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CONTRIBUTED PAPERS

An expert-based system to predict population survival rate from health data

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Article impact statement: Health data can be used to predict survival rates for wildlife populations, providing an effective monitoring tool to support conservation.

Abstract

Timely detection and understanding of causes for population decline are essential for effective wildlife management and conservation. Assessing trends in population size has been the standard approach, but we propose that monitoring population health could prove more effective. We collated data from 7 bottlenose dolphin (*Tursiops truncatus*) populations in the southeastern United States to develop a method for estimating survival probability based on a suite of health measures identified by experts as indices for inflammatory, metabolic, pulmonary, and neuroendocrine systems. We used logistic regression to implement the veterinary expert system for outcome prediction (VESOP) within a Bayesian analysis framework. We fitted parameters with records from 5 of the sites that had a robust network of responders to marine mammal strandings and frequent photographic identification surveys that documented definitive survival outcomes. We also conducted capture–mark–recapture (CMR) analyses of photographic identification data to obtain separate estimates of population survival rates for comparison with VESOP survival estimates. The VESOP analyses showed that multiple measures of health, particularly markers of inflammation, were predictive of 1- and 2-year individual survival. The highest mortality risk 1 year following health assessment related to low alkaline phosphatase (odds ratio

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[OR] = 10.2 [95% CI: 3.41–26.8]), whereas 2-year mortality was most influenced by elevated globulin (OR = 9.60 [95% CI: 3.88–22.4]); both are markers of inflammation. The VESOP model predicted population-level survival rates that correlated with estimated survival rates from CMR analyses for the same populations (1-year Pearson's $r = 0.99$, $p = 1.52 \times 10^{-5}$; 2-year $r = 0.94$, $p = 0.001$). Although our proposed approach will not detect acute mortality threats that are largely independent of animal health, such as harmful algal blooms, it can be used to detect chronic health conditions that increase mortality risk. Random sampling of the population is important and advancement in remote sampling methods could facilitate more random selection of subjects, obtainment of larger sample sizes, and extension of the approach to other wildlife species.

KEYWORDS
biomarker, dolphin, health assessment, survival, vital rate, wildlife monitoring

Un sistema basado en conocimiento experto para predecir la tasa de supervivencia a partir de datos de salud

Resumen: La detección y el entendimiento oportunos de la declinación poblacional son esenciales para que el manejo y la conservación de fauna tengan efectividad. La evaluación de las tendencias en el tamaño poblacional ha sido la estrategia estándar, pero proponemos que el monitoreo de la salud poblacional podría ser más efectivo. Recopilamos datos de siete poblaciones de delfines (*Tursiops trun*catus) en el sureste de Estados Unidos para desarrollar un método de estimación de la probabilidad de supervivencia con base en un conjunto de medidas sanitarias identificadas por expertos como índices para los sistemas inflamatorio, metabólico, pulmonar y neuroendocrino. Usamos la regresión logística para implementar el sistema de expertos veterinarios para la predicción de resultados (SEVPR) en un análisis bayesiano. Ajustamos los parámetros con los registros de cinco sitios que contaban con una buena red de respondientes a los varamientos de mamíferos marinos y censos de identificación fotográfica (foto-ID) que documentaron los resultados de supervivencia definitivos. También realizamos análisis de marcaje-recaptura (MR) en los datos de identificación fotográfica para obtener estimados separados de las tasas de supervivencia poblacional para compararlos con los estimados del SEVPR. Los análisis del SEVPR mostraron que varias medidas sanitarias, particularmente los marcadores de inflamación son buenos predictores de la supervivencia individual para uno y dos años. El riesgo de mortalidad más alto un año después de la valoración sanitaria se relacionó con una fosfatasa alcalina baja (cociente de probabilidades de 10.2 [95% CI 3.41-26.8]), mientras que la mortalidad a los dos años estuvo más influenciada por una globulina elevada (9.60 [95% CI 3.88-22.4]); ambas son marcadores de la inflamación. El modelo del SEVPR predijo las tasas de supervivencia a nivel poblacional en correlación con las tasas estimadas de supervivencia de los análisis de MR para las mismas poblaciones (Pearson de un año $r = 0.99$, $p = 1.52e\text{-}05$; dos años $r = 0.94$, $p = 0.001$). Aunque nuestra propuesta no detecta las amenazas agudas de mortalidad que en su mayoría son independientes de la salud animal, como la proliferación de algas nocivas, puede usarse para detectar las condiciones crónicas de salud que incrementan el riesgo de mortalidad. Es importante el muestreo aleatorio de la población y los avances en los métodos de muestreo remoto podrían facilitar una selección más aleatoria de los sujetos, la obtención de muestras de mayor tamaño y la expansión de la estrategia a otras especies de fauna.

PALABRAS CLAVE
biomarcadores, delfín, monitoreo de fauna, supervivencia, tasa de vitalidad, valoración sanitaria

INTRODUCTION

Effective wildlife management and conservation requires timely detection of changes in population status, typically measured as population size, and an understanding of the factors contributing to those changes. However, the number of individuals in a population is often difficult to measure, particularly for species that spend the majority of their lives out of human view. The

resulting lack of precision in estimates of population size and the need for repeated estimates over time can make it difficult to detect trends in a timely manner for all but the most precipitous declines (Jewell et al., 2012). Even when a decline is detected, the cause or contributing factors are generally not apparent, which hinders identification of effective management actions. Examining population vital rates (e.g., survival or fecundity), either to detect changes over time or to compare spatially across populations, may be a more sensitive method for assessing population status and trends. However, because of the difficulty in observing life-history events (e.g., births, deaths) for some species (Moore et al., 2020), obtaining robust estimates of vital rates may also require multiple years of monitoring effort, particularly for long-lived species that are slow to reproduce. In addition, direct monitoring of vital rates may not be informative of underlying causes when a decrease occurs.

Population health may provide an early warning of emerging issues prior to observable changes in vital rates. The importance of conservation medicine (i.e., integrating health into wildlife monitoring for responsive conservation efforts) has long been recognized (Deem et al., 2001). However, using health as a quantitative monitoring tool requires understanding of the link between a given health measureand population vital rates. Although few would question that health status affects an individual's chances of survival, defining the quantitative links between 1 or more health measures and survival probability is difficult, particularly if health status is measured at a single point in time. Studies of human subjects have had some success at identifying physiological measures that, taken at a single time point, are predictive of morbidity or mortality years into the future. Many of these measures focus on neuroendocrine dysregulation and resultant disruption of inflammatory, metabolic, cardiovascular, or pulmonary systems, collectively referred to as allostatic load (AL) (Beckie, 2012). Using multiple indices from these physiological systems and combining them into 1 or more indices of AL, researchers have identified links with numerous adverse health outcomes (reviewed by Beckie [2012]), including higher all-cause mortality (Castagne et al., 2018; Robertson et al., 2017). Similarly, Edes et al. (2018) demonstrated an association of AL indices with morbidity and mortality risk in western lowland gorillas (*Gorilla gorilla gorilla*) under human care and proposed that AL indices could be a predictive tool for wildlife populations.

