



NOTE

Decadal changes in adult size of salmon-eating killer whales in the eastern North Pacific

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ABSTRACT: Two populations of killer whales aggregate around Vancouver Island to feed primarily on Chinook salmon. Aerial photogrammetry of endangered southern residents has documented some adults growing to smaller lengths in recent decades, suggesting that early growth may have been constrained by low Chinook availability in the 1990s. We investigated whether growth and adult length were also constrained in the more abundant northern residents. Photographs were collected from an unmanned hexacopter at altitudes of 30 to 37 m over 4 yr, 2014 to 2017. Images were linked to 78 individuals of known age and sex based on distinctive saddle patch pigmentation. The length of each whale was estimated by measuring pixel dimensions between both the snout and dorsal fin and the dorsal fin and fluke; these were scaled to real size using camera lens focal length and altitude, determined by a laser or pressure altimeter. Total length, derived by summing the longest (flattest) of each measure, ranged from 2.42 m for a first-year calf to 7.45 m for the largest adult male. A Bayesian change point analysis revealed that adult whales <40 yr old were on average shorter by 0.44 m than older adults, which grew to typical lengths of 6.28 and 7.14 m for females and males, respectively. This mirrors the growth trends reported for southern residents, supporting demographic evidence of correlated prey limitation in both populations. The growth data suggest that the effects of nutritional stress are not only acutely lethal but also have long-term consequences for the condition of whales in both populations.

KEY WORDS: Photogrammetry · Drone · UAS · UAV · Growth · Nutrition · Orca

1. INTRODUCTION

Two populations of killer whales *Orcinus orca* frequent the waters around Vancouver Island to feed primarily on Chinook salmon *Oncorhynchus tshawytscha* returning to rivers off the west coast of Canada and the United States (Ford & Ellis 2006). The southern resident killer whale (SRKW) population is

listed as endangered by both countries (Fisheries and Oceans Canada 2008, National Marine Fisheries Service 2008) and currently numbers 75 individuals (K. Balcomb, Center for Whale Research, unpubl. data), while the northern resident killer whale (NKRW) population numbers around 300 individuals (Towers et al. 2015) and is listed as threatened in Canada (Fisheries and Oceans Canada 2008). Both popu-

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lations are hypothesized to be periodically food limited, with declines in coast-wide Chinook salmon (notably in the 1990s) coinciding with high mortality (Ford et al. 2010) and constrained reproduction (Ward et al. 2009) in both populations. However, despite these correlations, there is still uncertainty about if and when these whales are nutritionally stressed (Hilborn et al. 2012), which is constraining management recovery actions. For SRKWs, further evidence has come from aerial photogrammetry, which has documented declines in body condition of some whales (Fearnbach et al. 2018) and a trend for growth to smaller adult lengths in recent decades (Fearnbach et al. 2011). Fearnbach et al. (2011) hypothesized that this decline in adult length was likely the result of early growth being constrained by prey availability, but the sample size of older adults in the SRKW population was relatively small due to their low abundance. To investigate further, we used photogrammetry analyses of high-resolution photos to address the hypothesis that growth and adult length have also been constrained in the more abundant NRKWs.

2. MATERIALS AND METHODS

Aerial photographs of NRKWs were collected using an unmanned hexacopter launched from an 8.2 m boat (Durban et al. 2015) operating in the protected waters between Queen Charlotte Strait and Johnstone Strait, off northeastern Vancouver Island (Fig. 1). During a 3 wk field effort in August of each year from

2014 to 2017, vertical photographs of whales were collected from altitudes of 30 to 37 m using a micro 4/3 camera with a 25 mm lens that provided undistorted images with a water level resolution of <1.8 cm (Durban et al. 2015). We linked photographs to individual whales of known age and sex by matching distinctive saddle patch pigmentation in aerial images to a long-term boat-based photo-identification catalog (Durban et al. 2015, Towers et al. 2015; Fig. 2). Birth year was observed for 4 new calves born during the years of this study (Table 1) and reported in Towers et al. (2015) for all other whales. These were based on the first appearance of whales in the population census, except for whales born before 1973, for which birth years were estimated using techniques described in Olesiuk et al. (1990). Ages were standardized by assuming a February 1 birth date. Where known, sex for all whales was reported in Towers et al. (2015) and was classified as unknown for the 4 new calves.

