Body condition of gray whales (*Eschrichtius robustus*) feeding on the Pacific Coast reflects local and basin-wide environmental drivers and biological parameters

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ABSTRACT

A small subset of the Eastern North Pacific gray whale population does not make the full migration from wintering grounds in Mexico to feeding grounds in the Bering, Chukchi and Beaufort seas and instead feed along the Pacific Coast between northern California and northern British Columbia. This group is known as the Pacific Coast Feeding Group (PCFG). We evaluated the body condition of PCFG whales observed in northern Washington and along Vancouver Island to evaluate how body condition of gray whales changes within and between years. We found that PCFG gray whales improve in body condition through the feeding season and at varying rates by year and that they have variability in their body condition at the start and end of each feeding season. The inclusion of environmental factors, particularly the Pacific Decadal Oscillation, drastically improved the ability of regression models to predict average whale body condition for a given year as compared to models without environmental factors included. A comparison of our findings to a previously published study on body condition of gray whales at Sakhalin Island, Russia highlight the differences between these two distinct feeding groups. Whales feeding at Sakhalin Island gain body condition quicker and more predictably to a good body condition by the end of the feeding season than the whales we studied in the PCFG. This method of visual photographic assessment may be an effective method for monitoring the effects of climate change on PCFG gray whales.

KEYWORDS: GRAY WHALE; FEEDING; FEEDING GROUNDS; PACIFIC OCEAN; ECOSYSTEM; CLIMATE CHANGE

INTRODUCTION

The Eastern North Pacific (ENP) population of gray whales (*Eschrichtius robustus*) was twice seriously depleted due to unregulated commercial whaling (Darling, 1999), but with protection has recovered (Punt and Wade, 2012). The abundance of ENP gray whales increased to an estimated maximum of 26,960 whales in 2016 (Durban *et al*., 2017); the most recent estimate conducted in winter 2019/2020 decreased to 20,580 whales following the first year of an unusual mortality event (UME) in 2019 and 2020 (Stewart and Weller, 2021). The majority of the ENP population spends the summer feeding season in the Bering, Beaufort and Chukchi seas. A smaller number of gray whales feed along the Pacific coast of the US and Canada and are known as the Pacific Coast Feeding Group (PCFG; IWC, 2011). This smaller aggregation of whales was estimated to number 232 individuals in 2017 (Calambokidis *et al*., 2020). These PCFG whales are thought to remain off the coasts of northern California, Oregon,

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Washington and British Columbia during the feeding season (Calambokidis *et al*., 2002, 2020) and are defined by the International Whaling Commission (IWC) as gray whales observed during more than one year in the range of 41°N to 52°N (excluding the Puget Sound region) during the months of June through November (IWC, 2011; 2014). Roughly half of the gray whales observed in the PCFG range during the June to November feeding season are seen in only one year and never seen again and do not qualify as PCFG whales (Calambokidis *et al*., 2020). Some individuals that meet the IWC definition of the PCFG are sighted with regularity within the defined PCFG range whereas others are known to regularly use areas as far northwest as Kodiak Island (Gosho *et al*., 2011) and Icy Bay, Alaska (Lagerquist *et al.,* 2019), with one individual photographed a single time off Barrow, Alaska (Calambokidis *et al.*, 2012).

Within the PCFG range, individual gray whales show variability in their use and fidelity to a particular region (Calambokidis *et al*., 2020; Lagerquist *et al*., 2019; Scordino *et al*., 2017). For example, there is a higher degree of overlap of individual whales between feeding areas off northern Washington and southern Vancouver Island, BC as compared to feeding areas to the south or further north (Calambokidis *et al*., 2020). Individual whales show varying degrees of fidelity both in the length of time within a year that a whale uses the area and the likelihood that the whale will return to the area in future years (Calambokidis *et al.*, 2020; Scordino *et al*., 2017). Further, the total number of whales sighted is also variable between years, regardless of survey effort (Calambokidis *et al.*, 2020; Scordino *et al*., 2017). This variability in use likely reflects both foraging success in the region and changes in ecosystem productivity (Burnham and Duffus, 2016; 2018; Feyrer and Duffus, 2011; 2015; Scordino *et al*., 2017).

A whale's health, as shown by its body condition, changes throughout the year depending on factors such as reproductive status or fasting during migration and is positively correlated with greater food availability (Bradford *et al*., 2012; Braithwaite *et al*., 2015; Pettis *et al*., 2004; 2017; Williams *et al*., 2013). Food availability is affected by both bottom-up factors, including life history of prey (Burnham, 2015; Feyrer, 2010), ocean productivity and large-scale climate drivers (Fleming *et al*., 2015; Newell and Cowles, 2006; Seyboth *et al*., 2016) as well as top-down foraging pressure by the whales themselves (Burnham and Duffus, 2016; 2018; Feyrer and Duffus, 2011). Gray whale foraging in the PCFG range is positively correlated to the regional and local density of available prey such as mysid shrimp (family Mysidae) (Feyrer and Duffus, 2015; Newell, 2009; Pasztor, 2008). Off the west coast of Vancouver Island, temporal and spatial variation both in prey species and gray whale abundance were significantly related to environmental factors at varying timescales including local sea surface temperature and annual average upwelling (Garside, 2009; Kerr, 2005). In several studies, top-down feeding pressure leading to reduced prey resources appeared to cause reduced foraging effort and local abundance of whales (Burnham and Duffus, 2016; 2018; Feyrer and Duffus, 2015).

Given the relationship of food availability to foraging effort, it is likely that whale health (i.e. body condition) is similarly affected by seasonal and annual variations in prey and the factors that affect prey availability. In order to determine whether body condition could reflect the variability of whale sightings in the PCFG region, we evaluated the body condition of individually identified gray whales photographed between 1996 and 2013 off Northwest Washington and Vancouver Island, British Columbia. A method for visually assessing the body condition of gray whales was developed by Bradford *et al*. (2012) to evaluate the health of gray whales feeding at Sakhalin Island, Russia. Bradford *et al*. (2012) noted that whale body condition differed over the duration of the feeding season, between years and by reproductive status. A similar though less extensive method of photographic health assessment was developed by Newell (2009) to evaluate annual differences in the numbers of feeding gray whales on the Oregon coast (USA) observed in poor body condition. Newell (2009) found that body condition and foraging effort of gray whales were affected by the abundance and density of mysids, the whale's primary prey in the study area. Other studies have tied whale body condition to environmental variables through their effect on prey resources. In bowhead whales (*Balaena mysticetus*), body condition was positively correlated to environmental drivers responsible for an increase in primary and secondary productivity, including the length of the ice-free feeding period and other factors (George *et al*., 2015; Harwood *et al*., 2015). In humpback whales, body condition was positively correlated with winter sea ice extent, likely driven by greater abundance of their primary prey, krill (Braithwaite *et al*. 2015).

The primary goal of this project was to use the methods developed by Bradford *et al*. (2012) to determine body condition of Pacific Coast Feeding Group (PCFG) gray whales and to assess how the body condition of these whales changed over the feeding season and between years over an 18-year time span using photographs of whales primarily collected in northern Washington. We also investigated whether body condition affected fidelity to the region based on resight of individuals in the following year. Our secondary goal was to determine how whale body condition is affected by local and large-scale environmental drivers. Given the seasonal and annual variability in whale sightings in this region (Scordino *et al*., 2017), we hypothesise that whale body condition in the region would reflect food availability and ecosystem productivity. We also investigated whether biological factors, specifically ENP calf estimates, correlated to observed PCFG body condition. Last, we compare our results with previously published results from a body condition study of gray whales at Sakhalin Island, Russia.

MATERIALS AND METHODS

Photographs and sighting data

The Makah Tribe's Fisheries Management department and NOAA's Marine Mammal Laboratory conducted nearshore, small-boat surveys of northwest Washington and southern and western Vancouver Island from 1996 to 2013. On the Washington coast, the surveys were conducted from Cape Flattery to Sekiu, WA in the Strait of Juan de Fuca and from Cape Flattery south to Sea Lion Rock, WA in the Eastern North Pacific Ocean (Fig. 1). Surveys off Vancouver Island were conducted between 1996 and 2002 from Port Renfrew north to Barkley Sound (Fig. 1). In 1999, surveys were also conducted along western Vancouver Island from Port Renfrew to Cape Scott, east to Port Hardy and north to Cape Caution, BC (Fig. 1).

Each gray whale sighted during these surveys was photographed using SLR cameras with a 70–300 mm lens and the time and location of the sighting was recorded. Photographs of gray whales were sent to Cascadia Research Collective (Olympia, WA, USA) for comparison to, and inclusion in, their catalog focused on individually identified gray whales from the west coast of the contiguous USA and Canada. Each whale photographed was either matched to an existing whale and identification number in the catalog, assigned a new identification number if no match could be made or left unidentified if the photo was of insufficient quality (Calambokidis *et al*., 2002, 2020). Cascadia Research Collective provided identification numbers (CRC ID) from each sighting for this analysis. The sex of photographed whales was determined by comparing the CRC ID to biopsied whales of known sex based on genetic studies following the methods detailed in Lang *et al*. (2014; Aimée Lang, NOAA Southwest Fisheries Science Center, pers. comm.).

Body condition evaluation

We used methods developed by Bradford *et al*. (2012) to visually estimate the body condition of individual gray whales by evaluating the amount of visible depression (or lack thereof) as a measure of the whale's subcutaneous fat stores in the post-cranial, scapular and lateral regions of the body. Each body region was scored to provide a qualitative measurement of whether the whale was in good, fair or poor condition (see *Supplementary Material*). Body condition was evaluated using photographs displaying the profile of the whale's back (described in Pettis *et al.,* 2004). The post-cranial region was scored shortly after a whale's surfacing when the region from the blowholes to the start of the dorsal ridge is approximately parallel to the water to avoid misinterpretation of a concavity or convexity based on the whale's body position, e.g. lifting or dropping the head. Similarly, the scapular and lateral regions were scored following the surfacing event while the blowholes (whether or not visible in the frame) were still out of the water or just after they were lowered such that the back was approximately parallel to the water and not arched into a dive. The post-cranial region was scored on a 3-point scale based on the degree of depression behind the blowholes and skull, where a score of 3 indicates a flat or rounded post-cranial region with no visible concavity (i.e. good condition), a score of 2 indicates a slight to moderate concavity posterior to the blowholes (i.e. fair condition) and score of 1 indicates severe post-cranial concavity (i.e. poor condition) such that a convex, raised hump behind the blowholes is apparent. The scapular region was scored on a 2-point scale where a visible subdermal protrusion of the scapula was assigned a score of 1 (poor condition of scapular region) and no visible

