

Body Condition of Eastern North Pacific Blue Whales Across a 32 Year Timespan (1991–2023)
and Links to Abundance Estimates

An Internship Report

Submitted to the Faculty
of the University of Miami,
Rosenstiel School of Marine, Atmospheric, and Earth Science
in partial fulfillment of the requirements for the
Degree of Master of Professional Science

In cooperation with
Cascadia Research Collective



Jessie Meyer
Marine Mammal Science
Department of Marine Biology and Ecology

UNIVERSITY OF MIAMI
11 December 2024

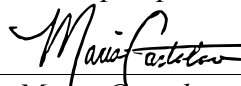
Approved:



Holli Eskelinen
Lecturer at UM Rosenstiel School of Marine, Atmospheric, and Earth Science
Committee Chair



John Calambokidis
Senior Research Biologist at Cascadia Research Collective
Internship Supervisor



Maria Carrilano
Lecturer of Marine Biology and Ecology at UM Rosenstiel School of Marine, Atmospheric, and Earth Science
Committee Member

Body Condition of Eastern North Pacific Blue Whales Across a 32 Year Timespan (1991–2023)
and Links to Abundance Estimates

Abstract of a master's degree internship report at the University of Miami, Rosenstiel School of Marine, Atmospheric, and Earth Science. Supervised by: *Dr. Holli Eskelinen, John Calambokidis, and Dr. Maria Cartalano*. Number of pages in text: 44

As a measure of health, body condition has been increasingly used to assess the impacts of environmental and physiological change on marine mammals. Such alterations can indicate widespread ecological effects in marine systems and inform the decision-making process to mitigate potential consequences to species of concern. Blue whale (*Balaenoptera musculus*) body condition in the Eastern North Pacific (ENP) has been previously assessed using 3,660 images of 1,112 individual blue whales collected by Cascadia Research Collective (CRC) from 2005–2018. This study expanded the body condition analysis previously done by adding CRC blue whale photo identification images collected in 1991, 1993, 1996 and from 2019–2023 with a focus on the relationship between body condition and population abundance estimates. 4,188 images of 1,319 individuals were grouped by year, decade, region, and season to investigate potential differences in body condition. Cumulative link mixed models (CLMMs) were used to determine the influence of reproductive class, photographic qualities, season, and environmental variables on blue whale body condition. Additionally, potential links between ENP blue whale body condition and survival were assessed using Cormack-Jolly-Seber survival models. Scoring agreement between raters of body condition was fair–good ($\kappa_w = 0.68$). Blue Whale body condition significantly varied over the study period ($\chi^2 = 615.47$, $df = 63$, $p < 2.2 \times 10^{-16}$) and with sighting season ($\chi^2 = 32.66$, $df = 12$, $p = 0.001$) showing better condition later in the year. Of the environmental drivers explored, the Habitat Compression Index (HCI) and Oceanic Niño Index (ONI) best accounted for variation in blue whale body condition. Survival estimates ranged from 0.994 (95% CI 0.971 – 0.999) in 2008 to 0.739 (95% CI 0.389 – 0.926) in 2021 with no significant correlation to annual body condition. Future work should investigate the influence of individual blue whale body condition on other measures such as reproductive output. These findings indicate the validity of this method of body condition assessment for use across multiple raters and further show the viability of body condition as an indicator of population health.

Keywords: blue whale, body condition, environmental drivers, apparent survival, modeling

Acknowledgements

I would like to thank Rachel Wachtendonk for her initial development of the scoring scheme, her guidance with the scoring criteria, and for access to her project resources; Georgina Whittome for her aid in developing the CJS models and help in results interpretation; Alexandra Vanderzee for her knowledge of the Cascadia databases; and all other Cascadia Research Collective interns, staff and collaborators who have contributed to the blue whale photo identification database. Furthermore, my committee members Dr. Holli Eskelinen, John Calambokidis and Dr. Maria Cartolano offered me invaluable assistance and feedback during the research process.

Table of Contents

1.0 Introduction	1
2.0 Materials and Methods	8
2.1 Photo Identification	8
2.2 Body Condition Scoring	8
2.3 Inter-rater Reliability	10
2.4 Body Condition Comparisons	11
2.5 Cumulative Link Mixed Modeling	12
2.6 Survival	14
3.0 Results	16
4.0 Discussion	31
5.0 Conclusions	36
6.0 References	37

List of Tables

Table 1. Definitions of body condition scores	10
Table 2. Sources and definitions of environmental indices included in CLMMs	14
Table 3. Body condition score agreement between Rater 1 (Jessie Meyer; JM) and Rater 2 (Rachel Wachtendonk; RW) for 90 randomly selected images.....	17
Table 4. All base models tested with sightings from 1991, 1993, 1996 and 2005–2023	23
Table 5. All base models tested utilizing the original dataset (2005–2018) analyzed in Wachtendonk et al. (2022).....	24
Table 6. Most parsimonious base model tested with each environmental covariate	25
Table 7. CJS models based on ENP blue whale sightings from 2005 to 2023	28

List of Figures

Figure 1. Representative images of scoring scheme visualization adopted from Wachtendonk et al. (2022)	10
Figure 2. Proportional representation of ENP blue whale (<i>Balaenoptera musculus</i>) body condition score (scale of 0 to 3) within each year from the 1990s (1991, 1993, and 1996) and every year between 2005–2023	18
Figure 3. Proportional representation of body condition score of ENP blue whales grouped by decade across the study period.....	19
Figure 4. Proportional representation of body condition score of ENP blue whales grouped by region sighted across the study period.....	20
Figure 5. Proportional representation of body condition score of ENP blue whales grouped by season (excluding data from Mexico) sighted across the study period	21
Figure 6. Mean (\pm SE) A) Habitat Compression Index (HCI) and B) Oceanic Niño Index (ONI) along the U.S West Coast from 1991–2023.....	26
Figure 7. Within-year A) apparent survival and B) recapture rate of ENP blue whales from 2006–2022 (ϕ ($\sim t + tr$) p ($\sim t * td$))	29
Figure 8. Linear regression model of apparent survival against average body condition score for ENP blue whales from 2006–2022	30
Figure 9. Proportion of ENP blue whales within each body condition score category resighted from 2010–2023.....	30

1.0 Introduction

Blue whales (*Balaenoptera musculus*) are the largest animals on Earth; however, they have and continue to face the consequences of both intentional and incidental anthropogenic impacts (NMFS, 2022). The Eastern North Pacific (ENP) stock of blue whales (*B. m. musculus*) was historically targeted by commercial whaling vessels during the 20th century, with catches estimated at 3,411 from 1905–1971 (Monnahan et al., 2014). Despite these catches, a population model predicted that the population did not drop below 460 individuals (Monnahan et al., 2015). Currently, this population of blue whales is estimated at just under 2,000 individuals with a range that extends from their northern reaches in the Gulf of Alaska to the Costa Rica Dome and the Gulf of California (Bailey et al., 2009; Calambokidis & Barlow, 2020; Calambokidis et al., 2009). Anthropogenic threats to ENP blue whales include fishing gear entanglement, vessel strikes, and habitat disturbance (e.g., noise pollution, shipping, fossil fuel extraction, and military activities) (NMFS, 2022). Blue whales are globally distributed with potentially nine distinct populations (Northeast Pacific, Southeast Pacific, Southwest Pacific, North Pacific, North Atlantic, Southern Ocean, North Indian, Southeast Indian, and Southwest Indian) identified through unique song types (McDonald et al., 2006).

Blue whale migration extents appear to vary in response to prey availability, and movements may be limited during reproduction (Bailey et al., 2009). Tagged individuals have shifted feeding north to higher latitudes (Bailey et al., 2009) in response to environmental variation, such as the 2005 warming event in the California Current (Pierce et al., 2006), that negatively impacted productivity further south in their range (Thomas & Brickley, 2006). Eastern North Pacific (ENP) blue whales have begun to expand their ranges towards the poles due to rising ocean temperatures, however, it is not known if this trend has continued (Bailey et

al., 2009; Barlow, 2016). Although ENP blue whales were calculated by one model to be at carrying capacity (Monnahan et al., 2015), the stock is considered “depleted” and “strategic” under the Marine Mammal Protection Act (MMPA) of 1972, with blue whales listed as Endangered under the U.S. Endangered Species Act throughout their range (ESA; NMFS, 2022). Additionally, human-caused mortality currently exceeds the potential for biological removal (PBR) of 4.1 whales/year at 19.5 whales/year due to fisheries and vessel strike mortality (NMFS, 2022).

Line-transect estimates of the ENP blue whale population have shown a decreasing trend since the 1990s (Becker et al., 2020), while mark-recapture estimates from photo-identification display an increasing trend (Calambokidis and Barlow, 2020). Blue whale abundance can be difficult to precisely evaluate, however, mark-recapture estimates appear to show greater sensitivity to changes in distribution (NMFS, 2022). Modification of existing shipping lanes, to reduce blue whale vessel strikes, has been recommended due to identification of preferential habitat zones (Irvine et al., 2014). To limit anthropogenic impacts to ENP blue whales, it is valuable to gain a full understanding of their population status and health.

The physiological and anatomical adaptations of marine mammals, that enable them to live in aquatic environments, also expose them to the variability and degradation of marine ecosystems (Moore, 2008). Blue whales can range up to 33m and 172 metric tons (Yochem & Leatherwood, 1985) and will selectively consume a maximum of two tons of euphausiids (krill) per day (Rice, 1978). In the Eastern North Pacific, blue whales have been documented preying upon two species of euphausiids (*Thysanoessa spinifera* and *Euphausia pacifica*) in the California Channel Islands (Fiedler et al., 1998). Additionally, blue whales in this region may utilize two different feeding strategies with more aggregated foraging around nearshore

upwelling centers and dispersed foraging around offshore areas of high productivity (Irvine et al., 2019).

Marine mammal body condition, therefore, can serve as an indicator of both individual and ecosystem health due to the innate link between top predators and environmental variability (Akmajian et al., 2021; Bradford et al., 2012; Pettis et al., 2004; Moore, 2008; Wachtendonk et al., 2022). Measures of blubber thickness and girth have been used to assess the body condition of fin (*Balaenoptera physalus*) and sei whale (*Balaenoptera borealis*) carcasses (Lockyer et al., 1985). In large whale species, health assessment scores that reflect poor body condition (e.g. low blubber thickness) may indicate compromised health (Pettis et al., 2004). Non-invasive, photographic assessments of body condition have been successfully conducted in North Atlantic right whales (*Eubalaena glacialis*; Pettis et al., 2004), gray whales (*Eschrichtus robustus*; Bradford et al., 2012), and blue whales (Wachtendonk et al., 2022). Through these investigations, the authors tracked changes in body mass recorded in the photographic record. Pettis et al. (2004) established a baseline methodology through a visual analysis of subcutaneous fat in North Atlantic right whales and monitored changes in body condition associated with the reproductive cycle. Female whales exhibited significantly lower body condition during, and post-calving compared to the year prior to calving. In gray whales, Bradford et al. (2012) utilized a similar visual analysis to track within-season changes in body condition and similarly linked body condition with reproductive class where lactating females had significantly worse body condition and calf body condition remained consistent.

These methods were further modified by Wachtendonk et al. (2022) to analyze body condition of blue whales in archival images collected by Cascadia Research Collective (CRC) from 2005 to 2018. Cascadia Research Collective is a registered non-profit, 501(c)(3)

organization based in Olympia, WA that currently focuses on marine mammal research along the West-Coast of the United States and Hawai'i (Cascadia Research Collective, 2024). Throughout the past 45 years of research, the organization has covered topics including bird and marine mammal behavior, ecology, and biology. The research goals of the institution mainly involve the use of photo-identification and telemetry techniques to track population dynamics of mysticetes (e.g. blue whales, gray whales, and humpback whales) on the U.S. West Coast and Hawaiian odontocetes (e.g. false killer whales, beaked whales). The results reported by Wachtendonk et al. (2022) showed further evidence for the correlation between body condition and reproductive cycles in mysticetes.

Following the birth of large whale species, lactation is more energetically costly than pregnancy, and calves completely depend upon this process for survival (Lockyer, 1984; Soledade Lemos et al., 2020). Lactating females have displayed poor body condition relative to their weaning calves, both in blue whales (Wachtendonk et al., 2022) and gray whales (Bradford et al., 2012). However, in some cases, lactating females may fare better than other reproductive classes (e.g. adults and juveniles) due to large fat reserves stored towards the mid-section of the body (Christiansen et al., 2021).

Due to large marine mammals' dependence on substantial energy stores (e.g., blubber), it is possible that reduced body condition could be linked to reduced survival and reproduction (Lockyer et al., 2007; Stewart et al., 2021). In gray whales, there is evidence for an association between reduced body condition, potentially due to starvation, and an unusual mortality event (UME) in 2019-2020 (Christiansen et al., 2021). Similarly, elevated mortality rates were observed in Southern Resident killer whales (SRKW; *Orcinus orca*) in poor body condition in an investigation from 2008 to 2019 (Stewart et al., 2021). Cormack-Jolly-Seber (CJS) mark-

recapture models have been used to determine apparent survival in large whales including fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence (Schleimer et al., 2019) and ENP blue whales in the Gulf of California (Whittome et al., 2024). However, to our knowledge, such estimates have not incorporated measures of body condition as covariates within models of apparent survival.