Body measurements in pixels were scaled to real size for the majority of whales (all those imaged in 2017) using data from a laser altimeter, which has been shown to have a typical error of ~0.1% (Dawson et al. 2017). For the remaining whales that were not imaged in 2017, scale was provided by a pressure altimeter with a typical error of <1% (Durban et al. 2015). The length of each whale was estimated in the most recent year it was photographed by measuring pixel dimensions between both the snout and dorsal fin (SNDF) and the dorsal fin and fluke (DFFL; Fig. 2). Total length was derived for each whale by summing the longest (flattest) of each measure.

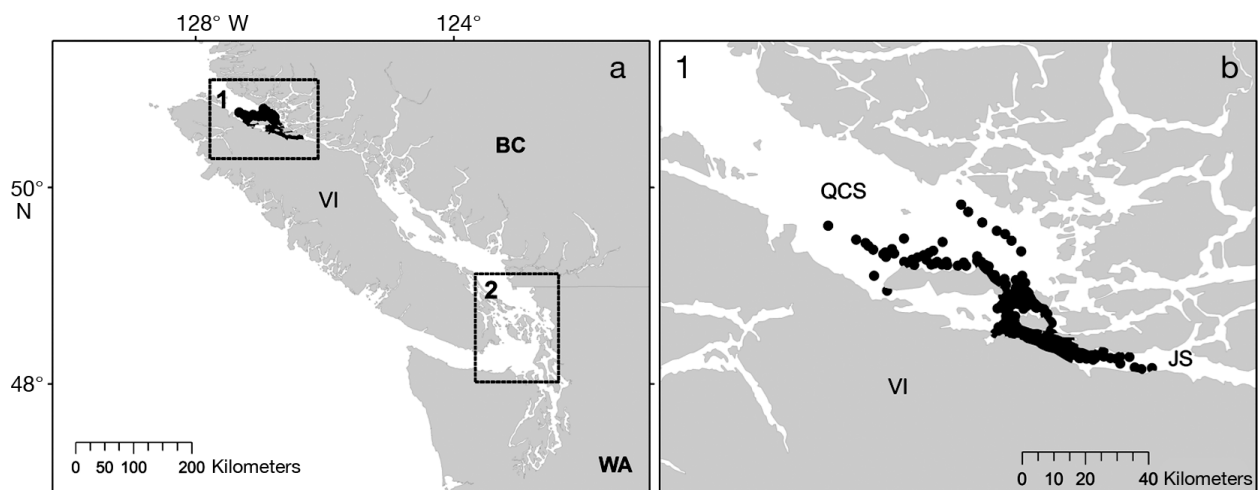


Fig. 1. Locations of 303 hexacopter flights used to collect vertical images of northern resident killer whales off the coast of British Columbia (BC), Canada. Rectangle 1 in (a) shows the location of the study area off northeastern Vancouver Island (VI) compared to the area between southern VI and Washington state (WA), USA, where comparative aerial images were collected from southern resident killer whales (rectangle 2; see Fearnbach et al. 2011). (b) shows a magnified view of rectangle 1, with flights (black dots: start locations) in the protected waters between Queen Charlotte Strait (QCS) and Johnstone Strait (JS)

