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

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

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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 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 (lagged two years) and September kelp canopy cover along the Washington coast (lagged one year), drastically improved the ability of a multiple regression model 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 of life history strategy between a group of whales with a long migration (Sakhalin whales) and those with a short migration. 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. Photogrammetry may be an effective method for monitoring the effects of climate change on PCFG gray whales.

KEYWORDS: GRAY WHALE; BODY CONDITION; HEALTH; ENVIRONMENT; PHOTOGRAMMETRY; PACIFIC COAST FEEDING GROUP; PACIFIC OCEAN

INTRODUCTION

The Eastern North Pacific (ENP) population of gray whales was twice seriously depleted due to unregulated commercial whaling (Darling, 1999), but with protection has recovered (Punt and Wade, 2012). Now numbering an estimated 26,960 whales (Durban *et al*., 2017), the majority of the population spends the summer feeding season in the Bering, Beaufort and Chukchi seas, while a smaller number feed along the Pacific coast of the U.S. and Canada. This smaller aggregation of whales, known as the Pacific Coast Feeding Group (PCFG; IWC, 2011), is estimated to number about 232 individuals (Calambokidis *et al*., 2019). These PCFG whales are thought to remain off the coasts of Northern California, Oregon, Washington and British Columbia during the June to November feeding season (Calambokidis *et al*., 2002, 2019), although some individuals are sighted with regularity as far northwest as Kodiak Island, Alaska (Gosho *et al*., 2011). The International Whaling Commission defines PCFG whales 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*., 2019).

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Within the PCFG range, individual gray whales show variability in their use and fidelity to a particular region (Calambokidis *et al*., 2019; 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*., 2019). 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*., 2019; Scordino *et al*., 2017). Further, the total number of whales sighted is also variable between years, regardless of survey effort (Calambokidis *et al*., 2019; 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 and Duffus, 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 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 in both 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). Conversely, top-down feeding pressure leading to reduced prey resources also causes reduced foraging effort and 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 (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 hypothesize that whale body condition in the region would reflect food availability and ecosystem productivity. 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 for comparison to, and inclusion in, their catalog of individually identified gray whales from the US West Coast. Each whale photographed was either matched to an existing whale and identification number in the Cascadia Research Collective catalogue, assigned a new identification number for the catalogue if no match could be made, or left unidentified if the photo was of insufficient quality (Calambokidis *et al.*, 2002, 2019). Cascadia Research Collective provided identification numbers (CRC ID) from each sighting for this analysis. The sex of photographed whales was determined by comparing their CRC ID to those of biopsied whales with sex determined during genetic studies following the methods detailed in Lang *et al*. 2014 (Aimée Lang, NOAA Southwest Fisheries Science Center, personal communication). In order to look at changes in body condition over the feeding season, we used photographs from June through November only. Furthermore, we restricted our analysis to only evaluating the body condition scores of whales that met the IWC definition of a PCFG whale (see IWC, 2011; 2014).

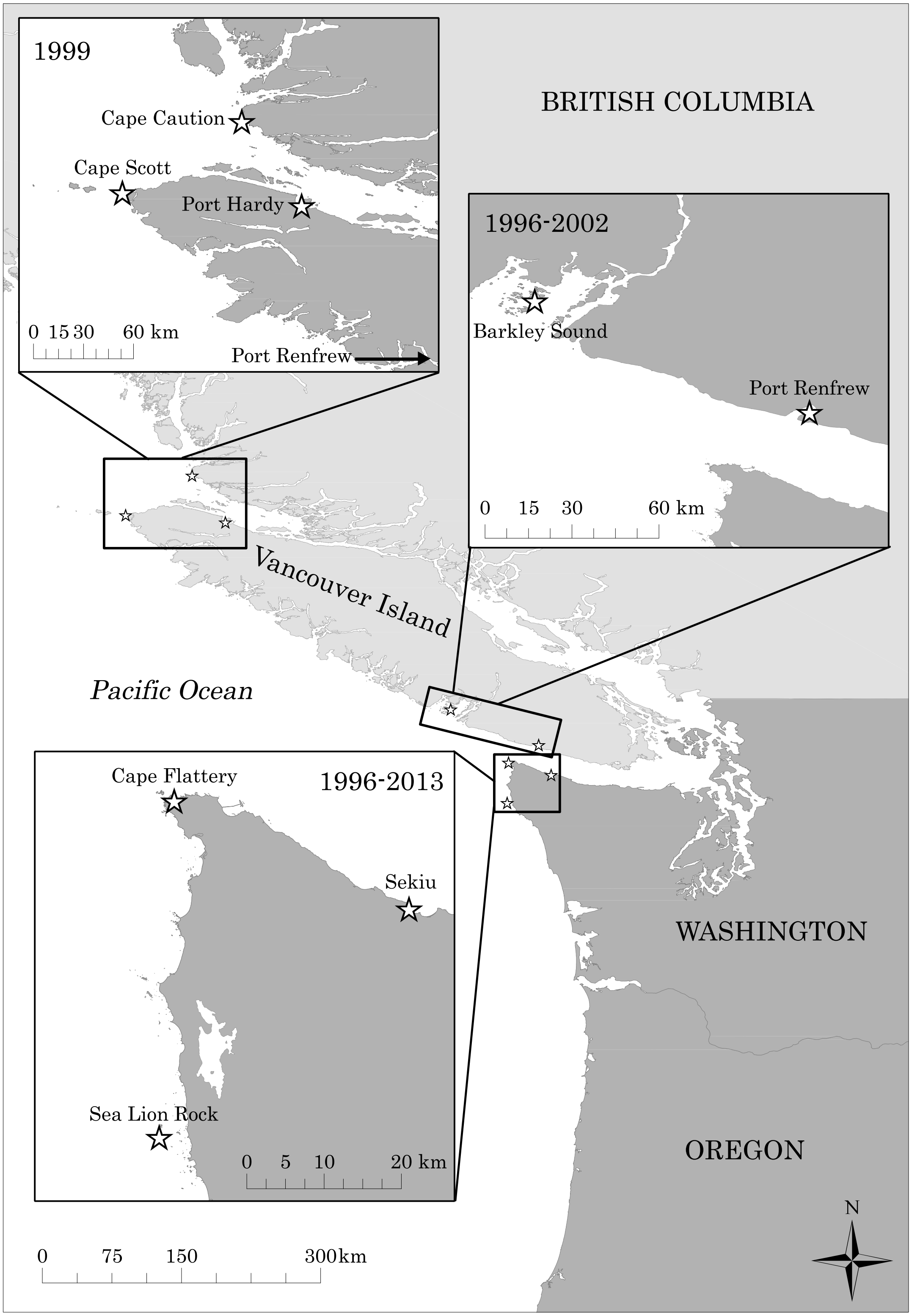

Fig. 1. Map of the study area with insets to display regions and years surveyed for gray whales in Washington State, USA, and Vancouver Island, British Columbia, Canada.