Blue whales have been shown to respond to variations in environmental factors such as sea surface temperature (SST; Whittome et al., 2024), with changes in body condition occurring in conjunction with long-term oceanographic cycles (e.g., the Pacific Decadal Oscillation) (Akmajian et al., 2021; Wachtendonk et al., 2022) and upwelling (Wachtendonk et al., 2022). Ecosystem shifts in primary production, caused by processes such as upwelling, may influence zooplankton prey dynamics that can impact the body conditions of large whales (Soledade Lemos et al., 2020). Wachtendonk et al. (2022) correlated longer upwelling seasons (and negative Pacific Decadal Oscillation) with improved body condition in blue whales. This analysis also revealed the relationship between reduced blue whale body condition and a marine heatwave in the NE Pacific from 2014–2016. Despite their enormous size, the high energetic costs of lunge-feeding during blue whale foraging dives limit dive duration and drive their feeding behavior to seek out dense accumulations of euphausiids (Acevedo-Gutiérrez et al., 2002). Additionally, blue whales may be sensitive to euphausiid population shifts because of their inability to dive for extended periods of time and relative dependence on highly productive ocean regions such as the California Current region (Acevedo-Gutiérrez et al., 2002; Croll et al., 1998). Although blue whales forage year-round, feeding is concentrated to highly productive waters of the California Current Ecosystem (CCE) from June–November (Bailey et al., 2009; Oleson et al., 2007). For large whales, prey availability and resulting alterations in body fat

accumulation may be linked to reproductive success as a function of fetal growth and calf survival (Lockyer, 1986; Lockyer, 2007). Body condition assessments may, therefore, provide insights into future population dynamics and could inform policy responses in the face of climactic shifts.

Human responses to alterations in the physical environment due to climate change are likely to impact cetaceans, including habitat loss, acoustic disturbance, and increased coastal development (Alter et al., 2010). Anthropogenic noise, including sonar and shipping traffic, can alter blue whale vocal behavior with disruptions to call production. For example, low frequency calls associated with foraging (D calls) are specifically impacted, despite the occurrence of noise disturbance at frequencies often above those utilized by blue whales (Melcón et al., 2012). Multiple cetacean species (including North Atlantic right whales) have altered their migration timing and shifted their distributions towards the poles in response to elevated sea surface temperatures, reduced sea ice extent, or a combination of both due to climate change (van Weelden et al., 2021). Similarly, ENP blue whales have appeared to demonstrate a poleward shift in their distribution (Bailey et al., 2009; Barlow, 2016). Variation in blue whale distribution is likely linked to environmental variation, as has been shown in the Gulf of California (Whittome et al., 2024).

Future policy measures for climate adaptation should include the potential for impacts on the health of cetacean populations (Alter et al., 2010). Biologically important areas (BIAs) for ENP blue whale feeding have been identified and updated with an outer shoreward boundary at 50m depth and a core boundary at 80m depth based on sighting data, satellite tag data, and line-transect model (Calambokidis et al., 2024). Changing environmental dynamics may therefore impact prey species, as reported for gray whales (Soledade Lemos et al., 2020), that could have a

cascading effect on blue whale populations. Dynamic ocean management (DOM) strategies may be utilized to plan for anomalous changes in prey distribution and habitat use of large whale species (e.g. blue whales) that can lead to greater overlap of whale habitat and areas utilized for commercial activities such as shipping (Hausner et al., 2021). While a few cetacean species may benefit from climactic shifts due to increased habitat (such as gray whales), this may lead to significant reductions in suitable habitats for other species, thus impacting their health (vanWeelden et al., 2021). To provide adequate regulatory measures to protect these sentinels of ecosystem health and prevent unintended mortality, it is important to fully understand the health of their populations (Alter et al., 2010).

Utilizing body condition, it is possible to understand the energetic demands of blue whales in the Eastern North Pacific and temporal variations in population health (Soledade Lemos et al., 2020). Wachtendonk et al. (2022) established a scoring methodology to assess body condition for blue whales following similar techniques used previously for gray whales (Bradford et al., 2012) and North Atlantic right whales (Pettis et al., 2004). This study aimed to extend the dataset on body condition scores for whales photographed between 2005–2018 by CRC to those photographed in selective years during the 1990s (1991, 1993, and 1996) and 2005–2023. The effect of body condition and links to abundance of ENP blue whales was investigated to assess the viability of this health measure as a predictor of population change. This study further aimed to explore the links between body condition and environmental indices of productivity with a broader dataset than initially utilized in Wachtendonk et al. (2022). Additionally, apparent survival was estimated for blue whales from 2005–2023 using mark-recapture methods to investigate the potential influence of body condition. Body condition was predicted to vary across years in accordance with Wachtendonk et al. (2022). Furthermore, given the seasonal

nature of blue whale feeding behavior, body condition was hypothesized to increase throughout the feeding season (June–November). Although there is some evidence for a relationship between body condition and survival in other cetaceans, body condition was not predicted to impact estimates of within-year apparent survival due to the long-lived nature of blue whales.

2.0 Materials and Methods

2.1 Photo Identification

Blue whale photographs were collected during annual photo identification efforts by CRC during 1991, 1993, and 1996 and from 2005–2023 along the West Coast of North America under NMFS permit #21678-01. This project extended the dataset of body condition scores (3,660 previously assessed images of 1,112 individual whales from 2005–2018) using methodology developed by Wachtendonk et al. (2022) with eight additional years of photo identification data (1991, 1993, 1996 & 2019–2023). Images from 1991, 1993, and 1996 were captured with a single lens reflex (SLR) camera on black and white film while images from 2005–2023 were captured in color on a digital SLR camera. Film images were viewed on a light table for inspection prior to scanning and were selectively digitized using the Nikon Super CoolScan 5000 ED at 4000 DPI. Scanned images were exported as .TIF files to maximize image quality for body condition analysis. Film photographs were scored using the same criteria as digital images. For all years, sightings without suitable photographs (e.g. only flukes visible) were not included in the analysis. This resulted in a dataset of 4583 sightings of 1376 individuals in 1991, 1993, 1996 and 2005–2023.

2.2 Body Condition Scoring

Lateral photographs were utilized for body condition scoring, with a preference for those

that displayed the most area forward of the dorsal fin. Blue whale photo ID focuses on the left and right lateral aspects of individual whales, which provides a way to measure individual body condition; this allows for analysis of archival images taken without the goal of body condition assessment. When lateral photographs are unavailable or of inadequate quality, photographs taken from behind or at a 45-degree angle to the whale will be scored as an alternative.

Following Wachtendonk et al. (2022), blue whale reproductive class was determined based on calf presence. Females photographed with a calf in a year were considered a “lactating female” for that entire year within this analysis. Similarly, calves were grouped within the “calf” reproductive class for the year they are first sighted with their mother. Individuals with unknown reproductive status were considered as “other.” Images were scored based on the body condition scoring scheme for blue whales developed by Wachtendonk et al. (2022) that was modified from methodologies established for determining the body condition of North Atlantic right whales (Pettis et al., 2004) and western gray whales (Bradford et al., 2012). Briefly, this method scores body condition on a 4-point ordinal scale from 0–3 based on the outlined criteria (Table 1). Examples of these criteria visualized in field photographs are provided in Figure 1. Photograph quality and visible proportion were also assessed using a scale from 1 (high quality/high proportion visible)–3 (low quality/low proportion visible) during image analysis. The presence of an arched back in photographs was additionally noted.

Table 1. Definitions of body condition scores.

Body Condition Score	Definition
0, Good	Rounded sides of whale and no visible vertebrae
1, Moderately good	Dorsal ridge visible with possible evidence of vertebrae
2, Moderately poor	More defined dorsal ridge and vertebrae visible
3, Poor	Clearly defined dorsal ridge and multiple vertebrae easily detectable

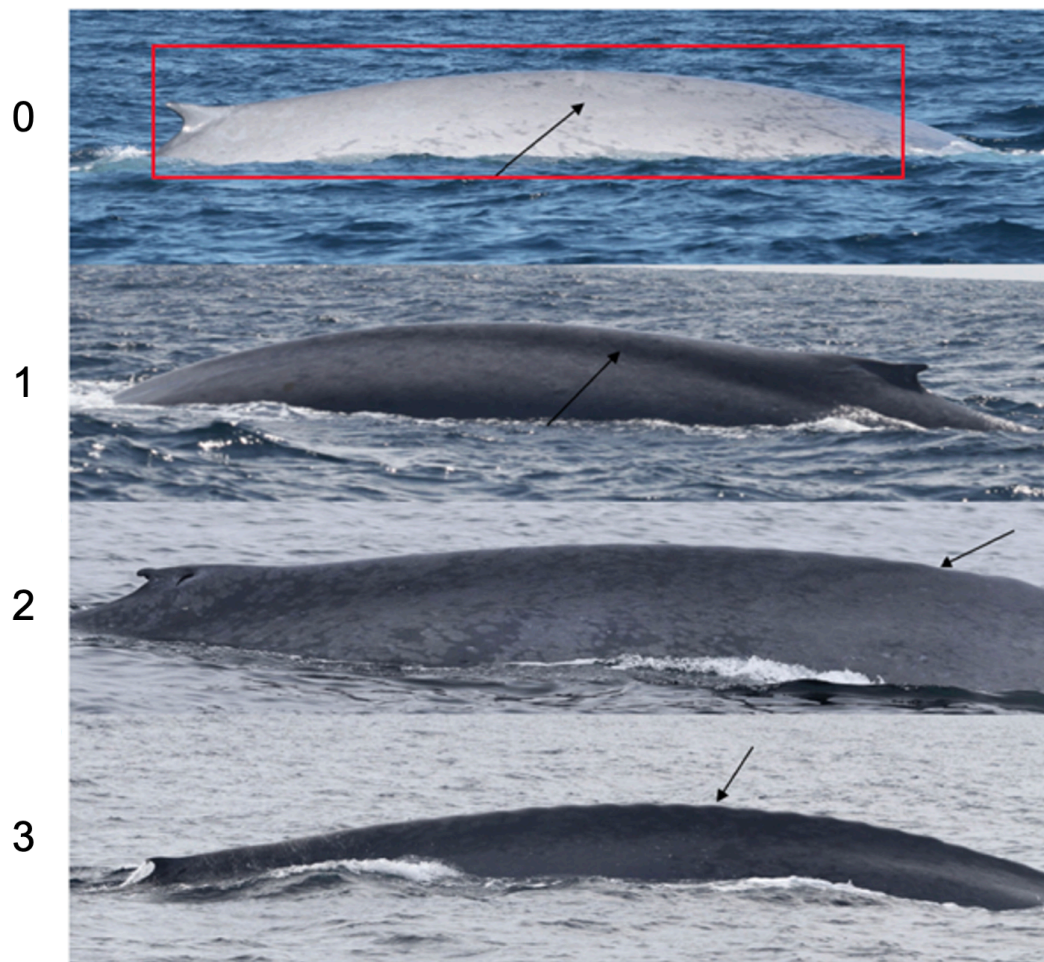


Figure 1. Representative images of scoring scheme visualization adopted from Wachtendonk et al. (2022). 0) Score 0, good body condition, clearly rounded shape. The red box represents the ideal section of the body for assessment of body condition. 1) Score 1, moderately good body condition with pronounced dorsal ridge. 2) Score 2, moderately poor body condition, evidence of vertebrae. 3) Score 3, poor body condition, clear presence of vertebrae. All images were taken by Cascadia Research Collective, NMFS Permit # 21678-01.

2.3 Inter-rater Reliability

To ensure continuity of the dataset, a 2-month training period occurred whereby body condition scores for three subsets of 10 images from the CRC blue whale database were compared between the primary analyst for this project (Jessie Meyer; JM) and the previous analyst (Rachel Wachtendonk; RW) of blue whale photographs from 2005–2018. Scores were then compared to ensure consistency in scoring methodology between raters. For the final analysis, a larger subset of images (~10% of digital and ~10% of film images) selected through proportional stratified random sampling was scored by Rater 1 (JM) and Rater 2 (RW). Three images within the subset were excluded from the analysis due to inadequate quality for scoring (90 images total). Scores were compared using weighted kappa coefficients (κ_w ; Cohen, 1968) following Bradford et al. (2012) for inter-rater reliability of ordinal measures in the software R (v4.3.3; R Core Team, 2024) using the irr package (Gamer et al., 2019). κ_w was calculated using quadratic weights to account for distances between scores. Weighted kappa statistics were interpreted following Fleiss (1981) with $\kappa_w > 0.75$ as “excellent”, $0.75 < \kappa_w < 0.40$ as “fair–good” and $\kappa_w < 0.4$ as “poor” agreement. Cohen’s kappa (κ ; Cohen, 1960) was used to test for agreement between ratings of arch presence or absence in score photographs. Cohen’s kappa statistics were interpreted as κ 0.01–0.20 (none–slight), κ 0.21–0.40 (fair), κ 0.41–0.60 (moderate), κ 0.61–0.80 (substantial), and κ 0.81–1.00 (almost perfect).