Of wildlife species, cetaceans are particularly challenging to monitor. Except for surfacing to breathe, cetaceans spend their lives underwater and out of human view. This, along with the fact that cetaceans are generally long-lived, makes it particularly challenging to estimate vital rates or monitor trends in populations. Even in the limited cases of some nearshore populations, where trends in abundance or vital rates have been documented, understanding of the mechanism underlying adverse trends is often lacking. Understanding health, and in particular what components of health are compromised, could provide that mechanistic link and help point to potential solutions. Therefore, cetaceans are an exemplar of how incorporating health into monitoring could support more effective management and conservation.

Bottlenose dolphins (*Tursiops truncatus*), hereafter referred to as dolphins, are considered a model species for understanding cetacean health due to the medical advances that have been made with populations under human care (Venn-Watson et al., 2011) and the breadth of health studies on free-ranging populations (Barratclough et al., 2019). A multidecade study of dolphin populations in Sarasota Bay, Florida, and other multiyear studies of populations in the Indian River Lagoon, Florida, and near Charleston, South Carolina, have contributed to a robust understanding of the physiology, environmental exposures, and endemic disease in free-ranging populations (Bossart et al., 2017; Reif et al., 2017; Wells et al., 2004). Targeted health assessments for other populations have also been conducted in response to specific events, such as unusual mortality events (UMEs), and hazardous chemical releases (Schwacke et al., 2010, 2012, 2014).

We developed the veterinary expert system for outcome prediction (VESOP), a quantitative model that links dolphin health data with individual mortality risk and population-level survival rates (Figure 1). We synthesized data collected during previous health assessment studies, follow-up photographic monitoring studies, and stranding response efforts for 7 dolphin populations in the southeastern United States. Relying on knowledge from a panel of veterinary experts, we integrated health measures from blood, physical examination, and pulmonary ultrasound into indices and hypothesized that 1 or more of the indices is predictive of individual survival. The indices include some of the same physiological measures used in human and managed primate AL indices, but also include measures identified as important from cetacean veterinary research or prior dolphin health assessment studies. Because our ultimate goal was the prediction of population vital rates, we computed the average VESOP survival probability for individuals that were sampled for health metrics in each population. We then compared these VESOP population-level survival rates with survival rates for the same population and period estimated through capture–mark–recapture (CMR) to test the hypothesis that rates between the 2 methods are correlated.

METHODS

Health data

We collated records from prior dolphin catch-and-release health assessment studies across 7 locations (Figure 2; Appendix S1). A standard suite of health measures was collected across studies: complete blood count, serum chemistry, serum cortisol, thyroid hormones, length, weight, and maximum girth. Samples from all studies were sent to the Cornell Animal Health Diagnostic Center (Ithaca, New York) for laboratory analyses to support comparability of data across studies and over time. Pulmonary ultrasound was added as part of the standard assessment process beginning in 2010 (Schwacke et al., 2014; Smith et al., 2017). Sampling methods and health data from the various studies have been reported (Balmer et al., 2018; Bossart et al., 2017;

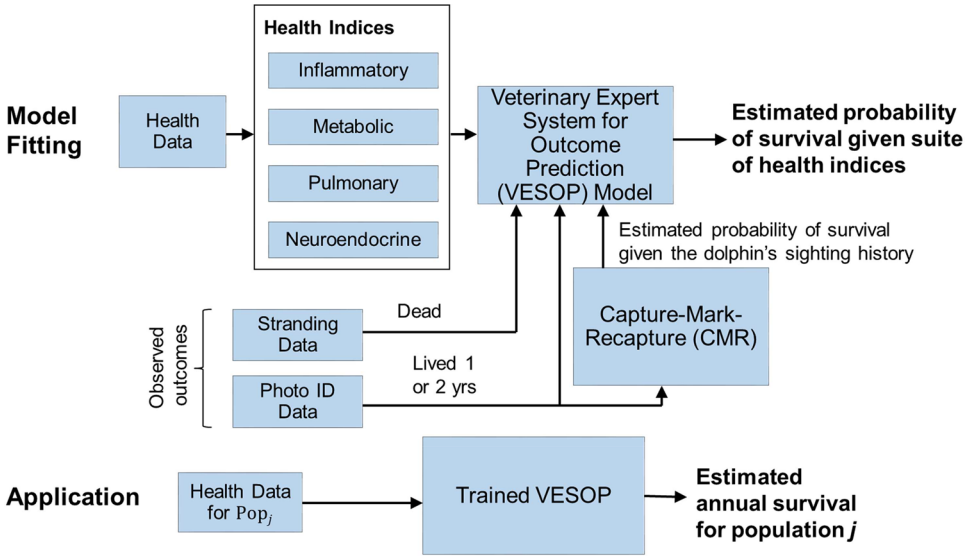

FIGURE 1 Overview of analytical approach for fitting coefficients for model parameters and application of the veterinary expert system for outcome prediction (VESOP) model. Health data are predictors; stranding and photographic identification (photo-ID) data provide observed outcomes and input for capture–mark–recapture models to estimate survival outcome for unknown fates. The fitted model can be applied for a new population (Pop_j) to estimate an annual survival rate.

