Received: 10 July 2023 | Accepted: 28 March 2024

DOI: 10.1111/mms.13132

ARTICLE

Marine Mammal Science

Changes in blue whale survival and abundance in the Gulf of California

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Abstract

Understanding the drivers of population abundance and distribution is fundamental to ecology and key to informing conservation actions, particularly in endangered species like blue whales (*Balaenoptera musculus*). Historically, some Eastern North Pacific blue whales have aggregated in the Gulf of California (GoC) each winter. Using photo-identification data collected around Loreto Bay from 1984 to 2020, we analyzed 453 sightings histories using mark-recapture models. Estimated apparent survival (including permanent emigration) decreased from 0.991, 95% CI [0.977, 0.997] in 1985 to 0.889, 95% CI [0.807, 0.939] in 2019. The estimated number of whales using the study area declined from 96 whales, 95% CI [50, 254] in 2012 to 13 whales, 95% CIs [12, 23 and 12, 28] in 2018 and 2019. Abundance of the whole Eastern North Pacific population is slowly increasing, so our results likely reflect declining usage of the GoC. Linear models found a relationship between the number of whales in the GoC and the difference in sea surface temperature between the study area and the Costa Rica Dome wintering area, suggesting that environmental variation could explain variation in blue whale numbers in the GoC. These results highlight the importance of tracking population dynamics as changing environmental conditions affect the range and distribution of populations.

KEYWORDS
abundance, *Balaenoptera musculus*, blue whale, Gulf of California, mark-recapture, photo-identification, Robust Design, survival

1 | INTRODUCTION

Knowledge of the population ecology of a species is essential to inform conservation assessments and management actions. For species that are wide-ranging, assessment can be particularly challenging because trends in abundance from studies that are spatially limited can be difficult to interpret. Furthermore, changing environments can lead to shifts in the distribution of a species, requiring continued study to understand where important habitats are. Obtaining robust information can be particularly challenging for threatened species. This study is focused on a historical winter concentration of Eastern North Pacific (ENP) blue whales (*Balaenoptera musculus*) around Loreto Bay in the Gulf of California and aims to understand the current relevance of this area to this population, and what may be driving any changes.

In summer, ENP blue whales feed off the West coast of North America, with large numbers sighted off Southern California (Calambokidis et al., 2015; Carretta et al., 2022). Most whales then migrate south for winter, where there are three known areas of aggregation, the Gulf of California (GoC), the Costa Rica Dome (CRD), and the West coast of Baja (WCB) (Busquets-Vass et al., 2020; Calambokidis et al., 1990; Calambokidis, Falcone, et al., 2009; Mate et al., 1999; Sears et al., 2013; Stafford et al., 1999). The GoC is believed to be an important habitat for blue whales based on a consistent annual presence that includes pregnant females and females with young calves (Costa-Urrutia et al., 2013; Melica et al., 2021; Sears et al., 2013; Valenzuela-Molina et al., 2018).

Blue whale abundance in the GoC was estimated to average 283 between 1993 and 1999, and to be 299 in 2005, but with wide confidence intervals (Gendron, 2002; Ugalde De La Cruz, 2008). Most sightings that contributed to these estimates were made on the western side of the GoC between Loreto and La Paz (Figure 1). Abundance in this limited area was estimated at ~200 whales per year between 1994 and 2006 and showed no obvious trend (Ugalde De La Cruz, 2008), suggesting that this area of the GoC may be used more heavily than the rest of the gulf. Ugalde De La Cruz (2008) also estimated annual survival rate in the GoC at 0.980, 95% CI [0.952, 0.991]. Additionally, age-specific annual survival has been estimated through a population dynamics model, with results ranging from 0.93 to 0.95 (Ortega-Ortiz, 2009).

These abundance estimates highlight that in the past, blue whales have consistently used the GoC habitat, but the most recent estimates of abundance and survival rate are >15 years old. Consequently, this study aims to provide updated information on abundance and survival rate of blue whales in the GoC that use the waters around Loreto (Figure 1).

Unlike many other baleen whale species, blue whales are believed to forage as they migrate, seeking out high productivity waters (Branch, Stafford, et al., 2007; Mercado-Santana et al., 2017; Reilly & Thayer, 1990) with enough resources to support their large body size. Blue whales must consistently find dense patches of their preferred prey krill (*Euphausiids*; Goldbogen et al., 2011) and their presence has been repeatedly shown to be associated with environmental covariates that indicate productivity, including sea surface height, sea surface temperature (SST), chlorophyll A (chl *a*), and wind speed (Barlow et al., 2021; García-Morales et al., 2017; Pardo et al., 2013; Shabangu et al., 2019). Underwater topography also plays an important role in creating the upwelling conditions that can aggregate krill, such as the submarine canyon systems in the California Current Ecosystem (Santora et al., 2018).

Additionally, Etnoyer et al. (2006) found that blue whales in the ENP were sensitive to subtle temperature gradients, potentially following temperature fronts as they foraged, and stronger dynamic aggregative current features have been linked with an increased blue whale feeding rate (Fahlbusch et al., 2022). Interannual variability in the timing of blue whale migration has been explained by an interaction between SST anomalies and krill abundance (Szesciorka et al., 2020) and by upwelling characteristics in the Monterey Bay region (Oestreich et al., 2022).