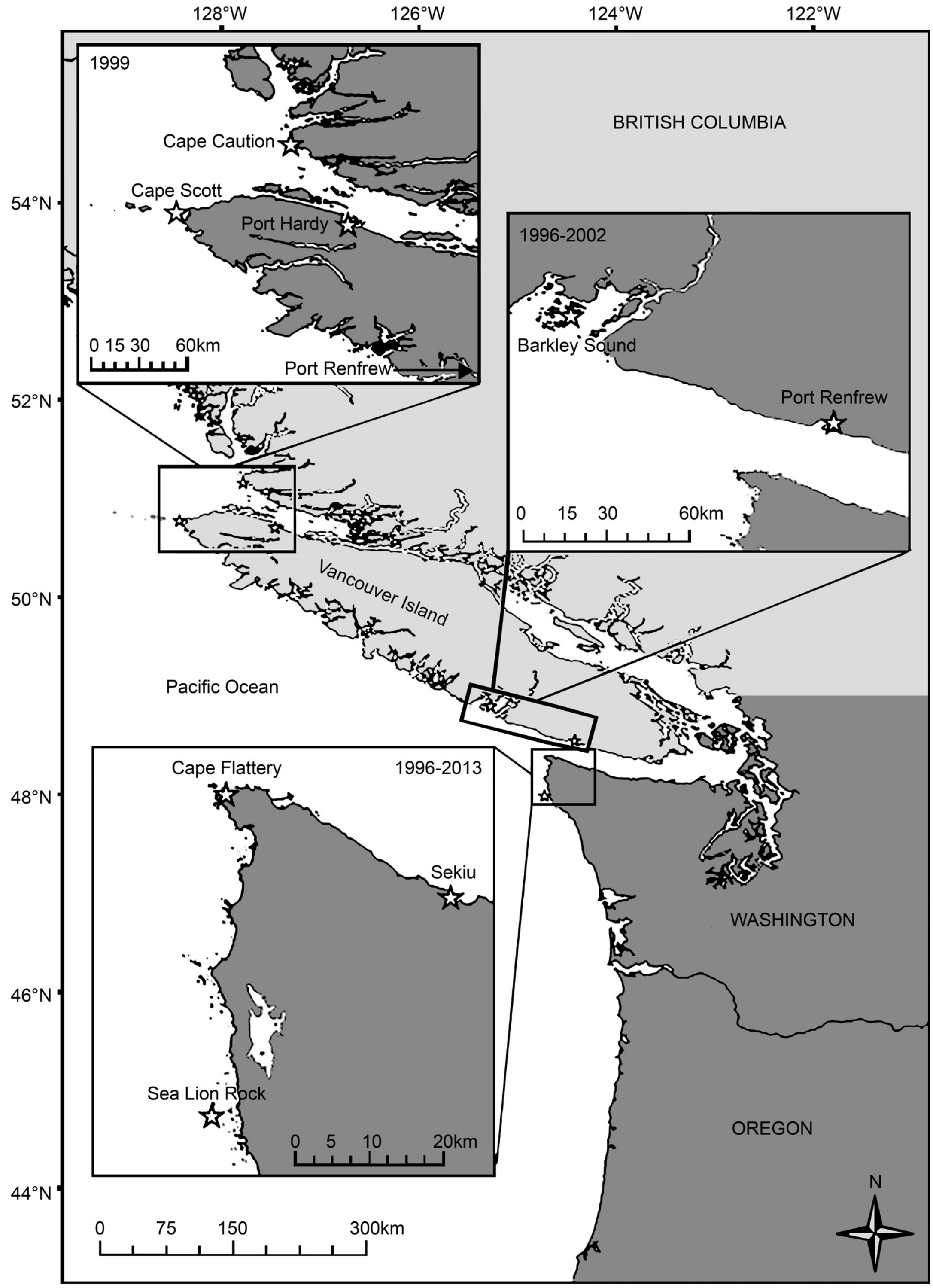

Fig. 1. Map of the study area with insets to display regions and years surveyed for gray whales in northwest Washington, USA, and Vancouver Island, British Columbia, Canada.

protrusion with rounded body in the scapular region was assigned a score of 2 (good condition of scapular region). The lateral flank was also scored on a 2-point scale where the lateral flank of a whale was scored a 2 (good flank condition) if rounded from the post-cranial region to the start of the knuckle ridge and scored a 1 (poor flank condition) when the whale had an obvious depression along the dorsal aspect of the lateral flank beginning mid-way along the dorsal ridge. An overall body condition score would thus read ‘322’ for a whale in good condition in all three evaluated regions.

Photos were selected for scoring based on their general quality (i.e. not blurry, grainy or with glare or extreme exposures), the amount of the body region showing (photographs that did not display the full body region were not scored) and their adherence to the angles and regions defined in Bradford *et al*. (2012). For a given sighting, the photographs required to assign an overall (complete) body condition score were not always available. In the case where a photograph was not available or was of poor quality, that particular body region was scored as an X. Bradford *et al*. (2012) found that the area most indicative of overall health was the post-cranial region, therefore a whale for which a post-cranial score could not be assigned (e.g. 'X22') was considered an incomplete body condition score. If at least a post-cranial score could be assigned (e.g. 3XX), then the score was considered complete (hereafter 'known'). Fig. 2 presents a list of the possible scores for good, fair and poor body condition. We created monthly composite scores of each individual whale following hierarchical decision rules described by Bradford *et al.* (2012; Appendix III) to increase the likelihood of having a known body condition score by pooling scores for that whale from all sightings in a given month. If a whale was sighted on more than one occasion within a month, then the composite was based on the most frequent body score given or the scores with the highest confidence (e.g. 322, 3X2 and XX2 would yield a 322 composite score; 221, 321, 3X1 and X21 would yield a 321 composite score).

This published method by Bradford *et al.* (2012) was validated using a formal interrater agreement study. Bradford *et al.* (2012) found good to moderate agreement between the scores of two separate researchers, suggesting that other researchers may conduct the same evaluation and come to a similar conclusion. In our study,

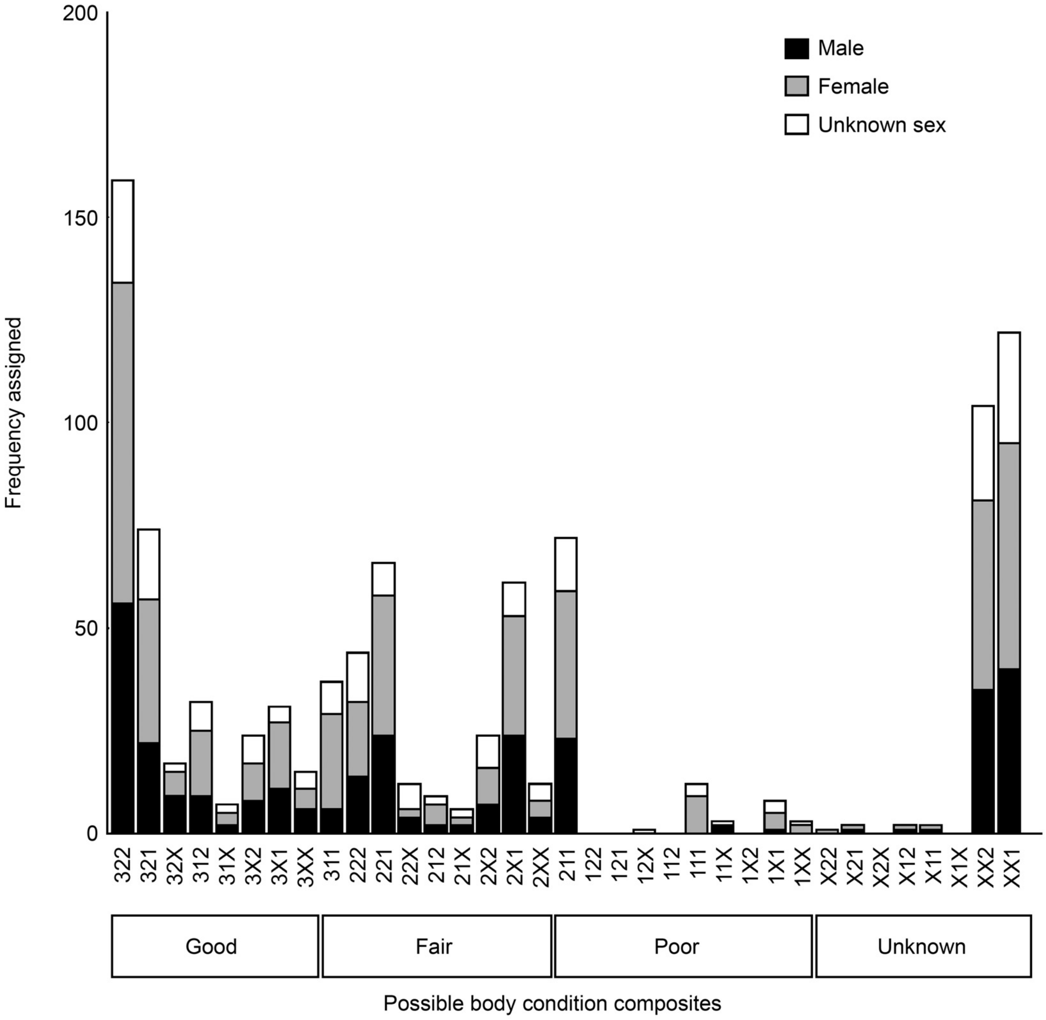

Fig. 2. Frequency of monthly body condition composite scores assigned to Pacific Coast Feeding Group gray whales by sex. The body condition composite score includes a score of 3 – good, 2 – fair, 1 – poor, and X – unknown for the post-cranial, scapular, and lateral body regions, respectfully.

all body condition scores were conducted by a single researcher (AMA) to eliminate any possibility of interrater differences affecting the results of our analyses.

Environmental and biological data

We compared gray whale body condition to environmental variables to investigate how the environment affected whale body condition on an annual scale as an indirect measure of ocean conditions and prey availability. We selected both large-scale and local measures of the environment because gray whales photographed off Washington and Vancouver Island may utilise feeding areas between northern California and British Columbia or as far north as Kodiak Island and Icy Bay, Alaska (Calambokidis *et al.*, 2020, 2002; Gosho *et al*., 2011; Lagerquist *et al.,* 2019). Large-scale environmental variables included in our analyses were the Pacific Decadal Oscillation (PDO[3]), Oceanic Niño Index (ONI[4]) and North Pacific Gyre Oscillation (NPGO[5]). Local environmental variables included annual and monthly upwelling index (UI), total kelp canopy cover along the Strait of Juan de Fuca and Washington outer coast and sea surface temperatures measured at the La Perouse Bank Buoy Station 46139 operated by Ocean and Climate Change Canada[6]. Upwelling indices were obtained from NOAA[7] for the northern Washington coast, 48°N, 125°W, as well as areas to the north and south including at 39°N, 125°W, 42°N, 125°W, 45°N, 125°W, 51°N, 131°W, 54°N, 137°W, 57°N, 137°W and 60°N, 146°W because PCFG whales are known to have large home ranges (Calambokidis *et al.*, 2020; Lagerquist *et al.*, 2019). We compared body condition to each of the individual upwelling locations as well as to an averaged upwelling score from all areas. Total kelp canopy cover was measured by the Washington Department of Natural Resources in September of each year from Port Townsend, WA (48°8’N, 122°46’W) to the Columbia River mouth (46˚15’N, 124°5’W), using aerial photography[8]. We used calf estimates for the ENP population of gray whales (Perryman *et al.*, 2020) to evaluate whether years of better or worse body condition correlated to years of higher or lower calf estimates.

Statistical analysis

All statistical tests were performed in the statistical program R (v. 3.4.4; R Core Team, 2018). Only complete body condition scores, containing at minimum a post-cranial score, were used for analysis. We used a multinomial logistic regression to determine the effects of month, year, sex and reproductive class on gray whale body condition (Bradford *et al*., 2012) and used Akaike’s Information Criterion (AIC) to select the most parsimonious model to represent the observed changes. Using body condition as an ordinal response variable, we compared a constant slope model (intercept model) to models with month, year, sex, reproductive class and the additive effects of the variables. Because individual whales could be represented multiple times within the model, we made whale identification numbers a normally distributed random effect variable within the models using the *clmm2* function in the Ordinal Package in R (Christensen, 2018).

Month and year were included in the logistic regression as categorical variables, with reference month of June and reference year set as 1997. Due to having no scores for whales in the month of November in half of the study years (Table 1), we only included scores from June through October in the models. The reference year, 1997, was selected rather than the first year of photographs available, 1996, for comparative purposes with Bradford *et al*. (2012) who used 1997 as the reference year in their study of body condition in Western North Pacific gray whales using the same scoring methodology.

