Journal of Mammalogy, 93(1):251–266, 2012

Leaner leviathans: body condition variation in a critically endangered whale population

Amanda L. Bradford,* David W. Weller, André E. Punt, Yulia V. Ivashchenko, Alexander M. Burdin, Glenn R. VanBlaricom, and Robert L. Brownell, Jr.

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA (ALB, AEP, GRV)
Protected Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3333 North Torrey Pines Court, La Jolla, CA 92037-1022, USA (DWW)
Seastar Scientific, Dzerzhinskogo Street, 5-30, Yaroslavl 150033, Russia (YVI)
Kamchatka Branch of Pacific Institute of Geography, Far East Branch of the Russian Academy of Sciences, Prospect Rybakov, 19-a, Petropavlovsk-Kamchatsky 683024, Russia (AMB)
Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 1352 Lighthouse Avenue, Pacific Grove, CA 93950-2097, USA (RLB)
Present address of ALB: Protected Species Division, Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 1601 Kapiolani Boulevard, Suite 1000, Honolulu, HI 96814-4700, USA

* *Correspondent: alb992@u.washington.edu*

The role of environmental limitation and density-dependent regulation in shaping populations is debated in ecology. Populations at low densities may offer an unobstructed view of basic environmental and physiological interactions that impact individual fitness and thus population productivity. The energy reserves of an organism are reflected in its body condition, a measure linking individual fitness and the environment. From 1997 to 2007, we monitored the critically endangered western gray whale (*Eschrichtius robustus*) population on its primary summer feeding ground off the northeastern coast of Sakhalin Island, Russia. This effort resulted in a large data set of photo-identification images from 5,007 sightings of 168 individual whales that we used to visually assess western gray whale body condition. We quantified temporal variation in the resulting 1,539 monthly body condition determinations with respect to observations of reproductive status and sex. Western gray whale body condition varied annually, and we identified years of significantly better (2004) and worse (1999, 2006, and 2007) body condition. This study is the 1st to track the within-season body condition of individual whales. Body condition improved significantly as the summer progressed, although results suggest that not all whales replenish their energy stores by the end of the season. The body condition of lactating females was significantly worse than that of other whales at all times and was most often determined to be compromised. The body condition of their weaning calves exhibited no temporal variation and was consistently good. It is possible lactating females provide an energetic buffer to their offspring at the expense of their own body condition and future reproductive success. Findings from the analysis establish a foundation for quantifying links between western gray whale body condition, demographic parameters, and environmental conditions; and provide a baseline for monitoring individual and population condition of an ecosystem sentinel species in a changing environment. Overall, this study highlights the presence of density-independent environmental and physiological mechanisms that affect the abundance and growth of populations.

Key words: density-independence, energy reserves, environmental variability, fitness, Okhotsk Sea, ordinal logistic regression, photo-identification, western gray whales

DOI: 10.1644/11-MAMM-A-091.1

The degree to which populations are limited by the environment and regulated by their density is a topic of much ecological interest and debate (e.g., Berryman 2004; White 2004). Recent mammalian studies have focused on the complex interactions between extrinsic and intrinsic factors that produce observed population dynamics, particularly in populations at high densities (e.g., Chamaillé-Jammes et al. 2008). Small or increasing populations are generally not discussed in this context, although by extension they are often used as a non–resource-limited reference in comparative population studies (e.g., Monson et al. 2000). However, it is clear that populations of all sizes are subject to environmental and physiological conditions and constraints that impose physical limits to population productivity. Populations at low densities may reveal these properties in a more fundamental form and merit investigation in this regard.

Depending on their metabolic needs and limitations, individuals in populations employ a variety of life-history tactics to contend with environmental variability. In pursuing these strategies, all organisms face some level of temporal reductions in body mass (Robbins 1993). Variation in stored energy is a response to current nutritional inputs and demands or to environmental cues regarding future conditions (Batzli and Esseks 1992). The dependency on energy reserves for reproduction varies across taxa, with animals that rely on endogenous energy stores to sustain reproduction during a period of fasting (i.e., capital breeders) representing 1 extreme (Thomas 1990). The body condition of an organism reflects its energy reserves relative to its size and can serve as a link to its ecological fitness. In that respect, the influence of a variety of environmental and physiological factors can be evaluated using a single metric, assuming an appropriate measure of body condition is identified (Speakman 2001).

Gray whales (*Eschrichtius robustus*) are extant only in the North Pacific Ocean, where they exist as geographically and genetically differentiated eastern and western populations (Lang 2010; Weller et al. 2002). Like most other baleen whales, gray whales feed in seasonally productive waters at high latitudes, while using warm waters at low latitudes to calve and breed. The eastern gray whale population migrates from winter breeding grounds off Baja California, Mexico, to summer feeding grounds that are encompassed primarily by the Bering and Chukchi seas. Eastern gray whales are potentially nearing the current carrying capacity of their environment at a population size of approximately 20,000 whales (Punt and Wade 2010). The western gray whale population returns to summer feeding grounds located principally in the Okhotsk Sea from unknown breeding grounds suspected to be along the southern coast of China (Wang 1984). Western gray whales are critically endangered (International Union for Conservation of Nature 2010) and number <150 individuals (Bradford et al. 2008).

Gray whales are in a negative energy balance after leaving the feeding grounds, relying on stored energy acquired during roughly 6 months spent foraging at high latitudes (Rice and Wolman 1971). These reserves are of particular importance to reproductive females, who have the potential to calve every other winter. After a 13-month gestation period, pregnant females give birth to a single calf, which is weaned during the subsequent feeding season (Rice 1983). In baleen whales, as in other mammals, energy stores are predominantly composed of fat (Young 1976), although energy reserves also can include other components such as carbohydrates and proteins (Atkinson and Ramsay 1995; Robbins 1993). Collectively, these sources of energy are catabolized from a variety of tissues, including blubber, muscle, skeleton, and viscera (Lockyer 1984; Worthy and Lavigne 1987).

Following a pilot effort in 1995 (Brownell et al. 1997), a collaborative Russia–United States research program was established in 1997 to conduct individual monitoring of western gray whales using photo-identification and genetic techniques (Weller et al. 1999, 2002). This project takes place annually during summer months on the primary feeding ground of the population, which is located in coastal waters off northeastern Sakhalin Island, Russia, in the western Okhotsk Sea. This feeding ground is utilized by western gray whales of both sexes and multiple age classes, including postparturient females and their weaning calves, and presumably offers access to most, if not all, of the western gray whale population (Bradford et al. 2006, 2008).

Several demographic parameters estimated over the course of this investigation have suggested that western gray whales are not realizing theorized levels of maximum productivity. The number of actively reproducing females is small, postweaning calf survival is low, the calf sex ratio is male-biased, and calving intervals are prolonged and variable (Bradford et al. 2006, 2008; Brownell and Weller 2002; Weller et al. 2002). Undoubtedly, there are anthropogenic sources of mortality to consider relative to these findings (Bradford et al. 2009; Weller et al. 2008), and small population effects cannot be ignored. However, concurrent with these demographic studies were visual observations of individuals with notable reductions in body mass (Brownell and Weller 2001), which appeared to vary in magnitude and over time, indicating that if western gray whale body condition could be appropriately measured, environmental links to individual fitness and thus population productivity could be explored.

Common methods for evaluating body condition in terrestrial mammals are generally impractical to apply to free-ranging whales. Standard techniques such as direct carcass analysis (e.g., Reynolds and Kunz 2001), mass-based morphometric indexes (e.g., Jakob et al. 1996), and electrical conductivity measurement (e.g., Wirsing et al. 2002) require capturing and handling individuals, lethally in the case of direct analysis. Given the migratory life cycle of most baleen whales, seasonal changes in body condition are expected, with whales reflecting more depleted energy stores while fasting than while feeding (Lockyer 2007). In fact, studies of whales killed in whaling operations have demonstrated that relative body mass increases as the feeding season progresses (e.g., Lockyer 1987). Although these studies showed that blubber thickness also can increase accordingly, particularly in pregnant females, lipid stores captured in other body components (e.g., muscle tissue) also are sensitive to changes in nutritional status and may better explain observed seasonal variations in body mass (Lockyer 1987; Víkingsson 1990). Further, there are many biases associated with measurements of blubber, suggesting that blubber thickness may not be the most reliable index of whale body condition (Aguilar et al. 2007).

In this regard, Rice and Wolman (1971) found that girth is a better indicator of body condition than blubber thickness in eastern gray whales and concluded that weight loss occurs primarily because of utilization of internal fat depots as opposed to blubber. Therefore, metrics of girth should theoretically be able to reflect the nutritional status of individuals. Indeed, aerial photogrammetry of eastern gray whales found that changes in body condition associated with fasting periods and reproductive status were reliably detected from measurements of width relative to length (Perryman and Lynn 2002). It is thus reasonable to assume such changes in body mass could be observed sidelong during boat-based photo-identification efforts and consequently recorded in the photographic record.

This assumption formed the premise of a recent evaluation of body condition in free-ranging North Atlantic right whales (*Eubalaena glacialis*). In a retrospective analysis of photo-identification data, Pettis et al. (2004) visually assessed the relative amount of subcutaneous fat in the postcranial area of whales in this population. This index accurately tracked known changes in body condition associated with the reproductive cycle (Pettis et al. 2004). Follow-up studies demonstrated that the visual assessment of body condition captured general trends in estimates of girth and blubber thickness (Angell 2006). Thus, this type of assessment represents a viable method of measuring right whale body condition, which was the main premise of the work of Pettis et al. (2004). The authors did not consider temporal variation in individual body condition.

The western gray whale photo-identification project produced a large data set of digital, film, and video images suitable for a visual assessment of western gray whale body condition. Therefore, our objectives in the present study were to develop a protocol to measure the body condition of western gray whales from photo-identification images; and to quantify temporal variation in the resulting determinations of body condition with respect to observations of reproductive status and sex. Specifically, we evaluated the relative amount of subcutaneous fat for individual whales and tested for interannual and within-season differences, with a particular interest in lactating females and their weaning calves and in males and females. Our overarching aim was to establish a baseline for monitoring western gray whale body condition that can ultimately be used to detect demographic and environmental linkages, in anticipation of future ecosystem changes.