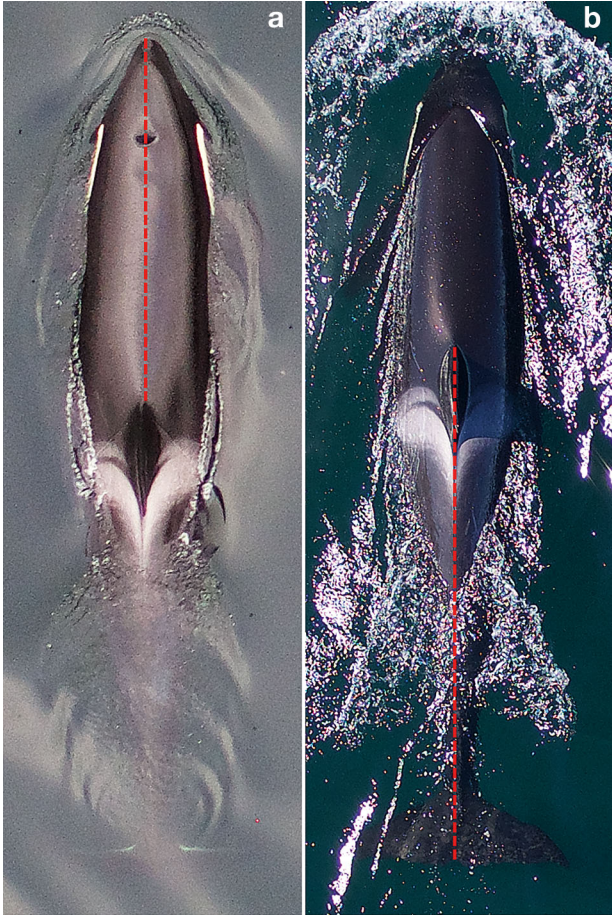


Fig. 2. Aerial images of the same adult female northern resident killer whale (A42) illustrating the 2 metrics of snout to dorsal fin (a) and dorsal fin to fluke (b) that were measured to derive total length. Also visible in both photos is the unique saddle patch pigmentation used to link measurements to individual whales of known age and sex (see Durban et al. 2015)

Trends in adult size were investigated by fitting a Bayesian change point model (Carlin et al. 1992) to length measurements for individuals of both sexes that were conservatively designated as adults by virtue of being >20 yr of age (Fearnbach et al. 2011). The total length (TL) measurements for each individual j of each sex i were assumed to be normally (N) distributed, with a residual standard deviation (σ) around a model μ that described 2 levels stratified by age:

$$TL_{ij} \sim N(\mu_{ij}, \sigma) \quad (1)$$

$$\mu_{ij} = \alpha_i + \beta\delta(\text{age}_{ij} - c) \quad (2)$$

where α represents the average length of adults of each sex before a change point at an unknown age c , to be estimated, and $\delta()$ represents a step function,

defined as 1 if its argument was zero or positive and zero otherwise; therefore, β describes the magnitude of a step change. We placed a flat uniform $U(20, 60)$ prior distribution on the timing of the change point and diffuse $N(0, 100)$ prior distributions on α_i and β to let these be informed by the data. Similarly a $U(0, 10)$ prior distribution was placed on σ .

We used WinBUGS software (Lunn et al. 2000) to implement Markov chain Monte Carlo (MCMC) sampling to estimate the posterior distribution for the unknown parameters, including the change point, after conditioning on the data.

To investigate if this change point model fit better than a simpler model with just a constant average adult size for each sex, we adopted the MCMC method of Carlin & Chib (1995) for simultaneous model selection. A model indicator k was included directly in the model, along with a parameter vector for each model: α^1 and σ^1 for the constant model; α^2 , β , c and σ^2 for the change point model. We then sampled from this joint model space simultaneously, updating the model indicator k at each iteration and then updating the parameters only for the model reflected by the current value of the model indicator. We assigned true priors for parameters when they were in the chosen model, and when they were not selected, we updated pseudo-priors that were precisely based on estimates of model parameters from separate pilot runs to facilitate switches between models. We set a discrete uniform prior distribution on the model indicator, to initially assign an equal probability of 0.5 to each model, and estimated the posterior probability $p(k = 2)$ of selecting the change point model. We based inference on 20 000 MCMC iterations following an initial burn-in of 20 000 iterations.

