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**Blue Whale Body Condition from Photographs Taken Over a
14-Year Period in the NE Pacific: Annual Variation and
Connection to Measures of Ocean Productivity**



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Mestrado em Biologia Marinha

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Abstract

Large marine mammals can serve as an indicator of the overall state of the environment due to their long lifespan and position in marine food webs. Reductions in prey, driven by changes in environmental conditions can have resounding impacts on the trophic system as a whole, which can manifest in reduced fat stores that are visible on whales. Poor health can lead to reduced survivorship and fitness, both of which can be detrimental to recovering populations. A non-invasive technique using digital photographs of blue whales taken in the NE Pacific from 2005-2018 (n=3,660) scored the overall body condition based on visible vertebrae and body shape. The data was analyzed to determine if there were patterns in the health of whales across years and whether overall poor health was related to oceanographic conditions and predictors of prey abundance. Overall, known females with calves had significantly poorer body conditions and calves had significantly better body conditions in comparison to the general population (Chi-Square, $p < 2.2e-16$). Year was a highly significant factor in body condition (Chi-Square, $p < 0.001$). The only two years where $>50\%$ of animals had poor body condition were 2015 and 2017 (no other year was above 45%). The 2015 maximum proportion of whales in poor body condition coincide with the marine heat wave that affected the NE Pacific 2014-16 and impacted other whale populations. We modeled the impact of various environmental indices on blue whale body condition and found the yearly average Pacific Decadal Oscillation value and yearly average Bakun Upwelling Index both influence body condition scores due to their role in promoting primary productivity and prey availability for these whales. This study indicates our scoring method effectively evaluated blue whale health and how they respond to a changing ocean.

Keywords Blue whale, body condition, environmental variability, photo-identification, marine heat wave

Resumo

Considerando a sua longevidade e a posição que ocupam nas teias tróficas marinhas, os mamíferos marinhos de grande porte podem constituir indicadores sobre o estado geral dos ecossistemas marinhos. A redução na disponibilidade de presas, determinadas por modificações ambientais pode determinar impactos consideráveis no sistema trófico global e que se podem manifestar através da redução da acumulação de gordura que é visível nas baleias. Este aspecto pode ter consequências directas na redução da condição física e na sobrevivência e que, por seu lado, interferem com a capacidade de recuperação das populações. Muitas espécies de cetáceos estão ainda numa fase de recuperação da actividade de pesca baleeira, incluído a baleia-azul (*Balaenoptera musculus*), que foi capturada quase até à extinção, antes de terem sido implementadas as medidas de protecção. A baleia-azul é o maior animal do planeta e, como tal, apresenta elevados requisitos alimentares. Esta espécie alimenta-se exclusivamente em eufausiáceos (*krill*) e precisa de consumir até cerca de duas toneladas deste alimento por dia recorrendo frequentemente, durante a época de alimentação, a manobras acrobáticas e exigentes do ponto de vista energético e que permitem manter a massa corporal durante o período restante do ano.

Devido à sua dieta extremamente limitada, a baleia-azul está extremamente dependente dos factores ambientais que determinam a abundância e concentração do *krill*. O manancial de baleia-azul do oceano Pacífico Nordeste, que habita no sistema de correntes da Califórnia, parece ter recuperado até níveis de abundância pré-era da pesca baleeira. Contudo, durante a última década, este ecossistema foi alvo de vários acontecimentos climáticos extremos que tiveram um impacto directo sobre a condição das baleias-azuis que aí ocorrem.

Os objectivos deste trabalho foram os seguintes: (1) determinar se a foto-identificação pode ser utilizada para avaliar a condição corporal e (2) determinar quais os factores que influenciam a condição corporal no ecossistema influenciado pela Corrente da Califórnia

Neste sentido, foi desenvolvida uma técnica não-invasiva que recorre a fotografia digital de 3660 baleias-azuis e que foram obtidas no Pacífico Nordeste entre 2005 e 2018, tendo sido avaliada a condição corporal geral baseada na observação das vértebras visíveis e na forma do corpo. As

imagens foram classificadas de acordo com uma escala de 0 a 3, onde 0 indica a melhor condição corporal e 3 a mais deficiente.

A informação foi analisada para avaliar a eventual existência de padrões no estado geral das baleias-azuis ao longo do tempo e quais as variações inter-anuais nas classes reprodutivas. Foi desenvolvido um modelo cumulativo misto para averiguar se a condição corporal está relacionada com condições oceanográficas e preditores de abundância de presas.

A quantidade de gordura acumulada nos flancos laterais variou e esta região apresentou a vantagem de permitir focar o alvo das imagens de foto-identificação, permitindo incluir a informação histórica na análise efectuada. De um modo geral, as fêmeas com crias apresentaram uma condição significativamente mais baixa enquanto que as crias apresentaram uma condição mais elevada, quando comparados com a população em geral (Qui-quadrado, $p < 2.2e-16$). A condição mais baixa em fêmeas que alimentam crias está bem documentada o que resulta dos requisitos energéticos elevados da amamentação, que utiliza entre 29-41% da energia obtida durante a época de alimentação. As crias apresentaram consistentemente uma boa condição, tendo 76% consideradas saudáveis (nível 0), independentemente de algumas variações terem sido observadas nos outros grupos. Este resultado pode ter sido determinado pela relação entre a condição e o sucesso reprodutivo observado em outras espécies. Se uma fêmea não tem a capacidade para suportar energeticamente uma cria, poderá abortá-la *in utero* de modo a maximizar a probabilidade de sobrevivência. Isto indica que condições limitadas na alimentação pode determinar uma diminuição na fertilidade, aspecto particularmente relevante em espécies ameaçadas. Um ano com condições de alimentação deficientes ou limitadas pode influenciar mais do que apenas a taxa de gravidez nesse ano, já que uma condição física deteriorada pode ter um impacto negativo em épocas reprodutivas dos anos seguintes. Se as condições de alimentação forem deficientes em anos consecutivos, como pode acontecer em resultado de ondas de calor, a recuperação de populações ameaçadas em termos de longo-prazo pode estar comprometida.

A variável *ano* foi igualmente um factor com influência significativa na condição (Qui-quadrado, $p < 0.001$). A proporção geral de animais apresentado uma condição deficiente (níveis 2 e 3) foi de 33%, tendo variado entre 18%, em 2008 e 55%, em 2015. Apenas em 2015 e 2017 menos de 50%

dos animais apresentaram uma condição baixa. O valor mais baixo da proporção de baleias com condição baixa obtido em 2015 coincidiu com uma onda de calor que afectou o oceano Pacífico Nordeste entre 2014 e 2016 e que demonstrou o seu impacto sobre as baleias-azuis. Esta onda de calor teve um impacto directo sobre a temperatura da água do mar com um aumento superior a 3°C com um máximo de 6.2°C registado ao largo da Califórnia do Sul. Este tipo de ondas de calor determinam uma diminuição na produtividade primária marinha e que pode perturbar a organização dos níveis mais baixos da teia trófica marinha que incluem os eufausiáceos, a principal fonte de alimento das baleias-azuis.

Foi modelado a relação entre diversos índices ambientais poderão desencadear e a condição da baleia-azul e desenvolvido um modelo incorporando a proporção entre as imagens, o valor médio anual da oscilação da década no Pacífico (Pacific Decadal Oscillation, PDO), a média anual do índice de ressurgimento (*upwelling*) de Bakun (BUI) e a inter-acção entre a classe reprodutiva e um intervalo de dois anos da onda de calor, que explicou cerca de 75% da variabilidade dos dados. Ambos os índices ambientais desempenha um papel importante ao promover a produtividade primária e a disponibilidade das presas da baleia-azul.

A PDO é o factor determinante da temperatura das águas superficiais indicando os valores mais reduzidos uma menor temperatura e, inversamente, os valores mais elevados uma temperatura mais alta. O ressurgimento sazonal, medido através do índice BUI determina a elevação para a superfície das camadas de água mais profundas e mais ricas em nutrientes o que tem um efeito directo no aumento da produtividade primária e secundária das águas superficiais o que determina o aumento do número de baleias-azuis decorrente deste fenómeno oceanográfico e que para aqui se deslocam para a estação de alimentação. De um modo geral, valores mais elevados de PDO coincidiram com uma diminuição dos valores de BUI. Em anos em que se registaram valores mais elevados de e em anos em que se registaram valores mais reduzidos de PDO verificou-se uma maior ocorrência de baleias-azuis com menor condição física (valores de 2 e de 3). Em anos onde se registaram valores mais baixos de PDO aumentou o número de baleias-azuis em boa condição física (valores de 0 e de 1). Um padrão inverso verificou-se para os valores de BUI, com um aumento de *upwelling* relacionado com o aumento de número de baleias-azuis em boa condição física, e vice-versa.

A monitorização da condição física das baleias-azuis com um indicador da produção aquática assumirá uma relevância crescente associada às alterações das condições ambientais do meio marinho. As alterações climáticas de origem antropogénica irão aumentar a frequência da ocorrência de ondas de calor. Este estudo contribuiu com informação de base para avaliar a condição física de baleias-azuis, podendo ser utilizado para monitorizar as populações numa perspectiva de um futuro previsivelmente em alteração.

General Introduction

Blue whales. Blue whales (*Balaenoptera musculus*) are the largest animals to have ever lived (Reeves et al. 1998; Jefferson et al. 2015). Adult blue whales in the Northern Hemisphere reach sizes of 23-27 m in length and 72,000-135,000 kg in mass (with females being larger than males). Blue whales are thought to have an average lifespan of 80-90 years, with killer whales (*Orcinus orca*) being their only natural predator since commercial whaling was banned. These whales have a cosmopolitan distribution and tend to inhabit the open ocean, however, they do come close to shore to feed. These whales are mainly solitary, often traveling alone or in pairs (Jefferson et al. 2015). But in highly productive feeding grounds these whales will gather in small areas of high krill density (Croll et al. 2005; Gill et al. 2011; Irvine et al. 2014; Jefferson et al. 2015; Lomac-MacNair and Smultea 2016).

Mating and reproduction of blue whales still has many unknowns. Their breeding grounds are not as well defined as other mysticete species like the humpback whale (*Megaptera novaeangliae*; Jefferson et al. 2015). Calving occurs in tropical and subtropical regions of the oceans in winter, although the exact location of these calving areas is unknown for most populations. At birth, calves are roughly 7.0 m in length and they will reach around 12.8 m in length by the time they are weaned (Lockyer 1984). Calves are weaned over 8 months and during that time they can gain 90 kg/day (Jefferson et al. 2015). Blue whale milk is highly caloric, with 3.99 Kcal/g and fats making up 34-50% of the wet weight (Lockyer 1984). Both males and females reach sexual maturity around 5 years of age (Lockyer 1984).