The need to feed leads to limited spatial and/or temporal separation between foraging and reproduction (Cotton Rockwood et al., 2020; Croll et al., 2005; Goldbogen et al., 2011; Sears & Perrin, 2009). This is evident in the GoC where females have been seen repeatedly with young calves in this productive body of water (Mercado-Santana et al., 2017; Sears et al., 2013). The observed relationships between blue whale presence and features of their environment that indicate productivity provides a motivation for this study to explore whether any of the variability in abundance or survival rate in the GoC can be explained by such environmental cues. This information could inform predictions of distribution throughout the year, including migration patterns and timings in this subgroup of the ENP population as the marine environment continues to be affected by the changing climate.

The photo-identification data analyzed in this study have been collected annually in the GoC from 1984 to 2020, offering a rare opportunity to improve our understanding of this subgroup of the ENP blue whale population. By estimating abundance and survival rate using mark-recapture methods, and exploring the relevance of changes in the environment, we aim to provide an updated perspective on the importance of the GoC to ENP blue whales.

2 | METHODS

2.1 | Study area and data collection in the Gulf of California

Annual photo-identification surveys were conducted in the GoC from 1984 to 2020 during February and March, the peak months for blue whale presence (Gendron, 1992, 2002; Sears et al., 2013). The study area was centered around Loreto, Mexico, extending 80 km along the coastline in both directions and 50 km offshore (Figure 1).

From 1984 to 2007, the area was surveyed by the Mingan Island Cetacean Study (MICS) during which period the average annual field effort was 18 days (Sears et al., 2013). Since 2008, the study area has been surveyed by an environmental nongovernmental organization, the Great Whale Conservancy (https://www.greatwhaleconservancy.org). From 2012 onwards, average annual effort was 24 days. Surveys were not undertaken according to a particular design, but the aim was to maximize the number of blue whale photo-identifications captured within the study area. When a blue whale was encountered, photo-identification images were taken of its flanks and back and data were recorded on GPS position, side of whale, and presence or absence of a calf. Calves were identified by their smaller size (half the size of an adult) and synchronous swimming during breathing sequences with the adult that was assumed to be its mother (Sears et al., 2013). Matching individuals between years was based on skin pigmentation patterns on the flank and back of both sides of the whale (Sears et al., 1990, 2013). To avoid duplication of individuals, only whales with a matched left side were used in the analysis. Matches were verified by three people and then included in the MICS photo-identification catalog with each whale being allocated a unique identification number. The catalog also included some opportunistic images shared by third parties (Sears et al., 2013).

2.2 | Data collection off the United States West Coast

The Cascadia Research Collective (CRC) and collaborators have collected photo-identification images of blue whales annually off the United States West Coast (USWC) since 1986 (Calambokidis et al., 1990; Calambokidis & Barlow, 2004, 2020). CRC surveys extended along the USWC from 32°N to 49°N although most photo-identifications of blue whales were obtained between 32°N and 42°N (see fig. 2 in Calambokidis & Barlow, 2004). Average annual effort ranged from 30 to 100 days predominantly between June and October. Survey areas were selected to maximize the number of encounters, while attempting to maintain coverage of a broad temporal and geographic range along the USWC (Calambokidis, Barlow, et al., 2009; Sears et al., 2013). The CRC catalog also included some