Materials and Methods

Whale sighting data.—From 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys off the northeastern coast of Sakhalin Island, Russia. Weller et al. (1999) contains detailed information about the study area and the photo-identification data collection and analysis protocols. We obtained biopsy samples (for genetic studies, including sex determination and relatedness analyses) in coordination with photo-identification efforts, following animal care guidelines in accordance with the American Society of Mammalogists (Sikes et al. 2011). These surveys produced 5,159 sightings of 169 individual western gray whales, which include 24 known reproductive females, 72 whales 1st identified as calves, and 142 individuals of known sex (59 females and 83 males). We considered a given female to be reproductive overall and lactating for the field season when genetic or behavioral observations, or both, linked her to a calf of the year. A sighting is represented by at least 1 high-quality photo-identification image, although we usually collected several photo and simultaneous video images during each sighting. We acquired 14 additional sightings of 12 of the 169 individuals during a survey of an ephemeral feeding area approximately 60 km southeast of the nearshore feeding area. In total, we examined more than 34,000 film and digital images and 38 h of digital video from 5,173 sightings of 169 photo-identified individuals to assess western gray whale body condition. However, we utilized only data collected during July–September of 1997–2007 in the statistical analysis of body condition, so that we could make temporal comparisons. The analysis subset consisted of 5,007 sightings of 168 individual whales, which include the same individual composition as above less 1 male 1st identified as a calf.

Body condition assessment.—We expanded the protocol developed for North Atlantic right whales (Pettis et al. 2004) to assess the body condition of western gray whales. We measured western gray whale body condition using a similar scoring approach, but along with the postcranial area, we evaluated 2 additional body regions also regularly captured during photo-identification. That is, we visually assessed the relative amount of subcutaneous fat in 3 body regions: the postcranial area, the scapular region, and the lateral flanks. Apparent reductions in body mass in these regions lead to 3 diagnostic features, respectively: a postcranial depression, a subdermal protrusion of the scapula, and a depression along the dorsal aspect of the lateral flanks (Brownell and Weller 2001). Although the underlying physiological mechanisms are not well understood, whales exhibiting these features are considered to be in compromised body condition (Brownell and Weller 2001).

We examined all available digital, film, and video images of individual western gray whales in the assessment of body condition. Specifically, for each survey sighting of a whale, we assigned a numerical score to the 3 body regions of interest, with higher values corresponding to better condition (Figs. 1–3). We scored the postcranial condition on a 3-point scale (Fig. 1), but scored the scapular and lateral flank conditions on a 2-point scale (Figs. 2 and 3) because distinguishing varying degrees of these characteristics would have been highly subjective. If we could not assign a reliable

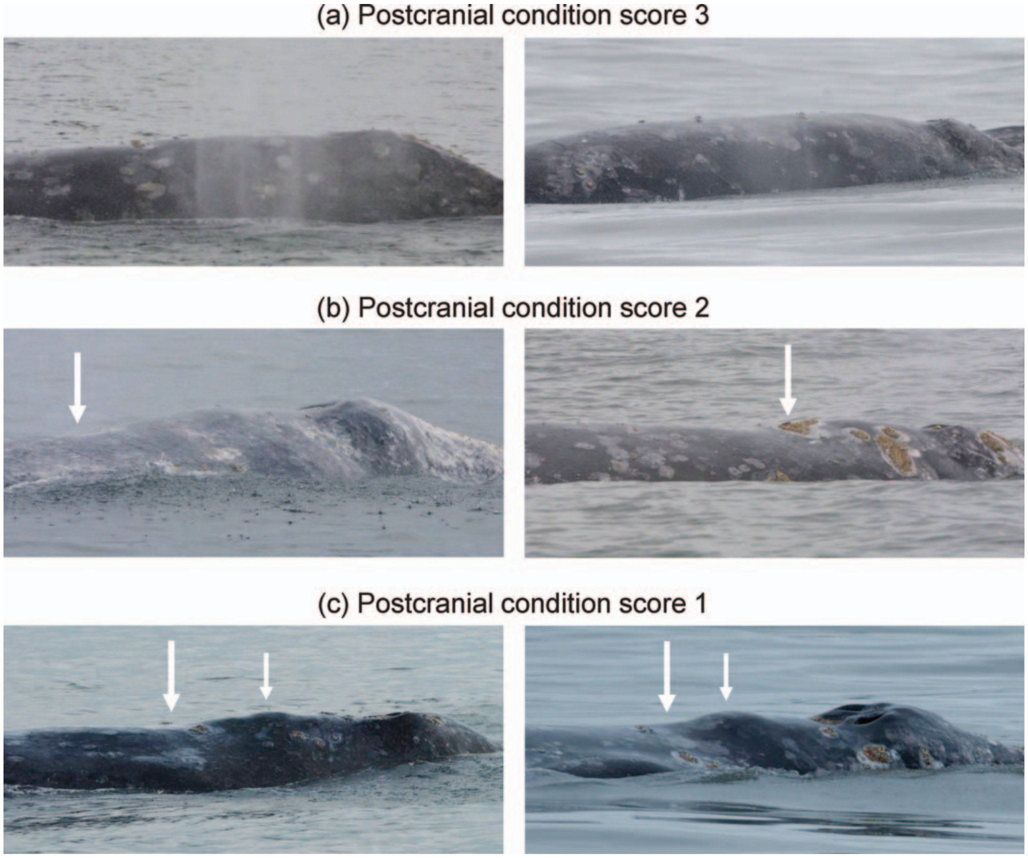

Fig. 1.—Example images depicting the 3-point scale we used to assess the postcranial condition of western gray whales (*Eschrichtius robustus*). We assigned a) a score of 3 to whales with a flat or rounded back; b) a score of 2 to whales with a slight to moderate postcranial depression, indicated by an arrow; and c) a score of 1 to whales with a significant postcranial depression such that a pronounced ''hump'' is visible posterior to the blowholes, noted by large and small arrows, respectively.

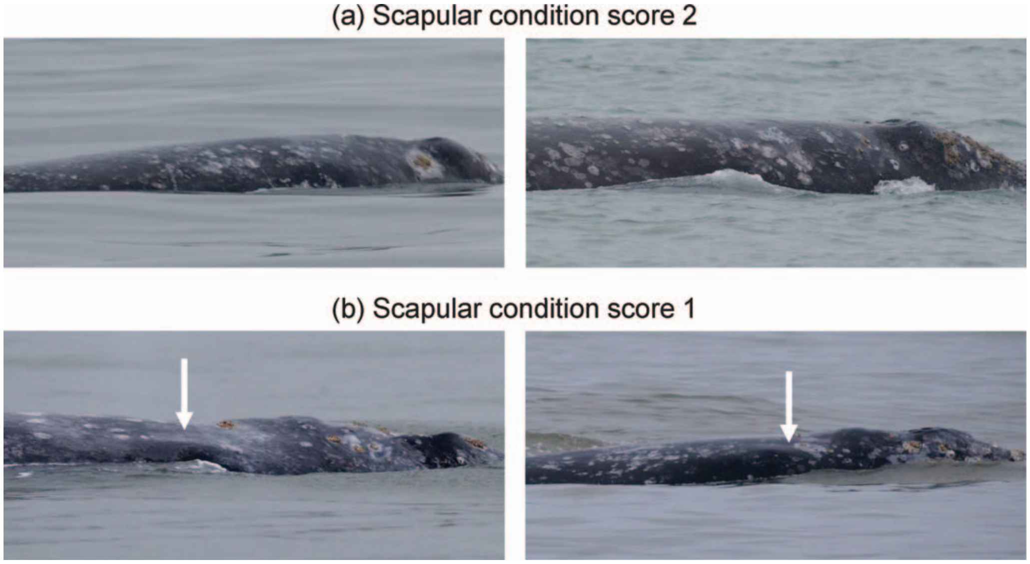

Fig. 2.—Example images showing the 2-point scale we utilized to evaluate the scapular condition of western gray whales (*Eschrichtius robustus*). We assigned a) a score of 2 to whales with rounded sides over the shoulder blades; and b) a score of 1 to whales with a subdermal protrusion of the scapula, identified by an arrow.

(a) Lateral flank condition score 2

(b) Lateral flank condition score 1

Fig. 3.—Example images showing the 2-point scale we employed to rate the lateral flank condition of western gray whales (*Eschrichtius robustus*). We assigned a) a score of 2 to whales with rounded sides from the postcranial area to the start of the caudal peduncle; and b) a score of 1 to whales with a depression along the dorsal aspect of the lateral flanks, indicated by an arrow.

numerical score to a body region (e.g., we did not take images of the body region or whale body position confounded body region condition), we coded the region as X. One analyst (ALB) performed all scoring to maintain consistency in the image review (Pettis et al. 2004). However, we demonstrated through an interrater agreement study that the western gray whale body region scoring protocol can be used by more than 1 trained researcher to achieve comparable results (Appendix I).

To maximize the use of irregular sightings with incomplete image coverage of the 3 body regions, we collapsed the scored data for each sighting into monthly composites of postcranial (P), scapular (S), and lateral flank (L) condition for each whale. We conducted sensitivity analyses to confirm that month was an appropriate and feasible scale at which to aggregate these data (Appendixes II–IV). We then needed a scheme to classify these composites to produce overall categorical determinations of individual body condition (i.e., good, fair, or poor) for use in the statistical analysis. Given that the postcranial condition is presently the standard visual measure of cetacean body condition (e.g., Pettis et al. 2004), we assumed this region to be most indicative of overall body condition. That is, we classified a composite of 3SL as good body condition, 2SL as fair body condition, and 1SL as poor body condition, unless we scored both the scapular and lateral flank conditions as poor. In those cases (i.e., composites of 311 and 211), we brought the body condition rating down a level (i.e., to fair and poor, respectively). Any other combination after the postcranial condition score (e.g., 3XX or 21X) did not change the rating suggested by the postcranial condition. If we coded the postcranial condition as X, then we considered the body condition as unknown and unusable for analysis. In summary, the possible composites within each body condition category are:

- good—322, 321, 32X, 312, 31X, 3X2, 3X1, 3XX;
- fair—311, 222, 221, 22X, 212, 21X, 2X2, 2X1, 2XX;
- poor—211, 122, 121, 12X, 112, 111, 11X, 1X2, 1X1, 1XX; and
- unknown—X22, X21, X2X, X12, X11, X1X, XX2, XX1, XXX.