Reproductive class was assigned to individuals based on biopsy sampling (Lang *et al*., 2014) and sightings of presumed females with calves (Calambokidis and Perez, 2017). Bradford *et al*. (2012) evaluated three levels of reproductive class: calf, post-partum (lactating) female and other. *A priori*, we knew that we only had nine calves identified in our study area during the years of the study and that Bradford *et al*. (2012) found that all calves were

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[3] *http://research.jisao.washington.edu/pdo/PDO.latest*

[4] *http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ ONI_change.shtml*

[5] *http://www.o3d.org/npgo/npgo.php*

[6] *http://www.ndbc.noaa.gov/*

[7] *http://www.pfeg.noaa.gov/*

[8] *http://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/kelp-monitoring*

Table 1

Number of Pacific Coast Feeding Group (PCFG) gray whales assigned complete body condition score by month and year and proportion of PCFG whales assigned a complete body condition score compared to total number of PCFG whales photographed in the study region.

Year	June	July	August	September	October	November	Total whales assigned score	Whales assigned score/ whales photographed
1996*	0	5	4	4	0	0	11	0.65
1997*	5	5	9	7	1	0	17	0.68
1998*	0	7	1	8	3	0	16	0.37
1999**	4	0	18	2	2	0	22	0.38
2000*	1	1	19	3	5	0	28	0.49
2001*	18	17	10	3	0	1	39	0.70
2002*	0	0	5	2	2	0	9	0.64
2003	2	1	2	6	3	0	12	0.55
2004	2	1	1	6	2	3	14	0.54
2005	1	3	2	6	3	3	13	0.42
2006	2	3	7	22	2	0	30	0.54
2007	0	9	10	8	2	5	17	0.71
2008	2	11	20	17	29	14	54	0.87
2009	7	6	22	18	16	1	40	0.83
2010	0	3	5	14	1	0	20	0.54
2011	9	7	4	10	14	3	32	0.74
2012	11	19	24	31	18	5	52	0.90
2013	7	5	23	26	21	10	55	0.96
Total scores by month	71	103	186	193	124	45		

*Years include whales photographed off Vancouver Island between Barkley Sound and Port Renfrew. **Includes whales photographed off Vancouver Island between Barkley Sound and Port Hardy.

in good body condition as their body condition is linked to nursing and not directly based on foraging success. To avoid the small sample size of calves and the fact that uniformity in calf scores observed by Bradford *et al*. (2012) could cause numerical challenges for fitting regressions (Hosmer and Lemeshow, 2000), we chose to exclude calves from our analysis. Thus, our reproductive classes were post-partum female and ‘other’ where other is all whales known not to have had a calf in the study year and non-calf whales of unknown reproductive class.

We compared predicted average gray whale body condition from our best ordinal regression model to environmental and biological variables using simple linear regression and multiple regression analysis. To calculate average gray whale body condition, we used the most parsimonious model selected by the ordinal regression and the *predict* function in the Ordinal Package in R (Christensen, 2018) to calculate the predicted probability of a whale being in good, fair or poor condition in each year of the study. We excluded post-partum females from the analysis because lactation increases their energetic demands relative to other whales resulting in their body condition being more a factor of reproductive status than environmental conditions (Bradford *et al*., 2012; Christiansen *et al*., 2018; Miller *et al*., 2012). Therefore, we averaged the predicted probability of ‘other’ whales being in each condition to assign a predicted average body condition for each year of the study. We used AIC adjusted for small sample sizes (AICc) in the MuMIn Package in R (v.1.42.1; Bartoń, 2018) to select among multiple regression models for the most parsimonious model to represent the average predicted body condition.

To investigate whether there may be a time lag between an environmental condition and its effect on whale body condition, we compared average body condition in year Y to environmental variables in the same year (year Y), from the winter (October to March) prior to the year Y feeding season, at a one year lag (Y–1), two year lag (Y–2) and to an average of the previous two years (average of Y–1 and Y–2). Each environmental variable at each time scale was graphically compared to average body condition to look for a linear relationship between the variable and gray whale body condition and to look for potential outlier years. When a linear relationship was observed, we performed simple linear regression to determine whether there was a significant linear relationship between the two variables and examined and removed outlier years based on QQ-normality plots, residual plots and residual versus leverage plots. We performed post hoc testing using a Bonferroni correction where the corrected alpha value was calculated as 0.05 divided by the number of linear regressions run for each environmental variable. Variables that were significant based on linear regression were further considered for multiple regression models. We used variance inflation factors to ensure that the variables included in the multiple regression were not collinear to one another where a score greater than 4 indicated collinearity and only one of the collinear variables was selected to be included in the multiple regression. We evaluated temporal autocorrelation of variables using the Durban-Watson statistic, where values of 1.5 to 2.5 indicated low autocorrelation and thus were considered for the multiple regression analysis.

We used simple chi-squared analyses to investigate whether apparent body condition in the latter half of the feeding season could predict whether or not a whale would return to the area in the subsequent year. We tabulated the number of whales seen in year Y by body condition score and whether or not the whale was photographed within the study area in the following year (year Y + 1). We used 2x2 contingency tables to compare whether whales scored in good body condition in August or later were more likely to return to the area than when considering all whales in any body condition. We then compared whether whales in good body condition were more likely than whales in Fair and Poor condition combined to return to the area in the following feeding season. We used 2x3 contingency tables to compare the three body condition scores (good, fair and poor) to whether or not a whale was resighted in the next year. Lastly, we conducted all three comparisons for whales of known sex, evaluating males and females separately.

RESULTS

Monthly composite scores

Out of 301 total whales photographed during the 18-year study period, 221 individual whales were classified as PCFG whales. Of those 221 whales, we were able to evaluate body condition from 195 whales with suitable photographs (Table 1). Between years of the study, we had variable sample size of both the number of whales scored and the proportion of whales photographed that were assigned scores (Table 1). The differences in proportions scored was likely related to differences in survey effort, which was difficult to quantify for the early years of the study, differences in numbers of whales using the survey area (see Scordino *et al*., 2017) and a switch to digital photography in later years (2005 onward) of the study allowing for more photographs to be taken during a sighting combined with increased effort to take photographs of the post-cranial and scapular regions. In total, we assigned 951 monthly composite scores, of which 76% (719 total) contained a post-cranial score (Fig. 2). Therefore, out of the 195 whales evaluated, we could assign known body condition for 181 individuals.

Of the known condition scores, 50% (359 total) represented good body condition, 37% (266 total) represented fair body condition and 13% (94 total) represented poor body condition (Fig. 2). Body condition was assigned for 118 individuals of known sex, disregarding reproductive status; 448 known scores were assigned to females and 314 known scores were assigned to males. Males and females were assigned in good, fair or poor body condition in similar proportions (Fig. 2). We were able to assign a known reproductive class (calf or post-partum female) in only 19 cases over the 18-year period. Out of nine known calves photographed in five of the study years, we assigned 14 known monthly composite scores, all in good condition. Out of 10 cases where a whale was identified as a post-partum female, we assigned 22 known monthly composite scores, of which 86% were scored in poor or fair condition. In general, body condition of whales improved over the duration of the feeding season, but varied between years, with peaks in poor condition occurring in the 2007, 2009 and 2010 feeding seasons (Fig. 3).

Ordinal logistic regression

We used multinomial logistic regression and model selection (AIC) to examine the influence of all additive combinations of the categorical variables month, year, sex and reproductive class on whale body condition. As noted earlier, calves were removed from the regression models. We initially used a subset of the scores for whales of known sex (n = 118). The resulting best model with the lowest AIC value included month, year and reproductive status, but not sex. Noting that sex was not included as a factor, we concluded that we could evaluate our entire dataset that included whales of unknown sex. The model selection using our full non-calf dataset (n = 181) found that the full additive model including month, year and reproductive class was most parsimonious with our data and had an Akaike weight of almost 1.0 (Table 2).

Gray whale body condition improved over the feeding season and varied significantly between years and by reproductive class (Table 3). Compared to the reference month, June, body condition of gray whales had

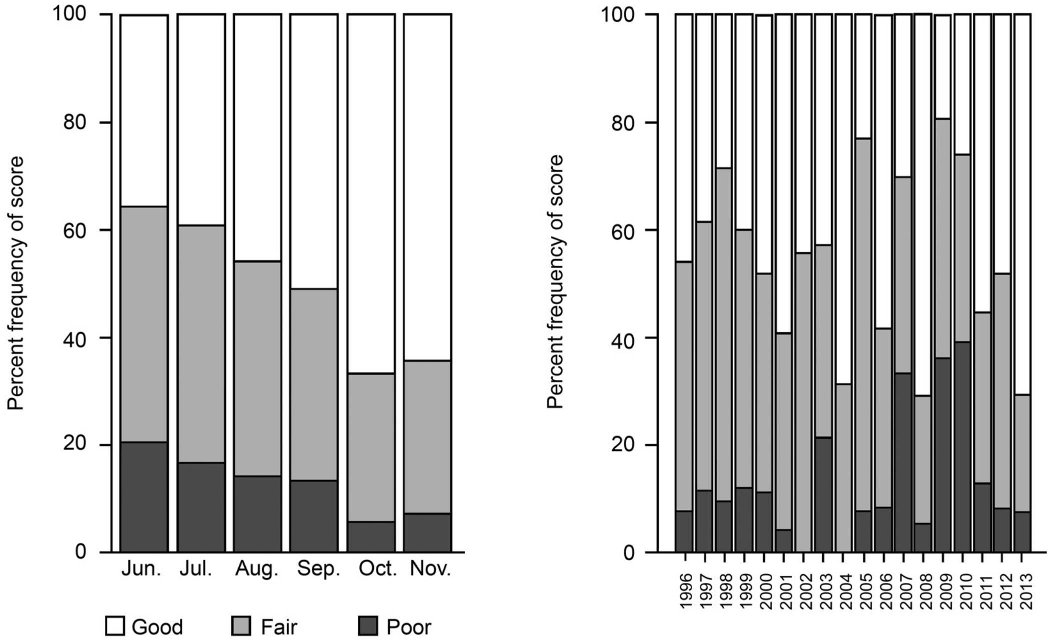

Fig. 3. Temporal trends in the percent frequency of known body condition scores assigned to Pacific Coast Feeding Group gray whales by month and year.

Table 2

Model selection of multinomial logistic regression analysis, log-likelihood, Akaike Information Criterion (AIC), delta AIC (ΔAIC) and Akaike weights (ω_i) for Pacific Coast Feeding Group gray whales in Washington, USA and Vancouver Island, Canada from 1996–2013. Month, year and reproductive class (Repro; 'Other' (noncalf) whales and 'Post-partum' females) are included as categorical independent variables, body condition is the ordinal response variable (Good, Fair, Poor) and individual whales (n = 181) are included as a random factor. The bolded model represents the most parsimonious model. The intercept model represents a constant slope model where the intercept = 1.0.

Model	*k*	Log-likelihood	AIC	ΔAIC	ω_i
Month + Year + Repro	**25**	–575.368	**1,200.74**	0.00	1.00
Month + Year	24	–591.358	1,230.72	29.98	0.00
Year + Repro	21	–596.289	1,234.58	33.84	0.00
Year	20	–612.648	1,265.30	64.56	0.00
Month + Repro	8	–636.629	1,289.26	88.52	0.00
Month	7	–645.523	1,305.05	104.31	0.00
Repro	4	–655.900	1,319.80	119.07	0.00
Intercept	3	–664.690	1,335.38	134.64	0.00

significantly improved by the month of August and continued to improve through the end of October (Table 3). Compared to the reference year, 1997, whales in each year had a higher or lower average body condition represented by a positive or negative Wald *z* statistic where 1997 is equal to zero (Table 3). Only five years were significantly different from 1997 (Table 3). Three years (2007, 2009 and 2010) had significantly lower average body condition than 1997. Two years (2001 and 2013) had significantly better average body condition. Known post-partum females were significantly more likely to be in worse body condition compared to whales of other reproductive states (Table 3).