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. 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 rounded post-cranial region with no visible depression (i.e. good condition), a score of 2 indicates a slight to moderate depression (i.e. fair condition) and score of 1 indicates severe post-cranial depression (i.e. poor condition). 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 protrusion 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 a 1 (poor flank condition) when the whale had an obvious depression along the flank. An overall body condition score would thus read "322" for a whale in good body 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 to increase the likelihood of having a known body condition score by pooling scores for that whale from all sightings in a given month (Bradford *et al.*, 2012). If whales were sighted on more than one occasion within a month, then the composite was based on the most frequent body score given or the score 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).

Environmental 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 utilize feeding areas between northern California and British Columbia or as far north as Kodiak Island (Calambokidis *et al*., 2019, 2002; Gosho *et al*., 2011). Large-scale environmental variables included in our analyses were the Pacific Decadal Oscillation (PDO, http://research.jisao.washington.edu/pdo/PDO.latest), Oceanic Niño Index (ONI, http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ ONI_change.shtml) and North Pacific Gyre Oscillation (NPGO, http://www.o3d.org/npgo/npgo.php). 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 (http://www.ndbc.noaa.gov/). Because PCFG whales are known to have large home ranges (Calambokidis *et al.*, 2019; Lagerquist *et al.*, 2019), upwelling indices were obtained from NOAA (http://www.pfeg.noaa.gov/) for the northern Washington coast, 48˚ N 125˚ W, as well as areas to the north and south including at 42˚ N 125˚ W, 45˚ N 125˚ W, 51˚ N 131˚ W and 54˚ N 137˚ W. 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 to the Columbia River mouth, using aerial photography (http://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/kelp-monitoring).

Statistical analysis

All statistical tests were performed in the statistical program R (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 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 *et al*., 2019). 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 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 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.

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). 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 prior to the year Y feeding season (October to March), 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 + 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. 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 and residual plots. 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 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 calculated the number of whales that had a body condition score from August or later in a given feeding season (year Y) that were also seen 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 number of whales scored and proportion of whales photographed that were assigned scores (Table 1). The differences in proportions scored are likely related to differences in survey effort, which were 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 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).

Table 1

Number of PCFG 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		

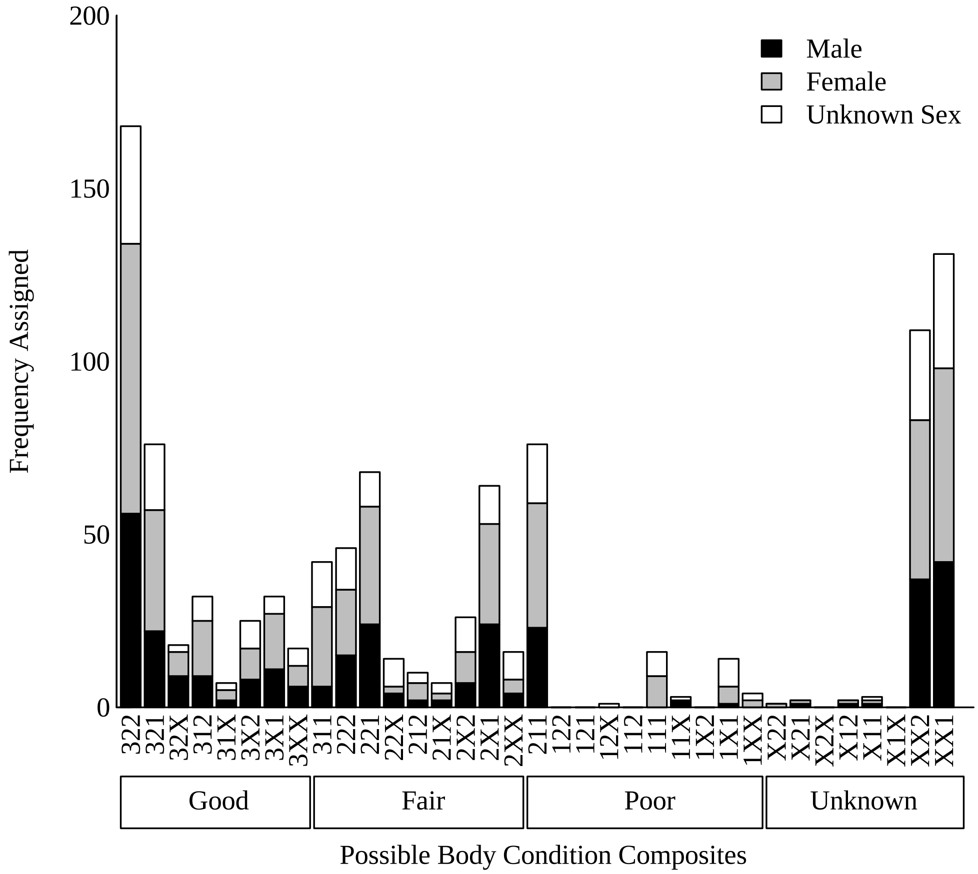

Fig. 2. Frequency of monthly body condition composite scores assigned to whales by sex.

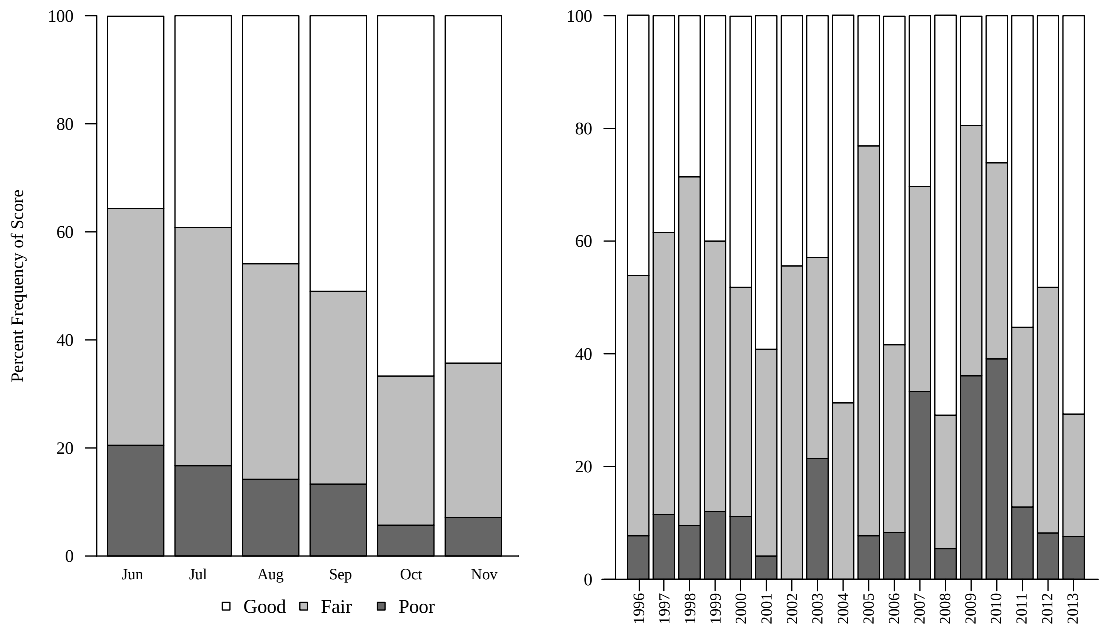

Fig. 3. Temporal trends in the percent frequency of known body condition scores assigned to PCFG whales by month and year.