This classification system is a conservative rating approach that allows composites with X entries to be incorporated into the 3 categories of known body condition and therefore utilized in the analysis.

Note that we use the body condition descriptors good, fair, and poor to refer to the amount of energy reserves available to a given whale and not to imply a prognosis of survival. Further, a determination of poor body condition does not equate to starvation, although if starving individuals were a part of this study, presumably we would have classified their body condition as poor. Instead, we regard whales in compromised body condition (i.e., fair or poor) as not completely buffered against the full suite of demands associated with their extreme life history, which could lead to a behavioral, physiological, or reproductive response.

Statistical analysis.—We employed multinomial logistic regression for ordinal responses to analyze variation in western gray whale body condition. Specifically, we used the proportional odds model (e.g., Agresti 2002) to evaluate the effect of 4 categorical variables (year, month, reproductive class, and sex) on body condition as a multinomial response (good, fair, or poor), where year is 1997–2007; month is July, August, or September; reproductive class is lactating female, calf, or other whale; and sex is male, female, or unknown. We specified these temporal and demographic covariates given their relevance to the study objectives. Further, preliminary univariable analyses suggested that these variables are each significant predictors of body condition. We utilized likelihood ratio tests to determine the most-parsimonious model, which we found by singly dropping each of the covariates

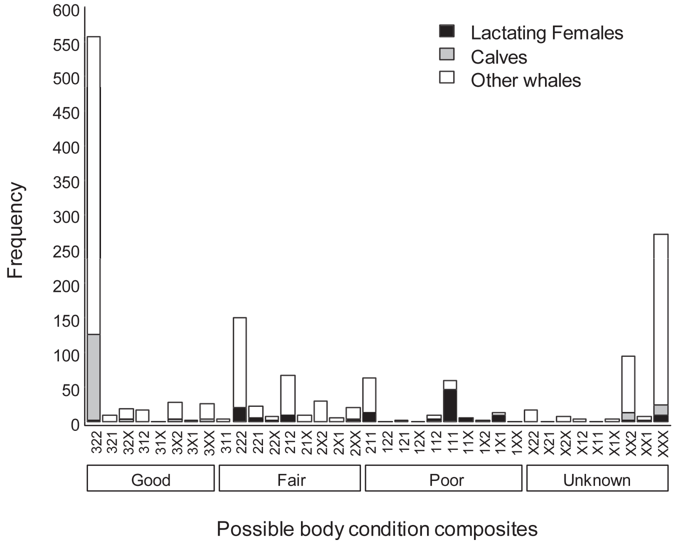

Fig. 4.—Frequencies of monthly body region condition composites of those possible within each of the 4 body condition categories (good, fair, poor, and unknown) for 1,539 composites of 168 western gray whales (*Eschrichtius robustus*). Frequencies are shown according to reproductive class (lactating females, calves, and other whales), with individual whales represented in as many months as the individual was sighted.

from the full model and, if required, from selected reduced models until we identified the most-parsimonious set of covariates. Individual whales were represented by a body condition category in as many months as the individual was sighted. To account for the correlation between these observations, we modeled individual whales as normally distributed random effects in the analysis, which we conducted using the Ordinal Package (Christensen 2010) within the program R (R Development Core Team 2010).

Results

We collapsed the 5,007 survey sightings between July and September of 1997–2007 into 1,539 monthly body region condition composites of 168 photo-identified western gray whales. The distribution of composites within each body condition category is: good—658 (42.8%), fair—317 (20.6%), poor—158 (10.3%), and unknown—406 (26.4%). Fig. 4 shows the frequencies of the possible composites within each body condition category. Within each category of known body condition, most of the composites are comprised of non-X entries (i.e., 322, 321, 312, 311, 222, 221, 212, 211, 122, 121, 112, and 111): good—583 (88.6%), fair—243 (76.7%), and poor—136 (86.1%). More information on the scored and collapsed body region data that led to the monthly determinations of body condition is available in Appendixes II–IV. Whales with known body condition determinations are represented by 165 individuals, with a median of 5 determinations per whale (range 1–24 determinations). Table 1 summarizes the distribution of these individuals and observations within the analytical framework.

Likelihood ratio tests indicated that sex is not a significant predictor of body condition in the presence of the covariates year, month, and reproductive class (Table 2). Because there was not support for dropping additional covariates, we selected the mixed model incorporating year, month, and class as the most parsimonious. When fit to the body condition determinations, this model revealed that, compared to the reference year of 1997, whales were in significantly better body condition in 2004 and in significantly worse body condition in 1999, 2006, and 2007 (Table 3). Moreover, whales were in significantly better body condition in August and September than in July, with the magnitude of the predictor coefficients pointing toward an improvement in body condition as the season progressed. Finally, lactating females were in significantly worse body condition relative to other whales, while weaning calves that were in significantly better condition than other whales.

The estimated predictor coefficients in Table 3 can be exponentiated and expressed as odds ratios. For example, a specific whale had about 3 times the odds of being in better body condition in 2004 (all other factors being equal) than in

Table 1.—Summary of observations used in the quantitative analysis of western gray whale (*Eschrichtius robustus*) body condition. Individual whales are represented once in the annual numbers of whales in known body condition and within each month, but are represented in as many months and years as the individual was sighted. Further, individual whales can be represented multiple times in the annual numbers within each reproductive class and sex category, depending on the number of known monthly body condition determinations for the individual. BC = body condition; LF = lactating female.

		Month			Reproductive class			Sex		
Year	Whales in known BC	Jul.	Aug.	Sep.	LF	Calf	Other	Male	Female	Unknown
1997	37	16	24	22	5	5	52	29	28	5
1998	48	33	28	22	16	15	52	35	41	7
1999	64	42	54	35	4	7	120	70	46	15
2000	54	7	50	38	3	5	87	58	34	3
2001	63	42	53	46	16	17	108	78	59	4
2002	70	38	47	50	16	21	98	68	62	5
2003	65	16	50	41	18	20	69	56	51	0
2004	55	22	50	1	11	13	49	31	37	5
2005	67	18	41	36	9	8	78	48	42	5
2006	61	33	45	0	7	5	66	41	28	9
2007	75	32	62	39	18	21	94	77	51	5

TABLE 2.—Results of comparing the full proportional odds mixed model of western gray whale (*Eschrichtius robustus*) body condition to reduced models formed by singly dropping each of the 4 covariates. We used likelihood ratio tests to compare the full model (top row) with each reduced model as a means to evaluate the significance ($P < 0.05$) of the dropped covariate. The selected model is shown in boldface type. *d.f.* = degrees of freedom; *LR* = likelihood ratio statistic (chi-square distributed).

Model predictors	Residual *d.f.*	Log-likelihood	*LR*	*LR d.f.*	*P*-value
Year + month + class + sex	1,114	−710.991			
Month + class + sex	1,124	−750.663	79.342	10	<0.001
Year + class + sex	1,116	−778.171	134.360	2	<0.001
Year + month + sex	1,116	−892.766	363.549	2	<0.001
Year + month + class	**1,116**	**−712.168**	**2.354**	**2**	**0.308**

TABLE 3.—Maximum-likelihood estimates resulting from fitting the proportional odds mixed model to determinations of western gray whale (*Eschrichtius robustus*) body condition, given year, month, and reproductive class. The first 2 rows represent model intercepts and the rest predictor coefficients. Note that year = 1997, month = July, and class = other whale served as the reference categories. Significant predictor coefficients ($P < 0.05$) are shown in boldface type. *SE* = standard error; LF = lactating female.

Variable	Estimate	*SE*	Wald *z*	*P*-value
$Y \geq$ fair	2.736	0.413	6.618	<0.001
$Y \geq$ good	−0.243	0.395	−0.616	0.538
Year = 1998	0.647	0.477	1.358	0.175
Year = 1999	**−1.071**	**0.404**	**−2.655**	**0.008**
Year = 2000	−0.511	0.435	−1.175	0.240
Year = 2001	−0.568	0.411	−1.381	0.167
Year = 2002	0.094	0.427	0.219	0.826
Year = 2003	0.116	0.450	0.258	0.796
Year = 2004	**1.128**	**0.507**	**2.225**	**0.026**
Year = 2005	−0.526	0.441	−1.192	0.233
Year = 2006	**−0.971**	**0.447**	**−2.171**	**0.030**
Year = 2007	**−1.706**	**0.422**	**−4.044**	**<0.001**
Month = Aug.	**1.235**	**0.188**	**6.553**	**<0.001**
Month = Sep.	**2.615**	**0.246**	**10.622**	**<0.001**
Class = LF	**−4.821**	**0.365**	**−13.195**	**<0.001**
Class = calf	**5.694**	**1.073**	**5.309**	**<0.001**

1997, had approximately 14 times the odds of being in better body condition in September than in July, and had roughly 124 times the odds of being in worse body condition when a lactating female than when classified as an other whale. However, when considering effect size, the calf coefficient and associated values merit particular attention. Of the 137 calf determinations of known body condition, 136 (99.3%) of them are classified as good. Thus, this covariate level perfectly predicts the outcome, which can create numerical problems when fitting a logistic regression model, typically manifested as a lack of convergence, a large estimated coefficient, and a large estimated standard error (Hosmer and Lemeshow 2000). In the present case, the model converged and although the estimated coefficient is large, the resulting standard error is not large enough to lead to a paradoxically small Wald test statistic (Hauck and Donner 1977). Further, compared to the original model formulation (see Table 2), eliminating the calf covariate level (residual degrees of freedom [*d.f.*] = 1,117, log-likelihood = −765.565) was not supported by a likelihood ratio test (chi-square distributed likelihood ratio statistic $[LR]_1 = 106.794$, $P < 0.001$). Also, completely removing calf observations from the statistical analysis did not produce appreciable differences in the estimates corresponding to the other covariates. Therefore, we retained the calf observations and covariate for illustrative purposes, but the resulting effect size should be interpreted with caution.