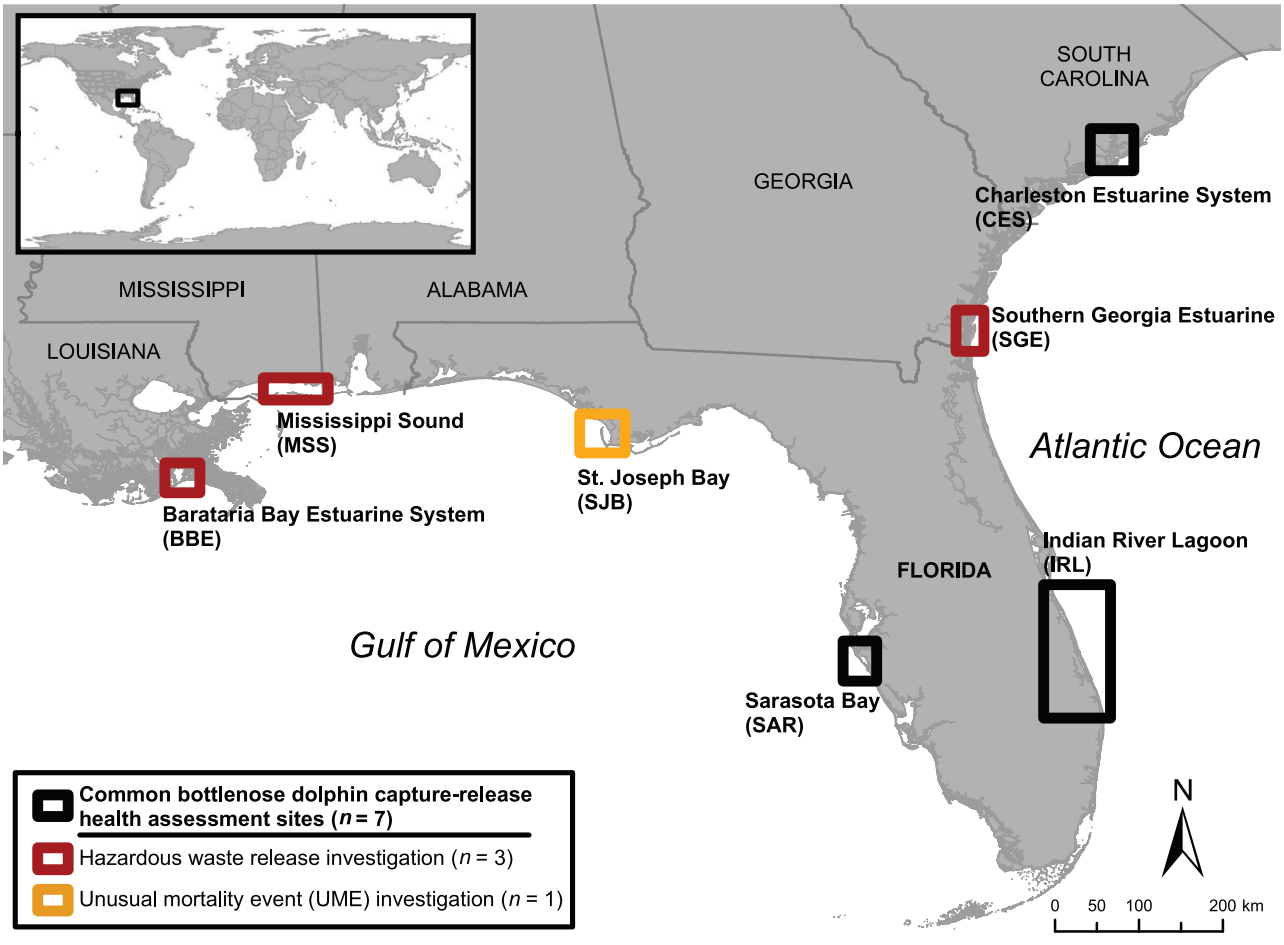

FIGURE 2 Bay, sound, and estuary stocks of bottlenose dolphins from which health data were obtained (boxes).

TABLE 1 Indices and criteria developed in consultation with the expert Veterinary Advisory Panel to classify cases of dolphin health abnormalities.

Physiological system	Index	Classification criteria
Inflammatory	Neutrophilia	Neutrophil count (thousand/μL) at or above 95th percentile: 7.3 (all age classes)
	Low albumin	Albumin (g/dL) at or below 5th percentile: $4.09 \times e^{-0.00018 \times \text{length}}$ or 3.9 (adult), 4.0 (subadult), 4.1 (calf)
	High globulin	Globulin (g/dL) at or above 95th percentile: $1.569 \times e^{-0.00393 \times \text{length}}$ or 4.4 (adult), 3.5 (subadult), 3.0 (calf)
	Low alkaline phosphatase (ALP)	Alkaline phosphatase (μ/L) at or below 5th percentile: $1101.6 \times e^{-0.1141 \times \text{length}}$ or 60.95 (adult), 119 (subadult), 185.5 (calf)
	Anemia	Hemoglobin (g/dL) at or below 5th percentile: 11.5 (adult female), 12.8 (calf, subadult, and adult male)
Metabolic	Low body mass index (BMI)	Mass (kg):length (cm) ratio at or below 5th percentile: mass $\leq 10^{-4.738} \times \text{length}^{2.889}$ (female), mass $\leq 10^{-5.366} \times \text{length}^{3.156}$ (male) Maximum girth (cm):length (cm) ratio used if weight was not obtained: max girth $\leq 10^{21.87} + 0.3981 \times$ length (female), max girth $\leq 10^{-0.7432} + 0.4963 \times$ length (female)
	Low cholesterol	Serum cholesterol (mg/dL) at or below 5th percentile: $171.03 \times e^{-0.00175 \times \text{length}}$ or 109 (adult), 117 (subadult), 142.8 (calf)
	Hypoglycemia	Serum glucose (mg/dL) at or below 5th percentile: $105.3 \times e^{-0.00156 \times \text{length}}$ or 70.0 (adult), 75.6 (subadult), 80.9 (calf)
Pulmonary	Lung disease	Moderate or severe lung disease as diagnosed via ultrasound
Neuroendocrine	Low cortisol	Serum cortisol (μg/dL) sampled postcapture at or below 5th percentile: 0.97 (all age classes)
	Low total triiodothyronine (total T3)	Serum total T3 (ng/dL) at or below 5th percentile: $1.46 \times e^{-0.00273 \times \text{length}}$ or 0.73 (adult), 0.87 (subadult), 0.84 (calf)

Reif et al., 2017; Schwacke et al., 2010, 2012; Smith et al., 2017) (additional details in Appendix S1).

The prior health assessment fieldwork was conducted under U.S. National Marine Fisheries Service scientific research permits 18786, 18986, 522–1785, 15543, 998–1678, and 14352. Protocols were approved by the Mote Marine Laboratory (Sarasota, Florida), Florida Atlantic University (Indian River Lagoon, Florida, and Charleston, South Carolina), or National Oceanic and Atmospheric Administration (all other health assessments) Institutional Animal Care and Use Committees.

We convened an expert veterinary advisory panel (VAP) that included 4 veterinary clinicians with extensive marine mammal experience and 3 additional veterinary researchers with specific expertise in toxicology, immunology, and infectious disease. We met with the VAP to review health indices previously described by Schwacke et al. (2014) and asked for their input on potential refinements for classification criteria; the diagnostic value of each index and how it might relate to pathways for disease; and identification of indices or other measures that would be most predictive of 1- to 2-year survival outcome. Through these discussions, we defined classification criteria for a final set of indices, organized by physiological system (Table 1; Figure 1).

For each index, we calculated the 5th percentile of measurements to provide a threshold for classifying cases. For some measurements, the threshold was defined as the 95th percentile, and for others the threshold was defined as the 5th percentile. For example, inflammation may be indicated by low values of alkaline phosphatase, but for serum globulins, which are antibodies, elevated values are of concern. For indices expected to vary with age, we used nonlinear quantile regression via the quantreg package in R (R Development Core Team, 2022) to estimate threshold as a function of length (Table 1). There were 18 records for which length was not recorded; therefore, we also estimated thresholds stratified by age class or sex to apply when length was missing. Additional details are in Appendix S3.

We applied the thresholds to evaluate cases for each health index and then estimated the prevalence of cases for each population. To visualize the differences in prevalence across the multiple sites, we used the R heatmap function with hierarchical clustering.