2.4 Body Condition Comparisons

Whales within each body condition score were summed and grouped by year, decade, geographic region, and season sighted. Geographic regions were binned by an internal identifier

(LocCode) based on latitude with the resulting groups of Mexico (LocCode 24–26; latitude 25–32), Southern California (LocCode 31–42; latitude 32–37), Central California (LocCode 51–59; latitude 34–39), Northern California (LocCode 61–63; latitude 39–42), Pacific Northwest (LocCode 71–75; latitude 42–47). Five seasons were defined as Early Season (January–May), June & July, August, September, and late season (October–December). These groupings were used to account for smaller sample sizes ($n < 1000$) from January–May, June–July and October–December. Data from Mexico were excluded in analyzing seasonal variation of body condition to examine individuals feeding in productive waters off the U.S. West Coast from Southern California to Washington. Chi-squared goodness of fit tests were utilized to assess the presence of statistically significant relationships between scores of year, decade, region and season groups across the study period using the software R. Images with a proportion seen or an image quality score of 3 were excluded from the final analysis due to significant differences between body condition scores when grouped by image quality ($\chi^2 = 37.85$, $df = 6$, $p = 1.2 \times 10^{-6}$) and proportion seen ($\chi^2 = 88.87$, $df = 6$, $p < 2.2 \times 10^{-16}$). 4,188 encounters of 1,319 individuals were examined as the final dataset after filtering.

2.5 Cumulative Link Mixed Modeling

Following Wachtendonk et al. (2022), cumulative linked mixed models (CLMMs) were created using the ordinal package (Christensen, 2019) in R to assess factors that may explain variations of blue whale body condition score. Components of the models investigated include RepClass (reproductive class; calf, lactating female, or other), Month (month of sighting), Month_group (season of individual sighting), BestQuality (quality of best image), and BestProp (proportion of whale seen in best image) with Year (year of sighting) and ID (identification

number of an individual) as random effects to account for pseudoreplication. We also investigated the inclusion of the following environmental covariates into a model of blue whale body condition: PDO.Value (Pacific Decadal Oscillation; average annual value), PDO (positive or negative), relative CPUE (Catch Per Unit Effort; average annual value) of krill, BEUTI (Biologically Effective Upwelling Transport Index; average annual value), Heatwave (the presence or absence of a marine heatwave from 2014–2016), HCI (Habitat Compression Index; average annual value), and ONI (Oceanic Niño Index; average annual value). This served to further explore the findings from Wachtendonk et al. (2022) that linked body condition to variations in environmental productivity and upwelling.

The PDO is the dominant pattern of SST fluctuations in the North Pacific (Mantua et al., 1997). Relative CPUE of krill serves as a proxy to krill abundance, which was used to measure the effect of prey population changes in relation to body condition. The BEUTI estimates vertical nitrate flux (i.e. upwelling of nitrates) within the water column (Jacox et al., 2018). HCI is derived from satellite observations of sea-surface temperature and outputs of ocean models describing the cool, nearshore (< 150 km from the coast) waters in the CCE (Schroeder et al., 2022). Higher HCI values represent expanded cool water habitat whereas lower HCI values indicate compressed cool water habitat (Schroeder et al., 2022). ONI, as a measure of the El Niño Southern Oscillation (ENSO), generally shows the opposite pattern from HCI with reduced upwelling occurring in the CCE during tropical El Niño years (Santora et al., 2020).

Sources of environmental indices and definitions are summarized in Table 2. Kruskal-Wallis tests were utilized to assess significant variation in each environmental covariate across the study period. This analysis utilized the Akaike's Information Criterion (AIC_c) adopted for small sample sizes (Akaike, 1973). The R package AICcmodavg (Mazerolle, 2023) was used to

create model selection tables.

Table 2. Sources and definitions of environmental indices included in CLMMs.

Index	Abbreviation	Spatial Coverage	Months Included	Source
Biologically Effective Upwelling Transport Index	BEUTI	31-39N	Jan-Dec	mjacox.com/upwelling-indices/
Catch Per Unit Effort (krill)	CPUE	32-42N	Jan	oceanview.pfeg.noaa.gov/whale_indices/
Habitat Compression Index	HCI	35-40N	Jun-Oct	oceanview.pfeg.noaa.gov/whale_indices/
Oceanic Niño Index	ONI	5N-5S	Jan-Dec	oceanview.pfeg.noaa.gov/whale_indices/
Pacific Decadal Oscillation	PDO	20-70N	Jan-Dec	ncdc.noaa.gov/teleconnections/pdo/

2.6 Survival

Apparent survival of ENP blue whales from 2005–2023 was estimated using Cormack-Jolly-Seber (CJS) open mark-recapture models in R based on annual capture histories. Methodology for the CJS analysis was modified from Schleimer et al. (2019). Prior to model fitting, goodness-of-fit component tests were performed on the dataset using the R package R2UCARE (Gimenez et al., 2017). The software MARK (White & Burnham, 1999) was utilized to run the CJS models through the RMark interface (Laake, 2013) in R.

First, the Overall_CJS test indicated a lack of fit ($\chi^2 = 245.42$, $df = 106$, $p = 0$). Second, the 2.CT test ($\chi^2 = 75.37$, $df = 16$, $p = 0.000$) also indicated a lack of fit. The probability of recapture (p) was allowed to differ as a constant (\cdot), which varied by annual sampling occasion (t) and was modeled to account for the lack of fit with the 2.CT test. A lack of fit with test 3.SR test ($\chi^2 = 72.51$, $df = 17$, $p = 0.000$) was accounted for by modeling survival as two “transience”

class (*tr*). The 2.CL test ($\chi^2 = 80.02$, $df = 43$, $p = 0.001$) additionally indicated a lack of fit while the 3.SM test ($\chi^2 = 17.52$, $df = 30$, $p = 0.966$) did not. However, a lack of fit for either the 2.CL or 3.SM necessitates accounting for overdispersion within the model. Trap dependence effect (*td*) was modeled as an individual time varying covariate; recapture probabilities can vary based on if an individual has been sighted (“captured”) within in a prior year.

Annual survival probability (ϕ) was modeled as a constant (\cdot), which varied by annual sampling occasion (*t*). Yearly average body condition score (*score*) of ENP blue whales was included as a covariate. Since average scores were an annual value, *t* and *score* were not included within the same model. Models allowed additive (+) and interactive (*) effects. The Akaike’s Information Criterion (AIC_c) adopted for small sample sizes was used, similar to the CLMMs (Akaike, 1973). Lastly, an overall χ^2 was adjusted to remove the 2.CT and 3.SR tests after modelling the trap dependence and transience effects. Thereby, a variance inflation factor (\hat{c}) was calculated (as total GoF χ^2 /degrees of freedom) which indicated a lack of fit ($\chi^2 = 97.54$, $df = 73$, $p = 0.03$; $\hat{c} = 1.34$). Accordingly, AIC_c were adjusted to quasi- AIC_c ($QAIC_c$).

In addition, resighting rates were used to determine if blue whales were more or less likely to be resighted as a function of their body condition. The last known sighting of an individual whale, with an associated body condition score, from 1991-2009 was utilized for this analysis. Years after 1996 (2005-2009) were included to account for the small sample sizes of whales in poor or moderately poor body condition during years in the 1990s. The “recapture” period was defined as 2010-2023. Lactating females were excluded due to the previously reported energetic expenditure of lactation and resulting impacts to blue whale body condition (Wachtendonk et al., 2022).

3.0 Results

There were a total of 4,188 images of 1,319 individual blue whales collected over 22 years of small boat operations that were scored for this analysis. Blue whale sightings were classified by reproductive class of the individual with 85 as “lactating female”, 60 as “calf”, and 4,043 as “other”. Across the dataset 35.1% of whales were in good body condition (score 0), 33.1% were in moderately good body condition (score 1), 18.5% were in moderately poor body condition (score 2), and 13.3% were in poor body condition (score 3).

Inter-rater Reliability

There was fair–good agreement between raters of body condition score (Table 3; $\kappa_w = 0.68$) for 90 images of blue whales utilized in the final analysis. The percentage agreement between Rater 1 (Jessie Meyer; JM) and Rater 2 (Rachel Wachtendonk; RW) was 63.33%. Investigating this further there was better agreement among scores of 0 & 1 ($\kappa_w = 0.42$) compared to scores of 2 & 3 ($\kappa_w = 0.26$). When accounting for photograph type (e.g., film or digital), there was higher agreement ($\kappa_w = 0.69$) in scores for the digital years (2005–2023) than the film years (1991, 1993, and 1996; $\kappa_w = 0.60$). For the additional components of image analysis, there was fair–good agreement between raters for proportion seen score ($\kappa_w = 0.67$) and image quality score ($\kappa_w = 0.65$). Raters consistently scored the presence of an arched back within the photograph with almost perfect agreement ($\kappa = 0.82$). Lastly, when removing images given proportion seen or quality scores of 3 by JM, there was fair–good agreement ($\kappa_w = 0.63$). There was similar agreement when filtering out images given proportion seen or quality scores of 3 by RW ($\kappa_w = 0.60$).

Table 3. Body condition score agreement between Rater 1 (Jessie Meyer; JM) and Rater 2 (Rachel Wachtendonk; RW) for 90 randomly selected images.

	Rater 1		Rater 2		Total
	0	1	2	3	
0	29	12	0	0	41
1	9	23	0	0	32
2	1	7	4	1	13
3	0	0	3	1	4
Total	39	42	7	2	90

Body Condition Across Time

The mean (\pm SE) number of sightings in each year was 190.36 (\pm 25.53). The lowest number of sightings occurred in 2022 (Figure 2; $n = 46$) while the highest number of sightings occurred in 2010 (Figure 2; $n = 415$). Within each decade, there was a mean (\pm SE) number of sightings of 1047 (\pm 481.03) with the highest number of sightings in the 2010s (Figure 3; $n = 2383$) and the lowest number of sightings in the 2020s (Figure 3; $n = 340$). Body condition scores varied significantly with year (Figure 2; $\chi^2 = 615.47$, $df = 63$, $p < 2.2 \times 10^{-16}$) and decade (Figure 3; $\chi^2 = 201.07$, $df = 9$, $p < 2.2 \times 10^{-16}$). The proportion of whales in good body condition (score 0) varied widely from a low of 13.5% in 2017 to a high of 66.8% in 1996; the proportion of whales in poor body condition (score 3) also varied from 0.5% in 1996 to 21% in 2015. Over 50% of whales in 2015 (during a marine heatwave) & in 2017 (post marine heatwave) were in poor (score 3) and moderately poor (score 2) body condition.

The percentage of whales in good body condition (score 0) exceeded 50% in 1993, 1996, and 2010. Accordingly, whales in the 1990s were more likely to be in good body condition (58.5% score 0) than whales in 2000s (36.7% score 0), 2010s (32.4 % score 0), and 2020s (25.3% score 0). Furthermore, whales in the 2010s had a higher probability of being in poor

body condition (17.4% score 3) than in the 1990s (0.8% score 3), 2000s (10.6% score 3), and 2020s (6.5% score 3).

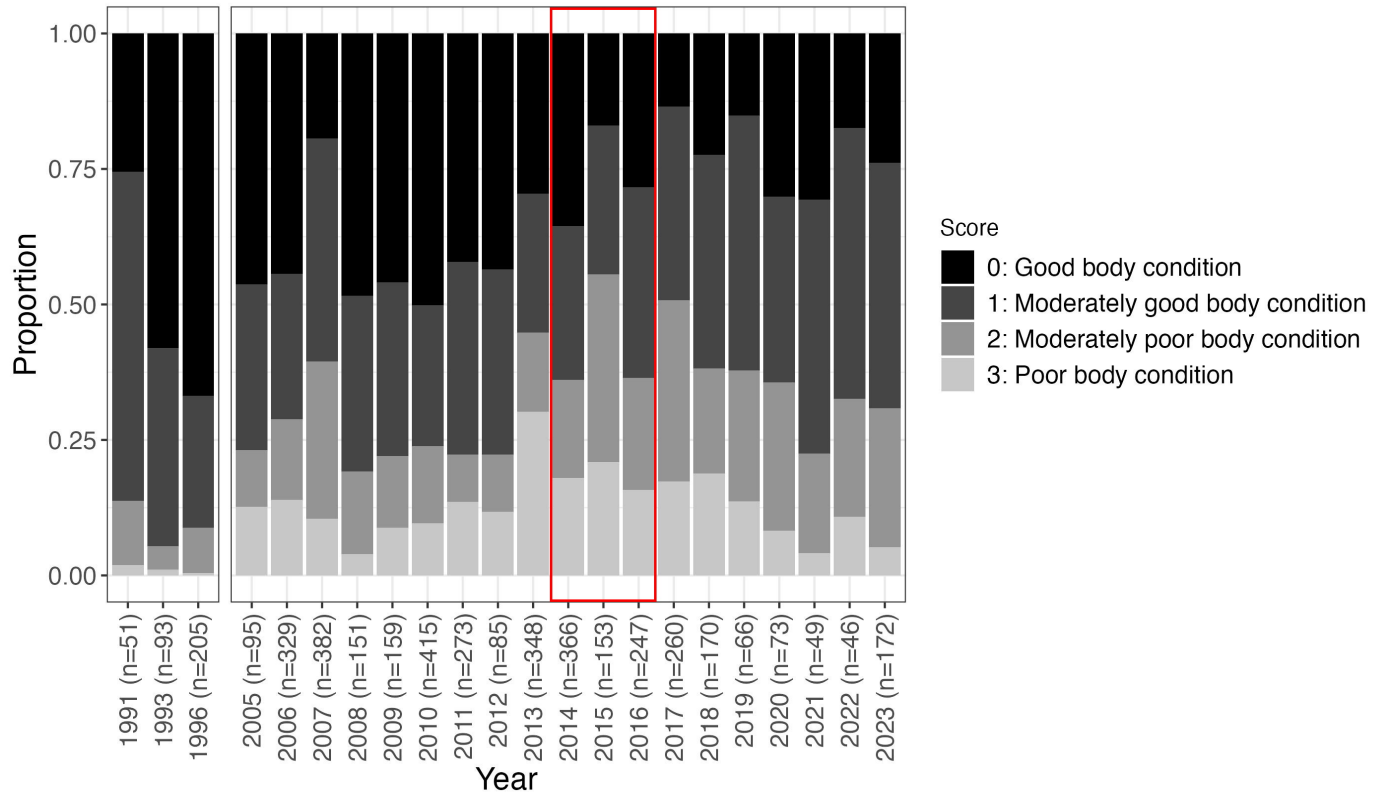


Figure 2. Proportional representation of ENP blue whale (*Balaenoptera musculus*) body condition score (scale of 0 to 3) within each year from the 1990s (1991, 1993, and 1996) and every year between 2005–2023. The red box indicates the occurrence of a marine heatwave in California Current from 2014–2016.