The predicted probabilities of an average whale (i.e., a random effect of zero) being in good, fair, and poor body condition according to various combinations of the covariates are shown in Fig. 5. The random effect estimates conformed to a normal distribution as intended. A random effects model allowed for the appropriate statistical treatment of the correlation between observations of individual whales. Additionally, compared to the same covariate model without random effects (*d.f.* = 1,117, log-likelihood = −798.273), the random effects model (see Table 2) provided a significantly better fit to the data ($LR_1 = 172.209$, $P < 0.001$).

DISCUSSION

Photo-identification of gray whales involves the comparison of natural and unique pigmentation patterns and generally focuses on the dorsal flank region of individual whales (Darling 1984; Weller et al. 1999). Thus, this body region was the primary target during western gray whale photo-identification efforts, but was not used to measure individual body condition, which explains the large number of unknown body condition determinations in the current retrospective assessment (Fig. 4). However, it is important to note that these unknown determinations are random with respect to the examined covariates.

Although the western gray whale body condition assessment protocol allows composites with X entries to be incorporated into the known body condition categories, most of the resulting known body condition determinations are composed of non-X entries (Fig. 4). These non-X composites offer 2 potential insights into patterns of weight loss in gray whales. First, there is individual variation in where on the body declines in mass occur, as evidenced by the frequencies of the various types of non-X composites (Fig. 4). Second, despite this variation, there is evidence that of the 3 body regions evaluated, the postcranial area is the most sensitive to reductions in subcutaneous fat. That is, the relatively high frequency of the composite 222 compared to frequencies of composites with normal postcranial and compromised scapular and lateral flank conditions (i.e., 321 and 312) suggests that discernible mass loss occurs 1st in the postcranial area and then in the other 2 body regions (Fig. 4), although unknown differences in the ease of mass loss detection between body regions also may have contributed to the perceived order of mass loss.

The decision to differentiate between the body condition categories of good, fair, and poor for western gray whales was primarily dictated by our ability to visually discern 3 levels of

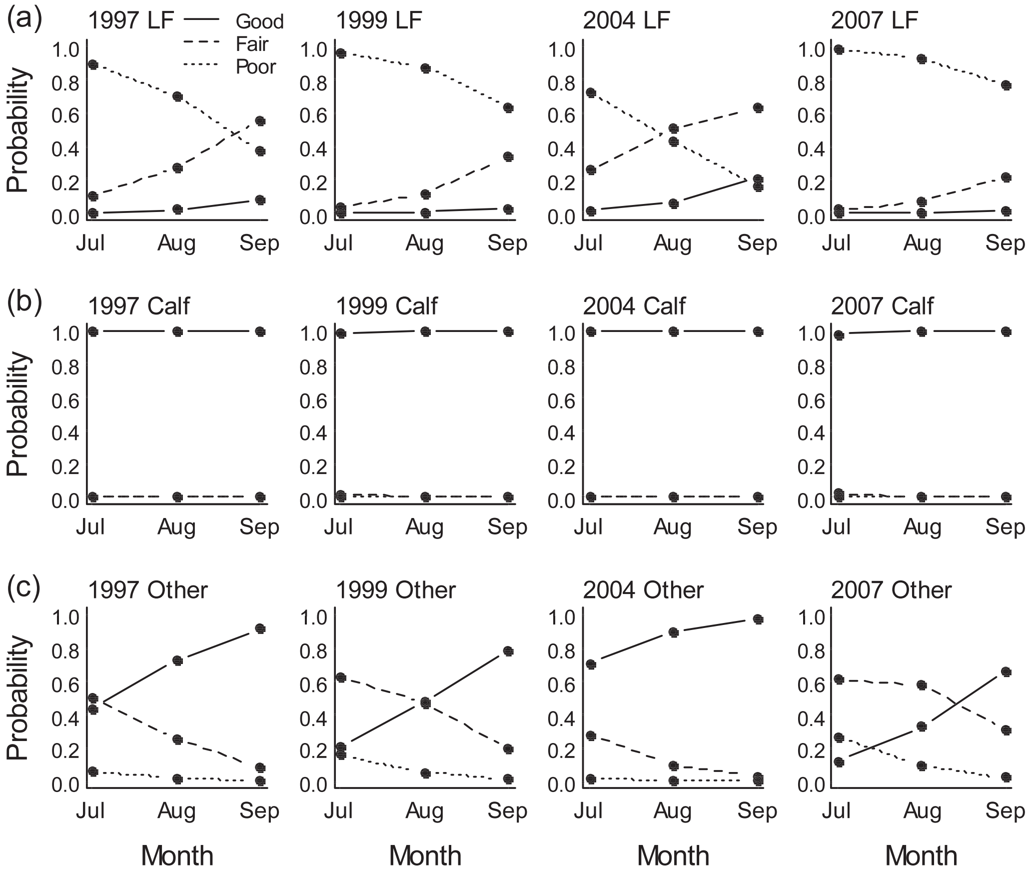

FIG. 5.—Predicted monthly probabilities of an average (i.e., a random effect of zero) western gray whale (*Eschrichtius robustus*) being in good, fair, and poor body condition during 1997 as compared to years in which body condition was significantly better (2004) and significantly worse (1999, 2007; 2006 not shown) for a a) lactating female (LF), b) calf, and c) other whale.

postcranial condition. However, during analyses associated with such categorical assessments, it may ultimately be difficult to statistically reconcile the resulting body condition determinations with particular covariates of interest, which may require restructuring the analysis or even revising the protocol. In the present case, the calf covariate level perfectly predicted the outcome of good body condition, which could have led to numerical problems when fitting the logistic regression model to the data set as a whole. Although this situation did not occur, the estimated effect size should nevertheless be considered unreliable. To a lesser degree, there also is reduced contrast in the body condition determinations for lactating females, with 121 (98.4%) of the 123 determinations of known body condition classified as fair or poor. If model instability had ensued, it might have been necessary to treat lactating females separately, perhaps in a binomial instead of a multinomial context. In general, flexibility in the treatment of covariate and response levels may be needed when statistically analyzing visual determinations of body condition.

Gray whale calves are weaned at approximately 7 months of age (Rice and Wolman 1971), a relatively short period of time given their body size, implying they rely on maternally derived energy for some period of time postweaning (Costa and Williams 1999). The comparatively good body condition of western gray whale calves (Table 3) is in line with findings from previous cetacean studies (e.g., Angell 2006) and reflects the significant energetic investment and high milk fat provided to them by lactating females (Rice and Wolman 1971). The consistently good body condition of calves (Fig. 5b) suggests that differences in maternal condition and environmental factors affecting calf development are not expressed in the stored energy of weaning calves, at least as measured by the present protocol. These differences may instead be manifested in the overall size of calves as opposed to their body condition. Perryman and Lynn (2002) found a positive correlation between the length of northbound migrating eastern gray whale females and the length of their calves, although the authors did not compare calf length to a metric more indicative of the body condition of associated females. Maternal and environmental effects also likely influence the growth of calves in ways that are not immediately apparent (Bernardo 1996), but that have long-term fitness consequences (Lindström 1999).

Still, the lack of variation in the body condition of calves is striking, particularly in light of the pronounced variation exhibited by noncalves (Figs. 5a and 5c). Perhaps reproductive females that are not nutritionally prepared to wean a calf with complete energy reserves remain anestrous or lose their calves prematurely (Lockyer 1984; Rice and Wolman 1971).

Calving intervals of eastern and western gray whales are variable (Bradford et al. 2008; Jones 1990), and there is evidence of high neonatal mortality in eastern gray whales (Swartz and Jones 1983). Further, it is conceivable that lactating females are able to energetically buffer their calves from adverse environmental conditions, although such an energy transfer would come at the expense of the body condition and future reproductive success of the female (Lindström 1999).

The high energetic costs of mammalian lactation (Young 1976) are particularly considerable for whales, who are fasting during much of this period (Lockyer 1984). As expected, the body condition of lactating female western gray whales was relatively worse than that of other whales (Table 3) and was most often determined to be compromised (Figs. 4 and 5a). Although there was some degree of monthly improvement in the body condition of lactating females, probabilities of complete within-season recovery were to a greater or less extent low in all years (Fig. 5a), indicating that postparturient females usually have not fully replenished their energy stores by the time of the next breeding opportunity (i.e., the subsequent winter).

There is a well-established correlation between body condition and reproductive success in female mammals (Loudon et al. 1983), with maternal body condition potentially impacting all aspects of the reproductive process, including the timing of reproduction (Hickling et al. 1991), probability of pregnancy (Cook et al. 2004), embryonic absorption (Belonje and van Niekerk 1975), fetal growth (Lockyer 2007), offspring mass (Atkinson and Ramsay 1995), offspring survival (Cameron et al. 1993), and progeny sex ratio (Wauters et al. 1995). Although the relationship between body condition and reproduction is not well understood for whales, a few basic scenarios have been proposed. It is generally presumed that if a reproductive female has insufficient energy reserves, she may either fail to ovulate, fail to conceive, fail to give birth, or fail to nurse. Alternatively, she may direct her own maintenance reserves into producing and weaning a calf (Lockyer 1986). Further, these mechanisms are thought to be regulated by environmental conditions, such that ovulation and conception rates are likely linked to 1 feeding season and abortion and calving rates to the next, although a series of good or bad years could mitigate or confound these connections (Lockyer 1987).