3. RESULTS

Images were collected during a total of 303 hexacopter flights, and analysis was constrained to 78 individuals with 3 or more measurements for each of the 2 body metrics (SNDF median images per whale = 14; range: 3–40; DFFL median = 11; range: 3–35). This dataset comprised whales from 6 of 15 NRKW pods and 2 of 3 of the vocal clans (Table 1; see Towers et al. 2015). The majority of whales (67 of 78) imaged were associated with laser altimetry in 2017, with 6 additional individuals imaged using pressure altimetry in 2016, 2 in 2015, and 3 in 2014. TL estimates ranged from 2.42 m for a first-year calf to 7.45 m for the largest adult male (Table 1).

Table 1. Length and age data by sex for 78 northern resident killer whales with ≥ 3 photogrammetry measurements. Total length (TL) was derived by combining the flattest (max.) of the total number (n) snout to dorsal fin (SNDF) and dorsal fin to fluke (DFFL) measurements for each individual. Sex (F: female; M: male; U: unknown) and age from Towers et al. (2015), assuming a February 1 birth date

Whale ID	Birth year	Age (yr)	Sex	n SNDF	n DFFL	TL (max.)	Whale ID	Birth year	Age (yr)	Sex	n SNDF	n DFFL	TL (max.)
A69	1997	20.5	F	21	15	5.79	A103	2013	3.5	U	19	17	3.91
I63	1990	24.5	F	11	11	5.60	I145	2014	3.5	U	22	11	4.36
G51	1992	25.5	F	13	7	5.77	A108	2014	3.5	U	24	15	4.05
I68	1991	26.6	F	11	13	5.97	G105	2013	4.5	U	6	6	4.30
G48	1990	27.5	F	7	3	5.74	A106	2013	4.5	U	14	12	4.50
I65	1990	27.5	F	25	21	6.24	I137	2012	5.5	U	4	3	4.44
A54	1989	28.6	F	16	15	5.78	G104	2012	5.5	U	14	4	4.13
I51	1986	31.5	F	21	18	6.21	A101	2012	5.6	U	18	17	4.20
C13	1985	32.5	F	9	9	5.77	C30	2009	6.5	U	7	10	4.08
G37	1984	33.5	F	14	15	5.92	A99	2011	6.6	U	21	14	4.96
A50	1984	33.5	F	18	17	5.77	G93	2010	7.5	U	4	3	4.62
A43	1981	36.5	F	21	21	5.60	A95	2009	8.5	U	14	10	5.21
A42	1980	36.5	F	19	16	5.82	I128	2009	8.5	U	15	9	5.08
I4	1980	37.5	F	15	9	6.06	C29	2009	8.5	U	6	3	4.92
G22	1979	38.5	F	21	11	5.93	I129	2009	8.5	U	40	35	4.25
I35	1974	43.5	F	13	9	6.49	G92	2009	8.5	U	12	9	5.08
I13	1974	43.5	F	4	8	6.22	A88	2008	8.5	U	11	12	4.35
I27	1974	43.6	F	21	18	5.86	G86	2008	9.5	U	12	6	4.45
C10	1972	45.5	F	15	13	6.28	C28	2007	10.5	U	7	5	4.89
G20	1972	45.5	F	8	7	6.14	I122	2007	10.6	U	23	17	5.59
I16	1969	48.5	F	32	23	6.51	G81	2006	11.5	U	8	3	6.04
G3	1957	60.5	F	17	16	6.23	I103	2003	11.5	U	11	11	4.60
I76	1997	20.5	M	14	4	6.57	G80	2006	11.5	U	8	10	5.28
A66	1996	20.5	M	14	9	6.65	A86	2006	11.5	U	18	14	5.65
I77	1997	20.6	M	29	23	6.35	A85	2005	12.5	U	9	6	4.84
A61	1994	23.5	M	19	9	6.81	A79	2004	12.5	U	13	13	5.67
A60	1992	25.5	M	19	14	6.80	A84	2005	12.6	U	17	12	5.60
G39	1986	31.5	M	8	4	6.51	C26	2004	13.5	U	7	10	5.96
G32	1982	35.5	M	19	15	6.76	I106	2004	13.5	U	22	15	5.96
A37	1977	37.5	M	11	10	6.87	G73	2004	13.5	U	6	8	6.06
A38	1971	44.5	M	15	9	7.45	I107	2004	13.5	U	24	14	4.93
G114	2017	0.5	U	12	13	2.90	I102	2003	14.5	U	17	16	5.89
I153	2016	0.6	U	9	11	2.42	I104	2002	15.5	U	11	9	5.69
I154	2016	1.5	U	16	12	3.45	I98	2002	15.5	U	25	15	6.37
A113	2016	1.5	U	19	15	3.92	A75	2002	15.6	U	16	16	5.82
I146	2014	3.5	U	5	7	4.08	G69	2001	16.5	U	15	14	5.63
A109	2014	3.5	U	17	14	4.87	G63	1999	18.5	U	3	4	5.79
G108	2014	3.5	U	7	9	4.26	A72	1999	18.6	U	17	16	5.65
G107	2014	3.5	U	6	8	4.00	C23	1998	19.5	U	13	11	6.02