Blue whales have an extremely limited diet, feeding almost exclusively on euphausiids (krill). Due to their large size, these whales have the highest prey demands of any predator, needing to consume up to two tones of krill per day during their feeding seasons (Croll et al. 2005). This often requires the use of high-energy acrobatic maneuvers during their feeding lunges to capture prey (Acevedo-Gutiérrez et al. 2002; Calambokidis et al. 2008; Goldbogen et al. 2011; Goldbogen et al. 2015). The energy outputs for these maneuvers seem to be inversely proportional to prey density, with whales often performing more acrobatic and energetic dives on shallow, low-density krill aggregations (Goldbogen et al. 2015). While foraging, blue whales will dive to depths greater than 100 m for durations up to 30 minutes (Jefferson et al. 2015); however, because of the energy

required for acrobatic diving maneuvers, most blue whale dives only last a couple of minutes (Acevedo-Gutiérrez et al. 2002; Goldbogen et al 2011).

Like many cetacean species, blue whales were hunted excessively during the whaling era (Jefferson et al. 2015). All populations of blue whales were exploited to near extinction until they became protected by the International Whaling Commission in 1966. However blue whales as a whole are still considered endangered (the Antarctic stock being considered critically endangered), though some populations are showing signs of recovering (Thomas et al. 2015). The eastern North Pacific stock of blue whales seems to be recovering well, with the most updated abundance estimates of 1,898 whales (Calambokidis et al. 2020). Modern concerns for large whales, such as blue whales include anthropogenic noise and ship strikes (Irving et al 2014; Monnahan et al. 2015; Thomas et al. 2015; Pirodda et al. 2021).

Costs of reproduction in mysticetes. The reproductive cycle of mysticetes lasts two to three years for most species, though minke (*Balaenoptera acutorostrata*) whales (and the occasional humpback) rear a calf every year (Lockyer 1984). This cycle consists of mating in low-latitudes, migrating to high-latitudes to feed, migrating back to breeding grounds to give birth and wean calves, resting for a year or two to recover, and then starting the cycle over again (Lockyer 1984; Christiansen et al. 2014). The gestation period for mysticete whales is one year with roughly 6 months of lactation; this means that for whales who reproduce annually they can be nursing one calf while pregnant with another, further depleting their energy stores (Lockyer 1984; Christiansen et al 2014). Mysticetes are capital breeders- they must gain all of the required energy for reproduction in high-latitude feeding grounds before giving birth in low-latitude breeding grounds (Christiansen et al. 2013; Christiansen et al. 2014). They store this excess energy after meeting their needs for metabolism, maintenance, and growth mainly in blubber stores, as well as in muscle and fat. This excess energy is used during the gestation of the fetus and the production of milk for the calf once it is born. The calves gain considerable mass before being weaned, they must be able to have enough blubber to survive in the cold waters of the feeding grounds and be able to survive the long migration to those waters (Miller et al. 2012). So the cost to the cows to produce and care for a calf, as well as keep themselves healthy enough to continue reproducing is high.

The cost of reproduction is substantial for baleen whales. To meet this cost, pregnant females must gain a considerable amount of fat and blubber stores while at feeding grounds. Pregnant females are usually the first to leave the breeding grounds and the last to leave to maximize their time in productive high-latitudes. For species like blue, fin, and humpback whales, pregnant females can spend up to 50% more time in the feeding grounds than other reproductive classes (Lockyer 1984). Cow/calf pairs are often the last to make it to the feeding grounds due to the slow travel of calves and because the cows maximize their time in breeding grounds for their calves to reach a mass to survive the trip (Lockyer 1984; Miller et al. 2012). While at the feeding grounds the pregnant females must acquire enough energy for themselves, gestation (uses 16-23% of total energy intake), and lactation (uses 29-41% of total energy intake) to support their calf. It is well documented that when food is abundant, the pregnant whales put on the most body fat which can be seen in girth and blubber measurements, with an overall body mass increase of 60-65% (compared to 50% for the resting population; Lockyer 1984; Lockyer 1986; Lockyer 2007; Miller et al. 2012; Christiansen et al. 2013). In mammals, during the beginning of gestation, the fetus grows at a slow but consistent rate until the prenatal phase where growth rapidly increases up until the calf is born (Christiansen et al. 2014). For balaenopterids, the prenatal phase coincides with the arrival of the pregnant whales at their feeding grounds; meaning up until this time females had been relying on body stores to provide the energy for fetal growth. Then during the last part of the pregnancy- as well as birth and lactation- females must again rely on energy stores to provide for their calves. Mysticetes have some of the highest fetal growth rates of any mammal (0.964 ± 0.138 cm/day for minke whales; Christiansen et al. 2014), so females need to gain as much mass as possible in feeding grounds. Lactation is the costliest part of reproduction, requiring 3-5 times more energy than gestation (Miller et al. 2012). During this time calves must grow to a size where they can survive the migration to the feeding grounds as well as have thick enough blubber to last in the colder waters. Right whale calves can grow up to 2.8 ± 0.7 cm/day from milk alone and width measurements of the mothers reaching a minimum around 2-4 months into lactation (Miller et al. 2012). Since the initial cost of pregnancy requires little energy, much of the energy gained in feeding grounds goes into milk production (Lockyer 1984). Whale milk has an exceptionally high-fat content, which allows calves to increase their body weight 5-8 times by the time they are weaned (Lockyer 1984).

Since the cost of reproduction is so high and relies heavily on gaining enough energy during the feeding season, cows can run into serious issues when they cannot amass the energy needed to raise a calf. The quality and quantity of prey at feeding grounds is linked to the increase of mass in whales (Lockyer 1986; Lockyer 2007; Bradford et al. 2012; Williams et al. 2013; Soledade Lemos et al. 2020). Cows almost always are the thinnest animals in the population while lactating (Pettis et al. 2004; Bradford et al. 2012; Miller et al. 2012; Christiansen et al. 2014), so this coupled with poor feeding conditions can put the life of the cow and calf in jeopardy. But the survival of reproductive females is much more important to the overall fitness of a population than the survival of a calf, so females will choose to put themselves before their calf if needed. How they reduce investment is based on the progression of the pregnancy. Some mammals might reduce the gestation time of the pregnancy if they do not have the energy reserves, but this is unlikely for mysticetes since their gestation time is linked so closely with their migration patterns (Christiansen et al. 2014). Instead, females may reduce the energy expended on their calf by decreasing the growth rate of the fetus in utero, so females with reduced body condition will have smaller calves at birth. However, reducing the energy expenditure to the fetus can impact the ability to carry the fetus to term or decrease their chance of survival in the long run (Christiansen et al. 2014). Poor foraging conditions can influence more than just pregnancies for that year- in a process known as the carry-over effect, a reduced body condition of a reproductive female can decrease their ability to carry a pregnancy to term in future years (Soledade Lemos et al. 2020). For right whales, documented decreases in their prey lead to a reduction in the calving rates (Greene et al. 2003). But the calving rate boomed after foraging conditions improved a few years later, almost doubling, then falling again when poor feeding conditions returned. The close relationship between feeding success and reproductive success of mysticetes has implications in the way these whales should be managed.

California Current System. The California Current System (CCS) is a highly productive region of the Pacific Ocean which spans from the North Pacific (~50°N) to Baja California, Mexico (~15-25°N) (Huyer 1983; Di Lorenzo et al. 2008; McClatchie et al. 2008; Checkley and Barth 2009; Palacios et al. 2019). Seasonally, upwelling occurs in the spring/summer and varies in strength along the current, which leads to high levels of primary and secondary production (Huyer 1983; Fiedler et al. 1998; Croll et al. 2005; Checkley and Barth 2009). Interannual to decadal variation

(1-20 y) is the dominant form of variation in the CCS. The most notable form of this is the El Niño-Southern Oscillation (ENSO) which can impact upwelling strength and the makeup of marine life at the base of the food web (Benson et al. 2002; Brinton and Townsend 2003; McClatchie et al. 2008; Bograd et al. 2009; Checkley and Barth 2009). The Pacific Decadal Oscillation (PDO; Mantua and Hare 2002; Brinton and Townsend 2003; Di Lorenzo and Mantua 2016) and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008; Di Lorenzo and Mantua 2016) are the primary and secondary drivers of sea surface temperature (SST) in the Pacific Ocean Basin respectively (Checkley and Barth 2009).

Several important climatic events occurred during the study period that are important to note. In 2005, the seasonal spring transition was delayed by a few months (one of the most delayed onsets in the previous 40 years), which had resounding impacts on the ecosystem (Schwing et al. 2006; McClatchie 2008; Checkley and Barth 2009). The delay in the commencement of upwelling resulted in warmer surface temperatures and reduced nutrients- leading to a reduction in primary productivity. This led to a spatial redistribution of zooplankton, low recruitment of rockfish and forage fish species as well as a reproductive failure of the Cassin's auklet (*Ptychoramphus aleuticus*, Schwing et al. 2006). However, when upwelling did begin in late July of that year, the sea surface cooled and normal primary productivity returned to this region. The other notable climatic event was the marine heat wave that lasted from 2014-2016 (Di Lorenzo and Mantua 2016; Gentemann et al. 2017; Thompson et al. 2018). The heat wave started in the Gulf of Alaska in November 2013 and then made its way down the CCS, with sea surface temperature anomalies (SSTa) exceeding 3°C (maximum SSTa of 6.2°C off Southern California). This marine heat wave had enormous impacts on the environment including reduced primary productivity and changes in the composition of zooplankton assemblages (Di Lorenzo and Mantua 2016; Gentemann et al. 2017). These changes had bottom-up impacts on many higher trophic levels such as a marine mammal mortality event of pinnipeds in California resulting from poor foraging conditions (Cavole et al. 2016; Di Lorenzo and Mantua 2016). The heat wave was the warmest three-year stretch on record, and while 2016-2017 did not have extreme SSTa, above normal SST and reduced primary productivity persisted in many areas of the CCS, especially in the south (Thompson et al. 2018).

Marine heat waves. Marine heat waves are not new phenomena, but their increasing frequency has led them to be a subject of focus (Di Lorenzo et al. 2016; Hobday et al. 2016; Gentemann et al. 2017; Frölicher et al. 2018; Oliver et al. 2018; Holbrook et al. 2019; Oliver et al. 2021). In general marine heat waves are periods of abnormally high SST, just as terrestrial heat waves are periods of abnormally high air temperatures. Quantitatively, marine heat waves are events that last for at least five days with temperatures above the 90th (Hobday et al. 2016) or 99th (Frölicher et al. 2018) percentile of a 30-year baseline for that region; or above a fixed threshold defined by the thermal limits of marine species or temporally fixed measure of temperature variance (Oliver et al. 2021). These events can have enormous detriments to marine life and are only increasing with their frequency, duration, and impact (Frölicher et al. 2018). Notable marine heat waves in the past decade include events such as the 2012 heat wave in the northwest Atlantic Ocean, the 2013-2016 heat wave in the northeast Pacific Ocean, and the 2015-2016 heat waves in the Tasman Sea and tropical Australian waters (Holbrook et al. 2019).