Given that western gray whale calving intervals do vary (Bradford et al. 2008), it is possible that some form of environmental regulation through maternal body condition is occurring (Brownell and Weller 2002). There are conflicting ideas about the primary method of nutritional control in gray whale reproduction. Rice and Wolman (1971) suggested that females are likely to suppress ovulation when in poor condition and unable to carry a pregnancy to term. However, Perryman et al. (2002) found that calf production in eastern gray whales was positively correlated with the length of the previous feeding season (as determined by ice cover), with no significant correlation when a 1-year lag was introduced, implying that existing pregnancies were affected, rather than ovulations or conceptions. The latter scenario is consistent with the differential costs of pregnancy in whales, which only become substantial during the last one-half or one-third of gestation (Lockyer 1984). Other baleen whale studies point to the importance of the feeding season prior to (e.g., Lockyer 1986) and during (e.g., Lockyer 2007) pregnancy, but it is unlikely that these links are mutually exclusive, particularly when interactions between years and other factors (e.g., previous calf production or maternal age) are considered. Regardless, it appears that western gray whale females do fully invest in their calves at a certain point, potentially even providing environmental amelioration. As the energetic costs of lactation are much greater than those of pregnancy (Millar 1977), there are likely to be consequences of this investment for female reproductive success.

Sex is not an important predictor of western gray whale body condition given the incorporation of reproductive class in the mixed model (Table 2), suggesting that lactating females were responsible for the significant differences detected during preliminary univariable analyses. However, the presence of pregnant females and juveniles of both sexes in the sample might have confounded the sex comparison. A variety of measures (e.g., blubber thickness, body girth, and lipid content) have shown that pregnant female whales have the highest energy stores relative to other whales (e.g., Lockyer 1986). With the exception of lactating females, juvenile whales generally have the lowest fat reserves (e.g., Víkingsson 1990), although some studies have found juvenile males to be leaner than all other whales (e.g., Lockyer 1987). Additionally, comparing the body condition of males and females at the same time may be inherently problematic because these whales may have been on the feeding ground for varying durations, since there appears to be some degree of temporal segregation by age, sex, and reproductive status in migrating gray whales (Rice and Wolman 1971). In any case, energy deposits are clearly needed by male and female gray whales for maintenance activities during the fasting period and by females to sustain substantial reproductive demands.

The monthly improvement in the body condition of western gray whales (Table 3; Fig. 5) demonstrates the significance of the feeding period for accumulating energy stores and is consistent with findings from previous whale research (e.g., Lockyer 1987; Perryman and Lynn 2002; Rice and Wolman 1971; Víkingsson 1990), although the current study is the 1st to monitor the within-season body condition of individual whales. The predicted probability that a nonlactating, noncalf (i.e., other whale) was in good condition at the end of the field season was generally, but not always, very high (Fig. 5c). Given patterns of seasonal sea-ice formation in the Okhotsk Sea, western gray whales presumably have access to the northeastern Sakhalin feeding area for at least 2 months beyond the monitoring period of the present assessment. Whales have been observed in the study area as late as mid-November, but in considerably reduced numbers, suggesting that most whales have left the region by that time (Blokhin

2004). Therefore, in addition to lactating females, other noncalf western gray whales have the potential to leave the study area with less than optimal energy stores.

The body condition of western gray whales varied annually, but was significantly better in 2004 and significantly worse in 1999, 2006, and 2007 (Table 3). Eastern gray whales experienced a high-mortality event in 1999 and 2000 that may have been caused by reductions in prey productivity brought on by short- and long-term climate effects in the North Pacific (Le Boeuf et al. 2000; Moore et al. 2001), leading Brownell and Weller (2001) to suggest an oceanographic link between the eastern gray whale mortality event and concurrent observations of western gray whales in relatively worse body condition. However, assuming males are most reflective of annual environmental conditions (Pettis et al. 2004), a post hoc analysis of the body condition of western gray whale noncalf males revealed that only the 2004 and 2007 year effects were maintained. This difference resulting from the exclusion of females implicates the interactions that can occur between the reproductive cycle and environmental variability (Lockyer 1987). Overall, the characteristics (e.g., prey quantity and quality and ice cover) of the years identified as significant in this study have not been evaluated and warrant additional attention.

Interannual variation in the energy reserves of whales has been previously detected and correlated with both prey availability (e.g., Ichii et al. 1998) and whale fecundity (e.g., Lockyer 1986). In that regard, a primary way environmental and associated foraging conditions affect population demography is by influencing maternal body condition and subsequent reproductive success (Le Boeuf and Crocker 2005), as has been demonstrated for North Atlantic right whales (Greene et al. 2003). The body condition of lactating female western gray whales was estimated to vary by year (Fig. 5a). However, the body condition of reproductive female whales likely exhibits complex and asynchronous dynamics that are a function of previous calf production and environmental factors. Thus, interannual variation in the body condition of reproductive female western gray whales merits a more thorough investigation.

Although a recent development in whale research, the use of visual body condition assessment methods is not new to animal ecology (e.g., Riney 1960; Robinson 1960). Visual determinations of body condition have been shown to successfully correlate with quantitative measures of energy stores for a variety of mammalian species (Kistner et al. 1980; Prestrud and Pond 2003; Stephenson et al. 2002; Stirling et al. 2008), including whales (Angell 2006), an important validation for any index of body condition (Schulte-Hostedde et al. 2005). Further, in cases such as free-ranging baleen whales, where a variety of components in a wide range of tissues reflect long-term energy reserves that cannot be comprehensively quantified, a more holistic assessment of relative body mass might offer some advantage over enumerating a specific measure of energy storage. That is, because energy is deposited in a number of forms and locales, which can vary according to age, sex, and reproductive status (Lockyer 1987), it could be limiting and potentially problematic to focus on 1 measurable attribute (e.g., blubber thickness—Aguilar et al. 2007).

In our study, differences in the relative amount of subcutaneous fat were detected collectively for the postcranial area, scapular region, and lateral flanks and presumed to reflect individual body condition. It is possible that body mass in these areas does not in fact correspond to important energy reserves, a problematic lack of correlation prevalent in the use of body condition indexes (Hayes and Shonkwiler 2001). However, findings of the analysis, particularly the compromised body condition of lactating females and the monthly improvement in noncalf body condition (Table 3; Figs. 5a and 5c), are consistent with well-supported patterns of mammalian and baleen whale life history, suggesting that the present assessment protocol can indeed measure western gray whale body condition. Results of research associated with whaling operations have indicated that for some balaenopterid species, the most substantial and variable, and therefore most useful, site of lipid storage is the dorsal tail region (e.g., Lockyer et al. 1985). Thus, the anterior body regions evaluated here may not represent the most sensitive or temporally precise gauge of internal fat depots, although it is also plausible that mass loss by body region may vary by species. Nevertheless, in addition to exhibiting meaningful variation, these areas are routinely documented during photo-identification efforts, providing an informative and practical means to infer body condition.

This assessment quantified temporal variation in western gray whale body condition given confirmed observations of reproductive class and sex. We suggest the next steps in the examination of western gray whale body condition are to evaluate the effect of inferred reproductive states (e.g., pregnant, resting, or immature) on body condition, and to explore the relationship between body condition and calving interval, calf sex ratio, and other life-history parameters; and between body condition and environmental indicators of food availability and access, such as indexes of sea-ice and oceanographic conditions. Assessing the body condition of free-ranging eastern gray whales also is recommended because it would allow for interpopulation comparisons, as well as illustrate the impact of density feedback mechanisms on the relationship between gray whale body condition and environmental variability. Finally, dead eastern gray whales strand in some numbers each year throughout their range (Le Boeuf et al. 2000). An anatomical and biochemical evaluation of these whales could be used to better understand subcutaneous fat deposition in the postcranial, scapular, lateral flank, and other body regions of gray whales.

The endogenous energy stores of mammalian capital breeders such as baleen whales allow individuals to sustain reproduction as well as survive periods of poor feeding, although trade-offs are involved (Lockyer 2007). Our study highlights linkages between the environmental conditions, physiological constraints, and reproductive costs of western gray whales. Further, we introduce a robust method for monitoring an aspect of individual condition, which will facilitate both following and elucidating population responses to a changing environment. Given that gray whales can track productivity changes at local scales and ecosystem alterations at ocean-basin scales, they have been referred to as bioindicators of environmental variability (Moore et al. 2003) and ecosystem sentinels (Moore and Huntington 2008), respectively. Incorporating the role of individual fitness is important for achieving a mechanistic view of these paradigms.

Fowler (1984) reported that cetacean populations are regulated through density-dependent changes in reproduction and survival that are a function of food resources. Others have argued that populations are not regulated by density-dependence but are limited by environmental capacity (e.g., White 2004) or that the 2 perspectives are indistinguishable (e.g., Berryman 2004). Whether ecologists will agree on regulation or limitation as the driver of population dynamics, it is clear that more effort is needed to identify ecological factors and mechanisms that affect individuals and ultimately population abundance and growth rate (Krebs 2002). The observed variation in western gray whale body condition indicates fundamental environmental and physiological interactions that will influence the productivity of the population regardless of its size, although a consideration of size is critical in a conservation context. That is, environmental variability can increase extinction risk in small populations (Stacey and Taper 1992), as well as compound the impact of demographic stochasticity and other small-population effects that may be contributing to the dynamics of the critically endangered western gray whale population.