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 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 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).

Table 2

Model selection of multinomial logistic regression analysis log-likelihood, Akaike Information Criterion (AIC), delta AIC and Akaike weights (ω_i). 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	**1200.74**	0.00	1.00
Month+Year	24	-591.358	1230.72	29.98	0.00
Year+Repro	21	-596.289	1234.58	33.84	0.00
Year	20	-612.648	1265.30	64.56	0.00
Month+Repro	8	-636.629	1289.26	88.52	0.00
Month	7	-645.523	1305.05	104.31	0.00
Repro	4	-655.900	1319.80	119.07	0.00
Intercept	3	-664.690	1335.38	134.64	0.00

Table 3

Results of the most parsimonious multinomial regression model 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".

Variable	Estimate	SE	Wald *z*	*P*-value
Poor|Fair	-2.379	0.738	-3.226	0.002
Fair|Good	0.580	0.721	0.804	0.031
Month = July	0.303	0.343	0.883	0.377
Month = August	**0.772**	**0.325**	**2.379**	**0.017**
Month = September	**1.142**	**0.333**	**3.427**	**0.001**
Month = October	**2.037**	**0.375**	**5.435**	**<0.001**
Year = 1996	0.492	0.758	0.649	0.516
Year = 1998	-1.088	0.652	-1.668	0.095
Year = 1999	-0.554	0.621	-0.893	0.372
Year = 2000	-0.165	0.607	-0.271	0.786
Year = 2001	**1.526**	**0.568**	**2.689**	**0.007**
Year = 2002	0.496	0.837	0.593	0.553
Year = 2003	0.035	0.764	0.046	0.963
Year = 2004	0.037	0.829	0.044	0.965
Year = 2005	-0.365	0.734	-0.497	0.619
Year = 2006	0.318	0.591	0.538	0.591
Year = 2007	**-1.534**	**0.622**	**-2.466**	**0.014**
Year = 2008	0.646	0.535	1.209	0.227
Year = 2009	**-2.087**	**0.547**	**-3.813**	**<0.001**
Year = 2010	**-1.730**	**0.663**	**-2.611**	**0.009**
Year = 2011	0.287	0.592	0.485	0.628
Year = 2012	-0.055	0.501	-0.110	0.912
Year = 2013	**1.184**	**0.553**	**2.143**	**0.032**
Repro = Post-partum	**-3.373**	**0.626**	**-5.387**	**<0.001**

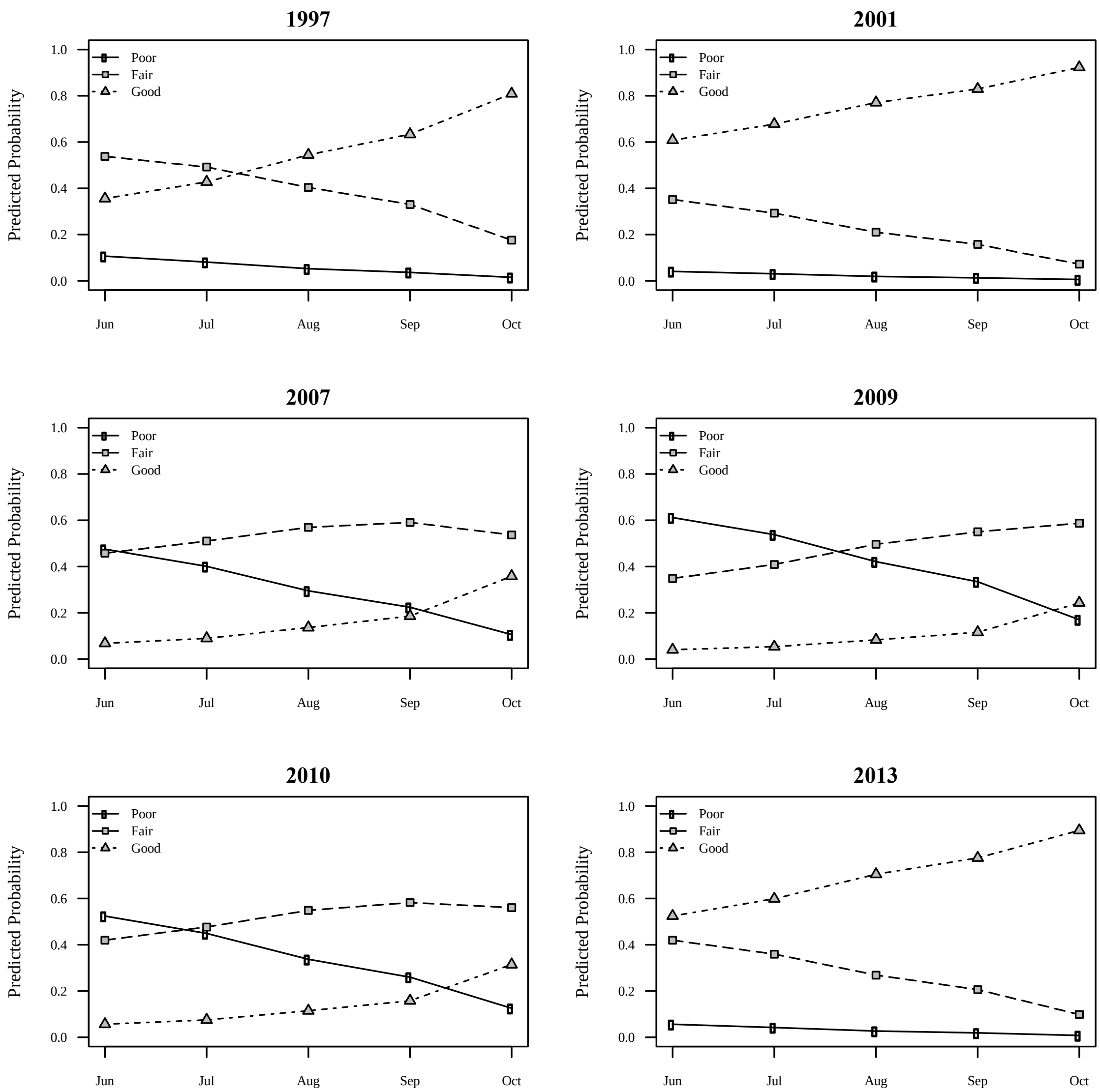

Fig. 4. Predicted probability of an average gray whale of being in poor, fair, or good body condition in each month of selected years of the study period. Selected years include the reference year (1997) and those that differ significantly from the reference year based on Wald *z* statistics and significant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