Photographic identification data

We collated data from photographic identification (photo-ID) studies across the same 7 locations to determine whether sampled dolphins were resighted following their health assessment. Different photo-ID research teams using similar survey methods, all previously described (Appendix S1), conducted surveys at the various sites. Using photo-ID data and working with members of the Southeast U.S. Marine Mammal Stranding Network, we examined 1-year survival from the time of the health assessment for each of the dolphins sampled. Dolphins documented via photo-ID as alive 1 year or more after sampling were assigned a 1. If there was strong evidence that the

dolphin had died during the follow-up period (i.e., the carcass was recovered or the dolphin was monitored by researchers through a period of deteriorating condition until death was imminent), then the dolphin was assigned a 0. We used the same process to assign values for 2-year survival. For some individuals, survival outcome could not be determined (unknown fate) (i.e., a carcass was not recovered but the dolphin was also not observed alive after the 1- or 2-year follow-up period).

CMR analyses

Using available photo-ID data collected over multiple years, including years in which health assessments were conducted, we performed site-specific CMR analyses to estimate individual survival probability for health-assessed dolphins with unknown fate and to obtain separate estimates of population survival rate from photo-ID data for comparison with VESOP survival estimates.

We developed CMR models for 3 genetically distinct populations (Hayes et al., 2022): Indian River Lagoon (IRL), Southern Georgia Estuarine System (SGE), and St. Joseph Bay (SJB) (Figure 2). For each population, we established a set of candidate models for survival and capture probability that included explanatory variables relating to time, season, geographic stratum, survey method, and survey effort as appropriate. Animals vary in the distinctiveness of the fin markings used to identify them; we used data only from individuals classified as being of average or high distinctiveness. We accounted for the possibility of nonresident (i.e., transient) individuals by truncating all individuals' first captures (SJB), analyzing data only from a core study area (SGE), or including in our candidate set models that allowed estimated survival to differ in the first period after capture (a transience effect) compared with subsequent time periods (IRL). We used maximum likelihood to fit all candidate models and selected the most parsimonious model for each population with small-sample Akaike information criterion as the model selection criterion. Analyses were undertaken with program MARK 9.0 (White & Burnham, 1999) and accessed via the RMark package in R (R Development Core Team, 2022). Additional details are in Appendix S4.

For 3 of the remaining populations, we used previously published survival estimates covering the required periods because no significant data collection efforts have taken place since these publications: Charleston Estuarine System (CES) (Speakman et al., 2010), Barataria Bay Estuarine System (BBE) (Glennie et al., 2021), and Sarasota Bay (SAR) (Lacy et al., 2021) (Figure 2). For the Mississippi Sound population (MSS) (Figure 2), there were insufficient photo-ID data available to conduct a CMR analysis for the years immediately following health assessments.

To estimate individual survival probability for each dolphin with an unknown fate, we used its sighting history together with the estimated capture and survival probabilities from the relevant CMR model to estimate 1- and 2-year survival probability after health assessment. This was achieved using custom-written R code (implementing an adaption of the forward–backward algorithm treating the CMR model as a special case of a hidden Markov model [Zucchini et al., 2016]). Uncertainty was quantified using parametric bootstrapping. To capture this uncertainty in the form of a parametric distribution that could be input into the VESOP modeling, we fitted via maximum likelihood beta distributions to the parametric bootstrap resamples for each animal. Additional details are in Appendix S5.

The fitted or literature-derived models for each site were also used to meet our second objective, which was to obtain estimates of population survival 1 and 2 years after each health assessment. Again, parametric bootstrapping was used to quantify uncertainty on these estimates (Appendix S5).

VESOP framework

We investigated models for predicting survival outcome from health indices using logistic regression within a Bayesian analysis framework. The Bayesian framework allowed us to use incomplete health records (i.e., records missing values for 1 or more predictor variables) for fitting the model via data augmentation and allowed inclusion of individuals with known outcomes (survival or death) and those with unknown fates by specifying probability distributions on the survival of unknown fate individuals derived from CMR analyses.

We let p_i be the survival probability of dolphin i, $i = 1, \ldots, N$, from sampling location $l(i)$, and modeled this with the linear predictor:

$$\text{logit}\left(p_i\right) = \alpha_{l(i)} + \sum_{j=1}^{J} \beta_j f_{i,j}, \tag{1}$$

where α_l is the baseline survival rate at location l, β_j is the additive contribution to survival rate of the jth health index, and $f_{i,j}$ is the value (1 or 0) of the jth health index for animal i.

We let the animals be ordered such that the first K animals are of known fate, where survival outcome, s_i, is known to be either alive (1) or dead (0). For these animals, we modeled each survival outcome as an independent Bernoulli random variable $s_i \sim \text{Bernoulli}(p_i)$, which gives the likelihood component:

$$\mathcal{L}_K = \prod_{i=1}^{K} \left\{ p_i^{s_i} \left[1 - p_i\right]^{\left[1-s_i\right]} \right\}. \tag{2}$$

The remaining $U = N - K$ animals were of unknown fate. For these animals, although we did not have a definite survival outcome, we did have information from the CMR study about their probability of survival. We represented this information in the form of a beta probability density function on survival probability q_i, which we denoted $f(q_i)$ (this is a function of 2 parameters of the beta distribution, which are assumed known for each unknown fate animal). To form the likelihood for the unknown fate animals, we summed over both possible survival

outcomes and integrated over all possible values of q:

$$\mathcal{L}_U = \prod_{i=K+1}^{N} \int_{q_i=0}^{1} \left\{ f(q_i) \sum_{s=0}^{1} Pr(S = s|q_i) \left[p_i^s (1-p_i)^{(1-s)} \right] \right\} dq_i,$$

$$= \prod_{i=K+1}^{N} \int_{q_i=0}^{1} \left\{ f(q_i) \left[q_i p_i + (1-q_i)(1-p_i) \right] \right\} dq_i, \quad (3)$$

where $Pr(S = s|q_i)$ is the probability the survival outcome is s given the value of q_i, which is equal to q_i when $S = 1$ and $(1 - q_i)$ when $S = 0$.

We implemented the model in R (R Development Core Team, 2022) with rjags 4–9 (Plummer, 2013); the integration and the sum in Equation (3) were computed within the Markov chain Monte Carlo sampler. For all analyses, 4 chains were sampled through an adaption phase of 200 samples and a burn-in period of 5000 samples. After the burn-in phase, 1000 samples (10,000 samples thinned by 10) from the posterior distribution were collected. Trace and density plots were used to assess convergence. Summary statistics were compared across the 4 chains to ensure consistency and then combined to provide 4000 samples from the posterior distribution. Additional details, including description of Bayesian prior parameter distributions, are in Appendix S6.

Data and code are publicly available through Dryad (https://doi.org/10.5061/dryad.h18931zqt).