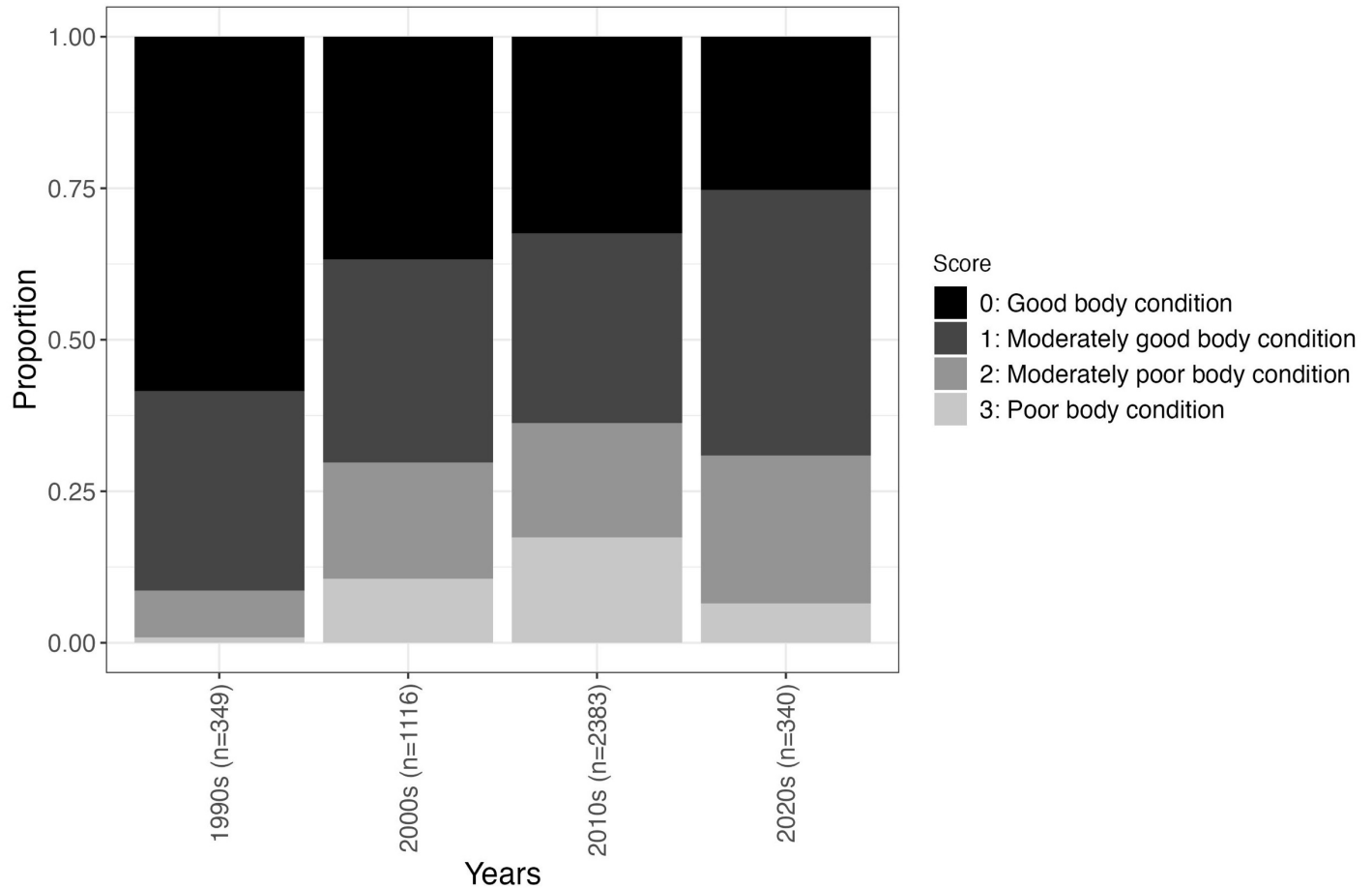


Figure 3. Proportional representation of body condition score of ENP blue whales grouped by decade across the study period.

Region & Seasonality

Across regions, the highest number of sightings occurred in Southern California (Figure 4; $n = 2908$) with the lowest number of sightings in Northern California (Figure 4; $n = 99$). The mean (\pm SE) number of sightings grouped by region was $837.6 (\pm 531.84)$. The association between body condition and geographic regions of the West Coast of North America was statistically significant (Figure 4; $\chi^2 = 54.96$, $df = 12$, $p = 1.84 \times 10^{-7}$). Whales spotted in Northern California were more likely to be in good body condition (40.4% score 0) compared to Mexico (39.8% score 0), Southern California (35.9% score 0), Central California (31.0% score

0), and the Pacific Northwest (30.8% score 0). Interestingly, whales in Mexico had a higher probability of being in poor body condition (14.8 % score 3) than whales in Southern California (14.7% score 3), Central California (9.2% score 3), Northern California (8.1% score 3), and the Pacific Northwest (9.4 % score 3).

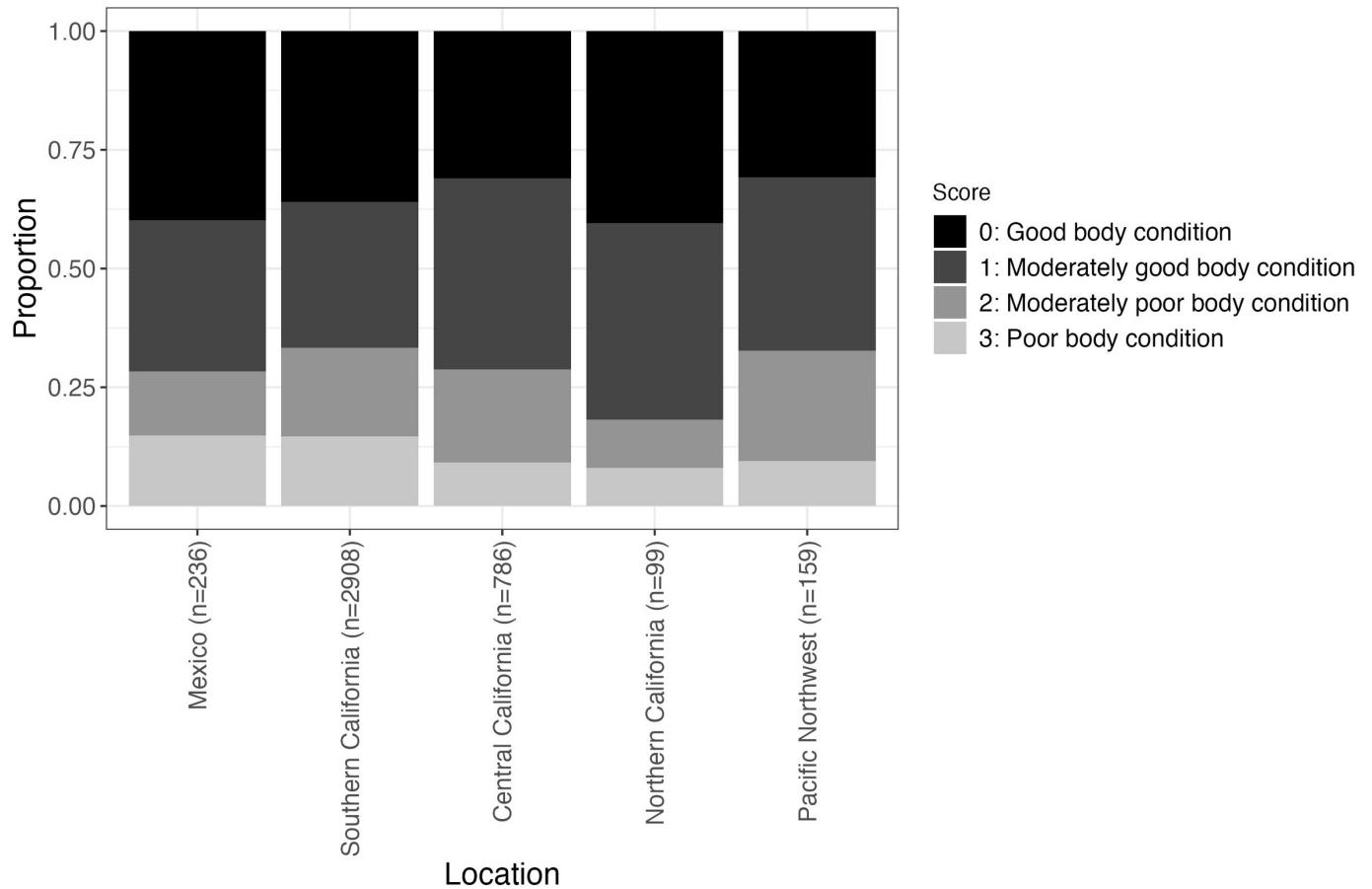


Figure 4. Proportional representation of body condition score of ENP blue whales grouped by region sighted across the study period.

When grouped by season (excluding data from Mexico) the mean (\pm SE) number of sightings was 790.4 (\pm 249.49) with the most sightings occurring in August (Figure 5; $n = 1431$) and the least number of sightings occurring in the early season (January–May; Figure 5; $n = 48$). There was also a statistically significant relationship between season of sighting and blue whale

body condition (Figure 5; $\chi^2 = 32.66$, $df = 12$, $p = 0.001$). Whales in late season (October–December) sightings were more likely to be in good body condition (38.8% score 0) compared to whales in early season (10.4% score 0), June & July (34.3% score 0), August (35.7% score 0), and September (33.9% score 0). Additionally, whales sighted in late season also had a lower probability of being in poor body condition (10.4% score 3) than whales sighted in early season (18.8% score 3), June & July (13.3% score 3), August (14.6% score 3), and September (12.0% score 3).

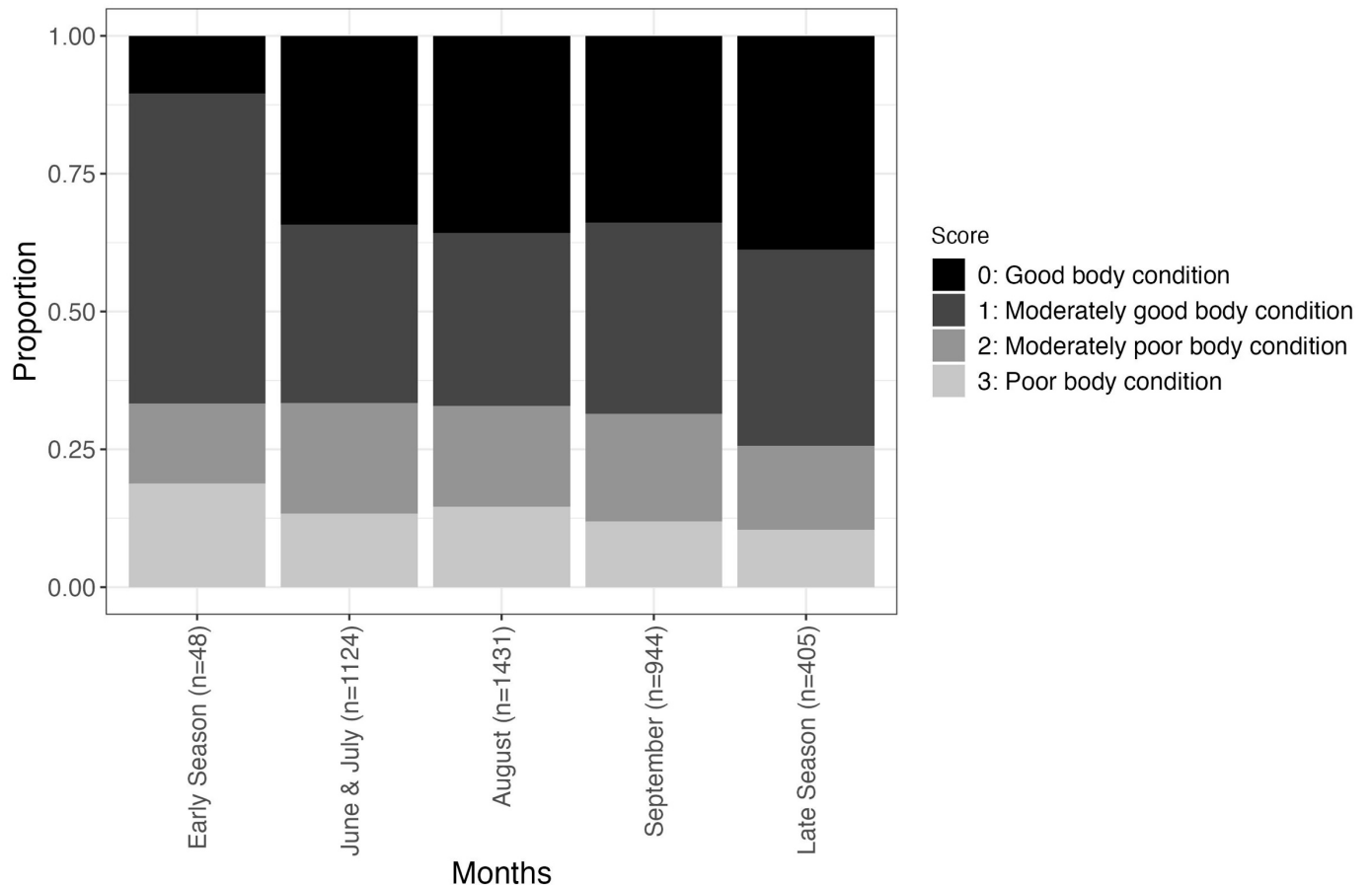


Figure 5. Proportional representation of body condition score of ENP blue whales grouped by season (excluding data from Mexico) sighted across the study period. Time periods are categorized by Early Season (January–May), June & July, August, September, and Late Season (October–December).