Influence of environmental variables

Based on simple linear regression, we found linear relationships between average body condition and several environmental variables when outlier years of 2007, 2009 and 2010 were removed (Table 4). Average body condition increased significantly with total September kelp canopy cover (in hectares) on the Washington coast lagged one year (Fig. 5). Average body condition increased significantly with decreasing annual average sea surface temperature (SST) at La Perouse Bank lagged one year (Fig. 6) and decreasing PDO lagged two years (Fig. 7). Body condition increased significantly when compared to annual upwelling index at 42˚ N and 54˚ N, but not at other individual latitudes (Fig. 8). When averaged across all areas (i.e. 42˚ N, 45˚ N, 48˚ N, 51˚ N and 54˚ N), upwelling index was also positively related to body condition (Fig. 8), though the relationship was not statistically significant at the p=0.05 level.

Using these four variables, we performed multiple regression analysis comparing average body condition to environmental indices with common outlier years removed (i.e. 2007, 2009 and 2010). For upwelling, we chose to use the average of all areas, rather than upwelling index at 42˚ N or 54˚ N because PCFG whales photographed in our research area are known to utilize a broad range of habitats encompassed between these latitudes (Calambokidis *et al.*, 2019; Lagerquist *et al.*, 2019).

Based on AIC model selection, ten models were strongly competing (<2 ΔAIC) as the best model. All of the environmental variables evaluated were included either independently or additively with other variables in strongly competing models. Eight of the ten strongly competing models included PDO lagged two years. The most parsimonious model included September kelp canopy cover lagged one year and PDO lagged two years (Table 5). The selected model accounted for 51.13% of variance in the body condition of "other" whales (Adjusted R^2=0.5113, *P*-value=0.0005; Fig. 9), although the only significant variable in the model was PDO lagged two years (Table 6). Based on evidence ratios of Akaike weights, the best model had 92 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 model from the multiple regression (PDO lagged 2 years + kelp canopy lagged 1 year) to the selected model from the ordinal regression (Month + Year + Repro) and found a significant positive correlation between the two (Fig. 9).

Table 4

Results of significant linear regressions of individual environmental variables to average whale body condition. Outliers are years that were removed from the model to improve normality and residuals.

Variable	Adjusted R^2	F	*P*-value	outliers
Kelp canopy, lagged 1 year	0.24	5.49	0.04	2007, 2009, 2010
PDO, lagged 2 years	0.36	9.59	0.008	2009, 2010
SST, lagged 1 year	0.44	12.21	0.004	2007, 2009, 2010
Upwelling, average of all areas	0.18	4.00	0.07	2007, 2009, 2010

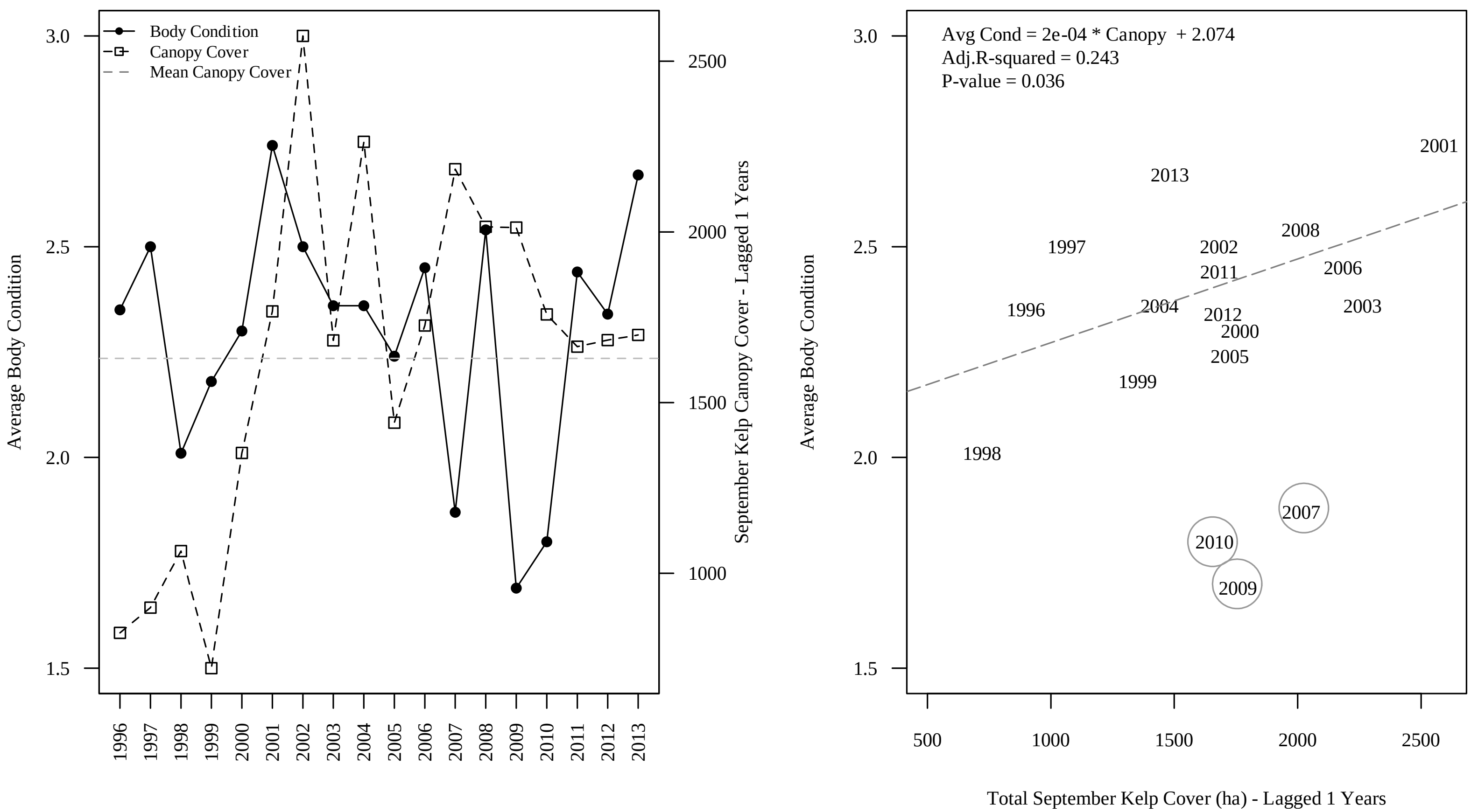

Fig. 5. Average September canopy cover (ha) on the Washington coast lagged one year compared to average whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model.