ACKNOWLEDGMENTS

We thank the many individuals who have provided field assistance over the years, especially S. Blokhin, H. W. Kim, A. Lang, S. Rickards, and G. Tsidulko. Participants in the 2006 NOAA Large Whale Health Assessment Workshop contributed valuable feedback on the body condition assessment protocol. N. Ellis, P. Heagerty, and R. Christensen offered useful advice on the statistical analysis. The edits of W. Perrin and 2 anonymous reviewers improved the manuscript. Support for ALB was funded in part by a grant from the Washington Sea Grant Program, University of Washington, pursuant to National Oceanic and Atmospheric Administration Graduate Fellowship Program in Population Dynamics and Marine Resource Economics. The views expressed herein are those of the authors and do not necessarily reflect the views of National Oceanic and Atmospheric Administration or any of its subagencies. Support and funding for the Russia–United States western gray whale research project were provided (in alphabetical order) by Alaska SeaLife Center, Exxon Neftegas Limited, the International Fund for Animal Welfare, the International Whaling Commission, the United States Marine Mammal Commission, the Marine Mammal Research Program at Texas A&M University at Galveston, the National Fish and Wildlife Foundation, the United States National Marine Fisheries Service, Ocean Park Conservation Foundation, Sakhalin Energy Investment Company, the School of Aquatic and Fishery Sciences at the University of Washington, the United States Environmental Protection Agency, and the Washington Cooperative Fish and Wildlife Research Unit. The project was conducted as part of the Marine Mammal Project under Area V: Protection of Nature and the Organization of Reserves within the United States–Russia Agreement on Cooperation in the Field of Environmental Protection.

LITERATURE CITED

AGRESTI, A. 2002. Categorical data analysis. John Wiley & Sons, Inc., Hoboken, New Jersey.

AGUILAR, A., A. BORRELL, AND E. GÓMEZ-CAMPOS. 2007. The reliability of blubber thickness as a measure of body condition in large whales. Paper SC/59/O17 presented to the International Whaling Commission Scientific Committee, June 2007, Anchorage, Alaska.

ANGELL, C. M. 2006. Body fat condition of free-ranging right whales, *Eubalaena glacialis* and *Eubalaena australis*. Ph.D. dissertation, Boston University, Boston, Massachusetts.

ATKINSON, S. N., AND M. A. RAMSAY. 1995. The effects of prolonged fasting of the body composition and reproductive success of female polar bears (*Ursus maritimus*). Functional Ecology 9:559–567.

BATZLI, G. O., AND E. ESSEKS. 1992. Body fat as an indicator of nutritional condition for the brown lemming. Journal of Mammalogy 73:431–439.

BELONJE, P. C., AND C. H. VAN NIEKERK. 1975. A review of the influence of nutrition upon the oestrous cycle and early pregnancy in the mare. Journal of Reproduction and Fertility 23:167–169.

BERNARDO, J. 1996. Maternal effects in animal ecology. American Zoologist 36:83–105.

BERRYMAN, A. A. 2004. Limiting factors and population regulation. Oikos 105:667–670.

BLOKHIN, S. A. 2004. Terms of grey whales' (*Eschrichtius robustus*) appearance near the northeastern Sakhalin, their abundance and behavior in the beginning and in the end of their stay in the area of Piltun Bay. Pp. 78–82 in Marine mammals of the Holarctic, collection of scientific papers (V. M. Belkovich, ed.). 3rd International Conference, Koktebel, Crimea, Ukraine, 11–17 October 2004.

BRADFORD, A. L., D. W. WELLER, Y. V. IVASHCHENKO, A. M. BURDIN, AND R. L. BROWNELL, JR. 2009. Anthropogenic scarring of western gray whales (*Eschrichtius robustus*). Marine Mammal Science 25:161–175.

BRADFORD, A. L., D. W. WELLER, P. R. WADE, A. M. BURDIN, AND R. L. BROWNELL, JR. 2008. Population abundance and growth rate of western gray whales *Eschrichtius robustus*. Endangered Species Research 6:1–14.

BRADFORD, A. L., ET AL. 2006. Survival estimates of western gray whales *Eschrichtius robustus* incorporating individual heterogeneity and temporary emigration. Marine Ecology Progress Series 315:293–307.

BROWNELL, R. L., JR., AND D. W. WELLER. 2001. Is the ''carrying capacity hypothesis'' a plausible explanation for the ''skinny'' gray whale phenomenon? Paper SC/53/BRG20 presented to the International Whaling Commission Scientific Committee, July 2001, London, United Kingdom.

BROWNELL, R. L., JR., AND D. W. WELLER. 2002. Prolonged calving intervals in western gray whales: nutritional stress and pregnancy. Paper SC/54/BRG12 presented to the International Whaling Commission Scientific Committee, April 2002, Shimonoseki, Japan.

BROWNELL, R. L., JR., ET AL. 1997. Observations on Okhotsk–Korean gray whales on their feeding grounds off Sakhalin Island. Report of the International Whaling Commission 47:161–162.

CAMERON, R. D., W. T. SMITH, S. G. FANCY, K. L. GERHART, AND R. G. WHITE. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

Chamaillé-Jammes, S., H. Fritz, M. Valeix, F. Murindagomo, and J. Clobert. 2008. Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. Journal of Animal Ecology 77:135–144.

Christensen, R. H. B. 2010. Ordinal: regression models for ordinal data. R package version 2010.06-12. cran.r-project.org/web/packages/ordinal/index.html. Accessed 30 June 2010.

Cicchetti, D. V., and A. R. Feinstein. 1990. High agreement but low kappa: II. Resolving the paradoxes. Journal of Clinical Epidemiology 43:551–558.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20:37–46.

Cohen, J. 1968. Weighted kappa: nominal scale agreement with provision for scaled disagreement or partial credit. Psychological Bulletin 70:213–220.

Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of northern Yellowstone elk. Journal of Mammalogy 85:714–722.

Costa, D. P., and T. M. Williams. 1999. Marine mammal energetics. Pp. 176–217 in Biology of marine mammals (J. E. Reynolds III and S. A. Rommel, eds.). Smithsonian Institution Press, Washington, D.C.

Darling, J. D. 1984. Gray whales off Vancouver Island, British Columbia. Pp. 267–287 in The gray whale *Eschrichtius robustus* (M. L. Jones and S. L. Swartz, eds.). Academic Press, Orlando, Florida.

Feinstein, A. R., and D. V. Cicchetti. 1990. High agreement but low kappa: I. The problems of the two paradoxes. Journal of Clinical Epidemiology 43:543–549.

Fowler, C. W. 1984. Density dependence in cetacean populations. Report of the International Whaling Commission Special Issue 6:373–379.

Greene, C. H., A. J. Pershing, R. D. Kenney, and J. W. Jossi. 2003. Impact of climate variability on the recovery of endangered North Atlantic right whales. Oceanography 16:98–103.

Hauck, W. W., Jr., and A. Donner. 1977. Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851–853.

Hayes, J. P., and J. S. Shonkwiler. 2001. Morphometric indicators of body condition: worthwhile or wishful thinking? Pp. 8–38 in Body composition analysis of animals: a handbook of non-destructive methods (J. R. Speakman, ed.). Cambridge University Press, Cambridge, United Kingdom.

Hickling, G. J., J. S. Millar, and R. A. Moses. 1991. Reproduction and nutrient reserves of bushy-tailed wood rats (*Neotoma cinerea*). Canadian Journal of Zoology 69:3088–3092.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley & Sons, Inc., Hoboken, New Jersey.

Ichii, T., N. Shinohara, Y. Fujise, S. Nishiwaki, and K. Matsuoka. 1998. Interannual changes in body fat condition index of minke whales in the Antarctic. Marine Ecology Progress Series 175:1–12.

International Union for Conservation of Nature. 2010. IUCN Red list of threatened species, version 2010.4. www.iucnredlist.org. Accessed 1 December 2010.

Jakob, E. M., S. D. Marshall, and G. W. Utez. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Jones, M. L. 1990. The reproductive cycle in gray whales based on photographic resightings of females on the breeding grounds from 1977–82. Report of the International Whaling Commission Special Issue 12:177–182.

Kistner, D. R., C. E. Trainer, and N. A. Hartmann. 1980. A field technique for evaluating physical condition of deer. Wildlife Society Bulletin 8:11–17.

Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 357:1211–1219.

Lang, A. R. 2010. The population genetics of gray whales (*Eschrichtius robustus*) in the North Pacific. Ph.D. dissertation, University of California, San Diego.

Le Boeuf, B. J., and D. E. Crocker. 2005. Ocean climate and seal condition. BMC Biology 3:1–10.

Le Boeuf, B. J., M. H. Pérez-Cortés, R. J. Urbán, B. R. Mate, and U. F. Ollervides. 2000. High gray whale mortality and low recruitment in 1999: potential causes and implication. Journal of Cetacean Research and Management 2:85–99.

Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14:343–348.

Lockyer, C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. Report of the International Whaling Commission Special Issue 6:27–50.

Lockyer, C. 1986. Body fat condition in northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. Canadian Journal of Fisheries and Aquatic Sciences 43:142–147.

Lockyer, C. 1987. The relationship between body fat, food resource and reproductive energy costs in north Atlantic fin whales (*Balaenoptera physalus*). Symposia of the Zoological Society of London 57:343–361.

Lockyer, C. 2007. All creatures great and smaller: a study in cetacean life history energetics. Journal of the Marine Biological Association of the United Kingdom 87:1035–1045.

Lockyer, C., L. C. McConnell, and T. D. Waters. 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Canadian Journal of Zoology 63:2328–2338.

Loudon, A. S. I., A. S. McNeilly, and J. A. Milne. 1983. Nutrition and lactational control of fertility in red deer. Nature 302:145–147.

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31:370–386.

Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. Oikos 90:457–468.

Moore, S. E., and H. P. Huntington. 2008. Arctic marine mammals and climate change: impacts and resilience. Ecological Applications 18:S157–S165.

Moore, S. E., et al. 2001. Are gray whales hitting ''K'' hard? Marine Mammal Science 17:954–958.

Moore, S. E., J. M. Grebmeier, and J. R. Davies. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81:734–742.

Perryman, W. L., M. A. Donahue, P. C. Perkins, and S. B. Reilly. 2002. Gray whale calf production 1994–2000: are observed fluctuations related to changes in seasonal ice cover? Marine Mammal Science 18:121–144.

Perryman, W. L., and M. S. Lynn. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. Journal of Cetacean Research and Management 4:155–164.