Marine heat waves impact the base of the food web which then ripples up the trophic chain. They reduce mixing and upwelling which leads to low primary productivity that causes changes in the makeup and distribution of organisms low on the food web, like copepods and krill (Di Lorenzo et al. 2016; Thompson et al. 2018; Barlow et al. 2020). This impacts the abundance and distribution of other organisms that feed on them, which can lead to reductions in prey species for many other marine animals. For example, in the 2016-2018 eastern North Pacific heat wave there were documented instances of a large number of dead or starving Cassin's auklets (*Ptychoramphus aleuticus*), and unusual mortality events for both California sea lions (*Zalophus californianus*) and whales which were related to the reductions in their prey (Di Lorenzo et al. 2016; Frölicher and Laufkötter 2018).

There can also be a reduction in the types of habitats or oceanographic features that certain species like to forage in. Marine mammals, for instance, often display high site fidelity for feeding grounds, breeding grounds, and migration paths that may be vulnerable to climate change and climate change related heat waves (Silber et al. 2017). For animals that can travel to follow prey, marine heat waves can lead to spatial and temporal changes in the distribution of those animals. These changes in distribution have led to overlapping with fisheries, often to the detriment of those

animals. In the Southern Taranaki Bight of New Zealand, the distribution and density of krill aggregations have shifted with warm and cool periods- with fewer and less dense aggregations during warm regimes (Barlow et al. 2020). This also changed the distribution of blue whales in the region as they moved with the prey patches, leading to a compression and shift of their habitat in the bight (Barlow et al. 2020). In the California Current System (CCS) there were also changes in the assemblages of marine species during and after the recent marine heat wave experienced there. Eleven warm-water copepod species uncommon to the area were found in the northern California Current shelf and slope region (Di Lorenzo et al. 2016), semi-tropical fish were found in southern California, and anchovy abundance was greatly increased (Cavole et al. 2016; Thompson et al. 2018). Certain species, like the wahoo (*Acanthocybium solandri*) were found 3,500 km north of their typical northernmost distribution (Cavole et al. 2016). The compression of certain species ranges also led to interactions with local fisheries, such as whale entanglement in fishing gear. Also during the 2014-2016 CCS heat wave, the reduction of krill led humpback whales to move shoreward to take advantage of the increased abundance of anchovy (Cavole et al. 2016; Santora et al. 2020). This led to the temporal and spatial overlap with a crab fishery that had an unexpected delay to their opening due to domoic acid contamination. During this time there was also a spike in entanglements of blue, grey, and especially humpback whales from about 25 entanglements in 2014 to over 50 entanglements in 2015 and 2016 (Santora et al. 2020). It is clear that marine heat waves have a large and disproportionately negative impact on marine life and threaten many of our fisheries. Some species may be able to change their distribution, but the rapid increase in heat waves will be hard for species to adapt to over generations. This is especially true for species, like marine mammals, who have long lifespans, low reproduction rates, and long generation times (Silber et al. 2017).

Marine heat waves have occurred more frequently, for longer periods of time, and at a higher intensity than in the past and that trend appears to be continuing. Comparing two 30-year time periods globally (1925-1954 and 1987-2016), the frequency of marine heat waves increased by 34% and duration increased by 17%, meaning a combined increase of 54% in the total number of marine heat wave days (Oliver et al. 2018). Anthropogenic climate change driven by the increase of fossil fuels in the atmosphere has on average, increased SST globally (Frölicher et al. 2018; Oliver et al. 2018).

Research gaps. Studying body condition as an indicator of health has been undertaken for many years in both the marine and terrestrial ecosystems (Lockyer et al. 1985; Lockyer 1986; Batzli and Esseks 1992; Pettis et al. 2004; Konishi 2006; Acevedo-Whitehouse and Duffus 2009; Bradford et al. 2012; Williams et al. 2013; Braithwaite et al. 2015; Soledade Lemos et al. 2020). These studies are important to gauge the health of recovering populations of animals and can be used to evaluate the environment as a whole. While “ecosystem health” can be a difficult thing to measure, especially in the marine environment, assessing the condition of large, long-lived predators can alert how an ecosystem is functioning (Williams et al. 2013).

Measuring the conditions of baleen whales has been shown to be difficult in body condition studies. Unlike smaller cetaceans and pinnipeds, large baleen whales cannot be weighed or removed from the water for extensive measurements (Konishi 2006). Additionally, only a limited portion of these animals are seen from the surface, and the remoteness of their habitat and variable sighting frequencies make health assessments more difficult compared to other species (Pettis et al. 2004). Many previous studies have used whaling data for their measurements of girth and blubber thickness (Lockyer et al. 1985; Lockyer 1986; Konishi 2006; Williams et al. 2013; Braithwaite et al. 2015). However, these studies often come with caveats such as limitations on the species and size classes that were authorized in the takes. Additionally, whaling was banned internationally in the 1980s (although Japan, Norway, and Iceland still hunt fin, minke, and sei whales) so many of these datasets are solely historical, and current patterns cannot be observed.

Thus, photographic data has been developed as a non-invasive way to monitor whale populations. Photographic data can be split into two categories, visual qualitative measurements, and drone photogrammetry. Drone photogrammetry is a newer development in body condition studies and has the added benefit of being able to record quantitative measurements (Durban et al. 2016; Soledade Lemos et al. 2020; Leslie et al. 2020). This method of study has produced valuable results in body condition research but it also has its drawbacks. Namely, drone research can be more logistically constraining, and historical images cannot be compared, so data stretches years, instead of decades. Visual health assessments based on photographs, therefore are extremely valuable for health studies. In addition to being non-invasive, the target area for assessment can often be seen

in images used for photo identification, allowing for long-term studies (Pettis et al. 2004; Bradford et al. 2012). Both types of studies have found clear temporal trends in the overall health of the animals both within a feeding season and over the years. Assessments have been performed on baleen whales such as North Atlantic right whales (*Eubalaena glacialis*) (Pettis et al. 2004), and grey whales (*Eschrichtius robustus*) (Bradford et al. 2012; Soledade Lemos et al. 2020). So while image-based assessments are not a new concept, this will be the first of its kind for blue whales.

Research approach. This research project aims to determine if blue whale health can be derived from photo identification images and if so, to see if the health of the population shows clear temporal trends. In order to determine how changes in the California Current System impact blue whale health, I will analyze images of whales from over a decade to assess temporal changes in body condition and see how these changes relate to environmental variables. This will be the first study of this kind to be performed on blue whales. Assessment of body condition based on photographic data has been successful for many mysticetes (Pettis et al. 2004; Bradford et al. 2012; Soledade Lemos et al. 2020), and animals showed clear trends in the health of a population both inter-annually and over longer time periods. Blue whales are expected to show a similar trend with noticeable increases in body fat during a feeding season and overall health varying across years with overall changes to the environment.

“Health” can be a relative term but is defined as “the state of the organism when it functions optimally without evidence of disease or abnormality” (Steadman 2000). Blue whales in this study will be scored on a scale of 0-3, with a score of 0 indicating a visually healthy whale, a score of 1 indicating a moderately healthy whale, a score of 2 indicating a moderately unhealthy whale, and a score of 3 indicating an unhealthy whale. It is important to note that a score of 3 does not mean that the whale is unlikely to recover and survive, although it can be presumed that starving whales would be scored as “unhealthy” in this study. Instead of a projection for survival, these scores are meant to indicate the relative energy stores that a whale possesses (Bradford et al. 2012). Due to the feast and famine lifestyle of large whales, individuals that are identified to be in a compromised body condition (a score of 2 or 3) may not be fully equipped for their extreme life history, which may result in declines in the physical and reproductive health of an individual (Bradford et al. 2012; Soledade Lemos et al. 2020).

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TITLE

Blue Whale Body Condition from Photographs Taken Over a 14-Year Period in the NE Pacific: Annual Variation and Connection to Measures of Ocean Productivity

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Abstract

Large marine mammals can serve as an indicator of the overall state of the environment due to their long lifespan and position in marine food webs. Reductions in prey, driven by changes in environmental conditions can have resounding impacts on the trophic system as a whole, which can manifest in reduced fat stores that are visible on whales. Poor health can lead to reduced survivorship and fitness, both of which can be detrimental to recovering populations. A non-invasive technique using digital photographs of blue whales taken in the NE Pacific from 2005-2018 (n=3,660) scored the overall body condition based on visible vertebrae and body shape. The data was analyzed to determine if there were patterns in the health of whales across years and whether overall poor health was related to oceanographic conditions and predictors of prey abundance. Overall, known females with calves had significantly poorer body conditions and calves had significantly better body conditions in comparison to the general population (Chi-Square, $p < 2.2e-16$). Year was a highly significant factor in body condition (Chi-Square, $p < 0.001$). The only two years where $>50\%$ of animals had poor body condition were 2015 and 2017 (no other year was above 45%). The 2015 maximum proportion of whales in poor body condition coincide with the marine heat wave that affected the NE Pacific 2014-16 and impacted other whale populations. We modeled the impact that various environmental indices have on blue whale body condition and found that the yearly average Pacific Decadal Oscillation value, and yearly average Bakun Upwelling Index both influence body condition scores due to their role in promoting primary productivity and prey availability for these whales. This study indicates that our scoring method effectively evaluated blue whale health and how they respond to a changing ocean.

Introduction

Large marine mammals can serve as an indicator of the overall state of the environment due to their long lifespan and apex position in marine food webs (Batzli and Esseks 1992; Williams et al. 2013). Changes in environmental conditions can manifest in reductions of prey at the base of the food web, which impacts predators further up the trophic chain (Acevedo-Whitehouse and Duffus 2009; Benoit-Bird and McManus 2012; Soledade Lemos et al. 2020). In the case of large whales, reduced food availability has been shown to result in visible reductions in fat stores (Lockyer 1986; Konishi 2006; Christiansen et al. 2013; Braithwaite et al. 2015). Whales with a compromised body condition may be unable to take on the challenges of their extreme life history which can lead to reduced survivorship and reproductive fitness (Greene et al. 2003; Lockyer 2007; Bradford et al. 2012; Soledade Lemos et al. 2020). This can have adverse impacts on the population or species as a whole, which is compounded in recovering populations (Acevedo-Whitehouse and Duffus 2009).

These impacts are magnified in pregnant and lactating females who rely on a bountiful foraging season in order to sustain themselves and their calf during the gestation (uses 16-23% of total energy intake from foraging) and lactation (uses 29-41% of total energy intake) phases of the pregnancy (Lockyer 1984; Miller et al. 2012; Christiansen et al. 2013; Christiansen et al. 2014). When females are unable to gather the necessary reserves to wean a calf they often have to choose between their own survival and the potential survival of the calf. Since reproductive females can give birth to a calf at a yearly to bi-yearly rate, the survival of the females is more important to the fitness of the population, and females will reduce the energy they invest in their calf (Christiansen et al. 2014). This can be done by decreasing the growth rate of the fetus in utero or by aborting the fetus entirely (Ichihara 1962; Christiansen et al. 2014). Poor foraging can also influence future pregnancies through a process known as the carry-over effect- where a reduced body condition of a reproductive female can decrease her ability to carry a pregnancy to term in future years, ultimately impacting population growth rates (Soledade Lemos et al. 2020).