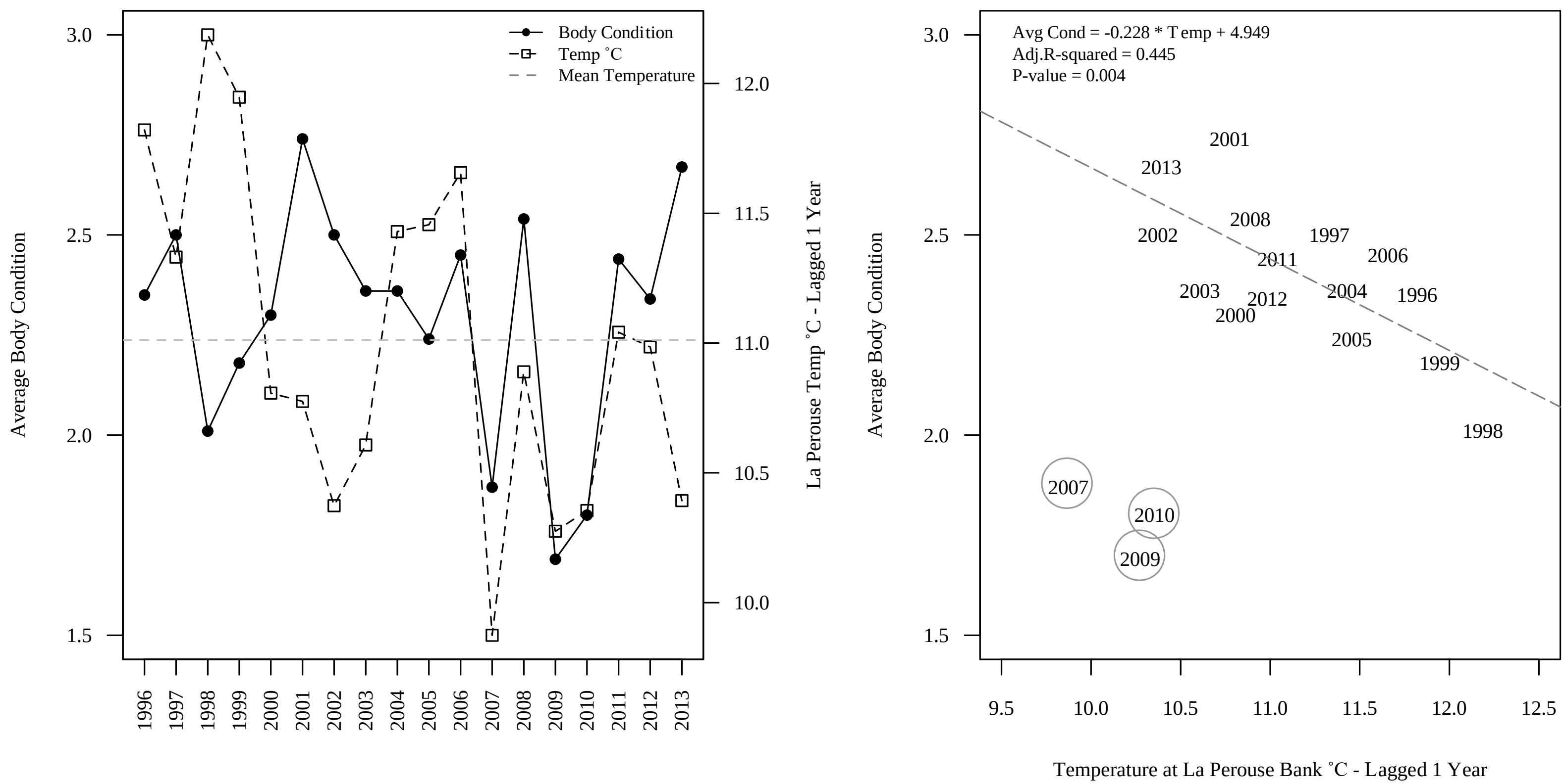

Fig. 6. Average annual sea surface temperature (˚C) at La Perouse Bank, Canada, lagged one year, compared to average whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model.