Cumulative Link Mixed Modeling

Incorporating seasonality (Month_group) as a covariate in a cumulative linked mixed model of blue whale body condition score improved the model (Table 4). The most parsimonious model included the covariates of reproductive class (RepClass), seasonality (Month_group), image quality (BestQuality), and proportion of image seen (BestProp) with year and ID as random effects. Significant components of the top model were reproductive class being a lactating female ($p < 2.0 \times 10^{-16}$), reproductive class as “other” ($p = 1.15 \times 10^{-8}$), season classified as “early season” ($p = 0.025$), season classified as “late season” ($p = 8.64 \times 10^{-8}$), season classified as “September” ($p = 0.027$), quality of best image (linear, $p = 0.029$), and proportion of best image seen (linear, $p = 0.000$).

When testing the updated base model with the dataset analyzed in Wachtendonk et al. (2022), seasonality improved the fit to the scoring dataset (Table 5). The top two models, based on AICc, included seasonality as a covariate within the model. Within the most parsimonious model, significant components were reproductive class being a lactating female ($p < 2.0 \times 10^{-16}$), reproductive class as “other” ($p = 5.89 \times 10^{-6}$), season classified as “early season” ($p = 0.005$), season classified as “late season” ($p = 1.54 \times 10^{-5}$), season classified as “September” ($p = 0.014$), and quality of best image (linear, $p = 0.000$).

Of the environmental covariates included in this analysis, HCI (Habitat Compression Index) best explained variation in body condition scores (Table 6). The second-best model, as determined by $\Delta\text{AICc} < 2$, included ONI (Oceanic Niño Index). HCI varied significantly across the study period (1991–2023; Figure 6a; Kruskal-Wallis $\chi^2 = 94.22$, $df = 32$, $p = 4.81 \times 10^{-8}$) while ONI also significantly fluctuated across the same period (Figure 6b; Kruskal-Wallis $\chi^2 = 213.83$, $df = 32$, $p < 2.2 \times 10^{-16}$). Significant components of the top model were reproductive

class being a lactating female ($p < 2 \times 10^{-16}$), reproductive class as “other” ($p = 1.06 \times 10^{-8}$), season classified as “early season” ($p = 0.024$), season classified as “late season” ($p = 7.93 \times 10^{-8}$), season classified as “September” ($p = 0.028$), quality of best image (linear, $p = 0.027$), proportion of best image seen (linear, $p = 0.000$), and HCI ($p = 0.03$).

Table 4. All base models tested with sightings from 1991, 1993, 1996 and 2005–2023. Models are listed from lowest to highest AIC value. The most parsimonious model is displayed in bold; the base model used in Wachtendonk et al. (2022) is italicized.

Model	K	AICc	Δ AICc	AICcWt
Score~ RepClass + Month_group + BestQuality + BestProp + (1 Year) + (1 ID)	13	9597.43	0.00	0.8
Score~ RepClass + Month_group + BestProp + (1 Year) + (1 ID)	12	9600.23	2.79	0.2
Score~ RepClass + Month_group + BestQuality + (1 Year) + (1 ID)	12	9609.87	12.43	0.0
Score~ RepClass + Month_group + (1 Year) + (1 ID)	11	9613.43	15.98	0.0
Score~ RepClass + Month + BestQuality + BestProp + (1 Year) + (1 ID)	10	9621.95	24.52	0.0
Score~ RepClass + Month + BestProp + (1 Year) + (1 ID)	9	9623.69	26.25	0.0
Score~ RepClass + BestQuality + BestProp + (1 Year) + (1 ID)	9	9625.74	28.30	0.0
<i>Score~ RepClass + BestProp + (1 Year) + (1 ID)</i>	8	9627.39	29.96	0.0
Score~ RepClass + Month + BestQuality + (1 Year) + (1 ID)	9	9634.02	36.59	0.0
Score~ Month_group + BestQuality + BestProp + (1 Year) + (1 ID)	11	9773.39	175.96	0.0
Score~ Month_group + BestProp + (1 Year) + (1 ID)	10	9775.36	177.92	0.0
Score~ Month_group + (1 Year) + (1 ID)	9	9787.17	189.73	0.0
Score~ Month + BestQuality + BestProp + (1 Year) + (1 ID)	8	9799.15	201.71	0.0

Score, body condition score; *RepClass*, reproductive class (calf, lactating female, or other); *Month_group*, season of individual sighting; *BestQuality*, quality of best image; *BestProp*, proportion of whale seen in best image. *K*, number of parameters; *AICc*, Akaike’s Information Criterion for small sample size; *AICcWT*, *AICc* weight.

Table 5. All base models tested utilizing the original dataset (2005–2018) analyzed in Wachtendonk et al. (2022). Models are listed from lowest to highest AIC value. The most parsimonious model is displayed in bold; the base model used in Wachtendonk et al. (2022) is italicized.

Model	K	AICc	ΔAICc	AICcWt
Score~ RepClass + Month_group + BestProp + (1 Year) + (1 ID)	12	8050.67	0.00	0.59
Score~ RepClass + Month_group + BestQuality + BestProp + (1 Year) + (1 ID)	13	8051.43	0.76	0.40
Score~ RepClass + Month_group + (1 Year) + (1 ID)	11	8061.85	11.18	0.00
Score~ RepClass + Month_group + BestQuality + (1 Year) + (1 ID)	12	8062.32	11.65	0.00
<i>Score~ RepClass + BestProp + (1 Year) + (1 ID)</i>	<i>8</i>	<i>8069.10</i>	<i>18.43</i>	<i>0.00</i>
Score~ RepClass + Month + BestProp + (1 Year) + (1 ID)	9	8070.09	19.42	0.00
Score~ RepClass + BestQuality + BestProp + (1 Year) + (1 ID)	9	8070.32	19.65	0.00
Score~ RepClass + Month + BestQuality + BestProp + (1 Year) + (1 ID)	10	8071.29	20.62	0.00
Score~ RepClass + Month + BestQuality + (1 Year) + (1 ID)	9	8081.13	30.46	0.00
Score~ Month_group + BestProp + (1 Year) + (1 ID)	10	8192.03	141.36	0.00
Score~ Month_group + BestQuality + BestProp + (1 Year) + (1 ID)	11	8193.19	142.51	0.00
Score~ Month_group + (1 Year) + (1 ID)	9	8202.28	151.61	0.00
Score~ Month + BestQuality + BestProp + (1 Year) + (1 ID)	8	8212.80	162.12	0.00

Score, body condition score; *RepClass*, reproductive class (calf, lactating female, or other); *Month* (month of sighting); *Month_group*, season of individual sighting; *BestQuality*, quality of best image; *BestProp*, proportion of whale seen in best image. *K*, number of parameters; *AICc*, Akaike's Information Criterion for small sample size; *AICcWT*, *AICc* weight.

Table 6. Most parsimonious base model tested with each environmental covariate. Models are listed from lowest to highest AIC value. The most parsimonious model is displayed in bold.

Model	K	AICc	Δ AICc	AICcWt
Score~ RepClass + Month_group + BestQuality + BestProp + HCI + (1 Year) + (1 ID)	14	9595.26	0.00	0.40
Score~ RepClass + Month_group + BestQuality + BestProp + ONI + (1 Year) + (1 ID)	14	9597.24	1.98	0.15
Score~ RepClass + Month_group + BestQuality + BestProp + HeatWave + (1 Year) + (1 ID)	14	9597.43	2.17	0.13
Score~ RepClass + Month_group + BestQuality + BestProp + RelativeCPUE + (1 Year) + (1 ID)	14	9597.91	2.65	0.11
Score~ RepClass + Month_group + BestQuality + BestProp + BEUTI + (1 Year) + (1 ID)	14	9598.07	2.82	0.10
Score~ RepClass + Month_group + BestQuality + BestProp + PDO + (1 Year) + (1 ID)	14	9598.72	3.46	0.07
Score~ RepClass + Month_group + BestQuality + BestProp + PDO.Value + (1 Year) + (1 ID)	14	9599.44	4.18	0.05

Score, body condition score; *RepClass*, reproductive class (calf, lactating female, or other); *Month_group*, season of individual sighting; *BestQuality*, quality of best image; *BestProp*, proportion of whale seen in best image; *HCI*, Habitat Compression Index; *ONI*, Oceanic Niño Index; *HeatWave*, presence or absence of a heatwave; *RelativeCPUE*, Relative Catch Per Unit Effort (krill); *BEUTI*, Biologically Effective Upwelling Transport Index; *PDO*, Pacific Decadal Oscillation (positive or negative); *PDO.Value*, Pacific Decadal Oscillation value. *K*, number of parameters *AICc*, Akaike's Information Criterion for small sample size; *AICcWT*, *AICc* weight.

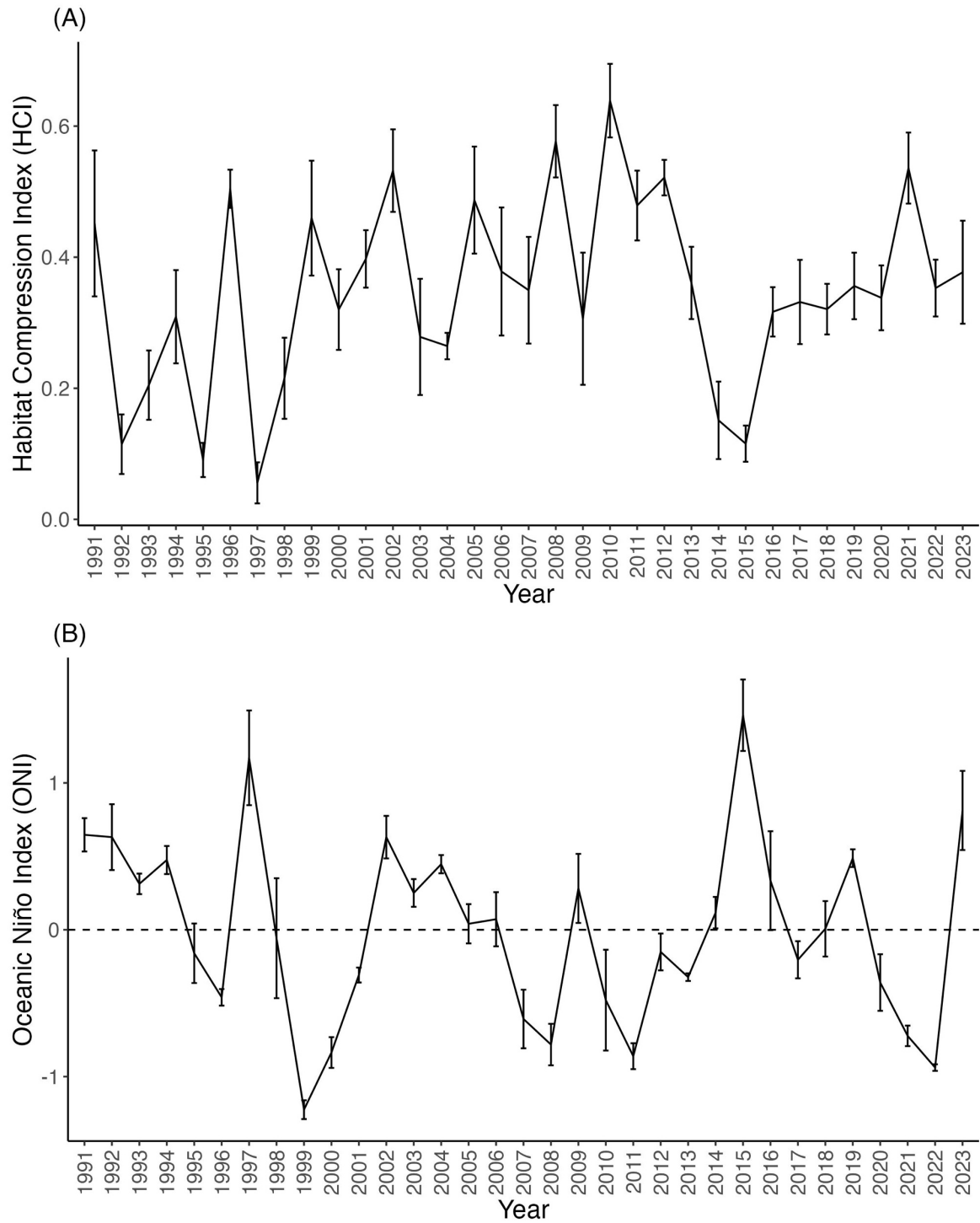


Figure 6. Mean (\pm SE) A) Habitat Compression Index (HCI) and B) Oceanic Niño Index (ONI) along the U.S. West Coast from 1991–2023.