The eastern North Pacific population of blue whales (*Balaenoptera musculus*) forage within the highly productive California Current System (CCS) that spans from the North Pacific (~50°N) to Baja California, Mexico (~15-25°N) (Huyer 1983; Di Lorenzo et al. 2008; McClatchie et al. 2008; Checkley and Barth 2009; Palacios et al. 2019; Calambokidis et al. 2020). These whales reach

sizes of 23-27 m in length and 72,000-135,000 kg in mass (with females being larger than males) and have an estimated lifespan of 80-90 years (Jefferson et al. 2015). Blue whales reach sexual maturity around 5 years of age and reproduce in tropical and subtropical regions of the Pacific Ocean in winter, although the exact location of these calving grounds is unknown (Lockyer 1984; Jefferson et al. 2015; Busquets-Vass et al. 2021). Blue whales are the largest animal on Earth and thus have the highest prey demands (Croll et al 2005). These large animals feed almost exclusively on euphausiids (krill) and must consume up to two tons of euphausiids per day, often employing costly energetic and acrobatic maneuvers, during their feeding season to maintain their masses for the remainder of the year (Acevedo-Gutiérrez et al. 2002; Croll et al. 2005; Calambokidis et al. 2008; Goldbogen et al. 2011; Friedlaender et al. 2015; Goldbogen et al. 2015; Barlow et al. 2020). Like all mysticetes, blue whales were hunted extensively during the whaling era, facing reductions in populations of as much as 90% (Jefferson et al. 2015; Thomas et al. 2015). After they became a protected species by the International Whaling Commission in 1966 blue whale populations started to increase, but they are still considered endangered. The eastern North Pacific population of blue whales is currently estimated to be at 1,898 individuals (Calambokidis et al. 2020).

Due to their extremely limited diet, blue whale health is closely linked with environmental factors that determine krill abundance and concentration (Croll et al. 2005; Calambokidis et al. 2007; Silber et al. 2017). The eastern North Pacific blue whales forage in the highly productive California Current System (CCS) which spans from the North Pacific (~50°N) to Baja California, Mexico (~15-25°N) (Huyer 1983; Di Lorenzo et al. 2008; McClatchie et al. 2008; Checkley and Barth 2009; Palacios et al. 2019). Productivity and sea surface temperature in the CCS is driven by patterns of variability on various spatial and temporal scales from local and seasonal upwelling to the ocean basin level interannual/decadal El Niño-Southern Oscillation and Pacific Decadal Oscillation. The CCS saw some climatic events during this study period that had resounding impacts on the ecosystem such as a delay in the spring transition in 2005 and a large marine heat wave that lasted from 2014-2016 with sea surface temperature anomalies (SSTa) exceeding 3°C (maximum SSTa of 6.2°C off Southern California) and was the warmest three year stretch on record (Schwing et al. 2006; McClatchie 2008; Checkley and Barth 2009; Di Lorenzo and Mantua 2016; Gentemann et al. 2017; Thompson et al. 2018). Marine heat waves can cause low primary productivity that then changes in the makeup and distribution of organisms low on the food web,

such as the main prey source for blue whales- euphausiids (Di Lorenzo and Mantua 2016; Thompson et al. 2018; Barlow et al. 2020). The 2015-2016 heat wave in the CCS caused unusual mortality events for Cassin's auklets (*Ptychoramphus aleuticus*), California sea lions (*Zalophus californianus*), and whales related to the reductions in their prey (Di Lorenzo et al. 2016; Frölicher and Laufkötter 2018).

Measuring body condition has become a reliable way to assess the health of an individual or a population in both terrestrial and aquatic ecosystems (Lockyer et al. 1985; Lockyer 1986; Batzli and Esseks 1992; Pettis et al. 2004; Konishi 2006; Acevedo-Whitehouse and Duffus 2009; Bradford et al. 2012; Williams et al. 2013; Braithwaite et al. 2015; Soledade Lemos et al. 2020). Body condition studies are incredibly important to gauge the health of recovering populations of animals and the environment as a whole. "Ecosystem health" can be a complex metric to measure, especially in the marine environment, therefore assessing the body condition of large, long-lived predators can alert how an ecosystem is functioning (Williams et al. 2013). However, the logistics of measuring the body condition of large baleen whales due to their size, sighting frequency, and remoteness is much more difficult than terrestrial or even pinniped and small cetacean studies (Pettis et al. 2004; Konishi 2006). In order to overcome this, previous studies have used blubber thickness as well as whaling measurements of girth to estimate health (Lockyer et al. 1985; Lockyer 1986; Konishi 2006; Williams et al. 2013; Braithwaite et al. 2015). But these studies have limitations in the species and size classes authorized for takes, especially after international whaling was outlawed in the 1980s.

To overcome these hurdles, the use of photographic data, such as visual qualitative measurements, and drone photogrammetry, has been developed as a non-invasive way to monitor whale populations. The use of drones to measure the body condition of marine mammals has become increasingly popular over the years (Durban et al. 2016; Soledade Lemos et al. 2020; Leslie et al. 2020). This methodology has the benefits of being able to gather quantitative measurements that can yield body index scores, and can track a female through her pregnancy. However, drone research can be more logistically constraining and historical images cannot be compared, limiting the study of long temporal trends. Qualitative visual body condition studies are both non-invasive and the target area for assessment can often be seen in photo identification images, making this

methodology valuable for long-term studies (Pettis et al. 2004; Bradford et al. 2012). Photographic studies show clear temporal trends in the body condition of baleen whales within feeding seasons and over years for species such as North Atlantic right whales (*Eubalaena glacialis*) (Pettis et al. 2004), and grey whales (*Eschrichtius robustus*) (Bradford et al. 2012; Soledade Lemos et al. 2020). A drone study of blue whale length and width found that there were measurable differences in whales due to variations in body condition (Durban et al. 2016), however, further analysis has not yet been performed. Therefore, this qualitative visual body condition study will be the first of its kind for blue whales.

The aims of this study were (1) to determine if photo ID images of blue whales can be used to assess body condition, (2) to determine what factors influence blue whale body condition in the California Current Ecosystem and to see if body condition varied by year, and (3) to test whether the methodology could detect differences by reproductive class. Furthermore, we explored various environmental indices to determine which ones impacted blue whale body condition. This research provides a non-invasive model for monitoring blue whale health in the future and determining how blue whales may respond to a quickly changing ocean.

Methods

Sighting data. Blue whale sighting data was collected by Cascadia Research Collective and contributors primarily from June to October from 2005 to 2018 from the US West Coast (Calambokidis et al. 2007; Calambokidis 2009; Calambokidis et al. 2020). All whales were put through a photo ID process before being recorded in the Cascadia Research Collective blue whale catalog. Each sighting consisted of the blue whale’s ID number, information on the sighting (date, coordinates, group size and type, and behavior), and corresponding photographs.

Body condition scoring. For each sighting, there could be up to three images used for body condition scoring based on the angle of the blue whale in relation to the photographer (Table 1).

Table 1. Description of the three possible photographic angles for body condition scoring.

Photograph angle	Description
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Right	Whale is perpendicular with the photographer
Oblique	Whale is swimming at an angle towards or away from the photographer
Inline	Whale is swimming directly towards or away from the photographer

The best image was chosen for each category when applicable. Right angle photos were the most common, as these are the preferred images to use in photo ID. Each photo chosen was first scored based on two criteria: photo quality and proportion visible (Table 2). Images that were too limited in their view or had poor image quality were removed.

Table 2. Description of the three possible scores for body photo quality and proportion visible.

Score	Photo quality description	Proportion visible description
1	Excellent quality- the whale was clearly able to be seen	Good view forward of the dorsal fin
2	Good quality- a slightly fuzzy image, but details on the whale were still able to be seen	More limited view forward of the dorsal fin
3	Fair quality- details on the whale were difficult to see	Very limited view forward of the dorsal fin

Then the selected images were scored to determine whale body condition. Methods in this study were modified from the protocol developed for determining the body condition of North Atlantic right whales (Pettis et al. 2004) and western grey whales (Bradford et al. 2012). One analyst (RKW) scored all images for consistent scoring. The lateral flanks forward of the dorsal fin were visually assessed for the amount of subcutaneous fat in this region. Visible losses of fat in this area led to the protrusion of the vertebrae as well as a depression along the lateral flanks. Body condition was scored on a scale from 0-3 where a score of 0 indicated a visually healthy whale (Figure 1A.), with rounded sides, and no vertebrae are seen. A score of 1 indicated a moderately healthy whale (Figure 1B.), where it is difficult to tell if vertebrae are visible, but the whale has a definite dorsal ridge and possible undulations. A score of 2 indicated a moderately unhealthy whale (Figure 1C.), where slight but multiple vertebrae are seen. Finally, a score of 3 indicated a visually unhealthy

whale (Figure 1D.), in which obvious multiple vertebrae are seen. Whales that could not be scored (where there were only fluke images or not enough of the whale could be seen) were removed.