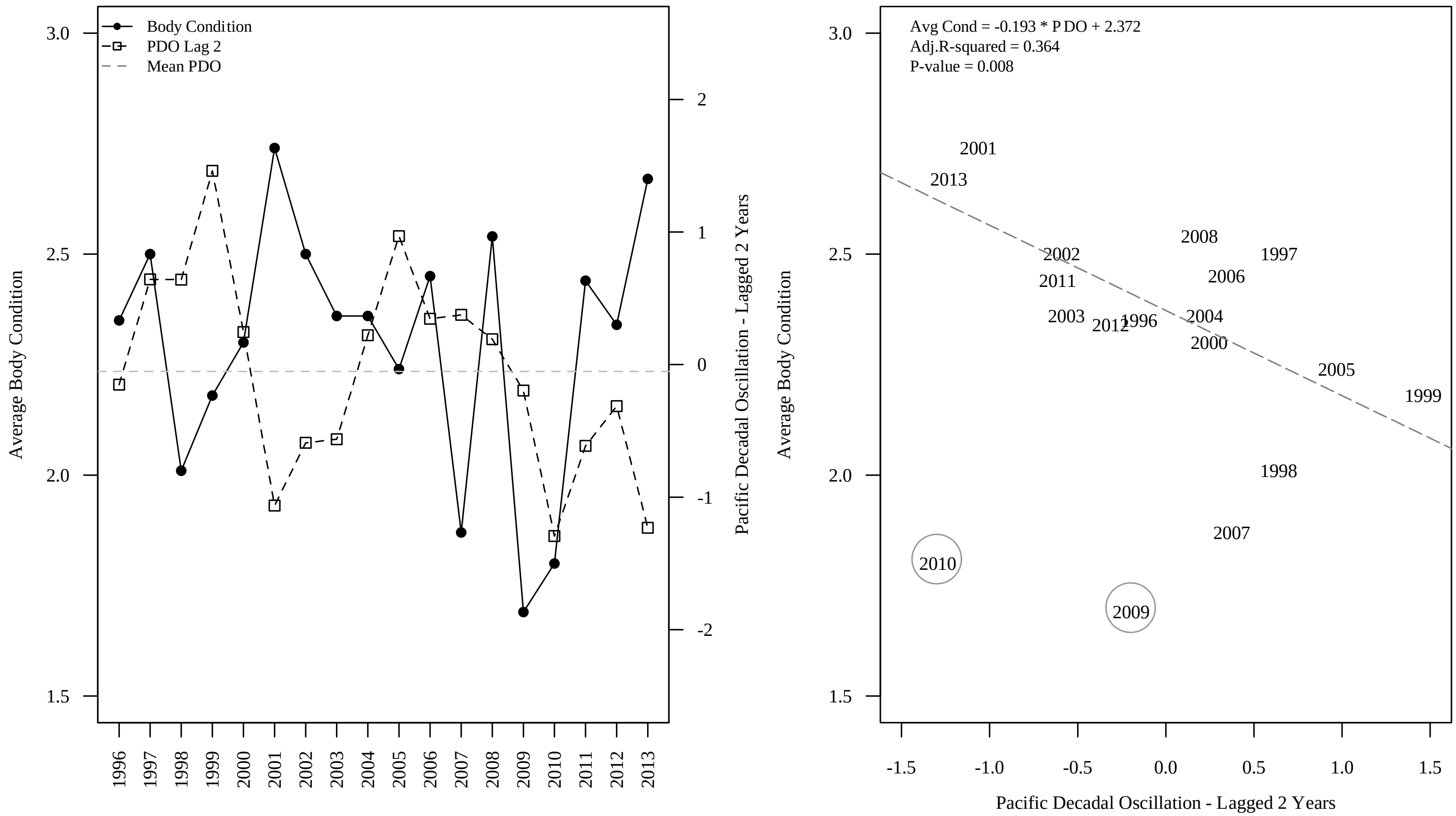

Fig. 7. Average annual PDO Index, lagged two years, compared to average whale body condition. Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model.

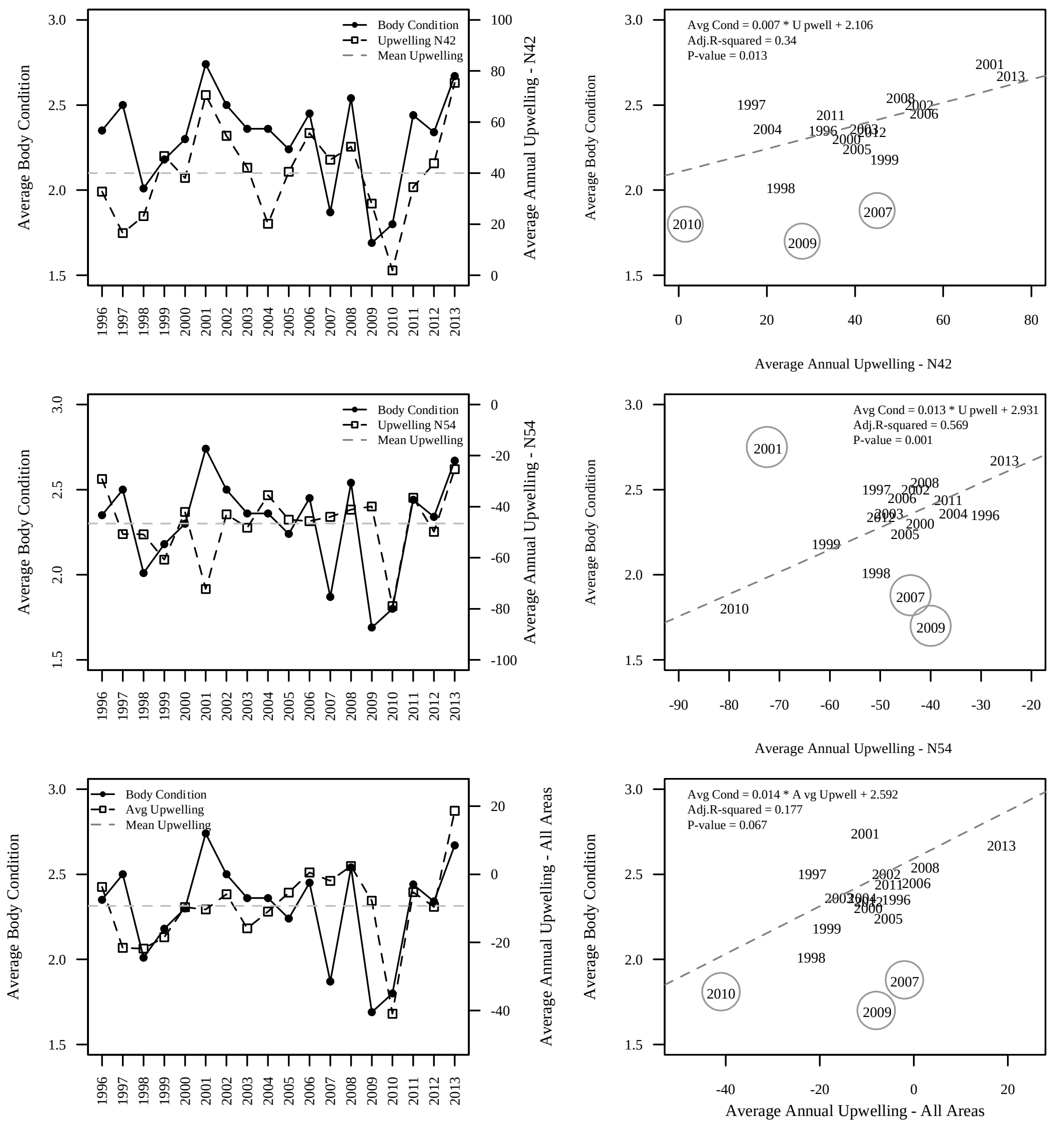

Fig. 8. Average annual Upwelling Index compared to average whale body condition at 42˚ N (top panels), 54˚ N (middle panels) and averaged across all areas (42˚ N, 45˚ N, 48˚ N, 51˚ N and 54˚ N; bottom panels). Circles represent years that were considered outliers based on QQ normality and fitted versus residual plots and were removed from the final model.

Table 5

Model selection of multiple regression analysis of environmental variables influencing average whale body condition using log-likelihood, Akaike Information Criterion (AIC), delta AIC and Akaike weights (ω_i). Variables included are September kelp canopy cover (ha) on the Washington coast lagged 1 year (Canopy), PDO lagged 2 years, SST at La Perouse Bank lagged 1 year, annual upwelling averaged between 42˚ N, 45˚ N, 48˚ N, 51˚ N and 54˚ N latitudes and an intercept model. The bolded model represents the most parsimonious model.