Pettis, H. M., R. M. Rolland, P. K. Hamilton, S. Brault, A. R. Knowlton, and S. D. Kraus. 2004. Visual health assessment of North Atlantic right whales (*Eubalaena glacialis*) using photographs. Canadian Journal of Zoology 82:8–19.

PRESTRUD, P., AND C. M. POND. 2003. Fat indices of arctic foxes *Alopex lagopus* in Svalbard. Wildlife Biology 9:193–197.

PUNT, A. E., AND P. R. WADE. 2010. Population status of the eastern North Pacific stock of gray whales in 2009. United States Department of Commerce, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-AFSC-207:1–43.

R DEVELOPMENT CORE TEAM. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing. www.r-project.org. Accessed 30 June 2010.

REYNOLDS, D. S., AND T. H. KUNZ. 2001. Standard methods for destructive body composition analysis. Pp. 39–55 in Body composition analysis of animals: a handbook of non-destructive methods (J. R. Speakman, ed.). Cambridge University Press, Cambridge, United Kingdom.

RICE, D. W. 1983. Gestation period and fetal growth of the gray whale. Report of the International Whaling Commission 33:539–544.

RICE, D. W., AND A. A. WOLMAN. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). Special Publication 3, The American Society of Mammalogists.

RINEY, T. 1960. A field technique for assessing physical condition of some ungulates. Journal of Wildlife Management 24:92–94.

ROBBINS, C. T. 1993. Wildlife feeding and nutrition. Academic Press, New York.

ROBINSON, W. L. 1960. Test of shelter requirements of penned white-tailed deer. Journal of Wildlife Management 24:364–371.

SCHULTE-HOSTEDDE, A. I., B. ZINNER, J. S. MILLAR, AND G. J. HICKLING. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SIMONOFF, J. S. 2003. Analyzing categorical data. Springer-Verlag, New York.

SPEAKMAN, J. R. (ED.). 2001. Body composition analysis of animals: a handbook of non-destructive methods. Cambridge University Press, Cambridge, United Kingdom.

STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18–29.

STEPHENSON, T. R., V. C. BLEICH, B. M. PIERCE, AND G. P. MULCAHY. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

STIRLING, I., G. W. THIEMANN, AND E. RICHARDSON. 2008. Quantitative support for a subjective fatness index of immobilized polar bears. Journal of Wildlife Management 72:568–574.

SWARTZ, S. L., AND M. L. JONES. 1983. Gray whale (*Eschrichtius robustus*) calf production and mortality in the winter range. Report of the International Whaling Commission 33:503–507.

THOMAS, V. G. 1990. Control of reproduction in animal species with high and low body fat reserves. Pp. 27–41 in Adipose tissue and preproduction. Progress in reproductive biology and medicine (R. E. Frisch, ed.). S. Karger AG, Basel, Switzerland.

VÍKINGSSON, G. A. 1990. Energetic studies on fin and sei whales caught off Iceland. Report of the International Whaling Commission 40:365–373.

WANG, P. 1984. Distribution of the gray whale (*Eschrichtius gibbosus*) off the coast of China. Acta Theriologica Sinica 4:21–26.

WAUTERS, L. A., S. A. DE CROMBRUGGHE, N. NOUR, AND E. MATTHYSEN. 1995. Do female roe deer in good condition produce more sons than daughters? Behavioral Ecology and Sociobiology 37:189–193.

WELLER, D. W., A. M. BURDIN, B. WÜRSIG, B. L. TAYLOR, AND R. L. BROWNELL, JR. 2002. The western gray whale: a review of past exploitation, current status, and potential threats. Journal of Cetacean Research and Management 4:7–12.

WELLER, D. W., ET AL. 1999. Gray whales (*Eschrichtius robustus*) off Sakhalin Island, Russia: seasonal and annual patterns of occurrence. Marine Mammal Science 15:1208–1227.

WELLER, D. W., ET AL. 2008. Photographic match of a western gray whale between Sakhalin Island, Russia and Honshu, Japan: first link between feeding ground and migratory corridor. Journal of Cetacean Research and Management 10:89–91.

WHITE, T. C. R. 2004. Limitation of populations by weather-driven changes in food: a challenge to density-dependent regulation. Oikos 105:664–666.

WIRSING, A. J., T. D. STEURY, AND D. L. MURRAY. 2002. Noninvasive estimation of body composition in small mammals: a comparison of conductive and morphometric techniques. Physiological and Biochemical Zoology 75:489–497.

WORTHY, G. A. J., AND D. M. LAVIGNE. 1987. Mass loss, metabolic rate, and energy utilization by harp and gray seals during the postweaning fast. Physiological Zoology 60:352–364.

YOUNG, R. A. 1976. Fat, energy and mammalian survival. American Zoologist 16:699–710.

Submitted 14 March 2011. Accepted 9 August 2011.

Associate Editor was William F. Perrin.

APPENDIX I

Report of an interrater agreement study that evaluated the comparability of results produced by 2 trained researchers using the body region scoring protocol developed to assess the body condition of western gray whales (*Eschrichtius robustus*).

We conducted an interrater agreement study to assess if the body region scoring protocol used to determine western gray whale body condition can be utilized by more than 1 qualified researcher to achieve similar results. To this end, a 2nd trained analyst (YVI) reviewed images from a subset of 300 randomly selected sightings and scored the 3 body regions of interest (i.e., postcranial area, scapular region, and lateral flanks) for the 98 individual whales represented in the subset. We then compared scored data from the 2 researchers in 2 separate tests of interrater agreement for each of the 3 body regions. First, we evaluated the decision to code each body region as visible (non-X) or not visible (X) for each of the 300 sightings. Next, when both analysts coded the body region as visible for a sighting, we assessed agreement in the assigned numerical postcranial (P), scapular (S), and lateral flank (L) condition scores.

We measured interrater agreement using the kappa (κ) coefficient (Cohen 1960), where $\kappa > 0.75$ is strong agreement, $0.75 > \kappa > 0.40$ is good-to-moderate agreement, and $\kappa < 0.40$ is fair-to-poor agreement (e.g., Simonoff 2003). Given that we scored the postcranial condition using a 3-point ordinal scale, we employed a weighted kappa (κ_w) coefficient (Cohen 1968) with linear weighting in this case. For each of the 6 tests, we expected the underlying prevalence of the observed entities to be imbalanced (e.g., more P scores of 3 than 2 and 1), which can lead to low values of κ despite relatively high values of total agreement (Feinstein and Cicchetti 1990). Therefore, for each test, we computed the proportional agreement (p) of each unit (e.g., p_{P3}, p_{P2}, and p_{P1}) along with κ as a recommended supplemental diagnostic (Cicchetti and Feinstein 1990).

For the decision to code the postcranial area as visible or not visible, κ indicates good agreement and both values of p are high ($\kappa = 0.67$, $p_{\text{Pnon-X}} = 0.85$, $p_{\text{PX}} = 0.83$, $n = 300$). For the postcranial condition score assigned when both raters coded the region as visible, κ_w denotes good agreement, while p is high for scores of 3 and only somewhat reduced for scores of 2 and 1 ($\kappa_w = 0.65$, $p_{\text{P3}} = 0.88$, $p_{\text{P2}} = 0.64$, $p_{\text{P1}} = 0.63$, $n = 135$). For the choice to code the scapular region as visible or not visible, κ shows moderate agreement and both p-values are high ($\kappa = 0.58$, $p_{\text{Snon-X}} = 0.74$, $p_{\text{SX}} = 0.83$, $n = 300$). For the scapular condition score assigned when both researchers coded the region as visible, κ demonstrates good agreement and p-values are high, particularly for scores of 2 ($\kappa = 0.69$, $p_{\text{S2}} = 0.94$, $p_{\text{S1}} = 0.76$, $n = 89$). For the judgment to code the lateral flanks as visible or not visible, κ reveals moderate agreement and both values of p are high ($\kappa = 0.59$, $p_{\text{Lnon-X}} = 0.82$, $p_{\text{LX}} = 0.76$, $n = 300$). For the lateral flank condition score assigned when both analysts coded the region as visible, κ specifies strong agreement and p-values are high, especially for scores of 2 ($\kappa = 0.83$, $p_{\text{L2}} = 0.98$, $p_{\text{L1}} = 0.85$, $n = 141$). Observed entities were imbalanced only in the 3 tests involving numerical condition scores. In these cases, values of p are higher for the more prevalent observation (i.e., the score indicating best condition) within each test.

Interrater agreement within the 6 tests was strong to moderate as measured by κ. Agreement was weakest for the choice to code each of the 3 body regions as visible or not visible. A closer examination of the decisions made by each rater revealed that 1 analyst reliably coded each body region as visible more frequently than the other analyst, suggesting slightly different, but consistent, interpretations of the body position and photographic extent and quality needed to assess body region condition. Determining the visibility of the scapular region and lateral flanks can be challenging, requiring the additional consideration of how much of the body is submerged, which is possibly reflected in the reduced κ coefficients for those regions. Agreement was strongest when assigning a numerical condition score to mutually visible body regions. Further, κ in these cases is likely biased low given the imbalance in prevalence of the observed entities (Feinstein and Cicchetti 1990), a suggestion that is generally supported by values of the p diagnostic. Unsurprisingly, agreement was highest when assigning the scapular and lateral flank condition scores, because these regions were scored on a 2-point scale. Overall, findings of the interrater agreement study suggest that although the sets of sightings with visible body regions identified by multiple researchers may vary marginally in size, the numerical scores assigned to these regions will be similar. Thus, the western gray whale body region scoring protocol can be used by more than 1 trained researcher to achieve comparable results.

Appendixes II–IV Overview

Overview of sensitivity analyses conducted to confirm that month was an appropriate and feasible scale at which to collapse the numerical body region condition scores for the body condition assessment of western gray whales (*Eschrichtius robustus*).