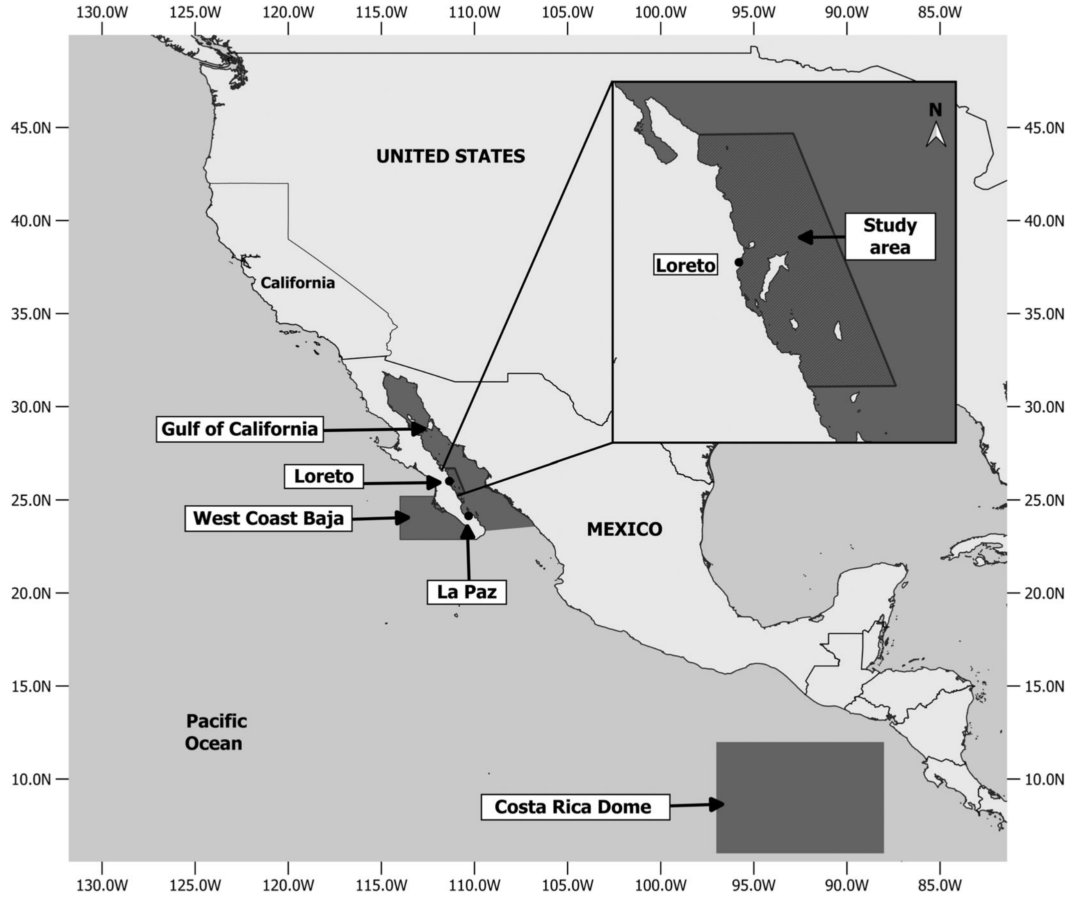

FIGURE 1 Map of the GoC study area centered around Loreto, Baja California, Mexico. Dark gray highlighted boxes represent areas for which environmental data were extracted (see section 2.3).

opportunistic images shared by third parties (Sears et al., 2013). CRC followed a similar procedure to MICS for matching and cataloging whales. For this study, as many individuals as possible were matched between the two catalogs. For whales that were matched, observations from the USWC of whales that were also seen in the GoC were included in the survival analysis.

2.3 | Environmental data

To explore whether any variability in estimates of survival rate or abundance in the GoC could be explained by features of the environment, data on variables that are known to be indicative of productivity were used (Mercado-Santana et al., 2017). Migratory plasticity has been demonstrated across the three known ENP wintering areas (GoC, WCB, and CRD), so data from all three areas were included. Data for the study area and for the rest of the GoC were included separately to allow investigation of how well variation in survival and abundance is explained by environmental conditions in waters of the GoC either inside or outside the study area.

Sea surface temperature (SST) can be indicative of productive waters (Chenillat et al., 2013; García-Morales et al., 2017). Based on Stafford et al. (2009) a lag of 1 month for SST to impact baleen whale presence was assumed. Peak blue whale abundance in the GoC is from February to March, so only data from January were used. SST data were extracted from the National Oceanic and Atmospheric Administration (NOAA) daily Optimum Interpolation Sea Surface Temperature (OISST) data set (Liu et al., 2021) at a resolution of 0.25°. Values within each of the areas (see Figure 1) were extracted for the complete study period of 1984 to 2020. Locations of the CRD and WCB areas were based on historical blue whale sightings (Etnoyer et al., 2006; Fiedler, 2002; Gendron, 2002). Values were averaged to give a single daily value for each area. Daily values were then averaged again to generate a single value for January in each year. Variability in SST within each year was calculated as the standard deviation of the daily values in January.

The longest direct primary productivity data set available was that from the European Space Agency Ocean Colour Climate Change Initiative, which was available from 1998 to 2020. Chl *a* (mg/m^3) data were extracted from the monthly v5.0 data set (Sathyendranath et al., 2019). As for SST, data were extracted for the defined study area, the rest of the GoC, CRD, and WCB areas based on a resolution of 0.042° and then averaged to generate a single monthly value for each area for January in each year.

Fluctuations in conditions in the Pacific Ocean caused by the El Niño-Southern Oscillation climate pattern were also explored. Oceanic Niño Index (ONI) data were extracted from the R package "rsoi" (Albers, 2022). The ONI represents temperature anomalies by comparing sea surface temperatures in the east-central tropical Pacific to an average. The index is based on three month rolling averages, and the annual January to March data point was taken as the index value for each year.

2.4 | Estimation of survival

Cormack-Jolly-Seber (CJS) mark-recapture models were used to estimate apparent survival rate from annual capture histories of uniquely identifiable individuals (Amstrup et al., 2010). Survival is defined as apparent because permanent emigration cannot be distinguished from death without additional information. The goodness of fit (GoF) of the CJS model was first evaluated using R (R Core Team, 2020) package "R2ucare" (Gimenez et al., 2017). Two component tests are particularly pertinent. Test 3.SR explores whether animals marked for the first time have the same probability of being captured as previously encountered individuals. Lack of fit in this test is known as a transience effect. Test 2.CT explores if recapture probability in the current sampling occasion is affected by whether an animal was captured or not during the previous sampling occasion (Gimenez et al., 2017). Lack of fit in this test is known as a trap dependence effect.

Survival analysis was carried out on the full data set from 1984 to 2020 with sightings of GoC blue whales from both the GoC and USWC using software MARK (White & Burnham, 1999) through interface RMark (Laake, 2013) in R (R Core Team, 2020). Using model notation after Lebreton et al. (1992), annual survival probability φ and annual recapture probability p were modeled as constant (.), varying annually over time (t), or varying as a linear temporal trend (T). In addition, because field effort from 2012 onwards was higher and more consistent than previous years, p was modeled as varying between, but constant within, the periods 1984–2011 and 2012–2020, denoted as period (pr). Survival was also estimated for this latter period (2012–2020) as part of the Robust Design model analysis (see below).

In this data set, tests 3.SR and 2.CT both showed significant lack of fit (Test 3.SR $\chi^2 = 256.77$, $df = 29$, $p < .001$; Test 2.CT $\chi^2 = 110.37$, $df = 34$, $p < .001$); therefore the CJS models were developed further to account for the sources of this lack of fit. For the transience effect, survival was modeled as two time-since-marking "transience classes" (tr), one for the year after first capture and a second for all subsequent years (Pradel et al., 1997). The survival estimate for the second transience class can be considered as unbiased in relation to transience (Pradel et al., 1997). For the trap dependency effect (td), recapture probabilities varied based on whether or not the animal had been captured in the previous year, modeled as an individual time varying covariate (Huggins, 1989; Schleimer et al., 2019). Models allowed for interactive (*) and additive (+) effects of parameters.