Models	k	Log-likelihood	AIC	ΔAIC	ω_t
Canopy+PDO	**4**	**11.096**	**-14.19**	**0.00**	**0.12**
Canopy+PDO+Upwelling	5	12.055	-14.11	-0.08	0.12
PDO+Upwelling	4	10.942	-13.88	-0.31	0.11
PDO+SST+Upwelling	5	11.796	-13.59	-0.60	0.09
PDO+SST	4	10.790	-13.58	-0.61	0.09
PDO	3	9.774	-13.55	-0.64	0.09
SST+Upwelling	4	10.646	-13.29	-0.90	0.08
SST	3	9.537	-13.07	-1.12	0.07
Canopy+PDO+SST	5	11.451	-12.90	-1.29	0.06
Canopy+PDO+SST+Upwelling	6	12.360	-12.72	-1.47	0.06
Canopy+SST+Upwelling	5	11.039	-12.08	-2.11	0.04
Canopy+SST	4	10.014	-12.03	-2.16	0.04
Canopy+Upwelling	4	8.634	-9.27	-4.92	0.01
Canopy	3	7.213	-8.43	-5.77	0.01
Upwelling	3	6.582	-7.16	-7.03	0.00
Intercept	2	4.569	-5.14	-9.05	0.00

Table 6

Results of the selected regression model including September kelp canopy cover (ha) on the Washington coast lagged one year and PDO lagged two years (Adjusted R^2=0.5113, model *P*-value=0.0005). *P*-values <0.05 represent significance and estimates provide degree of influence on average body condition.

Variable	Estimate	SE	*t* value	*P*-value
Intercept	2.215	0.127	17.514	6.53E-10
PDO.lag2	-0.143	0.050	-2.853	0.015
Canopy.lag1	0.0001	0.0001	1.521	0.154

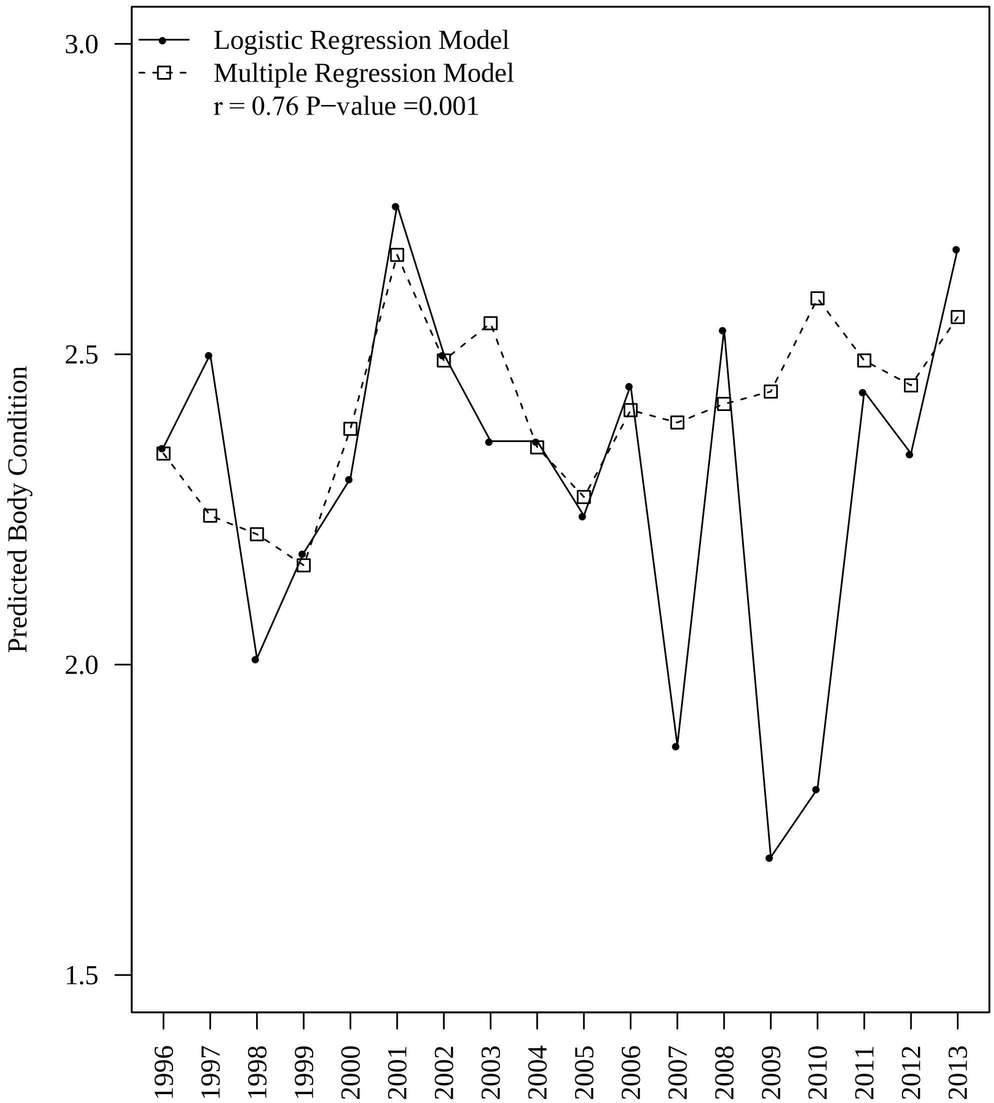

Fig. 9. Correlation of predicted body condition between the most parsimonious logistic regression model (Month + Year + Repro) and most parsimonious multiple regression model (Canopy_Lag1yr + PDO_Lag2yr).

Influence of body condition on fidelity to the study area

To evaluate the influence of body condition on the probability that an individual whale is 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) 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. 10).

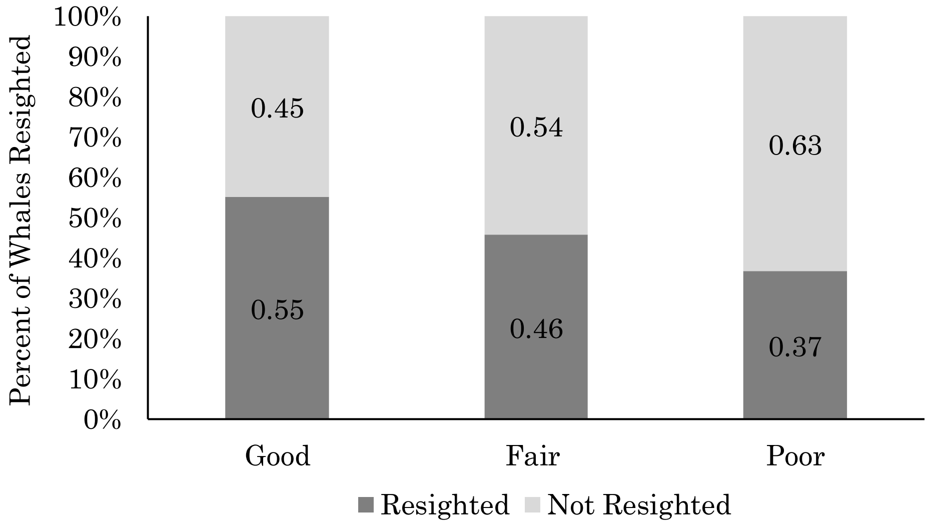

Fig. 10. Percent of PCFG whales resighted in year Y+1 compared to individual body condition (Good, Fair, or Poor) in August or later of year Y.