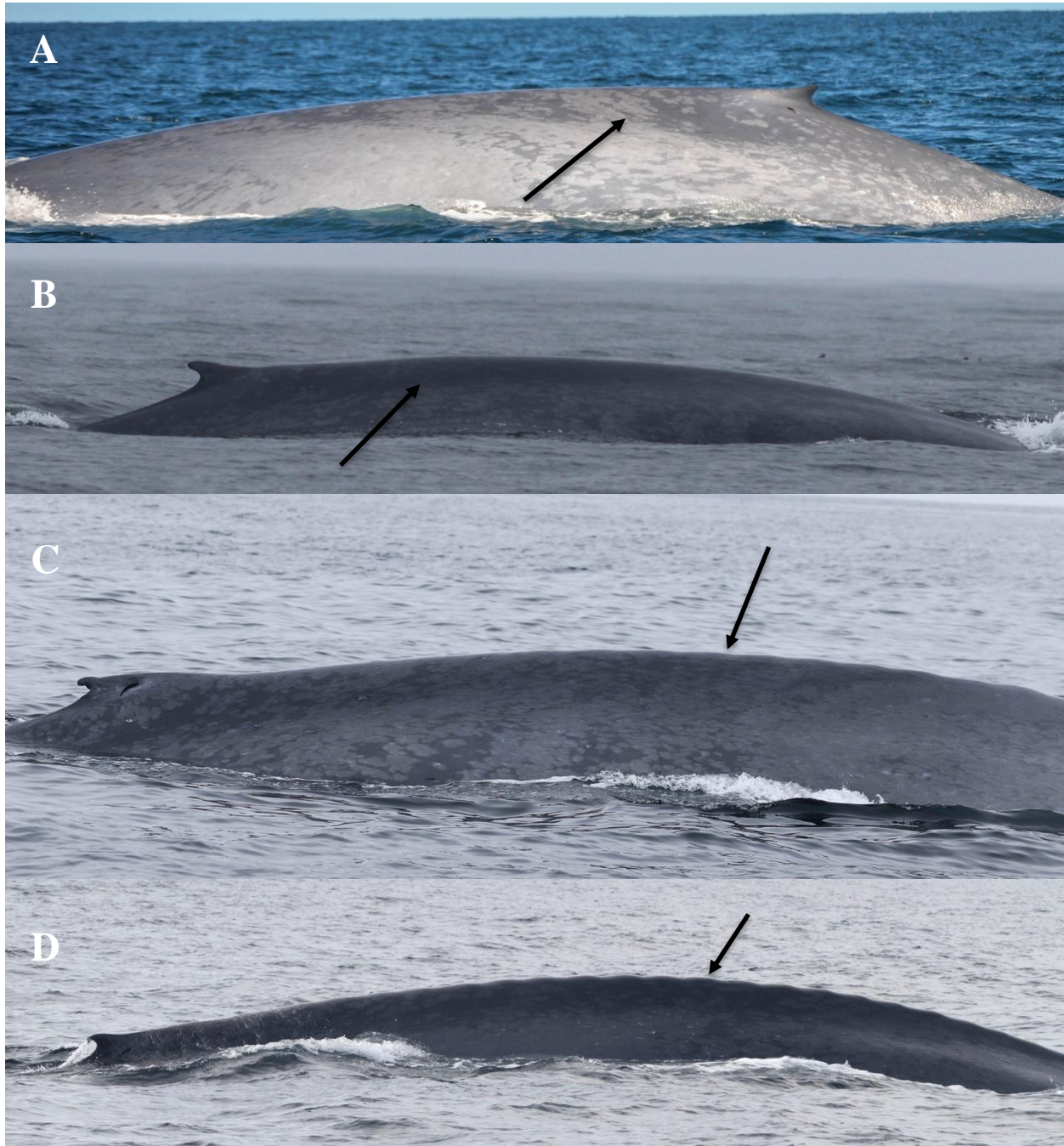


Figure 1. Examples of whales in each category of body condition. A) Score 0, a visually healthy whale, rounded sides (indicated by arrow), and no vertebrae are seen. B) Score 1, a moderately healthy whale, a definite dorsal ridge (indicated by arrow) and possible undulations. C) Score 2, a moderately unhealthy whale, slight but multiple detectable vertebrae (indicated by arrow). D) Score 3, a visually unhealthy whale, obvious multiple vertebrae seen (indicated by arrow).

Environmental data. Several environmental indices influence prey availability in the California Current System on different spatial and temporal scales (Brinton and Townsend 2003; Bograd et al. 2009; Checkley and Barth 2009). In this study, we included the Pacific Decadal Oscillation (PDO) and the Bakun Upwelling Index (BUI) in the creation of our model to see if they impact blue whale body condition. Monthly Pacific Decadal Oscillation values were accessed through a NOAA database (ncdc.noaa.gov/teleconnections/pdo/) and averaged for each year of the study. Similarly, monthly Bakun Upwelling Index values were accessed through a NOAA database (oceanview.pfeg.noaa.gov/products/upwelling/bakun) from 21-45°N. Bakun values were averaged across latitudes to come up with a singular overall upwelling index for each year of the study.

Statistical analysis and model creation.

In the first analysis, we tested the hypothesis that photographic assessments are a viable way to determine blue whale body condition, and that body condition would vary by year and reproductive class. First the number of whales in each body condition score (healthy, moderately healthy, moderately unhealthy, and unhealthy) were summed for each reproductive class (lactating female, calf, or other) and each year (2005-2018). Then a Chi-squared goodness of fit test was run in the program R (R Development Core Team 2019) for year and reproductive class to determine if they had an impact on body condition.

Then, to explore whether other environmental variables had an effect on blue whale body condition, we created an ordinal regression model. Using the Cumulative Mixed Model test from the Ordinal package (Christensen, 2019) within the program R, we determined the effect that four categorical variables (month, reproductive class, image quality, and proportion of image seen) and three environmental indices (Pacific Decadal Oscillation, Bakun Upwelling Index, and heat wave) had on body condition score (healthy, moderately healthy, moderately unhealthy, and unhealthy). In this analysis month is January-December; reproductive class is lactating female, calf, or other; and image quality and proportion of image seen is the score on the three-point scale (Table 2) for the primary image being scored. Since blue whales are highly mobile (Calambokidis et al. 1990; Mate et al. 1999; Calambokidis et al. 2009; Busquets-Vass et al. 2021) and body condition would

be determined by feeding success over an extended period and range, we used a single annual average value for both the Pacific Decadal Oscillation and the Bakun Upwelling Index. Finally, heat wave was the presence of unusually high sea surface temperatures (2014-2016; Di Lorenzo and Mantua 2016; Gentemann et al. 2017; Thompson et al. 2018). In each model blue whale ID number and year were included as random effects to account for pseudoreplication.

To determine the most parsimonious model, first a full model was created with the four categorical variables and then complexity and each covariate were singularly removed. Additional covariates were removed from selective models until we were able to determine the best fitting model using AIC scores. Then environmental indices were added to the model until the best model was found. This was repeated with a one-and two-year lag for each environmental variable to determine if environmental changes had a delayed effect. The three final models were then compared and the best fitting model was chosen (all models tested can be found in Appendix 1).

Results

Sighting data. We used sightings from the vessel surveys from 2005-2018 which represented 3,660 sightings of 1,112 unique blue whales (Table 3). Most sightings were in the summer feeding season between June and October (97%) and between 30-39°N (93%).

Table 3. Breakdown of sightings per reproductive class per year. Whales can be represented multiple times in the annual numbers within each reproductive class depending on the number of body condition determinations for that individual.

Reproductive class	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Calf	0	1	3	0	1	6	19	4	7	3	4	2	0	0
LF	0	7	3	0	2	8	35	3	7	5	4	2	0	0
Other	106	342	339	160	170	451	236	80	358	373	149	263	272	175
Total	106	350	405	160	173	465	290	87	372	381	157	267	272	175

LF, lactating female.

Body condition scoring. The lateral flanks forward of the dorsal fin showed large variations in body condition, confirming photographic assessments can be used for blue whales (Figure 1). The

distribution of scores for the study period was 34.5% healthy whales (score 0), 32% moderately healthy whales (score 1), 18.6% moderately unhealthy whales (score 2), and 14.9% unhealthy whales (score 3). The reproductive class had a significant impact on overall body condition (Chi-Square, $p < 2.2e-16$). Lactating females had a higher probability of being in poor body condition and calves had a higher probability of being in good body condition compared to the general population who had a fairly even spread across the body condition scores (Figure 2).

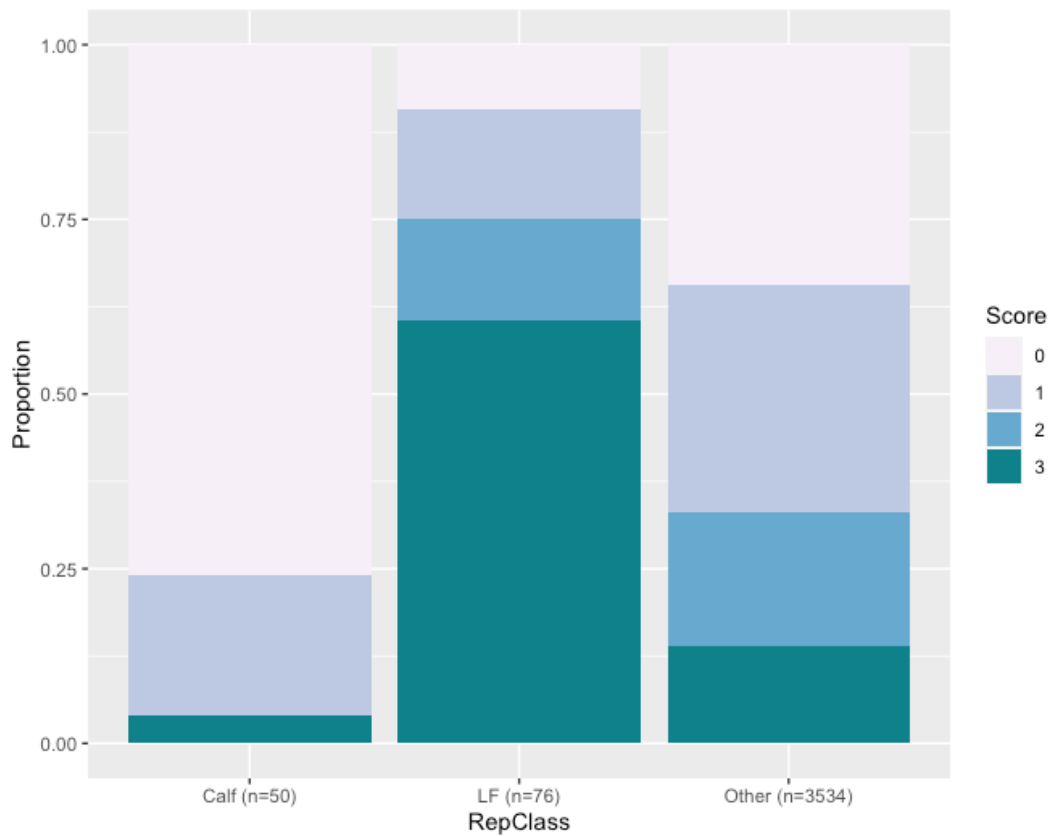


Figure 2. The proportion of each body condition score by reproductive class as a stacked bar graph. LF, lactating female.

The year was also a highly significant factor in the overall body condition score (Chi-Square, $p < 0.001$). For any given year the proportion of whales in poor body condition (scores 2 & 3) was 33%. But this varied widely across years with a low of 18% in 2008 to a high of 55% of whales in poor body condition in 2015. The percentage of whales in poor body condition did not exceed 45% except for 2015 and 2017 where over half of the whales scored had a compromised body condition (Figure 3).