Model selection was based on the small sample modification of Akaike's information criterion (AIC$_c$; Akaike, 1973). A variance inflation factor ($\hat{c}$) was calculated as total GoF χ^2 degrees of freedom but because both trap dependence and transience effects were included in the models, the overall χ^2 did not include the 2.CT and 3.SR components (Fletcher et al., 2012; Gimenez et al., 2018). This overall χ^2 test indicated some lack of fit ($\chi^2 = 140.33$, $df = 109$, $p = .02$; $\hat{c} = 1.29$), so AIC$_c$ values were adjusted to quasi-AIC$_c$ (QAIC$_c$). Models with a ΔQAIC$_c$ < 10 when compared to the lowest QAIC$_c$ model were considered to have some support from the data (Burnham & Anderson, 2002) and were used to generate model-averaged survival estimates.

CJS models were also run to explore the influence of the environmental covariates on survival. The additional variables of SST mean and standard deviation for all areas (study area, CRD, WCB and rest of the GoC) and the ONI index were included in the models as annually varying covariates influencing survival. Additionally, models were run over a shorter period (1998–2020) to allow inclusion of mean chl *a* for all areas as annually varying covariates.

2.5 | Estimation of abundance

Robust Design models, which combine open population models for primary sampling occasions (here years) with closed population models for secondary sampling occasions (here periods within a research season) were used to estimate annual abundance (Kendall et al., 1997). An important assumption of these models is that the whole study area is surveyed in every secondary sampling occasion. This could only be verified for the GoC data from 2012 onwards where the complete study area was surveyed every 14 days. Consequently, the annual primary sampling occasions were split into as many periods as possible with a minimum length of 14 days (Table 1). Only data collected in the GoC were included in this analysis so that estimates of abundance refer only to this area. Robust Design models also allowed for a second estimation of survival over this shorter time period.

Base model parameters included probability of capture/recapture (assumed equal) (*p*), probability of survival (φ), and the number of animals never seen (*f*0) from which annual abundance in the study area is derived. Capture/recapture probability (*p*) could be constant (.), vary by year (*t*) or vary both by year and secondary sampling occasion (*t*:*s*). Survival probability (φ) could be constant (.), vary by time (*t*) or as a linear trend over time (*T*). No goodness of fit tests are available for Robust Design models but because test 3.SR for the CJS model was significant, survival probability (φ) was also allowed to vary by “transience class” (*tr*).

Robust Design models also included parameters representing temporary immigration/emigration of animals into and out of the study area between years. γ''_i is the probability that an animal is not present in the study area in year *i* given it was present in year $i - 1$ (i.e., the probability of temporary emigration), and γ'_i is the probability that an animal is not present in year given it was also not present in year $i - 1$ (i.e. $1 - \gamma'_i$ is the probability of temporary immigration) (see, e.g., Arso Civil et al., 2019; Smith et al., 2013). These gamma parameters can be defined as no movement ($\gamma'' = 0$; $\gamma' = 1$), random movement ($\gamma'' = \gamma'$) or Markovian (nonrandom) movement ($\gamma'' \neq \gamma'$). Model selection was based on AIC$_c$ and results of models with some support (ΔAIC$_c$ < 10) were used to generate model-averaged estimates of survival rate and abundance.

2.6 | Modeling the influence of environmental covariates on abundance

To explore the influence of environmental covariates on the number of animals present in the GoC, linear models were fitted to annual abundance estimates from the Robust Design models with the environmental covariates as explanatory variables. In addition to the previously described covariates, the percentage difference in the annual value between the study area, WCB, CRD and rest of the GoC were included for both mean SST and chl *a* to investigate whether variation in annual

TABLE 1 Primary and secondary sampling occasions applied in Robust Design models to GoC blue whale sightings data.

Primary sampling occasions (*t*)	2012	2013	2014	2015	2016	2017	2018	2019	2020
Number of secondary sampling occasions (*s*)	2	3	2	2	3	3	3	2	2

abundance in the GoC could be related to the difference between wintering areas or within the GoC. The abundance estimates were logged to meet the model assumption of normality. Due to the relatively small number of abundance data points (nine) we fitted single covariate models to avoid overfitting. Models were compared using AIC (Akaike, 1973).

3 | RESULTS

3.1 | CJS estimates of apparent survival rate: 1984–2020

A total of 453 individual blue whales sighted in the GoC formed the basis of this analysis to estimate apparent survival rate. Of these whales, 140 were reconciled with the CRC USWC catalog; thus, data from the USWC were also included for these individuals. Over the 37-year period, 55% of individuals were only sighted once while some individuals were recaptured on many occasions, the most frequent being captured in 22 different years (Figure 2).

Six models had some support from the data (Table 2), all of which included survival probability varying as a linear temporal time trend and by transient class as either an additive or interactive effect, and recapture probability varying by trap dependence alone or with period as either an additive or interactive effect.