We computed the predicted probabilities of an average whale being in poor, fair or good body condition in each year of the study (Fig. 4); due to the small sample size for known post-partum females, we only present predicted probabilities for 'other' whales. The rate of body condition improvement and starting body condition in each year varied (Fig. 4). Whales in 2001 appeared to start and end the season in better body condition than other years (Fig. 4), however no whales were scored in October (Table 1), therefore predictions for that month are estimated. In 2007, 2009 and 2010, whales started the feeding season in worse body condition than in other

Table 3

Results of the most parsimonious multinomial regression model of Pacific Coast Feeding Group gray whale body condition in Washington, USA and Vancouver Island, Canada from 1996–2013 including month, year and reproductive class (Repro) as categorical independent variables, body condition as the ordinal response variable (Good, Fair, Poor) and individual whales (n = 181) as a random factor. The first two rows represent model intercepts. P-values < 0.05 represent a significant difference from the reference month, June; year, 1997; and reproductive class, 'Other'. The Odds Ratio represents the exponentiated estimate coefficient compared to the reference value.

Variable	Estimate	SE	Wald *z*	*P*-value	Odds ratio
Poor|Fair	−2.379	0.738	−3.226	0.002	0.1
Fair|Good	0.58	0.721	0.804	0.031	1.8
Month = July	0.303	0.343	0.883	0.377	1.4
Month = August	**0.772**	**0.325**	**2.379**	**0.017**	**2.2**
Month = September	**1.142**	**0.333**	**3.427**	**0.001**	**3.1**
Month = October	**2.037**	**0.375**	**5.435**	**<0.001**	**7.7**
Year = 1996	0.492	0.758	0.649	0.516	1.6
Year = 1998	−1.088	0.652	−1.668	0.095	0.3
Year = 1999	−0.554	0.621	−0.893	0.372	0.6
Year = 2000	−0.165	0.607	−0.271	0.786	0.8
Year = 2001	**1.526**	**0.568**	**2.689**	**0.007**	**4.6**
Year = 2002	0.496	0.837	0.593	0.553	1.6
Year = 2003	0.035	0.764	0.046	0.963	1.0
Year = 2004	0.037	0.829	0.044	0.965	1.0
Year = 2005	−0.365	0.734	−0.497	0.619	0.7
Year = 2006	0.318	0.591	0.538	0.591	1.4
Year = 2007	**−1.534**	**0.622**	**−2.466**	**0.014**	**0.2**
Year = 2008	0.646	0.535	1.209	0.227	1.9
Year = 2009	**−2.087**	**0.547**	**−3.813**	**<0.001**	**0.1**
Year = 2010	**−1.73**	**0.663**	**−2.611**	**0.009**	**0.2**
Year = 2011	0.287	0.592	0.485	0.628	1.3
Year = 2012	−0.055	0.501	−0.11	0.912	0.9
Year = 2013	**1.184**	**0.553**	**2.143**	**0.032**	**3.3**
Repro = Post-partum	**−3.373**	**0.626**	**−5.387**	**<0.001**	**0.03**

years (Fig. 4). During poorer condition years (2007, 2009 and 2010) the whales had slower improvement of body condition as compared to the reference year (1997) and compared to good condition years (2001 and 2013; Fig. 4).

Influence of environmental variables

Based on examination of simple scatterplots, we identified several environmental variables that appeared to have positive or negative linear relationships with average body condition. Three study years consistently stood out as potential outliers in the dataset: 2007, 2009 and 2010. These years had the lowest average body condition compared to other study years and consistently fell below the linear trends observed. We performed simple linear regression to further examine the relationship between average body condition and these variables. Regression analyses with all years, including the three potential outliers, were non-significant at the $p = 0.05$ level and Bonferroni corrected alphas. Using QQ-normality plots, fitted versus residual plots and residual versus leverage plots, these three years were consistent outliers and were removed from the regression analyses.

We found significant linear relationships between average body condition and several environmental variables when outlier years of 2007, 2009 and 2010 were removed (Table 4); when using the Bonferroni corrected alpha values only three comparisons remained significant, however others that fell within the $p < 0.05$ level were considered and are presented in Table 4 and in figures based on apparent linear relationships and *a priori* interest in certain environmental and biological parameters. Average body condition increased with total September kelp canopy cover (in hectares) on the Washington coast lagged one year (Fig. 5, Table 4). Average body condition increased with decreasing ONI lagged one year (Fig. 6, Table 4), decreasing PDO using the running average of the two prior years (Fig. 7, Table 4) and decreasing annual average sea surface temperature (SST) at La Perouse Bank lagged one year (Fig. 8, Table 4). Body condition showed a linear relationship to upwelling index at several latitudes, however only those which met normal distribution and variance assumptions are presented. Body condition increased when compared to annual upwelling index at 42°N, 45°N and 51°N (Table 4). When averaged across

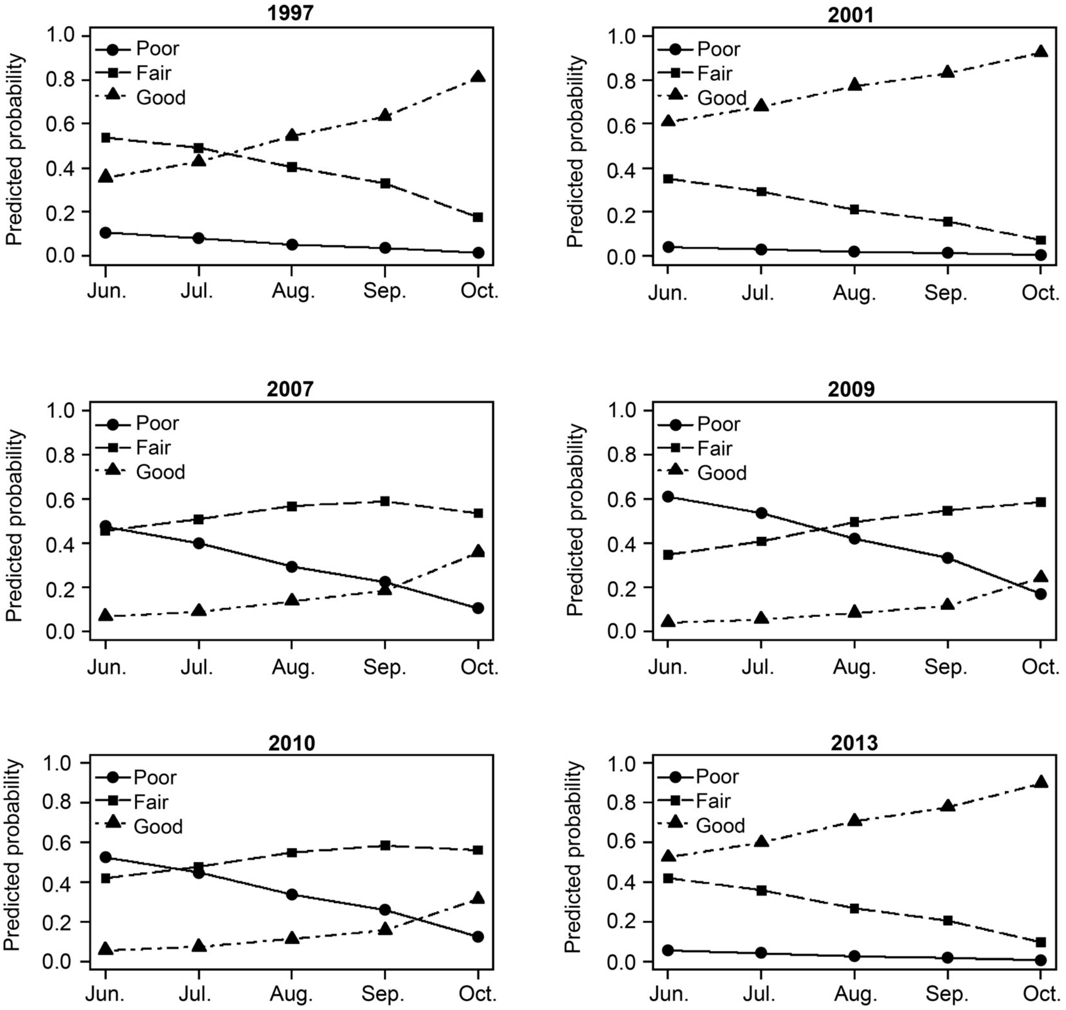

Fig. 4. Predicted probability of an average Pacific Coast Feeding Group gray whale (*Eschrichtius robustus*) being in poor, fair, or good body condition in each month of selected years of the study period. Selected years include the reference year (1997) and those that differ significantly from the reference year based on Wald *z* statistics and significant *P*-values (see Table 3). Predicted values were calculated from the selected model (Month+Year+Repro) for 'Other' non-calf whales and estimate predictions for month and year combinations where no data was available.

Table 4

Results of significant linear regressions of individual environmental variables compared to average Pacific Coast Feeding Group gray whale body condition. Environmental variables compared are September kelp canopy cover (ha) on the Washington coast lagged one year (Canopy Lag 1), Oceanic Niño Index lagged one year (ONI Lag 1), Pacific Decadal Oscillation running average (PDO Run) of the two prior years, sea surface temperature at the La Perouse Bank buoy Station 46139 lagged one year (SST Lag 1) and annual upwelling (no time lag) at N42, N45 and N51 and averaged between N42, N45, N48 and N51. Outliers are years that were removed from the model to improve normality and residuals. We performed post hoc testing using a Bonferroni adjustment where the corrected alpha value was calculated as 0.05 divided by the number of linear regressions run for each environmental variable. Bold values indicate significance after Bonferroni adjustment.

Variable	Adjusted R^2	F	*P*-value	Outliers
Canopy Lag 1	0.24	5.49	0.04 [a]	2007, 2009, 2010
ONI Lag 1	0.20	4.79	0.04 [b]	2007, 2009, 2010
PDO Run	0.44	12.18	**0.004** [b]	2007, 2009, 2010
SST at La Perouse Bank, lagged 1 year	0.44	12.21	**0.004** [b]	2007, 2009, 2010
Upwelling, N42	0.52	17.53	**0.001** [c]	2007, 2009
Upwelling, N45	0.35	9.03	0.009 [c]	2007, 2009
Upwelling, N51	0.23	5.57	0.033 [c]	2007, 2009
Upwelling, average of N42, N45, N48, N51	0.25	5.77	0.03 [c]	2007, 2009, 2010

[a] Bonferroni adjusted p-value < 0.0167
[b] Bonferroni adjusted p-value < 0.0125
[c] Bonferroni adjusted p-value < 0.006