VESOP model fitting and analyses

We used a subset of the dolphin health records to estimate coefficient values for the VESOP model parameters. For this model fitting, we selected study sites that had a robust network of responders for stranded marine mammals and relatively frequent (i.e., monthly or at least seasonal) photo-ID surveys conducted for the 2 years following health assessment sampling in order to minimize the potential bias that can be introduced by missing outcomes when missing outcomes are not random. Detection probability for dolphin mortalities (negative outcomes) is generally low. Wells et al. (2015) estimate that only 33% of resident SAR dolphin carcasses are recovered, and this likely represents an upper bound for the achievable detection rate due to the high human population density and shoreline accessibility near Sarasota, Florida. Conversely, detection of positive survival outcomes may be quite high, depending on the number and length of time that follow-up photo-ID surveys are conducted. For example, if photo-ID surveys are conducted for several years after health assessment, this provides many opportunities to observe the dolphin alive.

We used CMR analysis to estimate survival probability for unknown fate dolphins, but the precision of estimates depended on the degree of photo-ID effort for the given area and the length of time after health assessments surveys were conducted, which varied across study sites. This disparity in detection of positive versus negative outcomes had the potential to cause bias in estimation of survival rates when fitting the VESOP model. Given this, we selected the following sites with robust stranding response and photo-ID follow-up for inclusion in the data set for fitting model parameters: SAR, IRL, CHS, and SJB. We also included 2011 health records for BBE as part of the data set. Data for BBE 2013 and later were not included because systematic photo-ID surveys and support for stranding response in Louisiana were discontinued in 2014 when the *Deepwater Horizon* (DWH) Natural Resource Damage Assessment (NRDA) ended. The last NRDA photo-ID survey was in early 2014, and only 1 systematic photo-ID survey has been conducted since (in 2019).

We conducted preliminary analyses to examine the predictive potential for each index. For each of the 11 indices, we fitted the VESOP model including only that index. Samples from the posterior distribution for β were used to compute an odds ratio (OR) of 1- and 2-year mortality with 95% credible intervals. We considered an index significantly related to mortality when the credible interval for the OR excluded 1.

We then included all of the health indices simultaneously in the VESOP model to examine predictive potential for the combined indices. Following inference of the model parameters, we computed posterior predictive estimates of population-level survival probabilities. For dolphins from sites that were included in the model fitting, we used survival estimates from the posterior distribution. To compute a survival probability for dolphins that were not included in the model fitting, we applied Equation (1) with estimates for the coefficient for each health index (β_j) from the posterior distribution. For this computation, we selected α_l randomly by drawing with equal likelihood from the sites in the training set, excluding SJB. We excluded SJB because samples from this site were collected during a UME (Schwacke et al., 2010); therefore, we did not consider the underlying mortality rate to be representative of baseline (Appendix S6). After computing the survival estimate for each individual dolphin, we computed population-level mean and credible interval for each site from the combined survivals of all dolphins from that site.

To compare VESOP and CMR results, we computed the Pearson correlation coefficient for the mean population survival for the same period estimated from the 2 models.

For dolphins sampled during the health assessments at each site, individual survival outcomes were either observed or, for unknown fates, estimated from the CMR individual survival probability analysis. We also computed the mean estimated survival for dolphins that were sampled during health assessments and compared this survival estimate with CMR model estimates for the broader population. This comparison, which was based solely on dolphin sightings and CMR analyses without consideration of health data, was of interest to determine whether dolphins selected for health assessment have a survival rate similar to the overall population.

RESULTS

We obtained 812 dolphin health records from across the 7 study sites. We excluded records for dolphins that were known to be nonresidents, based either on sighting history ($n = 3$) or on radio or satellite-linked tagging data ($n = 4$). Of the remaining

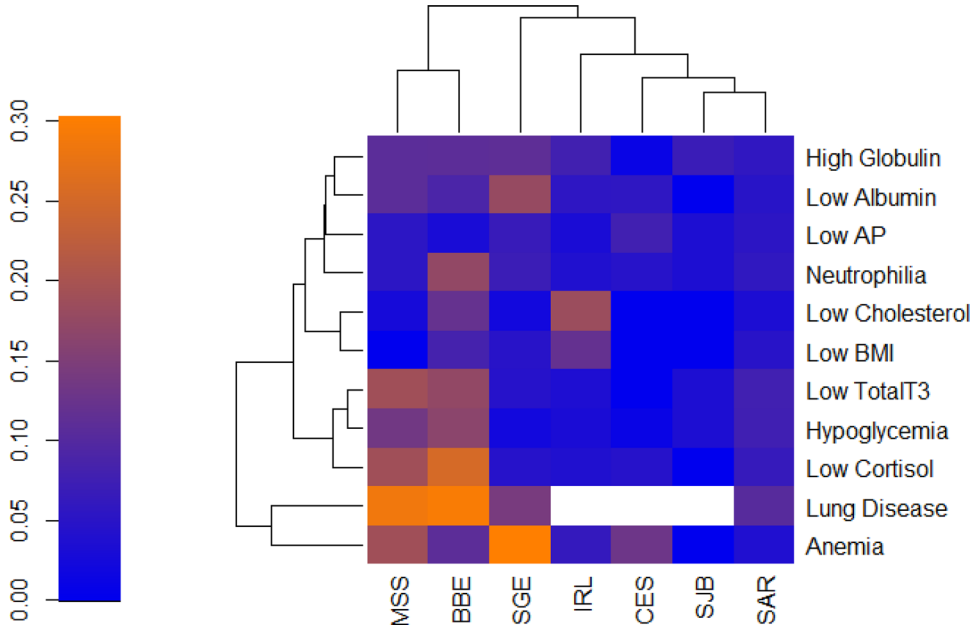

FIGURE 3 Prevalence of health abnormalities (rows) in 7 populations of bottlenose dolphins (columns), with hierarchical clustering of rows and columns (blue, lowest prevalence; orange, highest prevalence; scale on left, map for estimating prevalence; population abbreviations defined in Figure 1; health parameter abbreviations defined in Table 1).

805 records (Appendix S2), we confirmed 1-year survival for 692 individuals and 2-year survival for 649 individuals following their health assessment; 23 and 35 were confirmed mortalities within 1 and 2 years, respectively. Sufficient photo-ID data were available to estimate a probability of survival from the CMR analysis for an additional 53 (1 year) and 46 (2 years) dolphins. Survival estimates for the remaining animals could not be obtained because there were no photo-ID surveys more than 1 or 2 years after their health assessment date, so survival estimation would have involved an extrapolation in time. Health records were relatively complete (Appendix S2), with the exception of lung scores, which were completely missing for 3 sites (SJB, IRL, CES), and cholesterol, which was not measured in some years in IRL and CES.

Abnormal health indices were most prevalent in dolphins sampled from the BBE and MSS, and these 2 sites clustered together in the hierarchical clustering dendrogram (Figure 3, column clusters). The SGE also had a high prevalence of abnormalities and clustered separately from the remaining sites in the second clade. On the opposing axis (Figure 3, rows), inflammatory health indices (high globulin, low albumin, low alkaline phosphatase [ALP], and neutrophilia) clustered together, as did low cholesterol and low body mass index (BMI), both metabolic indicators.