Model-averaged results showed that estimated recapture probability was markedly different between 1985 and 2011 (mean $p = .260$; ranging from 0.253 to 0.269) and 2012–2020 (mean $p = .335$; ranging from 0.328 to 0.340). Estimated nontransient apparent survival probability declined over time from 0.991, 95% [CI 0.977, 0.99] in 1985 to 0.889, 95% CI [0.807, 0.939] in 2019 (Figure 3). The greater uncertainty in the estimates in the latter part of the time series and the possibility of negative terminal bias can compromise interpretation of a decline in the most recent years (Peñaloza et al., 2014). Terminal bias in the estimates was explored following Langtimm (2009) and Schleimer et al. (2019) by running CJS models with time-varying survival on three data sets with periods successively truncated by 5 years. Results showed that survival probability in the final year of each period did not drop in comparison to previous years, indicating no evidence of terminal bias. Models with SST, chl *a* and El Niño as covariates had no support ($\Delta QAIC_c > 10$).

3.2 | Robust Design models: estimates of temporary emigration/immigration and apparent survival 2012–2020

Robust Design models were fitted to the capture histories of 150 individual whales sighted in the GoC from 2012 to 2020. Thirteen models had some support from the data (Table 3). All these models included capture probability

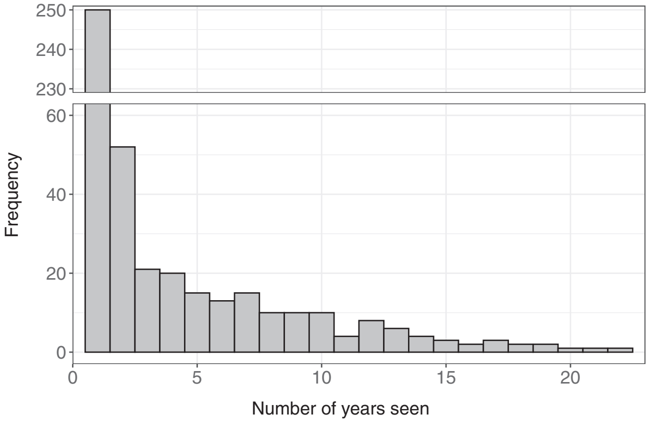

FIGURE 2 Frequency of annual captures of GoC blue whales from data in the GoC and USWC from 1984 to 2020.

TABLE 2 Summary of CJS models with $\Delta QAIC_c < 10$ fitted to GoC blue whales sighted in the GoC and USWC from 1984 to 2020.

Model description	No. of parameters	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
$\varphi_{(T+tr)}\ p_{(td+pr)}$	6	1,834.28	0.00	0.38
$\varphi_{(T^*tr)}\ p_{(td+pr)}$	7	1,835.15	0.87	0.25
$\varphi_{(T+tr)}\ p_{(td^*pr)}$	7	1,835.86	1.58	0.17
$\varphi_{(T^*tr)}\ p_{(td^*pr)}$	8	1,836.84	2.56	0.11
$\varphi_{(T+tr)}\ p_{(td)}$	5	1,837.78	3.49	0.07
$\varphi_{(T^*tr)}\ p_{(td)}$	6	1,839.29	5.01	0.03

Note: φ: apparent survival probability, *p*: recapture probability, *T*: linear temporal trend, *tr*: transience class, *td*: trap dependence, *pr*: periods 1984–2011 and 2012–2020, +: additive effect, *: interactive effect.

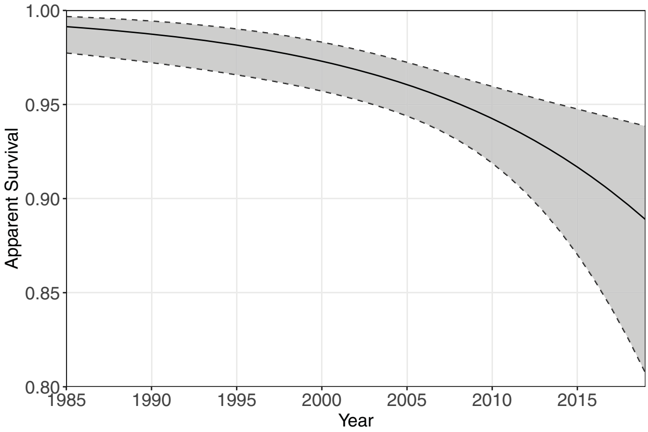

FIGURE 3 Long-term apparent survival of GoC blue whales from CJS models. The shaded gray area represents 95% CIs.

varying by both primary and secondary occasions. Over half of the models, including the top six models with 95% of the AICc weight, included transience class. Markovian temporary emigration was included in 62% of models but they only represented 50% of the AICc weight suggesting equal support for Markovian movement and random movement, which both varied by time in most models. Model-averaged estimates of γ'' (the probability of temporary emigration) ranged from 0.08, 95% CI [0.00, 0.94] to 0.68, 95% CI [0.44, 0.85]. Estimates of γ' ranged from 0.34, 95% CI [0.10, 0.70] to 0.76, 95% CI [0.18, 0.98], meaning that the probability of immigration ($1 - \gamma'$) ranged from 0.24 to 0.66, indicating similar average probabilities of temporary emigration (0.39) and temporary immigration (0.34). Model-averaged apparent survival varied little across the study period, averaging 0.84, 95% CI [0.68, 0.93].

3.3 | Robust Design estimates of abundance 2012–2020

Model-averaged estimates of annual abundance from the Robust Design models showed a declining trend in the number of blue whales present in the study area over the study period (Figure 4). The largest estimate was in

TABLE 3 Summary of robust design models with $\Delta AIC_c < 10$ fitted to data on blue whales sighted in the GoC from 2012 to 2020.