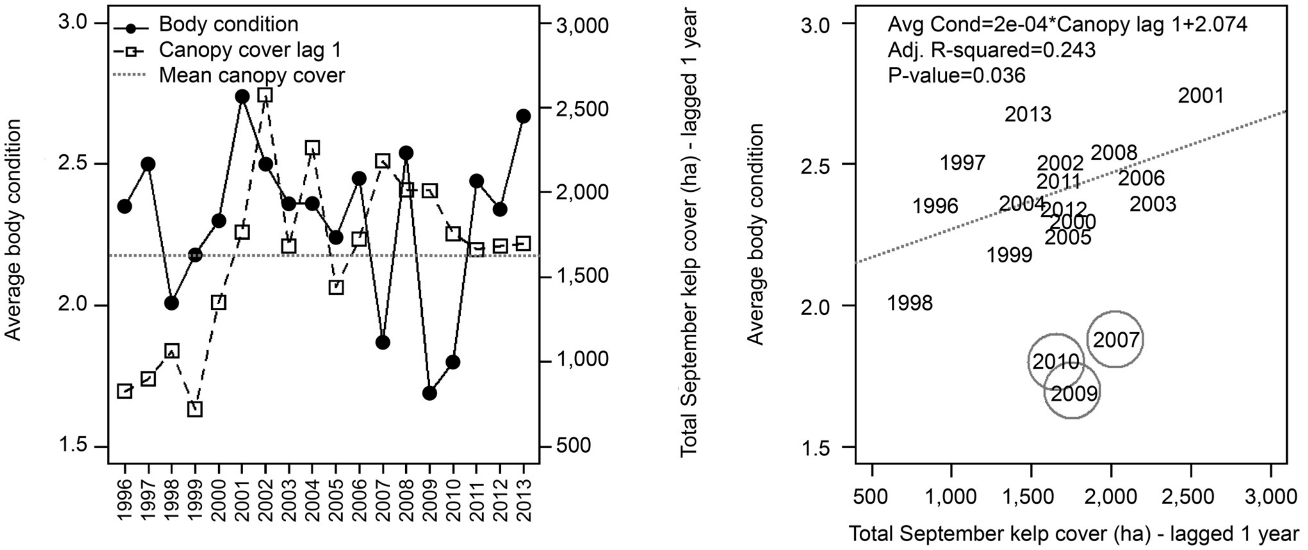

Fig. 5. Average September canopy cover (ha) of canopy forming kelp (bull kelp (*Nereocystis luetkeana*) and giant kelp (*Macrocystic integrifolia*)) on the Washington coast lagged one year compared to average Pacific Coast Feeding Group gray whale body condition. Circles represent years that were considered outliers based on QQ-normality and fitted versus residual plots and were removed from the final model. Regression is not significant following the Bonferroni adjustment ($p < 0.0167$).

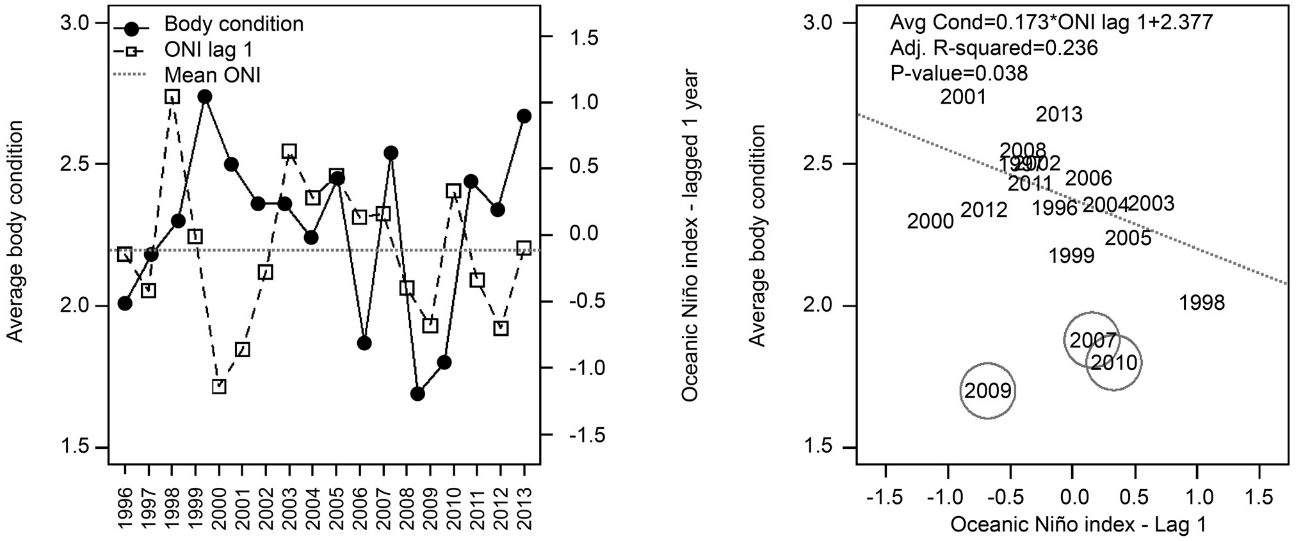

Fig. 6. Oceanic Niño Index (ONI) lagged one year compared to average Pacific Coast Feeding Group gray whale body condition. Circles represent years that were considered outliers based on QQ-normality and fitted versus residual plots and were removed from the final model. Regression is not significant following the Bonferroni adjustment ($p < 0.0125$).

the PCFG range (i.e. 42°N, 45°N, 48°N and 51°N), upwelling index was also positively related to body condition (Fig. 9, Table 4).

We performed a correlation matrix to investigate significant correlations between variables to help us select variables to include in the multiple regression analysis (Table 5). For upwelling, we chose to use the average of all areas, rather than upwelling index at individual latitudes because PCFG whales photographed in our research area are known to utilise a broad range of habitats encompassed between these latitudes (Calambokidis *et al.*, 2020; Lagerquist *et al*., 2019). We found a strong, positive correlation ($|r| > 0.70$) between PDO (running average) and sea surface temperature (SST; lagged one year) and moderate correlations ($0.5 > |r| < 0.7$) between the ONI (lagged one year) and PDO (running average) and between SST (lagged one year) and kelp canopy cover (lagged one year; Table 5). For the multiple regression analysis, we decided to include variables with moderate correlations, but to not include PDO and SST together in the same analysis due to the strong correlation between these two

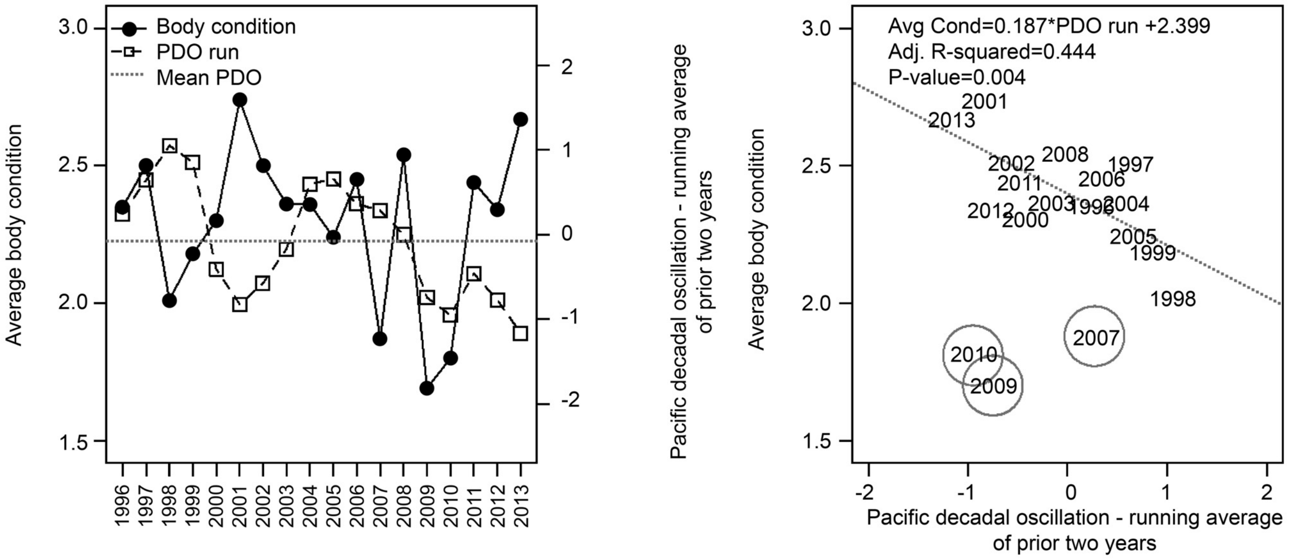

Fig. 7. Average annual Pacific Decadal Oscillation (PDO) Index, running average of two prior years, compared to average Pacific Coast Feeding Group gray whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model. Regression is significant following the Bonferroni adjustment (p < 0.0125).

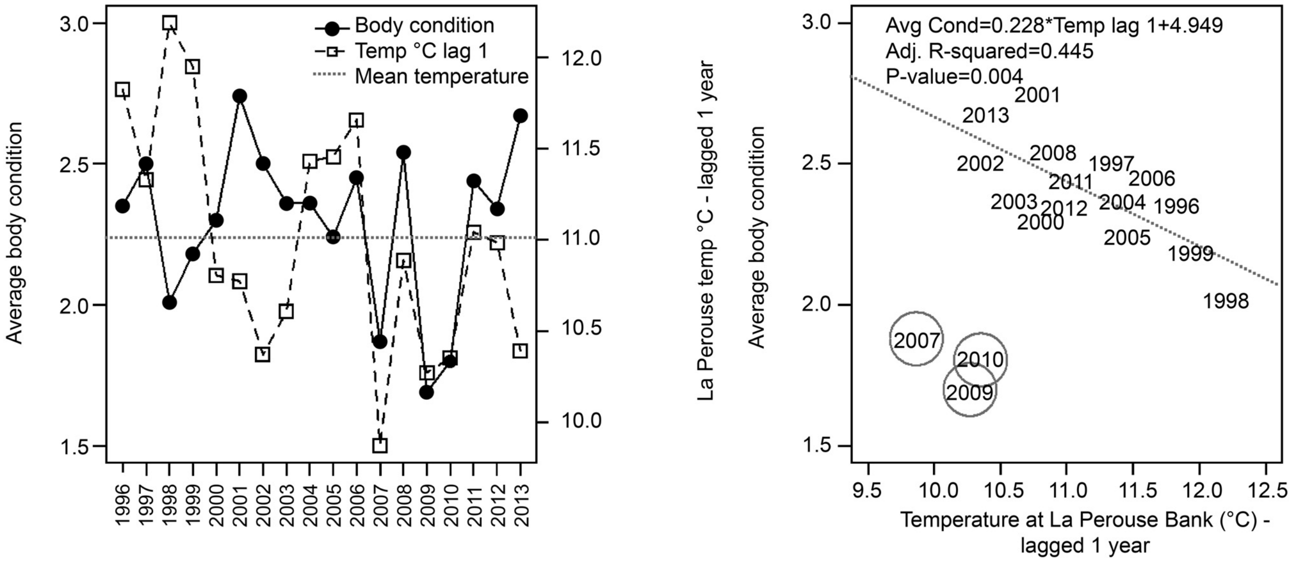

Fig. 8. Average annual sea surface temperature (°C) at La Perouse Bank, Canada, lagged one year, compared to average Pacific Coast Feeding Group gray whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model. Regression is significant following the Bonferroni adjustment (p < 0.0125).

variables. Of the two, we selected PDO to include in the multiple regression instead of SST because PDO includes conditions from the broader ocean basin including the full range of the PCFG feeding area. We performed multiple regression analysis comparing average body condition to the remaining environmental indices with common outlier years removed (i.e. 2007, 2009 and 2010).

Based on AICc model selection, the most parsimonious model included PDO using the running average of the two prior years (Table 6). The selected model accounted for 44.4% of variance in the body condition of ‘other’ whales (Adjusted $R^2 = 0.44$, P-value = 0.004; Fig. 8). Based on evidence ratios of Akaike weights, the best model had 29 times more evidence as being the most parsimonious model for the data than the intercept model that did not include environmental data. We compared the selected environmental model from the multiple regression (PDO running average of the two prior years) to the selected model from the ordinal regression (Month + Year + Repro) and found a significant positive correlation between the two (Fig. 10).