At all 3 sites for which CMR models were developed, survival probability was estimated to vary over time. It increased at SJB as a logit-linear function of time from 0.76 in 2005 to 0.99 in 2013 (Appendix S4), increased at SGE as a logit-linear function of time from 0.83 in 2008 to 0.92 in 2019 (Appendix S4), and fluctuated as a smooth function of time at IRL from 0.90 in 2003 to 0.94 in 2007 and 0.92 in 2016 (Appendix S4).

When health indices were analyzed separately, odds of both 1- and 2-year mortality increased for dolphins with any of the indices, with the exception of low BMI, low total triiodothyronine (T3), and hypoglycemia (Figure 4a,b). The highest 1-year mortality risk was for low ALP with an OR of 10.2 (95% CI: 3.41–26.8), whereas 2-year mortality risk was most influenced by elevated globulin (9.60 [3.88–22.4]), low ALP (8.80 [3.16–22.4]), and anemia (8.31 [3.14–20.3]). Pairwise comparison of 1-year ORs showed a high degree of association among the various indices (Appendix S1).

When all parameters were included simultaneously in the VESOP logistic regression for 1-year mortality, low ALP was still most influential (Figure 4c). All other indices, with the exception of hypoglycemia, had ORs >1 but wide 95% CIs that did not exclude 1. For 2-year mortality, high globulin and low cortisol had the greatest influence (Figure 4d).

Posterior baseline survivals (i.e., expected survival for a healthy dolphin) were similar across the sites: CES, 0.99 (95% CI: 0.97–0.99); IRL, 0.98 (0.95–0.99); SAR, 0.98 (0.97–0.99); BBE in 2011, 0.98 (0.94–0.99). The exception was SJB, for which baseline survival was much lower and credible intervals were broad (0.92 [0.78–0.98]).

Overall population survival estimated from the VESOP model, which incorporated both baseline and health index effects, varied across the 7 sites (Figure 5). The highest survival estimates were for CES (OR = 0.96 [95% CI: 0.93–0.98]) and SAR (0.96 [0.94–0.98]), followed by IRL (0.94 [0.91–0.97]) and MSS (0.94 [0.87–0.98]). The lowest estimates were for SJB (0.88 [0.74–0.97]), SGE (0.89 [0.79–0.96]), and BBE in 2011 (0.91 [0.83–0.97]) and 2013–2018 (0.91 [0.83–0.96]).

We found significant correlation between estimates from the VESOP model and the CMR models (1 year: Pearson's $r = 0.99$ [95% CI: 0.94–0.99], $p = 1.52 \times 10^{-5}$; 2 year: $r = 0.94$ [0.66–0.99], $p = 0.001$), but CMR estimates were consistently lower (Figure 5; Appendix S2). We found a similar pattern between CMR model estimates and mean survival for the dolphins sampled for health assessment at each site (Figure 5); correlation

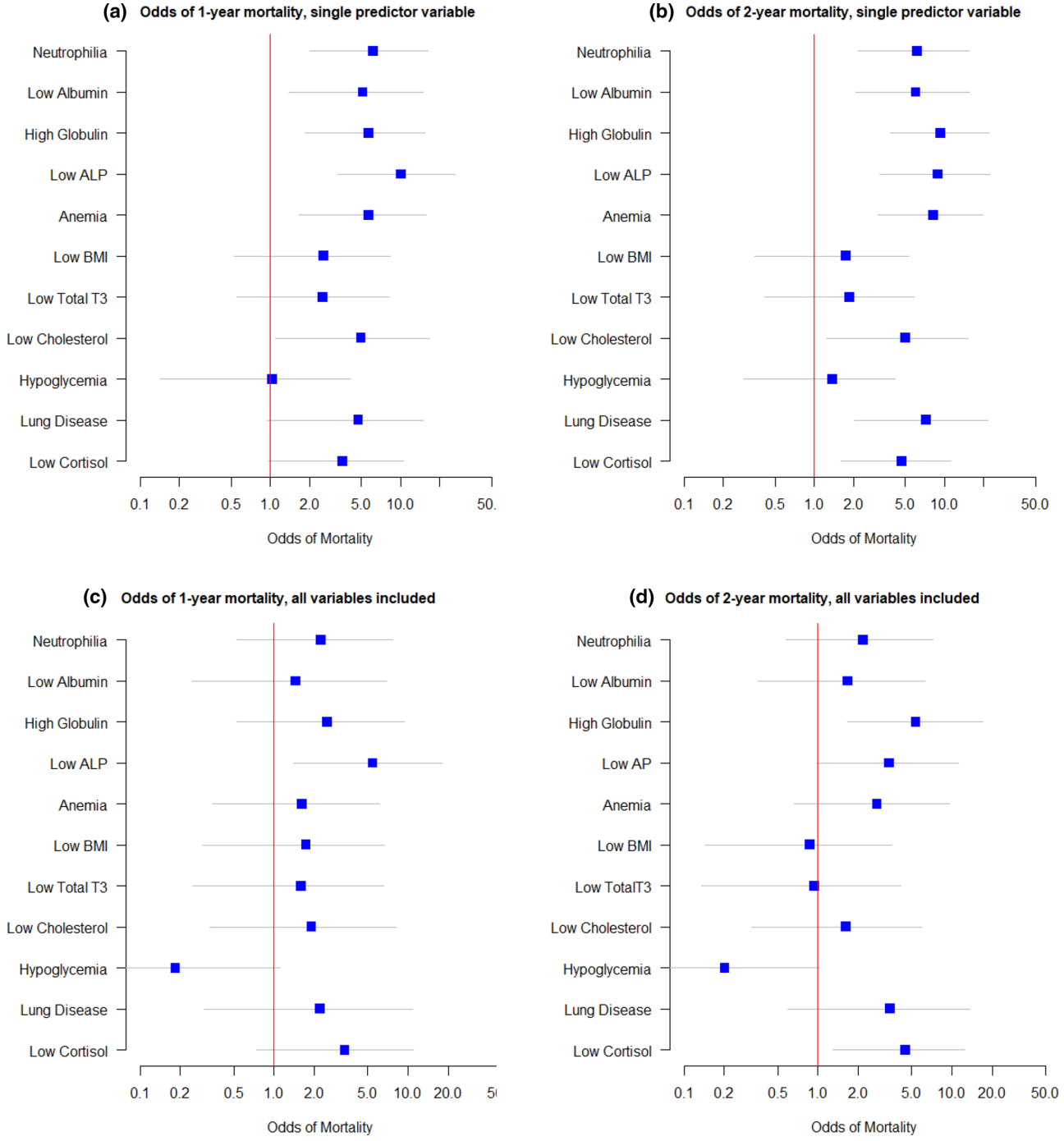

FIGURE 4 Estimated odds of mortality (a) within 1 and (b) 2 years for dolphins with a given abnormality versus those without derived from the veterinary expert system for outcome prediction (VESOP) analysis with 1 predictor and within (c) 1 and (d) 2 years derived from the VESOP analysis with all variables included (blue squares, median; gray lines, 95% credible intervals; vertical red line, equal odds; health parameter abbreviations defined in Table 1).

was high but CMR estimates were lower (Pearson's $r = 0.92$ [0.53–0.99], $p = 0.004$).