Model description	No. of parameters	AICc	ΔAICc	AICc weight
$\varphi_{(tr)}\ p_{(t:s)}\ \gamma''_{(t)} = \gamma'_{(t)}$	42	18.12	0.00	0.35
$\varphi_{(tr)}\ p_{(t:s)}\ \gamma''_{(t)} \neq \gamma'_{(t)}$	50	18.17	0.04	0.34
$\varphi_{(tr+T)}\ p_{(t:s)}\ \gamma''_{(t)} = \gamma'_{(t)}$	43	20.59	2.46	0.10
$\varphi_{(tr+T)}\ p_{(t:s)}\ \gamma''_{(t)} \neq \gamma'_{(t)}$	51	20.79	2.67	0.09
$\varphi_{(tr^{*}T)}\ p_{(t:s)}\ \gamma''_{(t)} = \gamma'_{(t)}$	44	23.12	4.99	0.03
$\varphi_{(tr^{*}T)}\ p_{(t:s)}\ \gamma''_{(t)} \neq \gamma'_{(t)}$	52	23.47	5.35	0.02
$\varphi_{(.)}\ p_{(t:s)}\ \gamma''_{(t)} \neq \gamma'_{(t)}$	49	24.21	6.08	0.02
$\varphi_{(tr)}\ p_{(t:s)}\ \gamma''_{(.)} \neq \gamma'_{(.)}$	36	24.74	6.62	0.01
$\varphi_{(tr+T)}\ p_{(t:s)}\ \gamma''_{(.)} \neq \gamma'_{(.)}$	37	25.77	7.65	0.01
$\varphi_{(T)}\ p_{(t:s)}\ \gamma''_{(t)} \neq \gamma'_{(t)}$	50	26.61	8.49	0.01
$\varphi_{(T)}\ p_{(t:s)}\ \gamma''_{(t)} = \gamma'_{(t)}$	42	26.93	8.81	0.00
$\varphi_{(.)}\ p_{(t:s)}\ \gamma''_{(t)} = \gamma'_{(t)}$	41	27.10	8.97	0.00
$\varphi_{(tr^{*}T)}\ p_{(t:s)}\ \gamma''_{(.)} \neq \gamma'_{(.)}$	38	27.21	9.09	0.00

Note: φ: apparent survival probability, p: capture/recapture probability, tr: transience class, T: linear temporal trend, (.): constant, t: varying by time (primary sampling occasion), t:s: varying by both primary and secondary sampling occasions, $\gamma'' \neq \gamma'$: Markovian temporary emigration, $\gamma'' = \gamma'$: random temporary emigration.

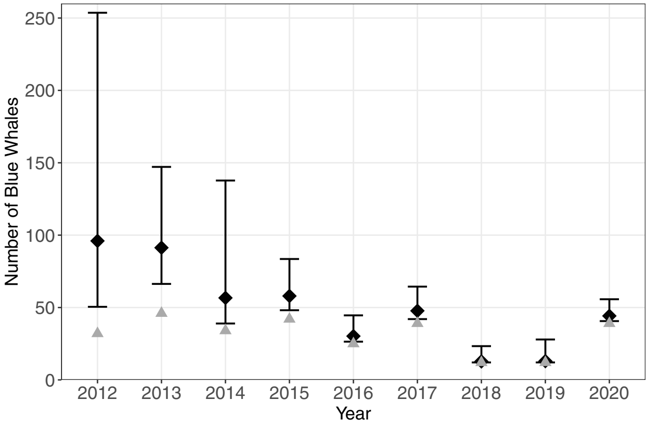

FIGURE 4 Annual estimates of blue whale abundance (black diamonds) and 95% log-normal confidence intervals (CIs) in the GoC study area from 2012 to 2020. Gray triangles represent the actual number of individual blue whales seen each year.

2012 at 96 whales, 95% CI [50, 254] and the lowest were in 2018 and 2019 at 13 whales, 95% CIs [12, 23 and 12, 28] respectively. The uncertainty in the estimates was much greater from 2012 to 2014, which was driven by lower capture probabilities during these years.

3.4 | Influence of environmental covariates on abundance

Four models had more support than a null model (Table 4). The most supported model included the covariate that described the difference in mean SST between the study area and CRD; it was significant at close to the 1% level ($p = .01$). This was

TABLE 4 Summary of environmental single covariate models which fitted the data better than the null model (A ~ 1).

Model description	AIC	ΔAIC	AIC weight	Covariate *p* value	% Deviance explained
A ~ mean SST SA vs. CRD	21.69	0.00	0.51	0.01	59.75
A ~ mean SST SA	23.86	2.17	0.17	0.04	48.77
A ~ mean SST rest of GoC vs. SA	24.37	2.68	0.13	0.05	45.78
A ~ mean SST WCB	24.95	3.26	0.10	0.06	42.16
A ~ 1	25.08	3.39	0.09	—	—

Note: Abundance (*A*), study area (*SA*), Costa Rica Dome (*CRD*), Gulf of California (*GoC*), West coast of Baja California (*WCB*).