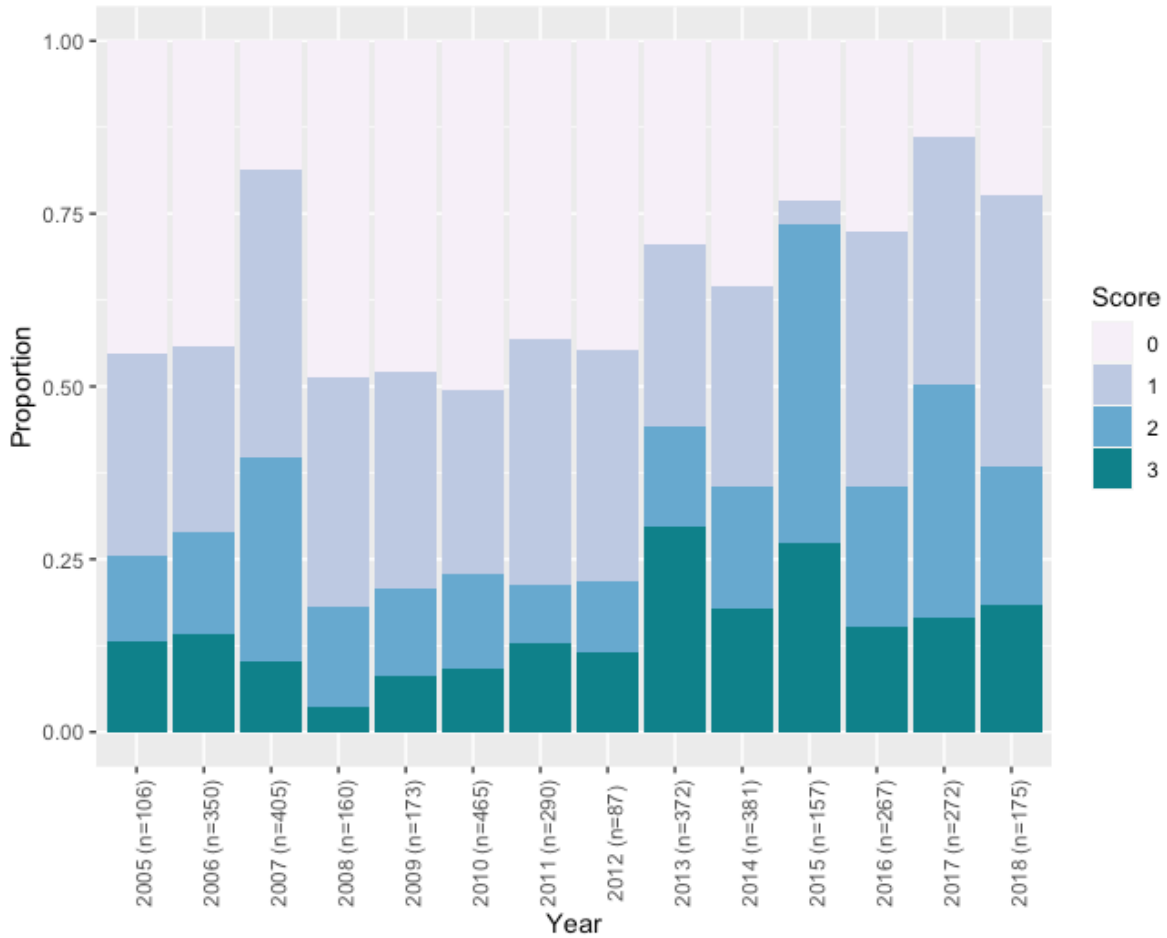


Figure 3. The proportion of each body condition score by year for the study period as a stacked bar graph.

Environmental data. There were significant annual variations in the Pacific Decadal Oscillation during the study period (Kruskal-Wallis, $p < 2.2e-16$) with high positive values from 2014-2016 and low negative values in 2008, 2011, and 2012 (Figure 4). Only four of the fifteen years had positive PDO values, and on average, the PDO was negative during the study period (-0.57 ± 1.09). PDO was lowest in 2011 with a value of -1.81 and highest in 2015 with a value of 0.92.

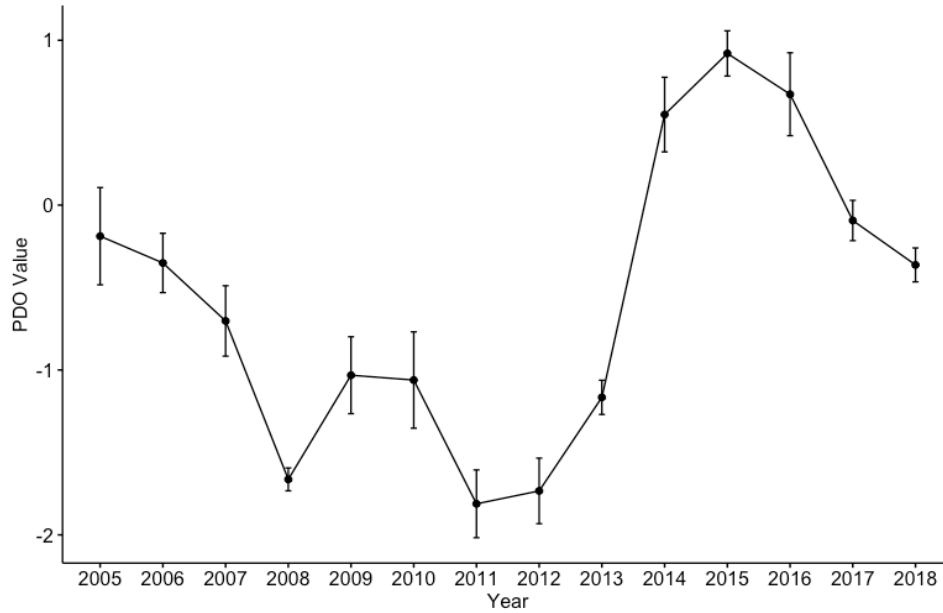


Figure 4. Average yearly PDO values over the study period in the Pacific Ocean Basin. Error bars show standard error.

The Bakun Upwelling Index did not vary significantly by year during the study period (Kruskal-Wallis, $p= 0.4983$). The average upwelling index varied from a low of 75 cubic M/s/100m coastline in 2009 and 2010 to a high of 104 cubic M/s/100m coastline in 2013 (Figure 5). Over all of the years, the average upwelling index was 88 ± 93 cubic M/s/100m coastline. While the variation in average upwelling was insignificant, the years of high upwelling match the years of low PDO values and vice versa.

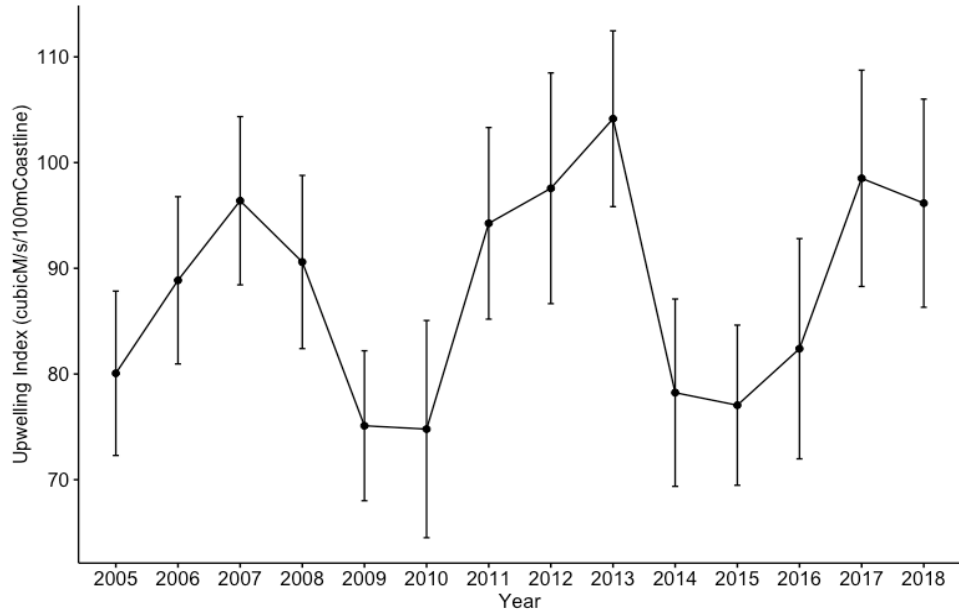


Figure 5. Average yearly Bakun Upwelling Index (cubicM/s/100m coastline) over the study period in the Pacific Ocean Basin. Error bars show standard error.

Model results. Of the five final models, the model incorporating the proportion of image seen, PDO value, Bakun Upwelling Index, and interaction between reproductive class and a two-year lag of a heat wave was most parsimonious (Table 4). This model explained 73% of the variation in the dataset. The variables that had the largest impact on the model were the two environmental indices (PDO value, $p= 1.18e-05$; Bakun Upwelling Index, $p= 0.002431$) and reproductive class (lactating female, $p < 2e-16$; other $p=0.000122$).

Table 4. Results comparing the three final Cumulative Mixed Models of blue whale body condition. Body condition score (Score) relative to predictor variables reproductive class (RepClass), the proportion of image seen (BestProp), PDO value, Bakun Upwelling Index (BUI), presence of a heat wave (heat wave), and PDO being positive or negative (PDO). Lag models have a one- or two-year lag of environmental predictor variables. Since the best two models with a 1-year lag had the same AIC score they were both included in the final model analysis. The most parsimonious model is bolded.

Model	K	AIC	Log-likelihood	AIC weight
Score~ RepClass * Lag2HeatWave + BestProp + PDO.Value + Upwelling + (1 Year) + (1 ID)	14	8514.2	-4243.04	0.73
Score~ RepClass + BestProp + PDO.Value + Upwelling + (1 Year) + (1 ID)	11	8516.3 9	-4247.16	0.24
Score~ RepClass * Lag2HeatWave + BestProp + (1 Year) + (1 ID)	12	1 8522.5	-4249.21	0.01
Score~ RepClass + BestProp + Lag1PDO + (1 Year) + (1 ID)	10	2 8523.2	-4251.58	0.01
Score~ RepClass + BestProp + Lag1HeatWave + (1 Year) + (1 ID)	10	2	-4251.58	0.01

K, number of groups; AIC, Akaike Information Criterion; AIC weight, relative likelihood of the model.

In general, peaks in PDO value coincided with dips in the Bakun Upwelling Index (Figure 6) and the two variables were moderately correlated (Pearson’s correlation test; -0.34). Years that had high PDO values had an increase in the number of whales in poor body condition (scores 2 and 3; Figure 6a) and years with low PDO values had an increase in the number of whales in good body condition (scores 0 and 1; Figure 6a). The opposite pattern was true for upwelling values, with an increase in upwelling leading to an increase in whales with good body condition and a decrease in upwelling leading to an increase in whales in poor body condition (Figure 6b). A two-year lag of a heat wave was moderately correlated PDO value (Pearson’s correlation test; 0.42), but only weakly correlated with upwelling (Pearson’s correlation test; 0.15).