Table 5

Results of correlation matrix showing Pearson's correlation coefficients (r). Bolded cells show significant correlations at the $\alpha = 0.05$ level. Environmental variables compared are September kelp canopy cover (ha) on the Washington coast lagged one year (Canopy Lag 1), Oceanic Niño Index lagged one year (ONI Lag 1), Pacific Decadal Oscillation running average (PDO Run) of the two prior years, sea surface temperature at the La Perouse Bank buoy Station 46139 lagged one year (SST Lag 1) and annual upwelling (no time lag) averaged between N42, N45, N48 and N51 (Upwelling). Coefficients where $|r| > 0.7$ are considered a strong correlation.

	Canopy Lag 1	ONI Lag 1	PDO Run	SST Lag 1
ONI Lag 1	–0.321			
PDO Run	–0.506	**0.602**		
SST Lag 1	**–0.573**	0.473	**0.859**	
Upwelling	0.258	–0.222	–0.503	–0.357

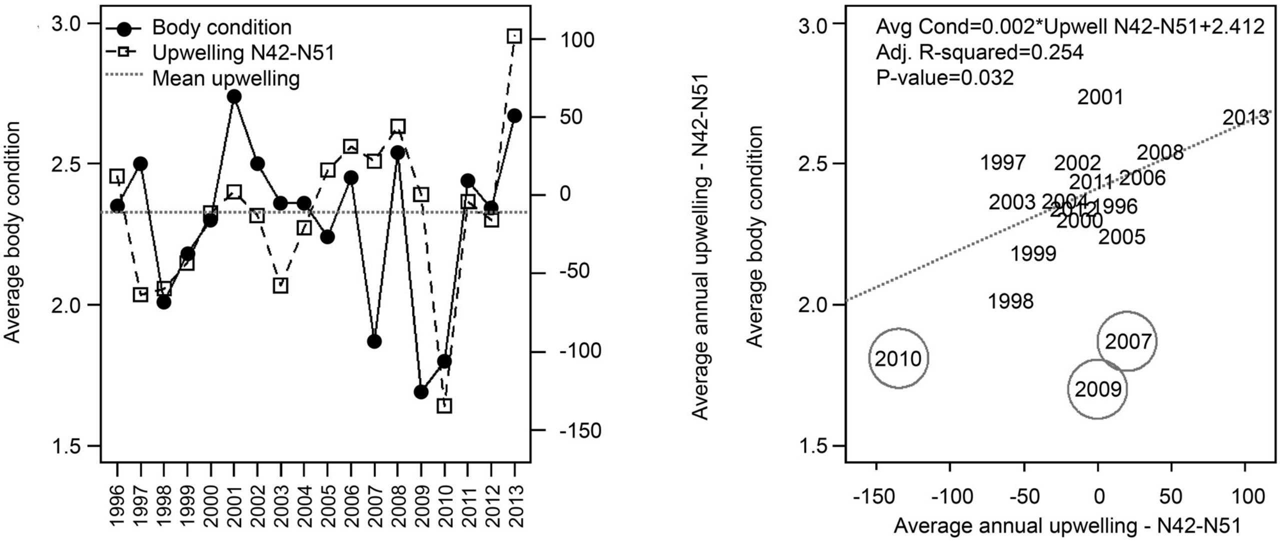

Fig. 9. Average annual Upwelling Index compared to average Pacific Coast Feeding Group gray whale body condition averaged across 42°N, 45°N, 48°N, and 51°N. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model. Regression is not significant following the Bonferroni adjustment ($p < 0.006$).

Table 6

Model selection of multiple regression analysis of environmental variables influencing average Pacific Coast Feeding Group gray whale body condition using log-likelihood, Akaike Information Criterion adjusted for small sample size (AICc), delta AICc (ΔAICc), Akaike weights (ω_i) and evidence ratio. Variables included are September kelp canopy cover (ha) on the Washington coast lagged one year (Canopy Lag 1), Oceanic Niño Index lagged one year (ONI Lag 1), Pacific Decadal Oscillation running average (PDO Run) of the two prior years, annual upwelling averaged between 42°N, 45°N, 48°N and 51°N latitudes (Upwelling) and an intercept model. The bolded model represents the most parsimonious model with $\Delta\text{AICc} > 2$.

Variables	df	logLik	AICc	ΔAICc	ω_i	Evidence ratio
PDO Run	**3**	**9.528**	**–10.87**	**0.00**	**0.35**	–
PDO Run + Upwelling	4	10.388	–8.78	2.10	0.12	2.9
Canopy Lag 1 + PDO Run	4	10.294	–8.59	2.29	0.11	3.1
ONI Lag 1 + PDO Run	4	9.866	–7.73	3.14	0.07	4.8
ONI Lag 1 + Upwelling	4	9.609	–7.22	3.66	0.06	6.2
Canopy Lag 1 + Upwelling	4	9.480	–6.96	3.91	0.05	7.1
Upwelling	3	7.324	–6.47	4.41	0.04	9.1
Canopy Lag 1	3	7.213	–6.24	4.63	0.03	10.1
ONI Lag 1	3	7.143	–6.11	4.77	0.03	10.8
Canopy Lag 1 + ONI Lag 1	4	8.984	–5.97	4.91	0.03	11.6
Canopy Lag 1 + PDO Run + Upwelling	5	11.244	–5.82	5.05	0.03	12.5
Canopy Lag 1 + ONI Lag 1 + Upwelling	5	11.162	–5.66	5.22	0.03	13.6
ONI Lag 1 + PDO Run + Upwelling	5	10.934	–5.20	5.67	0.02	17.1
Canopy Lag 1 + ONI Lag 1 + PDO Lag 1	5	10.643	–4.62	6.25	0.02	22.8
Intercept	2	4.569	–4.14	6.74	0.01	29.0
Canopy Lag 1 + ONI Lag 1 + PDO Run + Upwelling	6	11.821	–1.14	9.73	0.00	129.8

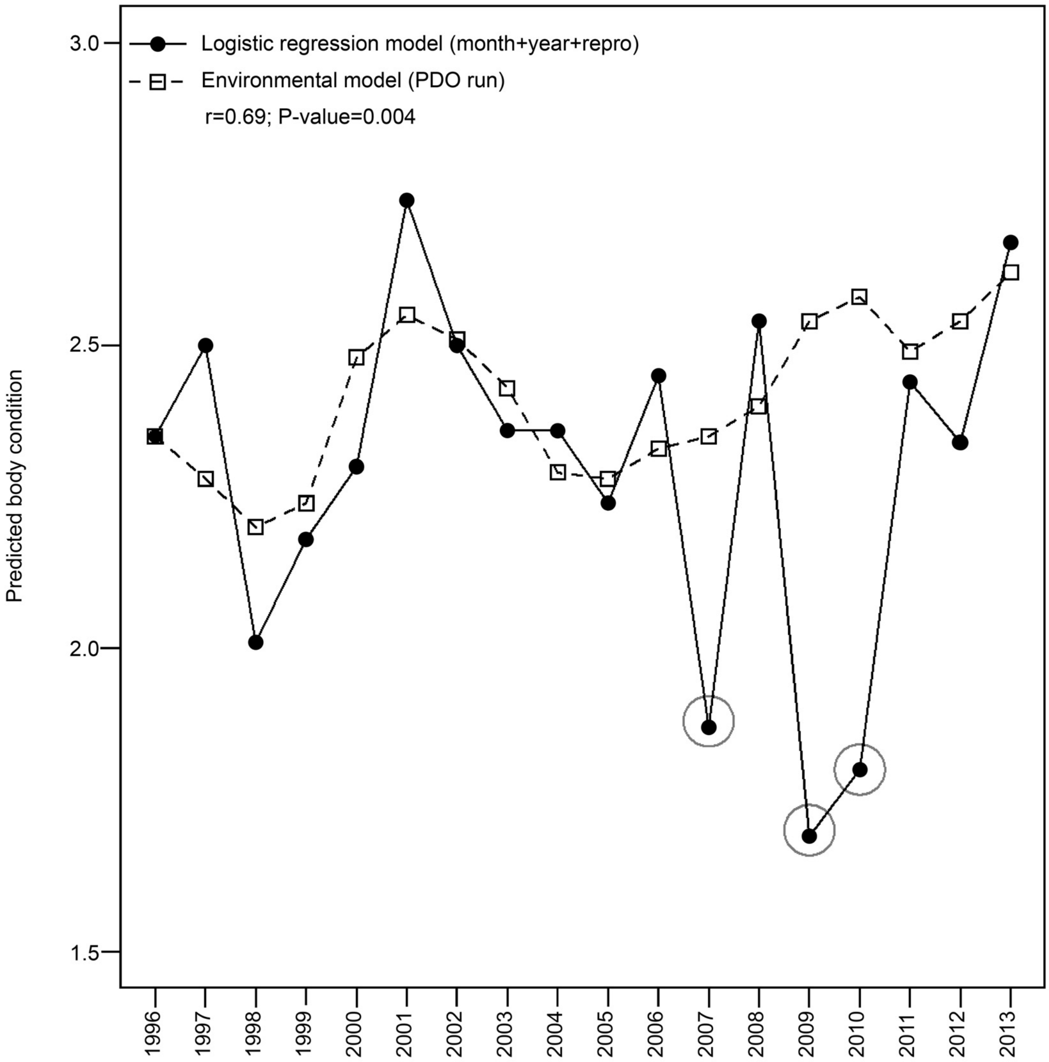

Fig. 10. Correlation of predicted Pacific Coast Feeding Group gray whale body condition between the most parsimonious logistic regression model (Month + Year + Repro) and most parsimonious environmental model (Pacific Decadal Oscillation running average of the two prior years; PDO Run). Reproductive class (Repro) includes 'Other' (non-calf) whales and 'Post-partum' females. Lighter grey circles represent years that were considered outliers and were not included in the correlation.

Influence of body condition on fidelity to the study area

To evaluate the influence of body condition on the probability that an individual whale was seen in the next feeding season, we compared body condition in the latter half (August or later) of the feeding season in a given year (year Y) as to whether or not the whale was seen the next year (year Y + 1). We did not find any significant association between a whale being in good body condition and whether it would return to the area in the following year when considering all whales or by sex, although whales in good body condition appeared slightly more likely to return to the region in the subsequent year (Fig. 11).

Comparison to ENP calf estimates

We used scatterplots to visually compare average body condition to ENP calf estimates at varying time lags (one year, two years and a running average of the two prior years) and observed linear relationships with calf estimates lagged one year and using a running average of the two prior years. Similar to our comparison with environmental variables, 2007, 2009 and 2010 appeared to be outliers from the data and were examined further. We performed simple linear regression to further examine the relationship between average body condition and the calf estimates (Appendix I). Based on QQ-normality plots, fitted versus residual plots and residual versus leverage plots, 2007,

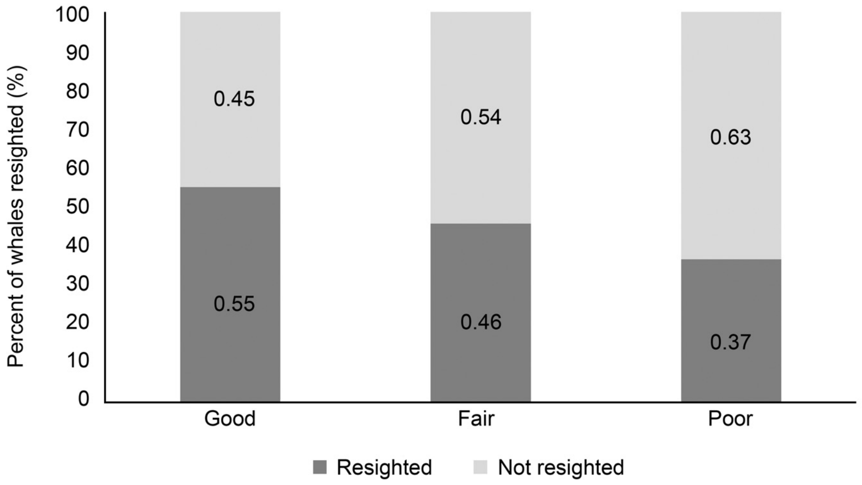

Fig. 11. Percent of Pacific Coast Feeding Group gray whales resighted in year Y + 1 compared to individual body condition (Good, Fair or Poor) in August or later of year Y.