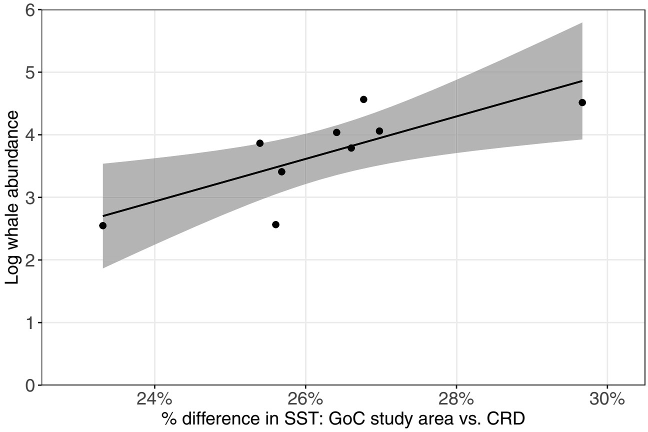

FIGURE 5 Relationship between log blue whale abundance and the percentage difference in mean SST between the study area and CRD (with higher temperatures in the CRD). The shaded gray area represents 95% CIs.

the most significant covariate in the model set with the next closest being mean SST in the study area ($p = .04$). The most supported model explained 59.75% of the deviance in the data, over 10% more than any other model and the model residuals showed no obvious patten. The second-best supported model had a ΔAIC of 2.17 suggesting support was not equivalent, additionally, it had only a third of the AIC weight when compared to the best model (0.17 vs. 0.51).

The most supported model indicated that as temperature difference between the two areas increased, abundance of animals in the GoC also increased (Figure 5). January SSTs in the study area were on average 26% lower than in the CRD during the period 2012–2020. SST has been increasing in both areas but the difference between them has concurrently declined. These results suggest that the decline in abundance of blue whales in the study area (Figure 4) could be related to the decline in difference in SST between these two areas.

4 | DISCUSSION

4.1 | Changing patterns in apparent survival and abundance in Gulf of California blue whales

As an established reproductive and feeding area, the Gulf of California (GoC) has been considered an important habitat for blue whales. In this study, mark-recapture models indicated a decline in both apparent survival and the number of blue whales in the study area, particularly in the latter half of the study period. Long term apparent survival estimated using CJS models declined over time from 0.991, 95% CI [0.977, 0.997] in 1985 to 0.889, 95% CI [0.807, 0.939] in 2019. Using Robust Design models for the most recent period (2012–2020), apparent survival was estimated to be constant at 0.84, 95% CI [0.68, 0.93], the lower end of the CJS model trend. Taken together, these results indicate that apparent survival has declined since 1985 but has now plateaued. Previous estimates of survival did not include any information on time trend (Ugalde De La Cruz, 2008, 2015). Abundance estimates in the study area also indicated a downward trend from 96 whales, 95% CI [50, 254] in 2012 to 13 whales, 95% CIs [12, 23 and 12, 28] in 2018 and 2019, respectively. Collectively, these results suggest that in the last decade this historically high-use area in the GoC may have had reduced importance as a blue whale habitat.

Over the past 30 years, abundance in the broader ENP population has been slowly increasing, with the highest estimates in the last decade (Calambokidis & Barlow, 2020). Some uncertainty remains because mark-recapture methods indicate a slowly increasing trend while species distribution modeling estimates much lower estimates with declining trend (Becker et al., 2020; Calambokidis & Barlow, 2020). However, line-transect methods would not capture shifts in distribution outside of the survey area so this could explain the diverging trends in the two methods (Becker et al., 2020; Calambokidis & Barlow, 2020). If the broader ENP population is stable, the decline in the GoC is likely to reflect a decline in the number of animals returning to this area, which would manifest as permanent emigration in estimates of apparent survival rate which is supported by lower-than-expected estimates in this study. Large whale species are long-lived and have high natural survival rates (e.g., Bradford et al., 2006; Ramp et al., 2010, 2014; Zeh et al., 2002). Our estimate of survival in the GoC in 2012–2020 of 0.84, 95% CI [0.68, 0.93] is too low to represent natural mortality alone for blue whales; much higher estimates would be expected (e.g., Ramp et al., 2006). A decline in abundance could also result from temporary emigration away from the study area. However, the Robust Design models estimated that the probability of temporary emigration was only slightly greater than the probability of reimmigration (0.39 vs. 0.34) so this is unlikely to be a major driver of the observed decline in numbers of blue whales in the study area.

Therefore, we conclude that blue whales are returning less frequently to the area around Loreto Bay in the GoC and that fewer whales are using this area in the last decade than over previous decades. To support their large body size, blue whales must seek out dense prey patches to meet their extreme calorific needs (Goldbogen et al., 2011) and migrations are therefore likely to be directed to high productivity areas (Branch, Abubaker, et al., 2007; Reilly & Thayer, 1990). If productivity (and hence blue whale prey) in the study area has declined in recent years, it could explain this trend of movement away from the area, with whales instead migrating to other areas within the GoC or more broadly within their wintering range. Alternatively, or in addition, productivity in other areas may have increased.

4.2 | Influence of the changing environment

Productivity is generally linked to cooler water temperatures, which drive upwellings providing nutrients that generate productivity at the lower trophic levels (Bond et al., 2015; García-Morales et al., 2017; Páez-Osuna et al., 2016; Sarmiento et al., 2004). The GoC has undergone a sustained period of warming since the late 1980s, which has been linked to a 65% decline in the population of another top marine predator, the California sea lion (*Zalophus californianus*; Adame et al., 2020). Additionally, baleen whale presence in the GoC has been correlated to colder SST periods (García-Morales et al., 2017).

We found no evidence that apparent survival of blue whales was influenced by SST or Chl *a*, but in simple models relating abundance in the study area to a range of environmental covariates we found most support for a relationship between estimated abundance in the GoC and the percentage difference in SST between the study area and CRD. This model indicated that abundance decreased as the difference between mean SST in the study area and CRD decreased, providing some evidence that the winter distribution of the ENP population could be influenced by SST differences within its range (Figure 5). Models relating estimated abundance to environmental covariates in other areas outside the study area, including the rest of the GoC, had some but much less support, suggesting that these were less likely scenarios. However, especially because of the limited number of abundance estimates available for analysis, it is not possible to make any stronger inferences.