DISCUSSION

Using a well-studied cetacean species for which hands-on health assessments are possible, we demonstrated that health data, particularly inflammatory indices, are strongly predictive of individual survival. Furthermore, we showed that these indices can be combined to estimate survival rate for the sampled population. This presents a promising new approach for estimating population vital rates in cetaceans and other species for which deaths cannot readily be observed.

At the individual level, we found a higher risk of mortality associated with the majority of health indices when

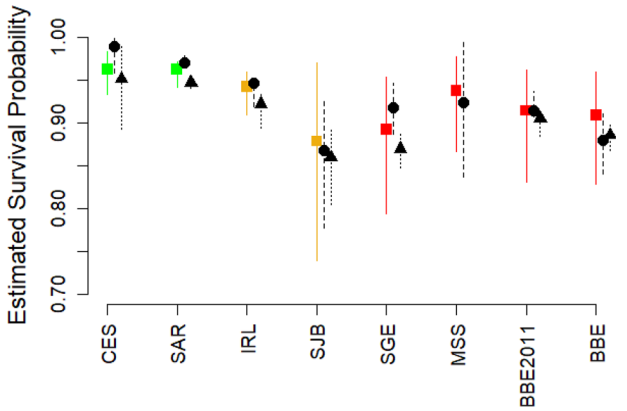

FIGURE 5 Estimated 1-year survival probability of dolphins for each sampled population (population abbreviations defined in Figure 1; squares, veterinary expert system for outcome prediction [VESOP] model estimates; colors, differentiate populations from which health data were obtained for varying purposes; green, basic biological or health research; red squares, hazardous waste release investigations; yellow, investigations of unusual mortality events; circles, proportion of dolphins sampled during health assessments that survived 1 year; triangles, population survival estimated from capture–mark–recapture [CMR] analyses; lines, 95% CIs for CMR survival estimates and VESOP model estimates).

analyzed separately as a single predictor. However, only low ALP remained strongly influential for 1-year mortality when all indices were combined in the VESOP model. In cetaceans, marked decrease in ALP is considered a strong negative prognostic indicator (Nollens et al., 2018), which was supported by our findings of an over 10-fold increased odds of dying within a year for dolphins with low ALP. Decline in ALP can occur during viral or bacterial infection; degree of decline corresponds with the severity of infection (Fothergill et al., 1991). However, the decrease may occur quite rapidly as disease progresses (Fothergill et al., 1991); therefore, low levels, particularly as extreme as the 5th percentile threshold we applied, may not be seen until a few weeks or months prior to death. All dolphins with low ALP that were later confirmed dead were lost within the first year, suggesting that ALP is a better measure of immediate (within 1 year) versus longer term survival. High serum globulin, also an indicator of inflammation, was a strong predictor of 2-year mortality, consistent with a human study showing increased all-cause mortality over a 5-year period in association with elevated globulin values (Juraschek et al., 2015).

The reduced importance of other inflammatory markers in the full VESOP model (i.e., with all indices included) versus the analysis with each index treated separately was likely due to the strong association among indices. For example, anemia was strongly associated with both low ALP and high globulin ($p < 0.0001$ for both) (Appendix S1). Although the univariate odds of 1-year mortality for dolphins with anemia was high (OR = 5.7 [95% CI: 1.8–16]), it became much less significant (1.6 [0.35–6.1]) when all indices were included in the model. A similar shift in importance was seen with neutrophilia, which was also strongly associated with low ALP and high globulin. However, the lesser influence of the multiple-index VESOP model does not discount the potential utility of the other indices.

In future applications, it may not be practical to measure the full suite of indices, and some indices may be more feasible to collect than others in logistically challenging field situations. For example, although a serum chemistry panel (including albumin, globulin, glucose, and ALP) requires 2 mL of separated serum, diagnostic markers of anemia can be measured from a very small amount of blood with a portable point-of-care system, and white blood cell counts (including neutrophils) can be estimated from a blood smear. For cetacean species for which hands-on blood collection is currently infeasible, researchers are pursuing analytical methods to measure cholesterol and total T3 in blubber, which can be remotely sampled. Therefore, our findings of some redundancy of information in the diagnostic indices are encouraging, suggesting that a limited suite can still be informative even when all measurements cannot be collected. Furthermore, exploration of other health indices could help identify alternative measures that are more applicable for predicting longer term survival. We were only able to look as far as 2-year survival due to data limitations in several of the sampling sites, but studies in humans show AL indices that are predictive of mortality over a decade or more (Castagne et al., 2018). In fact, 1 study showed an AL index that was not predictive of 5-year mortality, but was predictive of longer term (10-year) mortality (Robertson et al., 2017). Future studies with longer follow-up periods (i.e., including photo-ID surveys and stranding response) could help elucidate other health indices that supplement the VESOP suite and may be more sensitive for less severe or emerging population health issues.

At the population level, the VESOP model predicted survival rates that varied across the 7 sites, with the highest estimates for SAR and CES (both 0.96), followed by IRL and MSS (both 0.94), and the lowest estimates for SJB, SGE, and BBE (mean survival 0.91 or lower). This is consistent with what we know about the sites, in that SAR and CES are considered healthy populations that are stable or increasing in size (Lacy et al., 2021; Speakman et al., 2010) and have previously been used as reference populations for establishing physiological baselines (Hart et al., 2013, 2015; Schwacke et al., 2009) and for comparison with other potentially compromised populations (Schwacke et al., 2010, 2012, 2014; Twiner et al., 2012).

Conversely, the populations with the lowest estimated survival were under study due to concern about health effects from hazardous chemical exposure. Sampling in SGE was conducted to investigate potential adverse effects of exposure to extremely high levels of polychlorinated biphenyls (PCBs) (Balmer et al., 2011). Although exposure to PCBs and other persistent organochlorine pollutants has been reported for many dolphin populations along the southeast U.S. coast, PCB concentrations measured in SGE dolphins are 4- to 10-fold higher than other populations (Kucklick et al., 2011). Sampling in BBE, and later in MSS, was conducted as part of the investigation of injuries from the DWH oil spill and as part of the multiyear Northern Gulf of Mexico Cetacean UME investigation (Smith et al., 2017; Venn-Watson et al., 2015). For these sites

with high exposures to hazardous chemicals, the lower survival estimates from the VESOP model were driven by a high prevalence of multiple health abnormalities. The BBE, MSS, and SGE sites were separated from the others by the hierarchical clustering (Figure 3), and all had relatively high prevalence for multiple inflammation indices as well as other health problems. The BBE and MSS populations clustered together in the highest clade; both had a very high prevalence of lung disease and low cortisol, conditions previously reported in association with exposure to the DWH oil (Schwacke et al., 2014; Smith et al., 2017). Anemia was the most prevalent index for SGE, a finding consistent with previous analyses of this population and with high exposure to PCBs (Schwacke et al., 2012).