2009 and 2010 were removed from the regression analysis. With outlier years removed, we found a significant relationship between better body condition and decreasing calf estimates lagged one year and using the running average of the two prior years (Fig. 12).

DISCUSSION

Factors influencing gray whale body condition

Methods developed by Bradford *et al*. (2012) were used to evaluate the body condition of PCFG gray whales observed off the coast of northern Washington from 1996-2013 and off the coast of Vancouver Island from 1996–2002. It was found that gray whale body condition improved through the feeding season, but that the rate of improvement and body condition at the start and end of the feeding season was variable by year and found no overall trend in body condition (increasing or decreasing) over the study period. Gray whale body condition was also strongly affected by reproductive status, with postpartum females having much poorer body condition than other non-calf whales. We found that both local and basin-wide environmental drivers explained some of the observed annual variability in body condition of PCFG whales in our study area. In most years, oceanographic parameters such as PDO, SST and upwelling significantly improved the ability of regression models to predict the average body condition of whales observed in the study area during that year. Based on multiple regression analysis, PDO, using the running average of the two prior years, was the best predictor of body condition when outlier years (2007, 2009 and 2010) were removed (Table 6) and should be considered as an important variable in future investigations of PCFG gray whale health.

Changes in environmental conditions likely indirectly impact body condition through a more direct impact to the whales' prey resources throughout their range. In this regard, it is unsurprising that there was a significant effect of several environmental variables at one or more time lags. Whale body condition as mediated by prey availability and abundance cannot respond instantaneously to environmental factors; prey populations require time to increase reproduction and grow to body sizes suitable for gray whale foraging before the changes in environmental conditions can result in changes in the body condition of gray whales (Blanchard *et al*., 2019; Burnham and Duffus, 2018; Feyrer and Duffus, 2015). Gray whales in the PCFG region feed on a variety of prey taxa, including several species of mysid shrimps, crab larvae (*Petrolisthes* spp.) and ampeliscid amphipods, among other items (Darling *et al*., 1998; Dunham and Duffus, 2002; Feyrer and Duffus, 2011; Nelson *et al*., 2008). Whale abundance and distribution on the feeding grounds appear heavily mediated by prey location and abundance which, in turn, are affected by a combination of local and large-scale bottom-up forces (Burnham and Duffus, 2018; Feyrer and Duffus, 2015; Garside, 2009). Environmental conditions have been tied to changes in diet and reproductive success of large whales mediated through bottom-up forcing to their prey resources. The diet of

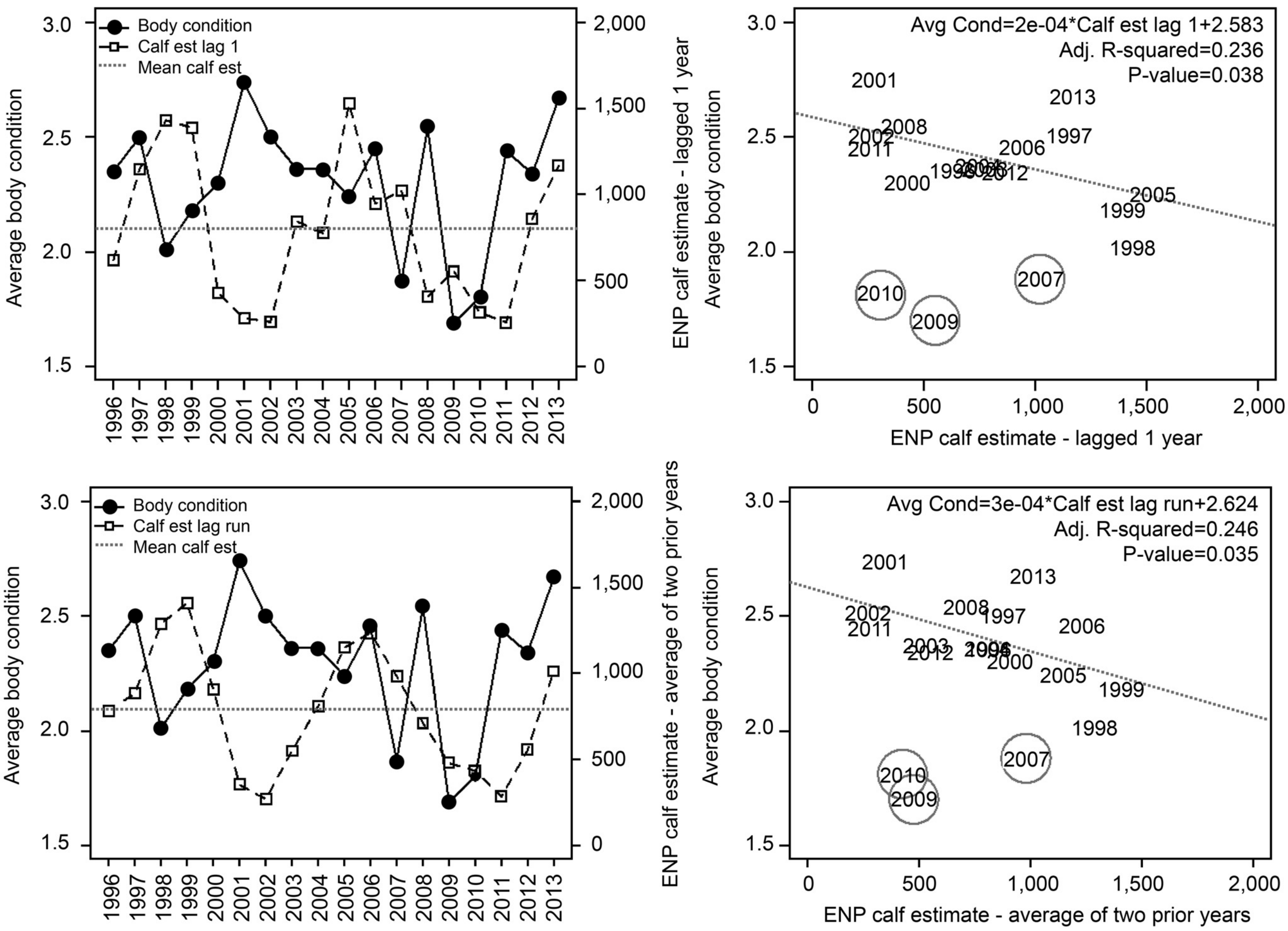

Fig. 12. Eastern North Pacific (ENP) gray whale population calf estimate (Perryman *et al.*, 2020), lagged 1 year (Lag 1; top panels) and running average of two prior years (Lag Run; bottom panels), compared to average Pacific Coast Feeding Group gray whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model.

humpback whales (*Megaptera novaeangliae*) varied from krill during cool ocean conditions with strong upwelling to schooling fish during warm ocean conditions and late season upwelling (Fleming *et al*., 2015). In southern right whales (*Eubalaena australis*), krill density, sea surface temperature and large-scale indices (Oceanic Niño Index (ONI) and the Antarctic Oscillation Index (AAO)), were significantly correlated to calf production at multiple time scales (Seyboth *et al*., 2016). Citta *et al.* (2008) found that bowhead whales favoured colder water temperatures and areas with high salinity gradients that are likely associated with greater densities of zooplankton prey. Several studies have found associations between gray whale calf production, apparent survival and sea ice extent on their Arctic feeding grounds (Gailey *et al*., 2020; Perryman *et al*., 2020; Salvadeo *et al*., 2015). Therefore, it is clear that environmental conditions have the potential to affect large megafauna at least indirectly.

Variables that reflected sea surface temperature, such as PDO and SST at La Perouse Bank, had high explanatory power for body condition in most years when lagged one or more years (Table 4). PDO exhibited a negative relationship with body condition (Fig. 7), where years of low index values (i.e. cold eras) correspond to years of better average whale condition, likely due to increased productivity off the US west coast during those years (Mantua *et al*., 1997). PDO represents sea surface temperature anomalies in the North Pacific poleward of 20°N and therefore more likely reflects environmental changes occurring over the entire PCFG range. Perryman *et al.* (2020) found that PDO and Arctic sea ice cover in May, the month pregnant females typically arrive back at Arctic feeding grounds, were strong predictors of ENP calf estimates the following spring (Perryman *et al.*, 2020). In the Arctic, colder years with greater ice cover reflect reduced foraging area and primary and secondary productivity (George *et al*., 2015; Stabeno *et al*., 2012), reducing reproductive potential. Similar to PDO, a negative relationship was observed between SST lagged one year and body condition (Fig. 8). SST measured at La Perouse Bank (48°50’24’’N 126°0’W) is well offshore of typical gray whale foraging areas along Washington and Vancouver Island and our decision to include temperature data from that buoy was two-fold: 1) temperature data was available from the buoy for the full time period of the study, and 2) temperature measured at the buoy would broadly reflect annual variations in temperature for the study region. Linear relationships between body condition of whales in our study with parameters that reflect ocean temperature at a lagged scale (e.g. local SST, ONI and PDO) suggests a lagged effect on prey productivity in the study area.

Significant positive relationships between average body condition and average upwelling index values were particularly strong for northern California (42°N; Table 4), but no linear trend was observed when compared to upwelling at or north of 54°N. This study supports the finding by Lemos *et al*. (2020) that PCFG gray whale body condition was lower during low upwelling years. Although some PCFG whales are known to spend time during and prior to the feeding season outside of the IWC defined range (Gosho *et al.*, 2011; Lagerquist *et al.*, 2019), we found that the upwelling conditions within the range of 41°N to 52°N appeared to be most reflective of the health of PCFG whales photographed in this study. Other studies have similarly found that health and regional abundance of whales reflect upwelling conditions. Croll *et al.* (2005) observed increased abundance of blue whales in Monterey Bay following seasonal periods of high upwelling that led to a peak in primary productivity and subsequent increase in their euphausiid prey. Garside (2009) considered the effect of environmental variables on gray whale abundance off Vancouver Island and found that upwelling index values, derived both locally and north of the study area, lagged two years, were good predictors of annual whale abundance during the feeding season. George *et al*. (2015) found that bowhead whale body condition was positively correlated to the loss of summer sea ice in the Beaufort Sea, as well as upwelling wind stress and mean open water from both the preceding summer and the average of three previous summers. The loss of summer sea ice is likely responsible for an increase in bowhead whale prey through the increased open water fraction and increased potential for upwelling favourable conditions leading to greater primary and secondary productivity (George *et al.*, 2015). The relationship between upwelling and body condition of PCFG whales likely reflects these bottom-up mechanisms that link upwelling to whale prey abundance.