These findings are consistent with previous evidence that blue whales in the ENP are responsive to SST and that it could be driving key behaviors including migration and foraging (Etnoyer et al., 2006; Szesciorka et al., 2020). This could also offer an explanation as to why some blue whales in the ENP demonstrate migratory plasticity between wintering areas (Busquets-Vass et al., 2017, 2020).

4.3 | Future prospects of the ENP blue whale population and further study needed

Assuming abundance in the ENP population is stable, a trend in apparent survival in recent years would not be expected. Further analysis to estimate survival over the full range of the ENP population would enable comparison to the estimates from the GoC, which may provide evidence of movement within the population rather than an actual decline in survival. If so, this would suggest that to date blue whales have been adaptable to changing conditions.

In the Eastern Pacific Ocean, other marine top predators have shown shifts in their distribution and behavior in response to environmental changes (Becker et al., 2019; Benson et al., 2002; Hazen et al., 2013, Ransome et al., 2024). As well as a shift away from the GoC in winter, ENP blue whales have expanded further north in summer, which could also be a response to changing prey availability (Calambokidis, Barlow, et al., 2009). Continued monitoring of population dynamics through photo-identification should be integrated with studies of individuals using other techniques (e.g., tagging and isotope analysis; Busquets-Vass et al., 2017, 2020) to investigate changes in individual movements and population distribution. Collecting additional data in the CRD would be valuable to inform whether the whales that apparently left the GoC study area are using these waters instead. Most of our knowledge about blue whales in the CRD comes from satellite tag data which demonstrate whales traveling to this area to feed (Bailey et al., 2009; Mate et al., 1999). Eleven blue whales were identified in the CRD in 2014, but none of these whales had a known match to the MICS GoC catalog.

As increased environmental variation is predicted with the changing climate, continued monitoring of the GoC will be informative of the permanence of this observed shift of blue whales away from this historical area of concentration within the GoC. While the number of whales using the study area was particularly low in 2018 and 2019, it was markedly higher in 2020 (Figure 4). Blue whales have demonstrated their plasticity in migration patterns (Busquets-Vass et al., 2017, 2020) so changes in prey availability across their range would be expected to create variation in habitat use and consequently, changes in the relative importance particular areas.

Blue whales forage almost exclusively on krill, which could limit their adaptability (Slijper, 1979). Other species of baleen whale can switch prey to small fish which can be more abundant in warmer SSTs (Fleming et al., 2016; Slijper, 1979). If krill resources become scarcer in future with warmer temperatures, limited food resources could reduce the carrying capacity of the ENP blue whale population. Consequently, monitoring krill availability could be key to understanding any changes in movements and distribution.

While ENP blue whales face challenges from the changing climate, they are also subject to more direct anthropogenic pressures, specifically ship strikes (Berman-Kowalewski et al., 2010; Cotton Rockwood et al., 2018; Lazcano-Pacheco et al., 2022). Numbers of deaths due to ship strikes are believed to be substantially underreported, with detection rates estimated to vary from <1% to 17% (Carretta et al., 2020). While, to date, overall population numbers appear not to have been affected (Monnahan et al., 2015), this may be masked by uncertainty in the abundance estimates (Cotton Rockwood et al., 2018), providing further motivation for a better understanding of population numbers and dynamics in ENP blue whales.

This study provides new insights into the component of the ENP blue whale population that frequents the GoC. The apparently reduced importance of this area indicates shifting patterns in the broader population and raises questions about its future in the face of a changing climate, potentially limited resources, and other anthropogenic pressures. This study estimated survival and abundance from data on individuals that had been observed in the study site in the Gulf of California, an unknown proportion of the Eastern North Pacific population. For abundance, the data were limited to a period of 9 years. A broader population dynamics study that covers the whole range and estimates reproductive parameters as well as survival over a longer timeframe would be necessary to further improve our understanding of how this population is responding to these pressures and to identify current and new habitats of the ENP blue whale population.

ACKNOWLEDGMENTS

We thank everyone involved in collecting blue whale photo-identification images in the Gulf of California from both the Mingan Island Cetacean Study and the Great Whale Conservancy. Data were collected under permit from Medio Ambiente, Subsecretaria de Política Ambiental y Recursos Naturales (current permit number is SPARN/DGVS/02075/23). We thank other staff, interns, and collaborators of the Mingan Island Cetacean Study who aided in obtaining, processing and matching photographs of blue whales. We are grateful to the Cascadia Research Collective for their contribution of photo-identification data to supplement the survival analysis which was collected under National Marine Fisheries Service permit (current permit number 21678-01), and everyone who aided in the processing and matching of these images. Finally, we thank three reviewers for their comments which helped to improve the manuscript.

AUTHOR CONTRIBUTIONS

Georgina Whittome: Conceptualization; data curation; formal analysis; writing – original draft; writing – review and editing. **John Calambokidis:** Data curation; writing – review and editing. **Annie B. Douglas:** Data curation; writing – review and editing. **Michael Fishbach:** Data curation; writing – review and editing. **Richard Sears:** Data curation; writing – review and editing. **Philip Hammond:** Conceptualization; formal analysis; validation; writing – review and editing.

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How to cite this article: Whittome, G., Calambokidis, J., Douglas, A. B., Fishbach, M., Sears, R., & Hammond, P. S. (2024). Changes in blue whale survival and abundance in the Gulf of California. *Marine Mammal Science*, e13132. https://doi.org/10.1111/mms.13132