The SJB population had the lowest survival rates and almost no health abnormalities. Sampling in SJB was part of an investigation into the 2005–2006 Florida Panhandle UME, which was ultimately attributed to blooms of a harmful algae (*Karena brevis*) and its neurotoxin, brevetoxin (Twiner et al., 2012). Rather than health-related mortality risk, the low VESOP survival estimate for SJB (0.88) was due to a low posterior baseline survival (0.92). Two of the 27 dolphins from SJB had no health abnormalities when sampled but later died in association with the UME: their carcasses were recovered and stomach contents were positive for brevetoxin. Five additional dolphins, also with no health abnormalities, were not observed a year or more after their assessment, but their carcasses were not recovered, and they potentially perished as part of the UME. Investigation of strandings during the UME showed dolphins in good nutritional state, no evidence of infectious disease, and no consistent gross or histological findings (Twiner et al., 2012). Mortalities appeared to occur either acutely during the bloom or shortly after the bloom due to the retention of *K. brevis* in the food web (Reif et al., 2017). In either case, the risk of mortality appeared to be related to brevetoxin exposure rather than a dolphin's underlying health state.

Although a high prevalence of eosinophilia (23%) was reported from the SJB health assessments (Schwacke et al., 2010), we found that all of the eosinophilia cases survived for at least 2 years after health assessment, providing no evidence that the eosinophilia increased near term (1- to 2-year) mortality risk. Eosinophilia was also not included in the health indices for the VESOP model because members of the VAP considered elevated eosinophils, which is often associated with common parasitic infections, less likely to be a strong predictor of survival. We applied the fitted VESOP model to SJB health data with posterior baseline survival from the other training sites, and the predicted survival was much higher (0.980), consistent with the CMR average survival estimates for SJB in the years following the UME (2007–2013) (Appendix S4). Our conclusion is that the SJB population was overall in good health and that acute mortality events, such as those associated with harmful algal blooms, cannot be predicted by monitoring health.

Estimated survival for the IRL population (0.94) was also low as compared with SAR and CES populations. Increased development and agricultural activity have led to environmental degradation in the IRL, including altered water quality and decreased sea grass habitat (Reif et al., 2017). The IRL population experienced 3 UMEs in 2001, 2008, and 2013 (Bossart et al., 2017). The specific causes of the UMEs were not determined, but ecological factors, such as poor water quality and habitat degradation, were believed to contribute. Although the recorded UMEs did not overlap with the health sampling used for our analyses, these same ecological factors certainly could be a chronic stressor for dolphin health in the IRL and may underlie our findings of slightly higher prevalence of metabolic abnormalities for IRL dolphins (low BMI, low cholesterol) (Figure 3) and somewhat lower survival.

Actual mortality for these populations cannot be directly measured because carcasses often sink, drift, or are consumed by scavengers (Moore et al., 2020), but open CMR models based on sighting histories from photo-ID data are currently a standard approach for estimating survival for dolphins and other cetacean populations. We found strong correlation between CMR and VESOP population survival estimates ($r = 0.99$), although the VESOP estimates were consistently higher (Appendix S2). Standard CMR models estimate apparent survival because an animal's disappearance due to mortality cannot be readily distinguished from a disappearance due to emigration from the survey area. It is possible that emigration created a downward bias in the CMR estimates, but we believe any such bias is likely low because we took specific measures to minimize it by mitigating any influence of transient animals.

Alternatively, there could have been a selection bias for the health assessment subjects in some instances, resulting in healthier dolphins being selected for sampling and creating an upward bias in the VESOP estimates. This alternative is supported by the fact that the observed survival of the dolphins sampled for health assessment was also higher than survival estimates derived from the application of CMR analyses to the broader photo-ID catalogs (which ranged from around 500 to over 2000 individual dolphins). Although protocols for sampling were consistent across studies, the sampling strategy for health assessments varied to some degree across sites and within some sites over time. In some SAR sampling years, younger dolphins believed to be on the verge of becoming independent from their mother were targeted to obtain basic life-history and health data while they were still identifiable through association with their mother and to mark them for future photo-ID study following separation. In the IRL, visibly emaciated dolphins or individuals with labored breathing were avoided, as were dolphins believed to be over 25 years old. This selection of younger dolphins could bias sampling toward healthier individuals, as could avoidance of visibly ill individuals.

There could be additional unconscious bias in the selection of subjects. Groups of dolphins (2–4 individuals) versus single individuals were often targeted for efficiency of the health assessment sampling. It is possible that compromised dolphins may exhibit "sickness behaviors" that lead to social isolation (Lopes, 2014), either self-imposed to avoid aggression from conspecifics or because conspecifics purposely avoid sick individuals. In this case, compromised individuals may be less likely to be sampled, and this bias would be more prominent for populations where there is a high prevalence of disease. If the goal of future health assessments is to derive a

survival estimate for the population, then these potential biases should be further explored and considered in developing the sampling design. Measuring health indices with remote sampling (e.g., sampling of blubber, blow, or feces) would greatly enhance researchers' ability to randomly select subjects and support collection of larger sample sizes due to the lower effort, risk, and cost. Research to develop methods to remotely collect blood from free-swimming cetaceans is also being pursued, and our findings support the need for such technological advancements. Such remote sampling approaches would expand the applicability of health assessment and VESOP models to other cetacean species for which hands-on health assessments are infeasible.

Our identification of a quantitative link between health and population survival is significant. The ability to estimate population survival rate from health measures, particularly those collected at a single point in time, provides a potential proactive approach for predicting survival rate to supplement current monitoring approaches. In addition to more timely detection of a decline, changes in health may suggest underlying factors when declines are detected. For example, a high prevalence of low cortisol, which we found in the BBE and MSS populations, is a relatively specific indicator of oil exposure. Aside from the implications for improved monitoring, the VESOP model supports an essential, and currently lacking, component in unified frameworks for assessing or predicting the effects of nonlethal effects of stressors on wildlife populations, such as population consequences of disturbance (PCoD) conceptual models (Pirotta et al., 2018). The PCoD framework, which links disturbance to physiological or behavioral responses, changes in health, and ultimately to population vital rates, has been widely applied for assessment of the nonlethal effects of disturbance, primarily noise disturbance, on marine mammals. However, implementations of PCoD models to date focus largely on body condition as the health indicator of interest and rely primarily on bioenergetic modeling and assumed relationships with reproduction or expert elicitation to estimate the level of energy below which starvation causes mortality (reviewed by Pirotta et al. [2018]). In contrast, the VESOP model provides a direct connection between health measures and both individual- and population-level survival, reducing the assumptions that must be made to determine the population consequences of anthropogenic stressors; this connection will greatly facilitate effective conservation, management, and regulatory decisions.

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SUPPORTING INFORMATION

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

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