Survival Modeling

Although the most parsimonious model, as suggested by QAICc, contains body condition score as a covariate, the model with the third lowest QAICc has a much lower QDeviance. This evidence suggests that the model $\phi(\sim t + tr) p(\sim t * td)$ explains more variability in the dataset with lower uncertainty (Table 7). The model excluding body condition is penalized for the higher number of parameters (55 parameters) compared to a model with body condition (39 parameters), which QAICc suggests as the top model. Based on these models we conclude that there is little evidence that average body condition can explain within-year variation in blue whale survival.

From 2006–2022 there was variation in apparent survival (including emigration; hereby referred to as “survival”) estimates with relatively higher within-year survival before 2010 (except for 2006) compared to after 2020 (Figure 7a). The highest estimate of survival was 0.994 (95% CI 0.971 – 0.999) in 2008, while the lowest estimate was 0.739 (95% CI 0.389 – 0.926) in 2021. However, estimates from 2013, 2020, 2021, and 2022 contain high uncertainty. The recapture rate for the model $\phi(\sim t + tr) p(\sim t * td)$ generally decreased throughout the study period (Figure 7b). The year with the highest rate of recapture was 2007 (0.478; 95% CI 0.325 – 0.637), while the lowest rate of recapture occurred in 2015 (0.054; 95% CI 0.033 – 0.086). There was no significant correlation between average body condition score and survival rates (estimated from $\phi(\sim t + tr) p(\sim t * td)$) utilizing a linear regression model (Figure 8; $F = 0.03$, $p = 0.864$, Multiple $R^2 = 0.002$). The survival estimate from 2013 was removed from this analysis due to high uncertainty.

There was no significant difference in the proportion of whales resighted among different

body condition scores (Figure 9; $\chi^2 = 3.88$, $df = 3$, $p = 0.275$) though these did follow an apparent trend of whales in poorer body conditions being resighted less often than those in good body condition. Regardless of body condition, whales were equally likely to be resighted within the “recapture” period (2010 – 2023). Nonetheless, the highest proportion of resighted whales (0.722) were in good body condition (score 0) at the last sighting while the lowest proportion of resighted whales (0.587) were in poor body condition (score 3) at the last sighting.

Table 7. CJS models based on ENP blue whale sightings from 2005 to 2023. ϕ : apparent survival probability, p : recapture probability, t : annual sampling occasion, tr : transience class, $score$: average body condition score, td : trap dependence, $+$: additive effect, $*$: interactive effect.

Model	Parameters	QAICc	Δ QAICc	Weight	QDeviance
$\phi (\sim tr + score) p (\sim t * td)$	39	4131.71	0	0.46038	4051.866
$\phi (\sim tr * score) p (\sim t * td)$	40	4131.91	0.2015771	0.41624	4049.972
$\phi (\sim t + tr) p (\sim t * td)$	55	4135.64	3.927187	0.06462	4021.961
$\phi (\sim tr + score) p (\sim t + td)$	22	4136.62	4.9101665	0.03953	4092.029
$\phi (\sim tr * score) p (\sim t + td)$	23	4138.48	6.763989	0.01564	4091.829
$\phi (\sim t + tr) p (\sim t + td)$	38	4141.42	9.7084599	0.00359	4063.668
$\phi (\sim t * tr) p (\sim t * td)$	72	4155.17	23.4605412	3.7E-06	4004.832
$\phi (\sim t * tr) p (\sim t + td)$	55	4156.93	25.2214357	1.5E-06	4043.255
$\phi (\sim t * tr) p (\sim td)$	38	4230.87	99.1613377	0	4153.121
$\phi (\sim t + tr) p (\sim td)$	21	4233.31	101.6010395	0	4190.772
$\phi (\sim tr + score) p (\sim td)$	5	4255.8	124.0829952	0	4245.76
$\phi (\sim tr * score) p (\sim td)$	6	4257.06	125.349439	0	4245.012

ϕ , apparent survival probability; p , recapture probability; t , annual sampling occasion; tr , transience class score, average body condition score; td , trap dependence; $+$, additive effect; $*$, interactive effect; QAICc, quasi Akaike’s information criterion for small sample sizes.

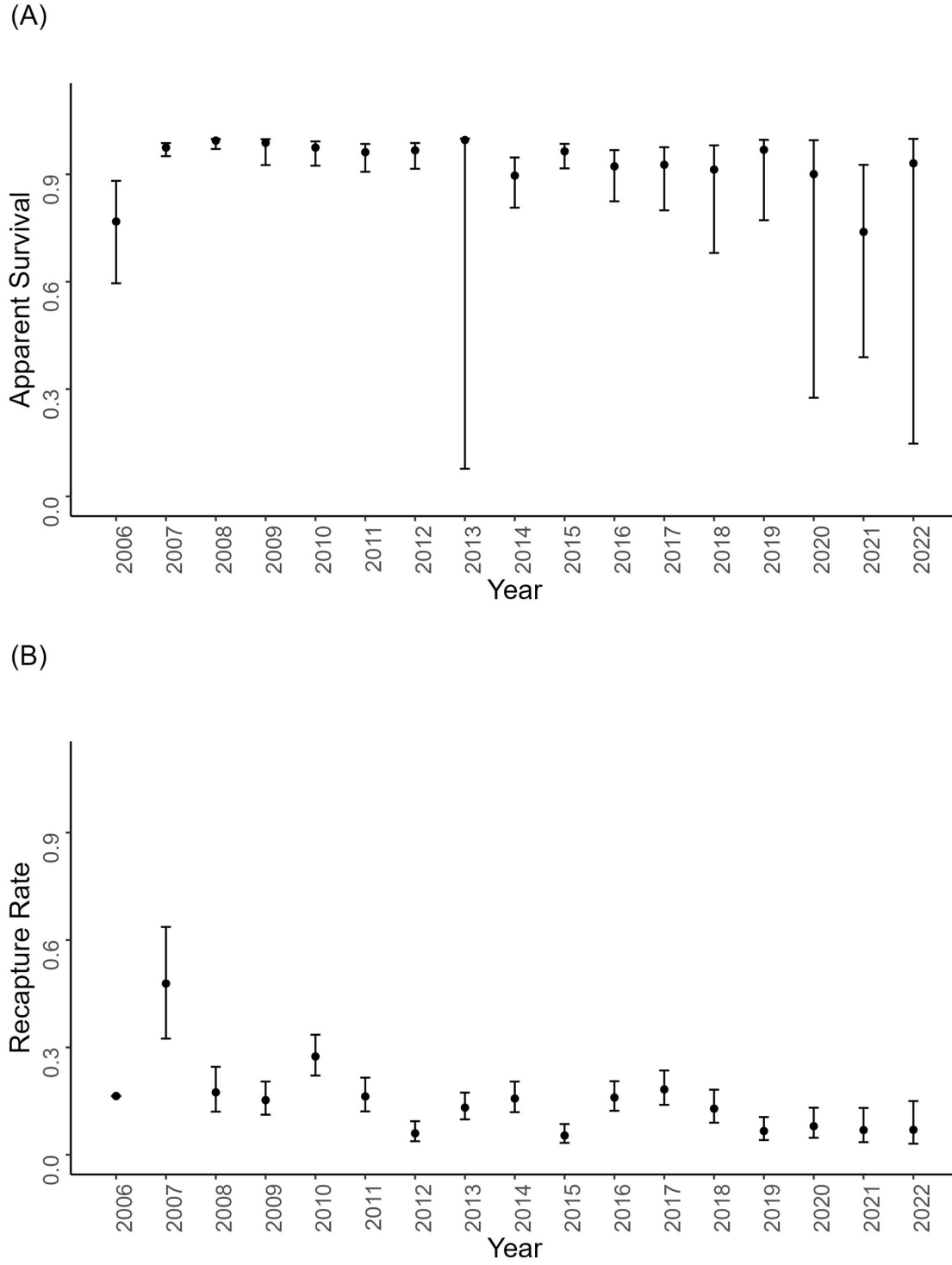


Figure 7. Within-year A) apparent survival and B) recapture rate of ENP blue whales from 2006-2022 ($\phi(\sim t + tr)$ $p(\sim t * td)$). Error bars represent upper and lower 95% confidence intervals.

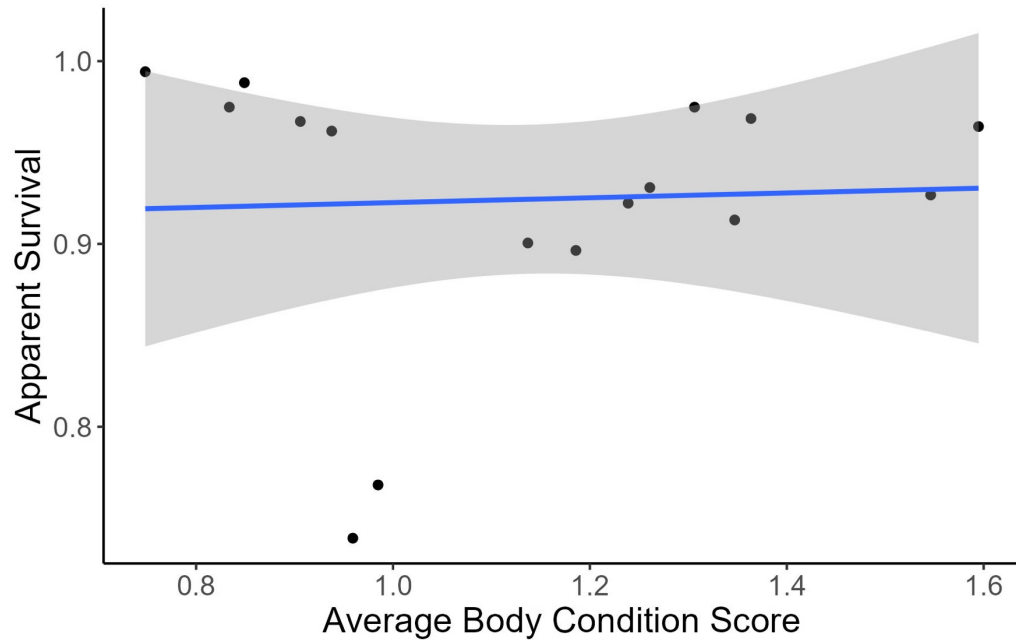


Figure 8. Linear regression model of apparent survival against average body condition score for ENP blue whales from 2006-2022.

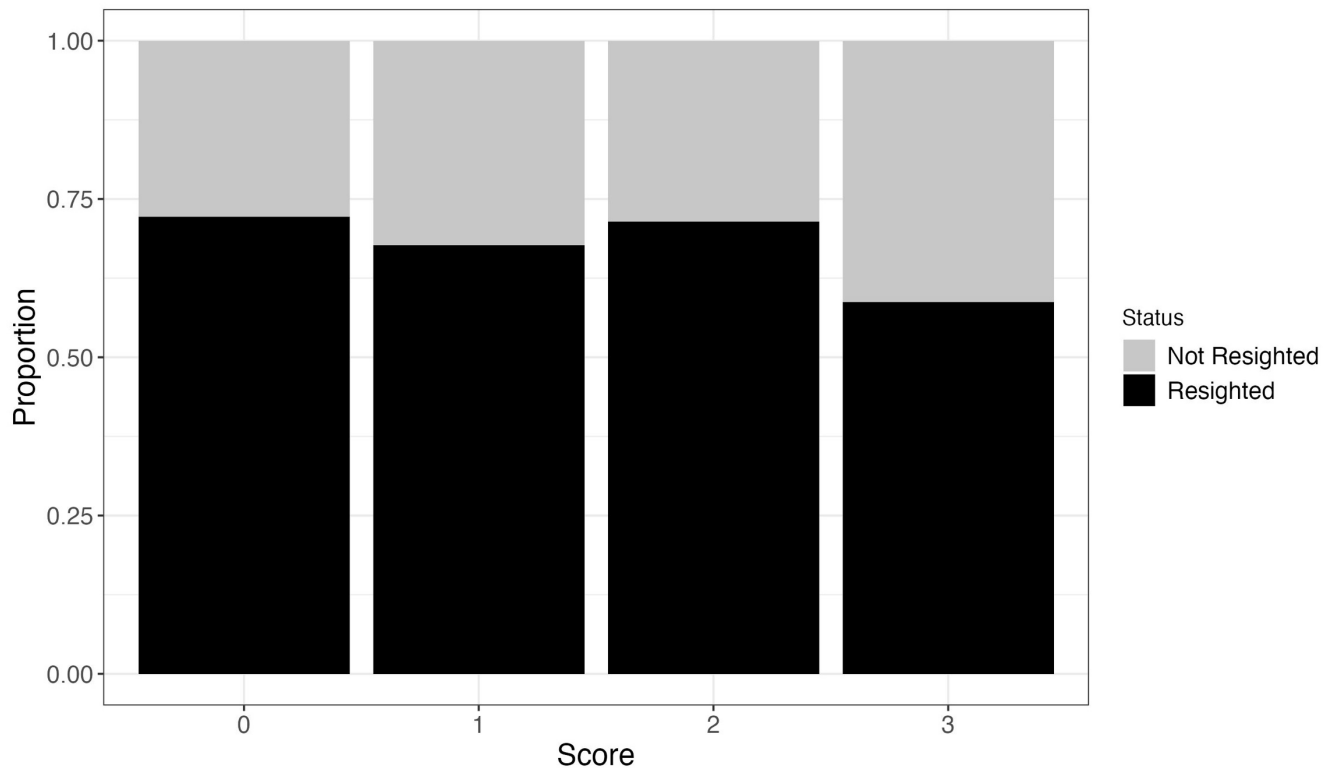


Figure 9. Proportion of ENP blue whales within each body condition score category at last sighting resighted from 2010–2023. A score of 0 indicates good body condition, 1 indicates moderately good body condition, 2 indicates moderately poor body condition, and 3 indicates poor body condition.