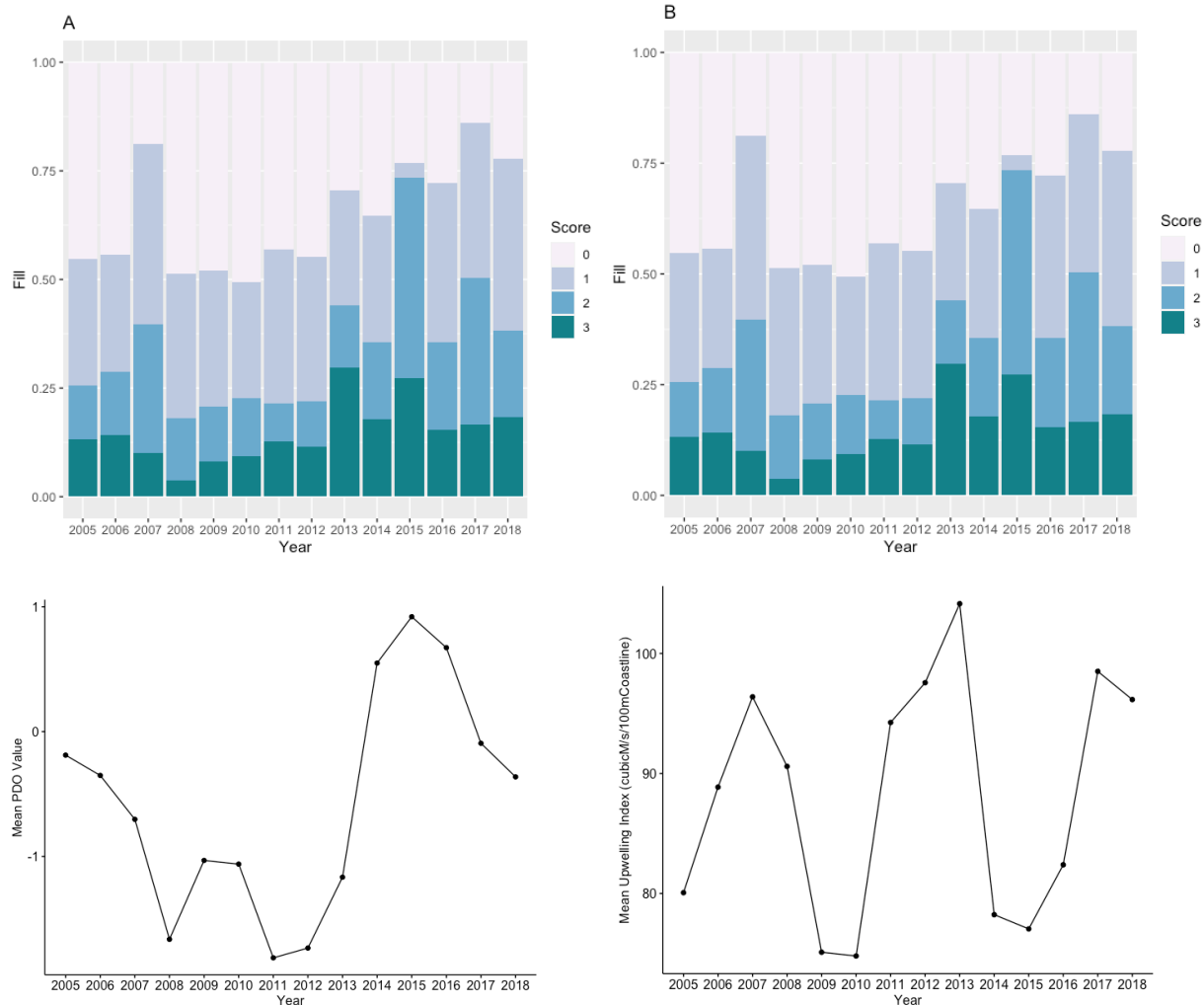


Figure 6. Average PDO value (A) and Upwelling Index (B) compared to yearly body condition scores.

Discussion

This study shows that visual health assessments based on foundational studies (Pettis et al. 2004; Bradford et al. 2012) can be applied to blue whales to track body condition over the years. The lateral flanks varied in the amount of subcutaneous fat accumulated in that area which made differentiation between condition scores possible (Figure 1). This region had the added benefit of being the target for photo identification images, making it possible to use historical data in our analysis. While previous studies focused on species in the *Balaenidae* and *Eschrichtiidae* families whose morphology is stocky with larger heads that allow study of the post-cranial regions, this is a pilot study for assessments on more streamlined animals in the family *Balaenopteridae*

(rorquals). Our study could be used as a basis to investigate other species in this family such as the minke (*Balaenoptera acutorostrata*), sei (*Balaenoptera borealis*), and fin (*Balaenoptera physalus*) whales.

The reproductive class of blue whales had a highly significant impact on body condition. Calves were the healthiest in the population and females who were assumed to be lactating were the least healthy. Other body condition studies have found that cows who are nursing their calves are in the worst condition of observed whales (Pettis et al. 2004; Bradford et al. 2012; Soledade Lemos et al. 2020). The high reproductive costs of weaning a mysticete whale calf has been well documented, as cows must consume enough during their feeding season to sustain themselves and their calf while in breeding grounds, although there is evidence that blue whales may forage year-round (Busquets-Vass et al. 2021). Blue whale calves are weaned over a period of 8 months (Jefferson et al. 2015) and this period of lactation is the costliest part of reproduction, requiring 3-5 times more energy than gestation (Miller et al. 2012). Calves must grow as quickly as possible during weaning in order to survive the migration to the feeding grounds as well as have thick enough blubber to last in the colder waters. For blue whales this increase in size can be as much as 90 kg/day (Jefferson et al. 2015).

Like Bradford et al. 2012 we saw small variations in the body condition of calves with 76% being scored as healthy (score 0) despite a variation of conditions being observed in the other groups (Figure 2). This could be due to the link between health and reproductive success seen in many species (Lockyer 1984; Lockyer 1986; Greene et al. 2003; Christiansen et al. 2013; Williams et al. 2013; Soledade Lemos et al. 2020). Females in poor body condition minimize the energy expended on their fetus to maximize their own chance of survival by reducing the growth rate of the fetus in utero (Christiansen et al. 2014). But decreasing the energy going to their fetus can impact the ability for the female to carry the calf to term or decrease the chance of long term survival (Christiansen et al. 2014). This means poor foraging conditions can lead to drops in calving rates—something that is especially concerning for an endangered species (Greene et al. 2003). A year of bad foraging can also influence more than just the pregnancies for that year, as a reduced body condition of a reproductive female can decrease their ability to carry a pregnancy to term in future years (carry-over effect; Christiansen et al. 2014; Soledade Lemos et al. 2020). If foraging

conditions are poor for consecutive years, the long term recovery of endangered populations can be in jeopardy.

As expected, blue whale body condition varied by year (Figure 3). But overall the variation of poor body condition was slight, with only two years (2015 and 2017) having more than half of the whales in poor health. While this study focused on the blue whales feeding on the US west coast, the eastern North Pacific population has a much broader feeding range (Calambokidis et al. 2009). After their numbers were greatly reduced from whaling, blue whales were rarely seen in British Columbia or Alaska; but starting in the late 1990s an increase of whales in more northern waters coincided with a decrease of blue whales off California (Calambokidis et al. 2009). It has been hypothesized that when foraging around California is poor due to decreased krill assemblages or increased competition, some blue whales may continue elsewhere to look for better foraging opportunities. It is likely that the pattern in blue whale body condition we observed results from a combination of some whales shifting foraging grounds and others being influenced by the feeding conditions off of California (Calambokidis et al. 2009; Busquets-Vass et al. 2021).

Variation in energy reserves (body fat) has been linked to prey availability, where oftentimes environmental conditions are used as a proxy (Braithwaite et al. 2015; Soledade Lemos et al. 2020). Since health varied by year, we created an exploratory model to determine what changes in environmental indices could explain this variation. We looked at several environmental indices that we believed would drive prey availability and therefore body condition in our model creation. Previous studies have linked upwelling strength with prey availability and cetacean body condition (Croll et al. 2005; Thompson et al. 2018, Barlow et al. 2020; Soledade Lemos et al. 2020), but ours was the first to look directly at the influence of the Pacific Decadal Oscillation on similar factors. The Pacific Decadal Oscillation (PDO), the Bakun Upwelling Index (BUI), and a two-year lag of a heat wave were the environmental drivers of the final model, with PDO and BUI being most significant to body condition score.

PDO varied significantly by year over our study period with high values in 2014-2016 (Figure 3). Only four years of our study period had positive PDO values (2014-2017), which followed the same pattern of poor body condition (Figure 6a). PDO is one of the main drivers of sea surface

temperature in the Pacific Ocean basin with positive PDO values signifying warmer ocean temperatures (Mantua and Hare 2002; Brinton and Townsend 2003; Di Lorenzo and Mantua 2016). We also looked at BUI since it occurs on a smaller temporal scale than PDO, seasonally leading to high levels of primary and secondary production (Huyer 1983; Fiedler et al. 1998; Croll et al. 2005; Checkley and Barth 2009). The seasonal upwelling coincides with the summer feeding period for blue whales (Croll et al. 2005; Barlow et al. 2020) and therefore could drive foraging success. While BUI did not vary significantly over the entire study period (Figure 4) the dips in upwelling match the peaks in PDO values and poor body condition scores (Figure 6). The worst body conditions followed the 2014-2016 marine heat wave which reduced primary productivity and changed the composition of zooplankton assemblages (Di Lorenzo and Mantua 2016; Gentemann et al. 2017; Thompson et al. 2018).

While not all environmental indices are highly correlated, they do play off one another and have a cumulative impact on the California Current System and the organisms that live there. Future studies may be required to quantitatively link specific indices and environmental events to whale body condition. It would be interesting to perform a similar study on humpback whales (*Megaptera novaeangliae*) over the same spatial and temporal scale to see if they were impacted the same way as blue whales. While both species forage for krill, humpbacks can also switch to forage fish like anchovy. During the marine heat wave humpbacks moved further inland to feed on anchovy which caused them to overlap with crab fisheries leading to record entanglements (Santora et al. 2020).

This study proved that it is possible to track body conditions of large whales using non-invasive tools. Monitoring large whale body condition as a proxy for overall environmental productivity will only become more important as the ocean rapidly changes. Marine heat waves are only expected to become more frequent and more intense in the future (Oliver et al. 2018) due to anthropogenically driven climate change (Frölicher et al. 2018; Oliver et al. 2018).

We provided a basis for evaluating large whale health that can be used to monitor populations well into the future. Blue whale body condition varied by year, matching the patterns of the Pacific Decadal Oscillation and Bakun Upwelling Index, with reduced productivity and warmer sea surface temperatures leading to decreased body condition. Additionally, our results supported prior

studies which have found that lactating females are often in the poorest health of a population due to the energetic demands of lactation. This study shows that our methodology is effective in evaluating blue whale health and how these whales respond to a changing ocean.

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Appendix

Appendix 1. All models that were tested and the indices used in model creation.

Table A1.1. Indices and their sources used in model creation.

Index	Abbreviation	Source
Bakun Upwelling Index	BUI	oceanview.pfeg.noaa.gov/products/upwelling/bakun
Biologically Effective Upwelling Transport Index	BEUTI	http://mjacox.com/upwelling-indices/ oceanview.pfeg.noaa.gov/whale_indices/
Catch Per Unit Effort (krill)	CPUE	oceanview.pfeg.noaa.gov/whale_indices/
Habitat Compression Index	HCI	oceanview.pfeg.noaa.gov/whale_indices/
Oceaninc Nino Index	ONI	oceanview.pfeg.noaa.gov/whale_indices/
Pacific Decadal Oscillation	PDO	ncdc.noaa.gov/teleconnections/pdo/
Spring Transition Index	STI	Derived from Bakun Upwelling Index

Table A1.2. All models tested with no temporal lag. Models are listed from lowest AIC to highest. Bolded model was used in the final analysis.