In general, each survey sighting of a western gray whale did not result in a comprehensive set of images that allowed us to assign a numerical score to each of the 3 body regions of interest (i.e., postcranial area, scapular region, and lateral flanks). Consequently, we could not produce an overall individual determination of body condition on a per-sighting basis. Additionally, a body condition determination made for a single sighting might be too sensitive to the effects of body position and other factors that can confound the body region scoring process. Thus, it was necessary to collapse the scored data for each sighting so that we could generate robust composites of postcranial, scapular, and lateral flank condition. Specifically, we needed to collapse the scored data at a scale that would be large enough to maximize the use of intermittent sightings lacking the full suite of body region condition scores, be small enough to minimize detectable transitions from one score to the next, and allow for temporal comparisons between annual field seasons. A preliminary assessment of the scored body region data suggested that month would be a useful, appropriate, and feasible scale at which to aggregate these data. We conducted 2 sensitivity analyses to evaluate this decision.

Analysis 1: body region score transitions.—The objective of the 1st analysis was to determine if the numerical scores assigned to each of the 3 body regions changed within each month of the study (July, August, and September). Accordingly, we used logistic regression to model the effect of the interaction between the categorical variable month and the continuous variable date on the body region condition score as a categorical response. We treated individual whales as random effects. Given the 3-point ordinal scale applied to the postcranial area, we utilized the proportional odds model formulation (e.g., Agresti 2002) in this case. From the 5,007 survey sightings of 168 western gray whales photo-identified between July and September of 1997–2007, 2,337 numerical (i.e., non-X) postcranial condition scores from 165 individual whales (median of 9 scores per whale, range 1–72 scores), 2,091 scapular scores from 165 whales (median of 8, range 1–62 scores), and 2,790 lateral flank scores from 167 whales (median of 11, range 1–75 scores) were available for this analysis.

Consistent with findings from the analysis of the body condition determinations (see Table 3), results from the 3 model runs indicate that condition in each body region improved as the field season progressed (i.e., by month), although significant recovery in the scapular region and lateral flanks was not detected until September (Appendix II). However, significant improvements in body region condition were not observed within each month, with the exception of the scapular region in September (Appendix II). Given that the overall body condition determinations were based primarily on the postcranial condition (see ''Materials and Methods: *Body condition assessment*,'' for explanation), and that the within-September recovery of the scapular region was not highly significant, we concluded that month was an appropriate scale to aggregate the scored body region data for interannual comparisons, because it was robust to detectable transitions between consecutive condition scores.

Collapsing the scored body region data.—We established a set of hierarchical decision rules to guide the process of collapsing the scored data into monthly determinations of postcranial, scapular, and lateral flank condition for each whale. Appendix III presents these decision rules and the frequency of their use. The 2,337 numerical postcranial scores resulted in 1,133 monthly determinations of postcranial condition, of which 1,010 (89.1%) are based on sightings that shared the same numerical score during the month (i.e., decision rule A was applied; Appendix III). Similarly, we collapsed the 2,091 scapular scores into 1,035 monthly scapular determinations, with 953 (92.1%) based on decision rule A, and the 2,790 lateral flank scores into 1,1,67 monthly lateral flank determinations, with 1,099 (94.2%) based on decision rule A (Appendix III). In other words, most of the monthly determinations of body region condition reflect no variation in numerical scores assigned within the month, which likely is at least partially explained by the aforementioned lack of detectable transitions between adjacent scores at a monthly scale, but could also be a function of the timing and number of monthly sightings. Therefore, we formed most of the overall body condition determinations from body region composites characterized by no within-month variation.

Analysis 2: effect of within-month variation.—The 2nd sensitivity analysis examined whether incorporating body condition determinations made from body region composites with possible within-month variation (i.e., we applied decision rules B–F; Appendix III) would refine or confound the statistical analysis of western gray whale body condition. To this end, we compared the analysis of the full set of body condition determinations (described in the main text, see Tables 2 and 3 for results) to an identical analysis performed using only the body condition determinations resulting from body regions composites based on decision rule A. Note that composites where we coded the scapular region or lateral flanks, or both, as X were included in the sensitivity analysis, as long as we made the associated postcranial condition determinations using decision rule A. Of the 1,133 determinations of known body condition (i.e., good, fair, or poor), 929 (82.0%) met the composite specification criteria for the sensitivity analysis. Identical to the full analysis, we employed ordinal logistic regression (in the form of the proportional odds model) in the sensitivity analysis to evaluate the effect of year, month, reproductive class, and sex on the body condition of individual whales, which we regarded as random effects.

As in the model selection procedure of the full analysis (Table 2), likelihood ratio tests revealed that the model incorporating year, month, and class as covariates is the most-parsimonious. Results of fitting this model to the reduced set of body condition determinations (Appendix IV) are equivalent to findings from the full analysis (Table 3). Specifically, body condition was significantly worse in 1999, 2006, and 2007 and significantly better in 2004 relative to the reference year of 1997. Further, body condition improved significantly with each month of the field season, whereas lactating females were in significantly worse body condition and calves in significantly better body condition as compared to other whales. The comparable results of the 2 analyses and the smaller standard errors associated with the predictor coefficients of the full analysis indicate that utilizing the full set of known body condition determinations refined the statistical analysis. Additionally, the complementary nature of the analyses suggests that our method of handling within-month variation when aggregating the scored body region data (Appendix III) was reasonable. In summary, most observations of body region condition did not vary within the month, but we found a suitable means for collapsing scores when there was variation. Thus, month offered a feasible, in addition to appropriate, scale at which to aggregate the numerical body region condition scores for the western gray whale body condition assessment.

APPENDIX II

Maximum-likelihood estimates resulting from fitting logistic regression mixed models to numerical scores of western gray whale (*Eschrichtius robustus*) postcranial, scapular, and lateral flank condition, given an interaction between month and date. We used the proportional odds formulation to model condition in the postcranial area. For each body region, the 1st row(s) represents the model intercept(s) and the rest predictor coefficients, with month = July serving as the reference category. Significant predictor coefficients ($P < 0.05$) are shown in boldface type. *SE* = standard error.

Body region	Variable	Estimate	*SE*	Wald *z*	*P*-value
Postcranial	$Y \geq 2$	2.845	0.351	8.112	<0.001
	$Y \geq 3$	−0.544	0.341	−1.594	0.111
	Month = Aug.	**0.904**	**0.321**	**2.818**	**0.005**
	Month = Sep.	**2.169**	**0.346**	**6.266**	**<0.001**
	Date	0.021	0.012	1.780	0.075
	Aug.:Date	0.007	0.015	0.498	0.618
	Sep.:Date	0.022	0.019	1.186	0.236
Scapular	$Y \geq 2$	1.180	0.436	2.706	0.007
	Month = Aug.	0.222	0.439	0.505	0.614
	Month = Sep.	**1.302**	**0.467**	**2.791**	**0.005**
	Date	0.003	0.017	0.150	0.880
	Aug.:Date	0.032	0.020	1.577	0.115
	Sep.:Date	**0.053**	**0.026**	**2.068**	**0.039**
Lateral flank	$Y \geq 2$	2.501	0.493	5.077	<0.001
	Month = Aug.	0.397	0.425	0.935	0.350
	Month = Sep.	**1.649**	**0.473**	**3.483**	**<0.001**
	Date	0.009	0.016	0.589	0.556
	Aug.:Date	0.035	0.020	1.788	0.074
	Sep.:Date	0.048	0.027	1.764	0.078

APPENDIX III

Hierarchical decision rules (DRs) used to collapse the scored western gray whale (*Eschrichtius robustus*) body region data into monthly determinations of postcranial (P), scapular (S), and lateral flank (L) condition for each whale. Decision rules were hierarchical in the sense that we did not consider a rule unless the previous rule(s) did not provide a resolution. An uncertain score refers to instances in which an image(s) within a sighting suggested a different score than that indicated by the majority of images.

		Frequency		
DR	Description of numerical score selected from those available	P	S	L
A	Only score assigned during the month	1,010	953	1,099
B	Majority score assigned when there were no uncertain scores	30	39	34
C	Majority score assigned after removing any uncertain scores	57	17	14
D	Score from 1st one-half of month when ≥10 days separate conflicting scores	8	3	4
E	Score that was not >score from next month or <score from previous month	3	2	3
F	Score that was most conservative (i.e., reflected better condition)	25	21	13

APPENDIX IV

Maximum-likelihood estimates resulting from fitting the proportional odds mixed model to western gray whale (*Eschrichtius robustus*) body condition determinations (formed from body region composites reflecting no within-month variation), given year, month, and reproductive class. The first 2 rows represent model intercepts and the rest predictor coefficients. Note that year = 1997, month = July, and class = other whale served as the reference categories. Significant predictor coefficients ($P < 0.05$) are shown in boldface type. *SE* = standard error; LF = lactating female.

Variable	Estimate	*SE*	Wald *z*	*P*-value
$Y \geq$ fair	3.173	0.470	6.755	<0.001
$Y \geq$ good	0.050	0.435	0.116	0.908
Year = 1998	0.471	0.519	0.907	0.364
Year = 1999	**−1.261**	**0.459**	**−2.749**	**0.006**
Year = 2000	−0.764	0.522	−1.463	0.143
Year = 2001	−0.801	0.483	−1.660	0.097
Year = 2002	−0.163	0.492	−0.332	0.740
Year = 2003	0.453	0.521	0.869	0.385
Year = 2004	**1.117**	**0.565**	**1.976**	**0.048**
Year = 2005	−0.873	0.471	−1.852	0.064
Year = 2006	**−0.989**	**0.494**	**−2.004**	**0.045**
Year = 2007	**−1.881**	**0.477**	**−3.947**	**<0.001**
Month = Aug.	**1.267**	**0.221**	**5.729**	**<0.001**
Month = Sep.	**2.841**	**0.297**	**9.577**	**<0.001**
Class = LF	**−5.480**	**0.467**	**−11.728**	**<0.001**
Class = calf	**5.533**	**1.086**	**5.094**	**<0.001**