DISCUSSION

Factors influencing gray whale body condition

We utilized methods developed by Bradford *et al.* (2012) 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. We found that gray whale body condition improved through the feeding season, but that the rate of improvement and the body condition at the start and end of the feeding season was variable by year. Gray whale body condition was also strongly affected by reproductive status, with postpartum females having much poorer body condition than other whales. 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. This change in finding was likely due in part 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*. (2019) 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.

We found that both local and basin-wide environmental drivers affected the observed annual variability in body condition of PCFG whales in our study area. In almost all years, inclusion of oceanographic parameters such as SST, PDO, upwelling and the environmentally driven biological parameter of kelp canopy cover improved the ability of regression models to predict the average body condition of whales observed in the study area during that year. The years that the model could not predict body condition well were 2007, 2009 and 2010. Scordino *et al*. (2017) found the greatest average daily density of gray whales observed in our study area in 2008. It is possible that the gray whales present in 2008 depleted prey resources to such an extent that the prey were unable to recover to support feeding gray whales in 2009 and 2010 and that low foraging success in the area may have resulted in poorer apparent body condition. 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 often had boom-bust dynamics with high whale use followed by 1-3 year periods of low whale use, which allowed the prey populations to recover. During the feeding season, gray whales may switch prey species (Nelson, 2008) and move from poorer to higher quality feeding locations (Burnham and Duffus, 2018; Feyrer and Duffus, 2015), which may in part explain within season movement of PCFG whales between regions of the full PCFG range (Calambokidis *et al*., 2019).

Changes in environmental conditions likely indirectly impact body condition through a more direct impact to the whales' prey resources throughout their range. 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, 2008). Whale abundance and distribution on the feeding grounds appears 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). Bottom-forcing environmental conditions have been tied to changes in diet and reproductive success of large whales mediated through changes to their prey resources. The diet of 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). Several studies have found associations between gray whale calf production and apparent survival and sea ice extent on their Arctic feeding grounds (Gailey *et al*., 2020; Salvadeo *et al*., 2015). Therefore, it is clear that environmental conditions have the potential to affect large megafauna at least indirectly.

The two environmental variables that best predicted the body condition of PCFG whales photographed in our area were PDO, lagged two years and September kelp canopy cover, lagged one year. At a local level, it is possible that kelp canopy is acting as habitat or food for gray whale prey, primarily mysid shrimp (e.g. *Holmesimysis* spp.) in the region (Garside, 2009). 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 may 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). However, kelp cover was only considered at a local scale and not over the entire PCFG feeding range.

The influence of PDO with a time lag of two years is less clear. 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). George *et al.* (2015) similarly found that bowhead whale body condition was influenced by mean open water and upwelling wind stress from both the preceding summer and the average of three previous summers. Seyboth *et al*. (2016) found that time lags as great as 6 and 7 years showed significant influence of large-scale indices (ONI and AAO, respectively) on southern right whale calf production. 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 in the area. Although the exact mechanism linking gray whale body condition to PDO is not known, PDO represents sea surface temperature anomalies in the North Pacific poleward of 20˚ N and therefore likely reflects environmental changes occurring over the entire PCFG range.

The inability of our 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. We were only able to assign reproductive status and age in the case of post-partum females and calves, however other age classes and reproductive states may 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. It is possible that we were not able to identify patterns further due to the presence of undocumented post-partum females and calves in our dataset or to our 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, our survey methodology for gray whales did not allow us to compute a daily rate of whales feeding in the survey area and thus we could not add that factor to our modeling to test whether gray whale feeding pressure affects body condition in future years.

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 providing a unique opportunity to compare the body condition of two feeding groups of gray whales with very different life history strategies. In the late 1990s and early 2000s, it was assumed that gray whales at Sakhalin Island were a remnant population of Western North Pacific gray whale population (Weller *et al*., 2002). However, further research has shown that at least a portion of this group of whales winters off Mexico (Mate *et al*., 2015; Weller *et al*., 2012). The International Whaling Commission conducted a thorough review of the stock structure of gray whales and found the two most plausible hypotheses for the stock structure of whales at Sakhalin Island are that 1) the whales are all a feeding group of Eastern North Pacific (ENP) gray whales or 2) that the whales using Sakhalin Island are a mixed stock feeding group of Western North Pacific gray whales and ENP gray whales (IWC, 2018). Under both of these hypotheses, all or some portion of the whales feeding at Sakhalin Island are a feeding group of ENP whales.

Whales feeding at Sakhalin Island that winter in Mexico must migrate roughly 10,000 km from wintering to feeding grounds (Mate *et al*., 2015) as compared to PCFG whales that have a much shorter migration of roughly 2,000 to 3,400 km. Whales migrating to Sakhalin Island must expend much more energy than those migrating to the PCFG feeding range making it very critical that they are able to forage efficiently once they arrive on their feeding grounds and that the prey can predictably be found (Villegas-Amtmann *et al*., 2017). A comparison of the body condition results from Bradford *et al*. (2012) and this study suggest that Sakhalin whales are rewarded with better payoff, in terms of predictably attaining body condition, than the whales we observed on PCFG feeding grounds.

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. These differences may have been driven by how the prey in the two feeding areas respond to 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 Sakhalin Island feeding grounds are positively correlated with both winter and summertime PDO (Blanchard *et al*., 2019). Conversely, we found a negative correlation of gray whale body condition with PDO suggesting that in warm phase years that 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 we studied in the PCFG. At Sakhalin Island in most years the vast majority of gray whales attained good body condition by September (Bradford *et al*., 2012), whereas in the PCFG we observed years in which only 60% had attained good body condition by October. To illustrate the difference in attainment of body condition by site, consider the similarity in predicted probability of gray whales in poor, fair, or good condition for 2013 in the PCFG (a year of significantly better body condition) to "other" whales at Sakhalin Island in 1999, a year that whales had significantly worse body condition (see Bradford *et al*., 2012, Fig. 5). By September similar proportions of whales in both studies were in good (~80%), fair (~20%) and poor (~0%) condition suggesting that a good body condition year in the PCFG is a significantly poor year for whales feeding at Sakhalin Island. This highlights the tradeoffs and payoff of two very different life history strategies for whales of two different feeding groups of ENP gray whales.

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*., 2019; Lagerquist *et al*., 2019). The results of our study clearly show that body condition of PCFG gray whales photographed in our study area vary within season and by year and that local and basin-wide environmental factors influence the observed variations. In the future, we should expect 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 photogrammetry can be an effective way to monitor individuals in a population over relatively short within-season timescales. Extending this analysis to include recent years of known environmental perturbations, such as the warm water "Blob" (Peterson *et al*., 2017), 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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