Model (no lag)	K	AIC	Log-likelihood	AIC weight
Score~ RepClass + BestProp + PDO.Value + BUI + (1 Year) + (1 ID)	11	8516.39	-4247.16	0.27
Score~ RepClass + BestProp + PDO.Value + BUI + CPUE + (1 Year) + (1 ID)	12	8516.81	-4246.36	0.22
Score~ RepClass * CPUE + BestProp + PDO.Value + BUI + (1 Year) + (1 ID)	14	8516.86	-4244.37	0.21
Score~ RepClass * PDO.Value + BestProp + BUI + (1 Year) + (1 ID)	13	8519.09	-4246.49	0.07
Score~ RepClass * BUI + BestProp + PDO.Value + (1 Year) + (1 ID)	13	8519.31	-4246.61	0.06
Score~ RepClass + BestProp + PDO.Value + BEUTI + (1 Year) + (1 ID)	11	8520.11	-4249.02	0.04
Score~ RepClass + BestProp + HCI + BUI + (1 Year) + (1 ID)	11	8521.44	-4249.68	0.02
Score~ RepClass + BestProp + PDO.Value + BUI + STI + (1 Year) + (1 ID)	15	8521.62	-4245.75	0.02
Score~ RepClass + BestProp + PDO.Value + BEUTI + CPUE + (1 Year) + (1 ID)	12	8521.81	-4248.86	0.02

Score~ RepClass + BestProp + PDO.Value + BUI + CPUE + STI + (1 Year) + (1 ID)	16	8521.88	-4244.87	0.02
Score~ RepClass + BestProp + PDO.Value + (1 Year) + (1 ID)	10	8522.95	-4251.45	0.01
Score~ RepClass + BestProp + HCI + BUI + CPUE + (1 Year) + (1 ID)	12	8523.29	-4249.6	0.01
Score~ RepClass + BestProp + HCI + (1 Year) + (1 ID)	10	8523.41	-4251.68	0.01
Score~ RepClass * STI + BestProp + PDO.Value + BUI + CPUE + (1 Year) + (1 ID)	20	8523.92	-4241.85	0.01
Score~ RepClass + BestProp + HCI + BEUTI + (1 Year) + (1 ID)	11	8524.83	-4251.38	0
Score~ RepClass + BestProp + ONI + (1 Year) + (1 ID)	10	8527.82	-4253.88	0
Score~ RepClass + BestProp + PDO.Value + BEUTI + STI + (1 Year) + (1 ID)	15	8527.99	-4248.93	0
Score~ RepClass + BestProp + ONI + BEUTI + (1 Year) + (1 ID)	11	8528.53	-4253.23	0
Score~ RepClass + BestProp + PDO + (1 Year) + (1 ID)	10	8528.55	-4254.24	0
Score~ RepClass + BestProp + HeatWave + (1 Year) + (1 ID)	10	8528.55	-4254.24	0
Score~ RepClass + BestProp + PDO + (1 Year) + (1 ID)	10	8528.55	-4254.24	0
Score~ RepClass + BestProp + HeatWave + (1 Year) + (1 ID)	10	8528.55	-4254.24	0
Score~ RepClass + BestProp + STI + BUI + CPUE + (1 Year) + (1 ID)	12	8538.21	-4254.04	0

Score, body condition score; RepClass, reproductive class (calf, lactating female, or other); BestProp, proportion of whale seen in best image; BUI, Bakun Upwelling Index; BEUTI, Biologically Effective Upwelling Transport Index; CPUE, Catch Per Unit Effort (krill); HCI, Habitat Compression Index; ONI, Oceanic Nino Index; PDO, Pacific Decadal Oscillation (positive or negative); PDO.Value, Pacific Decadal Oscillation value; STI, Spring Transition Index; HeatWave, presence or absence of a heatwave.

Table A1.3. All models tested with a one-year temporal lag for environmental indices. Models are listed from lowest AIC to highest. Bolded models were used in the final analysis.

Model (1-year lag)	K	AIC	Log-likelihood	AIC weight
Score~ RepClass + BestProp + Lag1PDO + (1 Year) + (1 ID)	10	8523.22	-4251.58	0.12
Score~ RepClass + BestProp + Lag1HeatWave + (1 Year) + (1 ID)	10	8523.22	-4251.58	0.12
Score~ RepClass + BestProp + Lag1PDO + Lag1BUI + (1 Year) + (1 ID)	11	8523.81	-4250.87	0.09

Score~ RepClass + BestProp + Lag1HeatWave + Lag1BUI + (1 Year) + (1 ID)	11	8523.81	-4250.87	0.09
Score~ RepClass + BestProp + Lag1PDO.Value + (1 Year) + (1 ID)	10	8524.38	-4252.16	0.07
Score~ RepClass + BestProp + Lag1PDO.Value + Lag1CPUE + (1 Year) + (1 ID)	11	8524.47	-4251.2	0.06
Score~ RepClass + BestProp + Lag1PDO + Lag1BEUTI + (1 Year) + (1 ID)	11	8524.54	-4251.23	0.06
Score~ RepClass + BestProp + Lag1HeatWave + Lag1BEUTI + (1 Year) + (1 ID)	11	8524.54	-4251.23	0.06
Score~ RepClass + BestProp + Lag1PDO.Value + Lag1BUI + (1 Year) + (1 ID)	11	8524.63	-4251.28	0.06
Score~ RepClass + BestProp + Lag1PDO + Lag1CPUE + (1 Year) + (1 ID)	11	8525.23	-4251.58	0.04
Score~ RepClass + BestProp + Lag1HeatWave + Lag1CPUE + (1 Year) + (1 ID)	11	8525.23	-4251.58	0.04
Score~ RepClass + BestProp + Lag1PDO.Value + Lag1BEUTI + (1 Year) + (1 ID)	11	8526.18	-4252.05	0.03
Score~ RepClass * Lag1PDO + BestProp + (1 Year) + (1 ID)	12	8526.33	-4251.12	0.03
Score~ RepClass * Lag1HeatWave + BestProp + (1 Year) + (1 ID)	12	8526.33	-4251.12	0.03
Score~ RepClass + BestProp + Lag1HCI + (1 Year) + (1 ID)	10	8526.34	-4253.14	0.02
Score~ RepClass * Lag1CPUE + BestProp + Lag1PDO.Value + (1 Year) + (1 ID)	13	8526.64	-4250.27	0.02
Score~ RepClass + BestProp + Lag1ONI + (1 Year) + (1 ID)	10	8526.77	-4253.36	0.02
Score~ RepClass + BestProp + Lag1PDO.Value + Lag1STI + (1 Year) + (1 ID)	14	8527.45	-4249.67	0.01
Score~ RepClass * Lag1PDO.Value + BestProp + Lag1CPUE + (1 Year) + (1 ID)	13	8527.88	-4250.89	0.01
Score~ RepClass + BestProp + Lag1PDO.Value + Lag1CPUE + Lag1STI + (1 Year) + (1 ID)	15	8529.06	-4249.47	0.01
Score~ RepClass + BestProp + Lag1PDO + Lag1STI + (1 Year) + (1 ID)	14	8529.33	-4250.61	0.01
Score~ RepClass + BestProp + Lag1HeatWave + Lag1STI + (1 Year) + (1 ID)	14	8529.33	-4250.61	0.01

Score, body condition score; RepClass, reproductive class (calf, lactating female, or other); BestProp, proportion of whale seen in best image; BUI, Bakun Upwelling Index; BEUTI, Biologically Effective Upwelling Transport Index; CPUE, Catch Per Unit Effort (krill); HCI, Habitat Compression Index; ONI, Oceanic Nino Index; PDO, Pacific Decadal Oscillation (positive or negative); PDO.Value, Pacific Decadal Oscillation value; STI, Spring Transition Index; HeatWave, presence or absence of a heatwave.

Table A1.4. All models tested with a two-year temporal lag for environmental indices. Models are listed from lowest AIC to highest. Bolded model was used in the final analysis.

Model (2-year lag)	K	AIC	Log-likelihood	AIC weight
Score~ RepClass * Lag2HeatWave + BestProp + (1 Year) + (1 ID)	12	8522.51	-4249.21	0.4
Score~ RepClass + BestProp + Lag2HeatWave + (1 Year) + (1 ID)	10	8524.32	-4252.13	0.16
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BUI + (1 Year) + (1 ID)	11	8525.19	-4251.56	0.1
Score~ RepClass * Lag2Upwelling + BestProp + Lag2HeatWave + (1 Year) + (1 ID)	13	8525.94	-4249.92	0.07
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BEUTI + (1 Year) + (1 ID)	11	8526.17	-4252.05	0.06
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BUI + Lag2CPUE + (1 Year) + (1 ID)	12	8527.2	-4251.56	0.04
Score~ RepClass + BestProp + Lag2PDO + (1 Year) + (1 ID)	10	8527.41	-4253.67	0.03
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BEUTI + Lag2CPUE + (1 Year) + (1 ID)	12	8528.18	-4252.05	0.02
Score~ RepClass + BestProp + Lag2PDO + Lag2BUI + (1 Year) + (1 ID)	11	8528.49	-4253.21	0.02
Score~ RepClass + BestProp + Lag2PDO.Value + (1 Year) + (1 ID)	10	8529.3	-4254.62	0.01
Score~ RepClass + BestProp + Lag2PDO + Lag2BEUTI + (1 Year) + (1 ID)	11	8529.32	-4253.62	0.01
Score~ RepClass * Lag2BEUTI + BestProp + Lag2HeatWave + (1 Year) + (1 ID)	13	8529.32	-4251.61	0.01
Score~ RepClass + BestProp + Lag2HCI + (1 Year) + (1 ID)	10	8529.49	-4254.72	0.01
Score~ RepClass + BestProp + Lag2ONI + (1 Year) + (1 ID)	10	8529.64	-4254.79	0.01
Score~ RepClass + BestProp + Lag2PDO.Value + Lag2BUI + (1 Year) + (1 ID)	11	8530.46	-4254.2	0.01
Score~ RepClass + BestProp + Lag2PDO.Value + Lag2BEUTI + (1 Year) + (1 ID)	11	8531.26	-4254.59	0.01
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BUI+ Lag2STI + (1 Year) + (1 ID)	15	8531.87	-4250.87	0
Score~ RepClass + BestProp + Lag2HeatWave + Lag2BEUTI + Lag2STI + (1 Year) + (1 ID)	15	8532.82	-4251.34	0

Score, body condition score; RepClass, reproductive class (calf, lactating female, or other); BestProp, proportion of whale seen in best image; BUI, Bakun Upwelling Index; BEUTI, Biologically Effective Upwelling Transport Index; CPUE, Catch Per Unit Effort (krill); HCI, Habitat Compression Index; ONI, Oceanic Nino Index; PDO, Pacific Decadal Oscillation (positive or negative); PDO.Value, Pacific Decadal Oscillation value; STI, Spring Transition Index; HeatWave, presence or absence of a heatwave.