are observed, thereby necessitating some adjustment, whether implicit or explicit, in the overall assessment of the importance of each COD.

As pointed out by Peltier et al. (2013, 2014) for cetacean strandings, carcass detection may be thought of as a complex function involving biological components (abundance and mortality rates), physical components (location or, if at sea, carcass drift as determined by buoyancy, winds and tides) and finally a societal component relating to the reporting of carcasses encountered by people. Some components within that framework may operate equally on all CODs, while others likely vary by COD and could conceivably contribute to bias in our COD determination and probabilities. For example, a partially consumed seal carcass drifting at sea will have less buoyancy than would a fully intact carcass resulting from a near-shore death (Moore & Read, 2008). More generally, deaths that take place in areas regularly visited by humans are more likely to be reported than are deaths that take place in remote settings. Further, for many CODs, there are opposing factors that could conceivably act, or interact, to render a carcass either more or less detectable in individual cases.

It is one matter to recognize that an assortment of factors might lead to bias in our carcass recovery and COD determinations, and quite another to decide how such factors differentially affect each COD and to then conjure some acceptable means for handling that bias. Ideally, we would apply correction coefficients to our COD probability vectors to address inequalities in the likelihood of detecting and diagnosing the various CODs. A similar approach was adopted by Roberts, Webber, Roe, Edwards, & Doonan (2019) in assuming (for one set of runs) a detection probability of 0.10 for dolphin predation deaths, thereby magnifying the proportion of nonfishery deaths attributed to predation. This 10-fold adjustment stemmed from the concern that partially consumed carcasses, especially those in which the body cavity was breached, would be less buoyant and hence less likely to be beachcast. However, at present we have no reliable way of estimating the true proportion of deaths of each type for monk seals and hence any correction factors would be largely speculative and simply introduce a different layer of bias to our analysis.

Another potential source of bias in our COD probability assignment is unequal confidence in our ability to recognize and assign the true COD, or to properly apportion COD probabilities across the set of nonexcluded CODs, for carcasses that have been detected, necropsied or examined, and reviewed by our panel. Standardized criteria and case definitions have been developed for some CODs (e.g., Moore et al., 2013 for anthropogenic trauma and Barbieri et al., 2016 for toxoplasmosis), but in many of our cases COD determination necessarily relied on expert opinion, elimination of some CODs from consideration, and logical inference using the entire body of available evidence. We were certain of the COD for 55% of the deaths we reviewed, and only 31% had a maximum probability of <0.75 (i.e., less confidence in the COD determination). In general, CODs characterized by unambiguous evidence, such as skeletal fractures from blunt force trauma, or hookings with conspicuous or exposed gear, were more likely to be definitively diagnosed than were those CODs that required, for example, fresh tissue samples for laboratory assays. Drowning is also notoriously difficult to diagnose even with a fresh carcass and a full necropsy (Moore et al., 2013).

Our methods recognize and preserve some of the inherent uncertainty by apportioning unassigned probability across all CODs that could not be specifically ruled out, and also through random COD allocation implemented within a Monte Carlo context. The resultant uncertainty is manifest in the vertical bars in Figures 3 and 4 which show, for example, considerable overlap in most of the natural CODs. This overlap can be interpreted as lack of evidence of a true difference in the expected effects of these CODs. However, the means and distribution for at least three individual CODs (protozoal disease, anthropogenic trauma, and anthropogenic drowning) are different enough from that of the other CODs to warrant special concern and further investigation or mitigation.

Another important aspect of our analysis is that it was designed to represent the status quo, in which many mitigations and interventions to rescue seals were conducted and without which additional mortalities certainly would have occurred (Harting, Johanos, & Littnan, 2014). Hookings provide a salient example of how such interventions affect our relative rankings of COD occurrence. Dedicated volunteers and public reports facilitate the detection and reporting of hooked seals, especially in cases where there is exposed gear (trailing line, visible hooks, or other). Once a report of a hooked seal is received, response staff can evaluate and, when necessary, institute capture and treatment to mitigate the situation. During the time period covered by our survival analysis (2004–2019), 46 successful dehooking interventions for serious life-threatening incidents took place (Gobush, Wurth, Henderson, Becker, & Littnan, 2016, as updated with NMFS unpublished data). This means that our estimate of the overall impacts of hookings (mean increased from 1.043 to 1.052 when the effect of hooking mortality was removed), while not insignificant, would be greater without the dehooking interventions that regularly take place.

Our analysis highlights the overall importance of anthropogenic mortalities to the demographics and recovery of monk seals in the MHI. The increase in mean growth rate associated with the removal of all anthropogenic CODs (from 1.043 to 1.090) is striking. That difference is not only greater than the result for natural CODs ($\bar{\lambda} = 1.066$), but there is also an important distinction between these two classes of mortality factors that bears on their interpretation. That is, unlike most of the natural CODs, which can be viewed as endogenous risks integral to the species' life history, the anthropogenic risks are, to varying degrees, accessible for mitigation and reduction. An exhaustive discussion of the types of management actions (education, regulatory, or other) that would be required to achieve effective mitigation for each COD is beyond the scope of this study. However, recognition of the importance of anthropogenic factors in monk seal population dynamics is certainly not new and considerable effort is already invested in addressing these threats. It is our hope that by quantifying the potential impacts of specific mortality factors, our results will provide a more complete science-based context for prioritizing conservation efforts.

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AUTHOR CONTRIBUTIONS

Albert Harting: Conceptualization; formal analysis; investigation; methodology; software; writing-original draft. **Michelle Barbieri:** Conceptualization; data curation; investigation; methodology; supervision; validation; writing-review and editing. **Jason Baker:** Conceptualization; methodology; writing-review and editing. **Tracy Mercer:** Data curation; investigation; methodology; writing-review and editing. **Thea Johanos:** Data curation; supervision; validation; writing-review and editing. **Stacie Robinson:** Conceptualization; methodology; writing-review and editing. **Charles Littnan:** Conceptualization; project administration; supervision; writing-review and editing. **Katie Colegrove:** Data curation; investigation; methodology; resources; writing-review and editing. **Dave Rotstein:** Data curation; investigation; resources; writing-review and editing.

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ENDNOTES

[1] As defined in the Marine Mammal Protection Act (Section 10), a seal is considered stranded when it is found dead on land or in the water, or is alive but unable to return to the water on its own.

[2] Pups were excluded from this test because there were no inferred deaths for pups (all 24 pup deaths were confirmed).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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