4.0 Discussion

Although there were some discrepancies in scoring between raters, the finding of fair–good agreement between raters is consistent with reports of inter-rater reliability in body condition scoring of other marine mammals. In body condition scoring of gray whales, Bradford et al. (2012) reported fair to excellent agreement ($\kappa = 0.58\text{--}0.83$). Notably, the agreement between raters of post-cranial condition on a 3-point ordinal scale, using linear weighted kappa coefficients ($\kappa_w = 0.65$), was similar to agreement between body condition scores reported within this study ($\kappa_w = 0.68$). Our finding of the highest inter-rater agreement when scoring for the presence or absence of an arch is consistent for ratings on smaller scales (2 options vs. 4 options) (Bradford et al., 2012). Although there was slightly better agreement in scores of digital images compared to film images, these scores remained within a range of fair–good agreement. Body condition assessments of short-beaked common dolphins (*Delphinus delphis*) on a 4-point ordinal scale have also shown moderate-strong agreement between raters (Kendall's $W = 0.664$) using non-parametric methods (Joblon et al., 2008). These findings suggest that the methods of blue whale body condition scoring outlined in Wachtendonk et al. (2022) are applicable for different qualified raters across varied photographic formats (film & digital).

Since the 1990s, blue whale body condition has fluctuated with a greater proportion of whales in poor and moderately poor body condition during the past two decades. However, there has been a slight increase in abundance since the 1990s according to the most recent mark-recapture estimates (Calambokidis & Barlow, 2020). This is concurrent with evidence suggesting that this population has reached its carrying capacity (Monnahan et al., 2015). Nonetheless, the discrepancy between mark-recapture abundance estimates and those estimated from line-transect surveys (Barlow, 2016), which show decline since the 1990s, provides some uncertainty. Given

the northward shift in blue whale distribution since the 1990s (Bailey et al., 2009; Barlow, 2016; Calambokidis et al., 2009; Whittome et al., 2024), apparent changes in ENP blue whale body condition may be due to appearance of different individuals during photo-identification efforts. Most sightings within this study occurred along the coasts of Southern and Central California during the months of June – September. Body condition scores across time may be representative of varying subsets of the ENP blue whale population that utilize the highly productive upwelling regions of the California Current. This is further supported by age and sex-specific differences in migratory strategies (Blevins et al., 2022) and the low resighting rates within the study period. Consistent with Wachtendonk et al. (2022), the years with the worst body condition throughout the study period (2015 & 2017) were during and in a year immediately following the 2014 – 2016 marine heatwave in California Current. Relating trends in blue whale body condition to prey abundance, relative krill biomass was lower in 2015 and 2016 during the marine heatwave and ~30% higher in 2013 and 2018 (Dorman et al., 2023). In years following the heatwave, the slight increase in body condition may be linked to increased krill biomass.

Sighting season had a significant impact on body condition of blue whales sighted off the U.S. West Coast. This trend is generally reflected by differences in body condition across geographic regions; as ENP blue whales migrate northward body condition tends to improve. However, whales sighted in the Pacific Northwest do not appear to follow this trend. For ENP blue whales, recently identified biologically important feeding areas are centered around the California Current region (Calambokidis et al., 2024) which is reflected by the relatively good body condition of whales sighted in Northern California. Furthermore, the incorporation of seasonality significantly improved the ability of a CLMM to explain variations blue whale body condition score for this dataset and the original dataset explored in Wachtendonk et al. (2022).

Although blue whales feed year-round, these findings add to the growing body of evidence that confirms the importance of summer feeding off the US West Coast, particularly in the California Current region, for the ENP blue whale population (Bailey et al., 2009; Calambokidis et al., 2024; Oleson et al., 2007).

Further investigating the potential cause for inter-annual fluctuations in blue whale body condition, this measure appears to be closely linked to environmental conditions that influence aggregations of their krill prey. Within this study, the inclusion of either HCI or ONI into the most parsimonious base CLMM improved the model's ability to explain variations in body condition, in contrast to the final model explored in Wachtendonk et al. (2022) that included both PDO value and LUSI as covariates. Model predictions of krill CPUE have shown lower than average values during El Niño years compared to La Niña years (Cimino et al., 2020).

Furthermore, shifts in humpback whale distribution and changes in associated prey species (krill and anchovy) have been documented to correspond with HCI (Santora et al., 2020). In 2015, the year in this investigation with highest proportion of blue whales in poor and moderately poor body condition, total krill abundance in the CCE declined from previously positive values in 2008 – 2014 (Santora et al., 2020). In contrast to HCI, the decline in blue whale body condition occurred during an ONI spike in 2015. Nonetheless, a relatively high proportion of whales in poor and moderately poor was recorded during years with lower ONI values such as 2007 and 2013.

Overall, euphausiid aggregations differ from year to year (Fiechter et al., 2020) with significantly lower abundances in the CCE during the 1990s compared to the 2000s (Ralston et al., 2015). Despite relatively lower abundances of krill in the 1990s, shifts per-capita prey availability could correlate to changes in blue whale body condition given the likely increase in

the ENP blue whale population abundance since the 1990s. In fin whales off western Iceland, body condition was reported to increase with per capita prey availability (Williams et al., 2013). Nonetheless, concurrent fluctuations in krill and ENP blue whale abundance may not account for observed variations in body condition. Blue whales have been shown to exhibit behavioral plasticity in the face of environmental change. The earlier arrival of blue whales to the Gulf of the Farallones, by 100 days, in 2016 compared to 1993 was associated with warm, non-productive years (Ingman et al., 2021). During a marine heatwave in New Zealand, blue whales exhibited reduced calls associated with foraging behavior (D calls) followed by lower song intensity associated with reproduction (Barlow et al., 2023). Within the scope of this analysis, environmental drivers appear to contribute to variability in blue whale body condition as reported by Wachtendonk et al. (2022).

In an exploration of within-year blue whale survival, as it relates to yearly averaged body condition, there was no evidence suggesting a strong relationship between these two variables. Survival estimates were consistent with an estimate of ENP blue whale survival in the Gulf of California (GoC) that displayed changing patterns of habitat usage with shifts linked to environmental variation (Whittome et al., 2024). Although poor body condition has been correlated with reduced survival in killer whales (Stewart et al., 2021) and gray whales (Christiansen et al., 2021), currently the relationship between blue whale survival and body condition seems unclear. Nonetheless, individual declines in body condition could serve as a stressor with potential long-term impacts to the greater population (Cerini et al., 2023). Given the limited time scope of this project, future work could consider body condition of ENP blue whale individuals sighted within a year (rather than averaged across the sightings for a year) and whether a more fine-scale analysis could yield further insights into population-wide effects.

Additionally, this analysis was limited to the continuous body condition dataset (2005–2023) and thus excluded estimates from the 1990s and sightings without images suitable for body condition scoring. A wider time-scope, especially for a long-lived species such as the blue whale, may provide more accurate estimates of survival as it relates to long-term trends in individual body condition.

As indicators of ecosystem health (Moore, 2008), changes in blue whale body condition could signal the detrimental effects of a warming climate to the highly productive CCE. Furthermore, decreased body condition can provide an additional stressor to marine mammals with the potential for population-wide impacts. Poor body condition of lactating female North Atlantic right whales (NARW) has been related to calf size, with an estimated reduction in calf length compared to southern right whales (SRW; *Eubalaena australis*; Christiansen et al., 2020). Female minke whales in poor body condition will provide proportionately less investment to a fetus compared to individuals in good body condition (Christiansen et al., 2014). Declines in ENP blue whale body condition have the potential to influence reproductive output and resulting population health. Along the U.S West Coast, blue whales remain vulnerable to anthropogenic impacts such as ship strike mortality (Rockwood et al., 2017) and mid-frequency active sonar (MFAS; Friedlaender et al., 2016) which impacts feeding behavior. These factors could compound in years with unfavorable environmental conditions that could impact blue whale body condition. Large whales in worse body condition may be less resilient to ecological change as has been described in Pacific Coast Feeding Group (PCFG) gray whales (Torres et al., 2022). Understanding the links between environmental variation, anthropogenic disturbance, abundance estimates, and body condition will be essential in continuing to monitor and manage the ENP blue whale population.

5.0 Conclusions

This research displays the value of archival film and digital imagery and provides validation for the visual assessment of blue whale body condition from vessel-based photographs developed by Wachtendonk et al. (2022). Future work could consider the addition of aerial-based imagery as a validation method for subjective body condition. Blue whale body condition varied throughout the study period with a general decreasing trend since the 1990s and was linked to fluctuations in environmental drivers such as HCI and ONI. Body condition tended to improve throughout the period described in the literature as the feeding season (June – November) within the California Current region (Bailey et al., 2009; Calambokidis et al., 2024; Oleson et al., 2007). Although body condition was not found to correlate to within-year survival, there is potential for future analyses to expand the survival estimates from this study using individual scores of body condition to conduct a fine-scale assessment. Analyses of the relationship between blue whale reproductive output and body condition may provide a deeper understanding of potential future impacts to the population. Additionally, the sensitivity of blue whales in poor body condition to ecological and anthropogenic disturbance should be further explored. As a measure of health (Pettis et al., 2004), body condition estimates serve as a proxy for the health of the greater ecosystem (Moore, 2008). Therefore, these assessments are necessary to monitor not only the ENP blue whale population but the greater ocean ecosystem as a whole.

6.0 References

- Acevedo-Gutiérrez, A., Croll, D. A., & Tershy, B. R. (2002). High feeding costs limit dive time in the largest whales. *The Journal of Experimental Biology*, 205, 1747–1753. <https://doi.org/10.1242/jeb.205.12.1747>
- Akaike, H. (1973). Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, 60(2), 255–265. <https://doi.org/10.1093/biomet/60.2.255>
- Akmajian, A. M., Scordino, J. J., Gearin, P., & Gosho, M. (2021). Body condition of gray whales (*Eschrichtius robustus*) feeding on the Pacific Coast reflects local and basin wide environmental drivers and biological parameters. *J. Cetacean Res. Manage.*, 22, 87–110. <https://doi.org/10.47536/jcrm.v22i1.223>
- Alter, S. E., Simmonds, M. P., & Brandon, J. R. (2010). Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. *Marine Policy*, 34(5), 943–954. <https://doi.org/10.1016/j.marpol.2010.01.026>
- Bailey, H., Mate, B. R., Palacios, D. M., Irvine, L., Bograd, S. J., & Costa, D. P. (2009). Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, 10(1), 93–106. <https://doi.org/10.3354/esr00239>
- Barlow, J. (2016). *Cetacean abundance in the California Current estimated from ship-based line-transect surveys in 1991-2014*. NOAA Southwest Fisheries Science Center Administrative Report LJ-16-01.
- Becker, E. A., Forney, K. A., Miller, D. L., Fiedler, P. C., Barlow, J., & Moore, J. E. (2020). *Habitat-based density estimates for cetaceans in the California Current Ecosystem based on 1991-2018 survey data*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-638.
- Blevins, C., Busquets-Vass, G., Pardo, M. A., Gendron, D., Jacobsen, J. K., Gómez-Díaz, F., Pérez-Puig, H., Ortega-Ortiz, C. D., Heckel, G., Urbán R, J., Vilorio-Gómora, L., & Newsome, S. D. (2022). Sex- and age-specific migratory strategies of blue whales in the northeast Pacific Ocean. *Frontiers in Marine Science*, 9. <https://doi.org/10.3389/fmars.2022.944918>

- Bradford, A. L., Weller, D. W., Punt, A. E., Ivashchenko, Y. v., Burdin, A. M., Vanblaricom, G. R., & Brownell, R. L. (2012). Leaner leviathans: Body condition variation in a critically endangered whale population. *Journal of Mammalogy*, 93(1), 251–266.
<https://doi.org/10.1644/11-MAMM-A-091.1>
- Calambokidis, J., & Barlow, J. (2020). *Updated Abundance Estimates for Blue and Humpback Whales Along the U.S. West Coast Using Data Through 2018*. U.S. Department of Commerce, NOAA Technical Memorandum.
- Calambokidis, J., Barlow, J., Ford, J. K. B., Chandler, T. E., & Douglas, A. B. (2009). Insights into the population structure of blue whales in the Eastern North Pacific from recent sightings and photographic identification. *Marine Mammal Science*, 25(4), 816–832.
<https://doi.org/10.1111/j.1748-7692.2009.00298.x>
- Calambokidis, J., Kratofil, M. A., Palacios, D. M., Lagerquist, B. A., Schorr, G. S., Hanson, M. B., Baird, R. W., Forney, K. A., Becker, E. A., Rockwood, R. C., & Hazen, E. L. (2024). Biologically Important Areas II for cetaceans within U.S. and adjacent waters - West Coast Region. *Frontiers in Marine Science*, 11.
<https://doi.org/10.3389/fmars.2024.1283231>
- Cascadia Research Collective. (2024). *About Cascadia Research Collective*.
<https://cascadiaresearch.org/about/>
- Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology and Evolution*, 7(3), 320–331. <https://doi.org/10.1038/s41559-023-01985-2>
- Christensen, R. (2023). *Ordinal-Regression Models for Ordinal Data*. R package version 2023.12-4.1. Available at <https://CRAN.R-project.org/package=ordinal>.
- Christiansen, F., Rodríguez-González, F., Martínez-Aguilar, S., Urbán, J., Swartz, S., Warick, H., Vivier, F., & Bejder, L. (2021). Poor body condition associated with an unusual mortality event in gray whales. *Marine Ecology Progress Series*, 658, 237–252.
<https://doi.org/10.3354/meps13585>
- Cimino, M. A., Santora, J. A., Schroeder, I., Sydeman, W., Jacox, M. G., Hazen, E. L., & Bograd, S. J. (2020). Essential krill species habitat resolved by seasonal upwelling and ocean circulation models within the large marine ecosystem of the California Current System. *Ecography*, 43(10), 1536–1549. <https://doi.org/10.1111/ecog.05204>

- Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and psychological measurement*, 20(1), 37–46. <https://doi.org/10.1177/001316446002000104>
- Cohen, J. (1968). Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit. *Psychological Bulletin*, 70(4), 213–220. <https://doi.org/10.1037/h0026256>
- Croll, D. A., Tershy, B. R., Hewitt, R. P., Demer, D. A., Fiedler, P. C., Smith, S. E., Armstrong, W., Popp, J. M., Kiekhefer, T., Lopez, V. R., Urban, J., & Gendron, D. (1998). An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 45(7), 1353–1371. [https://doi.org/10.1016/S0967-0645\(98\)00031-9](https://doi.org/10.1016/S0967-0645(98)00031-9)
- Dorman, J. G., Sydeman, W. J., Thompson, S. A., Warren, J. D., Killeen, H. J., Hoover, B. A., Field, J. C., & Santora, J. A. (2023). Environmental variability and krill abundance in the central California current: Implications for ecosystem monitoring. *Frontiers in Marine Science*, 10. <https://doi.org/10.3389/fmars.2023.1099482>
- Fiechter, J., Santora, J. A., Chavez, F., Northcott, D., & Messié, M. (2020). Krill Hotspot Formation and Phenology in the California Current Ecosystem. *Geophysical Research Letters*, 47(13). <https://doi.org/10.1029/2020GL088039>
- Fiedler, P. C., Reilly, S. B., Hewitt, R. P., Demer, D., Philbrick, V. A., Smith, S., Armstrong, W., Croll, D. A., Tershy, B. R., & Mate, B. R. (1998). Blue whale habitat and prey in the California Channel Islands. *Deep Sea Research Part II: Topical Studies in Oceanography*, 45(8-9), 1781–1801. [https://doi.org/10.1016/S0967-0645\(98\)80017-9](https://doi.org/10.1016/S0967-0645(98)80017-9)
- Fleiss, J. L., Levin, B., & Paik, M. C. (2003). The Measurement of Interrater Agreement. In: *Statistical methods for rates and proportions* (3rd Edition; pp. 596–626). John Wiley & Sons, New York.
- Friedlaender, A. S., Hazen, E. L., Goldbogen, J. A., Stimpert, A. K., Calambokidis, J., & Southall, B. L. (2016). Prey-mediated behavioral responses of feeding blue whales in controlled sound exposure experiments. *Ecological Applications*, 26(4), 1075–1085. <https://doi.org/10.1002/15-0783>
- Gamer, M., Lemon, J., Pupendra Singh, I. F. (2019). *irr: Various Coefficients of Interrater Reliability and Agreement*. R package version 0.84.1. Available at <https://CRAN.R-project.org/package=irr>.

- Gimenez, O., Lebreton, J. D., Choquet, R., & Pradel, R. (2018). R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models. *Methods Ecol Evol.*, 9, 1749–1754. <https://doi.org/10.1111/2041-210X.13014>
- Hausner, A., Samhouri, J. F., Hazen, E. L., Delgerjargal, D., & Abrahms, B. (2021). Dynamic strategies offer potential to reduce lethal ship collisions with large whales under changing climate conditions. *Marine Policy*, 130, 104565. <https://doi.org/10.1016/j.marpol.2021.104565>
- Ingman, K., Hines, E., Mazzini, P. L. F., Rockwood, R. C., Nur, N., & Jahneke, J. (2021). Modeling changes in baleen whale seasonal abundance, timing of migration, and environmental variables to explain the sudden rise in entanglements in California. *PLoS ONE*, 16(4 April). <https://doi.org/10.1371/journal.pone.0248557>
- Irvine, L. M., Mate, B. R., Winsor, M. H., Palacios, D. M., Bograd, S. J., Costa, D. P., & Bailey, H. (2014). Spatial and temporal occurrence of blue whales off the U.S. West Coast, with implications for management. *PLoS ONE*, 9(7). <https://doi.org/10.1371/journal.pone.0102959>
- Irvine, L. M., Palacios, D. M., Lagerquist, B. A., & Mate, B. R. (2019). Scales of blue and fin whale feeding behavior off California, USA, with implications for prey patchiness. *Frontiers in Ecology and Evolution*, 7, 338. <https://doi.org/10.3389/fevo.2019.00338>
- Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal Upwelling Revisited: Ekman, Bakun, and Improved Upwelling Indices for the U.S. West Coast. *Journal of Geophysical Research: Oceans*, 123(10), 7332–7350. <https://doi.org/10.1029/2018JC014187>
- Joblon, M. J., Pokras, M. A., Morse, B., Harry, C. T., Rose, K. S., Sharp, S. M., Niemeyer, M. E., Patchett, K. M., Sharp, W. B., & Moore, M. J. (2014). Body condition scoring system for delphinids based on short-beaked common dolphins (*Delphinus delphis*). *J. Mar. Anim. Ecol.*, 7(2), 5–13.
- Laake, J.L. (2013). *RMark: An R Interface for Analysis of Capture-Recapture Data with MARK*. NOAA Alaska Fisheries Science Center Processed Rep 2013-01.

- Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62(1), 67–118. <https://doi.org/10.2307/2937171>
- Lockyer, C. (1984). Review of Baleen Whale (Mysticeti) Reproduction and Implications for Management. *Rep. Int. Whal. Commn.*, 6, 27–50.
<https://www.researchgate.net/publication/282383861>
- Lockyer, C. (1986). Body fat condition in northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. *Canadian Journal of Fisheries and Aquatic Sciences*, 43(1), 142–147. <https://doi.org/10.1139/f86-015>
- Lockyer, C. (2007). All creatures great and smaller: A study in cetacean life history energetics. *Journal of the Marine Biological Association of the United Kingdom*, 87(4), 1035–1045. <https://doi.org/10.1017/S0025315407054720>
- Lockyer C., McConnel L., & Waters T. (1985). Body Condition in Terms of Anatomical and Biochemical Assessment of Body Fat in North Atlantic Fin and Sei Whales. *Can. J. Zool.*, 63, 2328–2338. <https://doi.org/10.1139/z85-345>
- Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the american Meteorological Society*, 78(6), 1069–1080. [https://doi.org/10.1175/1520-0477\(1997\)078<1069:APICOW>2.0.CO;2](https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2)
- Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.3. Available at <https://cran.r-project.org/package=AICcmodavg>
- McDonald, M. A., Mesnick, S. L., & Hildebrand, J. A. (2006). Biogeographic characterization of blue whale song worldwide: using song to identify populations. *J. Cetacean Res. Manage.*, 8(1), 55–65. <https://doi.org/10.47536/jcrm.v8i1.702>
- Melcón, M. L., Cummins, A. J., Kerosky, S. M., Roche, L. K., Wiggins, S. M., & Hildebrand, J. A. (2012). Blue whales respond to anthropogenic noise. *PLoS ONE*, 7(2). <https://doi.org/10.1371/journal.pone.0032681>
- Monnahan, C. C., Branch, T. A., & Punt, A. E. (2015). Do ship strikes threaten the recovery of endangered eastern North Pacific blue whales? *Marine Mammal Science*, 31(1), 279–297. <https://doi.org/10.1111/mms.12157>

- Monnahan, C. C., Branch, T. A., Stafford, K. M., Ivashchenko, Y. v., & Oleson, E. M. (2014). Estimating historical eastern North Pacific blue whale catches using spatial calling patterns. *PLoS ONE*, 9(6). <https://doi.org/10.1371/journal.pone.0098974>
- Moore, S. E. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, 89(3), 534–540. <https://academic.oup.com/jmammal/article/89/3/534/859859>
- National Marine Fisheries Service. (2022). *Blue Whale (Balaenoptera musculus musculus): Eastern North Pacific Stock*.
- Oleson, E. M., Wiggins, S. M., & Hildebrand, J. A. (2007). Temporal separation of blue whale call types on a southern California feeding ground. *Animal Behaviour*, 74(4), 881–894. <https://doi.org/10.1016/j.anbehav.2007.01.022>
- Pettis, H. M., Rolland, R. M., Hamilton, P. K., Brault, S., Knowlton, A. R., & Kraus, S. D. (2004). Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. *Canadian Journal of Zoology*, 82(1), 8–19. <https://doi.org/10.1139/z03-207>
- Pierce, S. D., Barth, J. A., Thomas, R. E., & Fleischer, G. W. (2006). Anomalously warm July 2005 in the northern California Current: Historical context and the significance of cumulative wind stress. *Geophysical Research Letters*, 33(22). <https://doi.org/10.1029/2006GL027149>
- R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>.
- Ralston, S., Field, J. C., & Sakuma, K. M. (2015). Long-term variation in a central California pelagic forage assemblage. *Journal of Marine Systems*, 146, 26–37. <https://doi.org/10.1016/j.jmarsys.2014.06.013>
- Rice, D.W. (1978). Blue whale. In: D. Haley (Ed.), *Marine Mammals of Eastern Pacific and Arctic Waters* (pp. 30–35). Pacific Search Press, Seattle.
- Rockwood, R. C., Calambokidis, J., & Jahncke, J. (2017). High mortality of blue, humpback and fin whales from modeling of vessel collisions on the U.S. West Coast suggests population impacts and insufficient protection. *PLoS ONE*, 12(8). <https://doi.org/10.1371/journal.pone.0183052>

- Santora, J. A., Mantua, N. J., Schroeder, I. D., Field, J. C., Hazen, E. L., Bograd, S. J., Sydeman, W. J., Wells, B. K., Calambokidis, J., Saez, L., Lawson, D., & Forney, K. A. (2020). Habitat compression and ecosystem shifts as potential links between marine heatwave and record whale entanglements. *Nature Communications*, *11*(1).
<https://doi.org/10.1038/s41467-019-14215-w>
- Schleimer, A., Ramp, C., Delarue, J., Carpentier, A., Bérubé, M., Palsbøll, P. J., Sears, R., & Hammond, P. S. (2019). Decline in abundance and apparent survival rates of fin whales (*Balaenoptera physalus*) in the northern Gulf of St. Lawrence. *Ecology and Evolution*, *9*(7), 4231–4244. <https://doi.org/10.1002/ece3.5055>
- Schroeder, I. D., Santora, J. A., Mantua, N., Field, J. C., Wells, B. K., Hazen, E. L., Jacox, M., & Bograd, S. J. (2022). Habitat compression indices for monitoring ocean conditions and ecosystem impacts within coastal upwelling systems. *Ecological Indicators*, *144*.
<https://doi.org/10.1016/j.ecolind.2022.109520>
- Soledade Lemos, L., Burnett, J. D., Chandler, T. E., Sumich, J. L., & Torres, L. G. (2020). Intra- and inter-annual variation in gray whale body condition on a foraging ground. *Ecosphere*, *11*(4). <https://doi.org/10.1002/ecs2.3094>
- Stewart, J. D., Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Casler, P. K., Ward, E. J., & Dapp, D. R. (2021). Survival of the fattest: linking body condition to prey availability and survivorship of killer whales. *Ecosphere*, *12*(8). <https://doi.org/10.1002/ecs2.3660>
- Thomas, A. C., & Brickley, P. (2006). Satellite measurements of chlorophyll distribution during spring 2005 in the California current. *Geophysical Research Letters*, *33*(22).
<https://doi.org/10.1029/2006GL026588>
- Torres, L. G., Bird, C. N., Rodríguez-González, F., Christiansen, F., Bejder, L., Lemos, L., Urban R, J., Swartz, S., Willoughby, A., Hewitt, J., & Bierlich, K. C. (2022). Range-Wide Comparison of Gray Whale Body Condition Reveals Contrasting Sub-Population Health Characteristics and Vulnerability to Environmental Change. *Frontiers in Marine Science*, *9*. <https://doi.org/10.3389/fmars.2022.867258>
- van Weelden, C., Towers, J. R., & Bosker, T. (2021). Impacts of climate change on cetacean distribution, habitat and migration. *Climate Change Ecology*, *1*, 100009.
<https://doi.org/10.1016/j.ecochg.2021.100009>

- Wachtendonk, R., Calambokidis, J., & Flynn, K. (2022). Blue Whale Body Condition Assessed Over a 14-Year Period in the NE Pacific: Annual Variation and Connection to Measures of Ocean Productivity. *Frontiers in Marine Science*, 9.
<https://doi.org/10.3389/fmars.2022.847032>
- White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, 46, S120–S139.
<https://doi.org/10.1080/00063659909477239>
- 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>
- Yochem, P.K. & Leatherwood, S. (1985). Blue whale *Balaenoptera musculus* (Linnaeus, 1758). In: S. H. Ridgway & R. Harrison (Eds.), *Handbook of Marine Mammals* (Vol. 3; pp. 193–240). Academic Press, London.