A positive (though not significant following Bonferroni adjustment) relationship was observed between September kelp canopy cover, lagged one year, and gray whale body condition where greater kelp canopy cover (ha) corresponded to better body condition. Kelp canopy cover data was only available for the Washington portions of the study area and it is possible that having kelp canopy data over the entire study area would have yielded different results. At a local level, it is possible that kelp canopy acts as habitat or as food for gray whale prey, primarily mysid shrimp (e.g. *Holmesimysis* spp.) (Burnham, 2015; Garside, 2009; Graham, 2004). Four primary species of mysids have been documented in feeding areas off Vancouver Island, with *Holmesimysis sculpta*, being the most dominant (Burnham, 2015; Feyrer and Duffus, 2011). Generally, mysid brood production peaks in summer months with increased nutrients and warming temperatures and at least three broods hatch between late May and early September, with only *H. sculpta* having a fourth brood in November (Burnham, 2015; Burnham and Duffus, 2018). Although the larvae reach maturity at relatively short scales (60 days), high foraging pressure by gray whales in a given season is typically followed by at least one summer of lower predation pressure in which the mysids are likely able to re-establish larger swarms (Burnham and Duffus, 2018). The winter brood of *H. sculpta* is likely responsible for the dominance of this species observed off Vancouver Island as the hatching and breeding of the subsequent brood take place prior to seasonal gray whale foraging (Burnham, 2015). Sullivan (2017) found an association between gray whale foraging behaviour and distance from kelp at fine, site-specific scales, suggesting that the presence of kelp may be a more reliable predictor of available prey compared to searching for dynamic mysid swarms that are patchy in time and space. In the current study, kelp cover was only considered at a local scale and not over the entire PCFG feeding range and we are not aware of any studies that have directly correlated mysid density with kelp canopy cover. Additionally, kelp canopy cover was negatively correlated to sea surface temperature and the observed relationship between body condition and kelp cover may be spurious.

The inability of these models to predict body condition in the poorer condition years (2007, 2009 and 2010), indicates that there are likely other factors (biotic or abiotic) that influence whale health that are unaccounted for in this study. Reproductive state and age were only recorded in post-partum females and their calves, however other age ranges and reproductive stages in whales may cause them to be vulnerable to changes in productivity and food availability (Bradford *et al*., 2012; Pettis *et al*., 2017). In a study of North Atlantic right whales (*Eubalaena glacialis*) using a similar methodology, Pettis *et al*. (2017) found that younger juvenile whales (age 1–2 years) and older juveniles (3–8 years), improved body condition during the feeding season at different rates, as did adult males and anestrous females. Similarly, George *et al.* (2015) found that yearling bowhead whales had lower body condition in the years after weaning. It is possible that this study was not able to identify further patterns due to the presence of undocumented post-partum females and calves or due to the inability to assign other whales to known age classes or reproductive states. In addition, gray whale foraging pressure in a previous year could have influenced the availability of prey in the year the body condition was determined (Burham and Duffus, 2018). Unfortunately, the survey methodology for gray whales did not allow the recoding of a daily rate for whales feeding in the survey area and thus it was not possible to add that factor to our modeling to test whether gray whale feeding pressure affects body condition in future years. The selected time lags may also have been too broad. Perryman *et al.* (2020) compared ENP calf production to environmental variables and found that models performed best at monthly time scales (e.g. sea ice cover and PDO in May influenced calf counts the following spring) compared to seasonal and annual averages. It is possible that the averaged seasonal and annual indices masked the influence of environmental variables on predicted body condition.

Several local observations may help explain the years that the models could not effectively predict body condition. In 2007 an aggregation of 28 gray whales were observed feeding 20–25km offshore (60m depth) of Grays Harbor, WA during the feeding season (Oleson *et al.* 2009). All but one of these 28 whales were known PCFG individuals. Given the overall poorer body condition of whales observed in that year, it is possible that poor feeding conditions elsewhere led to the whales exploring this offshore area. Scordino *et al*. (2017) found the greatest average daily density of gray whales observed in our study area in 2008. This was followed by the two years of poorest body condition over the 18-year study. The high number gray whales present in 2008 may have depleted prey resources meaning the prey were unable to recover to support feeding gray whales in 2009 and 2010, resulting in low foraging success in the study area and poorer apparent body condition of the whales present. Burnham and Duffus (2018) observed that PCFG gray whales feeding off Vancouver Island exert top-down control on mysid shrimp (Family Mysidae) populations and that numbers of whales using their area exhibit boom-bust dynamics with years of high whale use followed by 1–3 year periods of low whale use, which allowed the prey populations to recover. 2010 was a year of low whale use in the survey area and the whales using the area did not remain for long periods (i.e. had low minimum tenure, see Scordino *et al.*, 2017). In the same year, Burnham and Duffus (2018) observed a higher than average year for whales per survey in Clayoquot Sound, Vancouver Island. During the feeding season, gray whales may switch prey species (Nelson *et al.*, 2008) and move from poorer to higher quality feeding locations (Burnham and Duffus, 2018; Feyrer and Duffus, 2015), which may in part explain the differences in local abundance in these two areas and contribute to within season movement of PCFG whales between regions of the full PCFG range (Calambokidis *et al.*, 2020).

In contrast to findings from a previous study (Akmajian *et al*., 2013), body condition did not predict apparent fidelity to the study region, however we did see suggestive evidence that a larger proportion of whales in good condition and a lower proportion of those in poor condition were seen in the subsequent year. These findings were likely due to a change in our methodology and the inclusion of an additional eight years of data. In the current study, we restricted the analysis to body condition scores from August or later because we expected whales should have had the opportunity to attain good body condition by August, but not necessarily by June or July. We also restricted the analysis to known PCFG whales, which we had not done previously. Calambokidis *et al*. (2020) found that roughly half of the whales observed in the PCFG range during the feeding season were only observed in one year and did not meet the definition of a PCFG whale. By removing non-PCFG whales from the analysis, we prevented the lack of observation of non-PCFG whales in subsequent years from influencing our results.

A significant relationship was observed between PCFG body condition and ENP calf estimates where a higher number of ENP calves in the year prior corresponded to lower PCFG body condition. Several studies have noted that juvenile whales lose blubber thickness during the post weaning period as they began to forage on their own

(George *et al.*, 2015; Miller *et al.*, 2011; Pettis *et al.*, 2017). Post-lactation females may take longer than whales in other reproductive states to recover their blubber thickness (Bradford *et al.*, 2012; Miller *et al.*, 2011; Pettis *et al.*, 2017). The observations likely reflect a combination of unidentified juvenile whales and post-lactation adult females that were unidentified in this study. However, Bradford *et al.* (2012) found that body condition of females, regardless of reproductive status, may have an interactive effect with environmental variables, which may confound the analysis. Similar to this study's comparisons with environmental variables, 2007, 2009 and 2010 were apparent outliers underlining the assertion that additional factors unaccounted for in this study drive body condition of PCFG whales.

Within the years of this study, ENP gray whales experienced an unusual mortality event (UME) across their range. In 1999 and 2000, 651 gray whales washed ashore between Mexico and Alaska and though the ultimate cause remains unknown, starvation was considered the most likely scenario (Le Boeuf *et al.*, 2000; Gulland *et al.*, 2005). In this study, body condition of PCFG whales was lower in 1998, 1999 and 2000 compared to our reference year of 1997, but not significantly so and body condition was not as low as the three lowest years (2007, 2009 and 2010; Table 3). Body condition was highest in 2001, just following the 1999/2000 UME. Given the differences between the Arctic and the PCFG feeding areas (discussed above), it is unsurprising that the health of PCFG whales does not mirror the broader ENP population. Following a second UME in the ENP gray whale population in 2019 and 2020, Christiansen *et al.* (2021) investigated the body condition of gray whales wintering in San Ignacio Lagoon, Baja California Sur, Mexico in the years leading up to the morality event. Whales in 2018 and 2019 appeared to have poorer body condition compared to their reference year of 2017 (Christiansen *et al.*, 2021). A similar analysis of body condition was not available for the previous UME.

Comparisons of observations of body condition with whales studied at Sakhalin Island

Bradford *et al*. (2012) studied the body condition of gray whales at Sakhalin Island, Russia providing a unique opportunity to compare the body condition of two feeding groups of gray whales. At both Sakhalin Island and in the PCFG, gray whale body condition was variable by year. The years of significantly better or worse body condition were different for the two feeding areas, although both were compared to the same reference year of 1997. A notable exception was 2007, in which whales had significantly worse body condition compared to the reference year in both studies. As noted above, 2007 was a frequent outlier in this study when comparing environmental variables and a unique year for whales utilising the Washington coast in that a large group of PCFG whales was observed in an unusual feeding location. For Sakhalin Island gray whales, 2007 was the year with the lowest body condition and when only non-calf males were considered, was the only year of significantly worse body condition compared to other years suggesting that environmental drivers rather than reproductive condition may have been the cause (Bradford *et al.*, 2012). While this similarity in poorer body condition may be coincidental, further investigation of environmental and biological factors affecting these two separate feeding groups is warranted.

Given that these two groups of whales feed in areas far removed from one another, it is not surprising that conditions and years of good or poor body condition are generally unrelated. For example, these differences may have been driven by how the prey in the two feeding areas respond to large-scale environmental drivers such as the Pacific Decadal Oscillation (PDO). Mantua *et al*. (1997) found that PDO governed salmon production regimes with warm phases having greater production of salmon at more northerly latitudes and lower production at more southerly latitudes in the North Pacific and vice versa in cold phases. Prey of gray whales may have a similar response. Total available prey at offshore Sakhalin Island feeding grounds are positively correlated with both winter and summertime PDO (Blanchard *et al*., 2019). Perryman *et al.* (2020) found a positive relationship between PDO and ENP gray whale calf production where several cold years (negative PDO and/or extensive sea ice cover) translated to lower calf estimates in the following spring. These lower calf counts are likely the result of reduced available foraging area and prey resources translating to a reduced potential for successful pregnancy (Williams *et al*, 2013; Perryman *et al.*, 2020). In contrast, a negative correlation of PCFG gray whale body condition with PDO was found suggesting that in warm phase years the whales had less available prey.

The rate of improvement of body condition was not equal between the whales using the Sakhalin and PCFG feeding ranges. Whales feeding at Sakhalin Island attained body condition faster and to a better condition (Bradford *et al*., 2012) than the whales that were studied in the PCFG. At Sakhalin Island the majority of gray whales attained good body condition by September, being 14 times more likely to be in good body condition in September when compared to July (Bradford *et al*., 2012). In the PCFG, some years were observed in which only 60% had attained good body condition by October (see Fig. 4) and whales were only 7 times more likely to be in good condition in October compared to the reference month of June (see Table 3). Further, 58% of Sakhalin Island whales that could be assigned a complete body condition score were scored in good condition (Bradford *et al*., 2012) compared to 50% of known scores in this study. Together these findings suggest that Sakhalin whales are rewarded with better payoff, in terms of more predictably attaining body condition likely through a difference in availability or density of prey resources, than the whales we observed on PCFG feeding grounds.

CONCLUSIONS

The surveys informing this analysis were conducted over a limited portion of the PCFG range, making our scope of inference unclear. However, observations from photo-identification studies and from satellite telemetry have found that some PCFG whales will use a large portion of the PCFG range within a feeding season whereas others exhibit spatially limited home ranges (Calambokidis *et al*., 2020; Lagerquist *et al*., 2019). The results of this study clearly show that body condition of PCFG gray whales photographed in the study area vary within season and by year and that local and basin-wide environmental factors may influence the observed variations. In the future, it is expected that the body condition of gray whales will continue to fluctuate in response to environmental changes, particularly those like PDO that reflect ocean temperature and productivity in the PCFG range. Using a similar methodology to the one in this study, changes in body condition of whales were detected over short periods (11–12 days) (Pettis *et al*., 2017), suggesting this method of visual examination can be an effective way to monitor individuals in a population over relatively short within-season timescales. Note that this study did not detect a long-term change in body condition (positive or negative) over the 18-year period of this study (e.g, Fig 5). Extending this analysis to include recent years of known environmental perturbations, such as the warm water 'Blob' (Peterson *et al*., 2017) and the 2019–2020 gray whale UME, may provide further understanding of how anomalous conditions and climate change will impact PCFG gray whales and their prey resources. To be more representative of the PCFG as a whole, any future study of body condition should target collaborations with researchers throughout the PCFG range to ensure that the results are representative of the whole group and not just the portion that entered a spatially confined study area within a given year.

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