The change point model was fit to the length data for 22 females and 9 males over 20 yr of age (20.5–60.5 yr for females and 20.5–44.5 yr for males; Fig. 3, Table 1) and estimated a likely change point between 40 and 41 yr of age (95% probability interval [PI] = 36–44 yr). For whales younger than the change point, the average total length for females was 5.85 m (95% PI = 5.74–5.96 m) and for males 6.70 m (95% PI = 6.56–6.85 m), increasing by an estimated step magnitude of 0.44 m (95% PI = 0.25–0.62 m) after the change point to average sizes of 6.28 m (95% PI = 6.07–6.44 m) and 7.14 m (95% PI = 6.91–7.35 m), respectively. The model selection procedure estimated

a high probability ($p = 0.99$) of selecting the change point model compared to the base model with no change in the sex-specific average lengths. This was supported by the residual standard deviation, which was lower around the change point model (0.21 vs. 0.29).

4. DISCUSSION

These analyses provide strong support for a change in the adult length of NRKWs that grew in recent decades compared to older whales that are still alive.

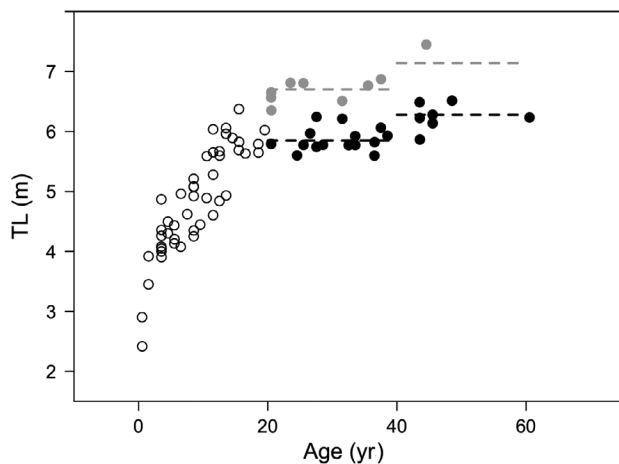


Fig. 3. Plot of total length (TL) against known age for 78 individual northern resident killer whales (22 females, black circles; 9 males, gray circles; 47 unknown sex and/or <20 yr of age, open circles). Also plotted are the medians of the posterior distributions for the estimated average sizes of both males and females before and after a change point estimated at 40 to 41 yr of age by a Bayesian model fit to whales >20 yr of age

Specifically, adult whales that are 20 to 40 yr old have significantly shorter body lengths than those >40 yr of age, which are typically ~0.44 m longer. This pattern is driven primarily by the larger sample size of adult females but is consistent with the relatively large size of the single adult male over 40 yr old in this data set. These data suggest that these younger adults experienced relatively constrained growth during their maturing years (0–15 yr of age for females and 0–20 yr for males; Fearnbach et al. 2011), which align with notable declines in Chinook salmon returns in the 1990s (Ford et al. 2010). The growth period of younger adults also coincides with declines in the size and proportional abundance of older Chinook salmon in more recent decades (Ohlberger et al. 2018), particularly the older age classes (>2 yr) that are targeted by resident killer whales (Ford & Ellis 2006).

The reduced adult size of NRKWs <40 yr of age is similar to that found for SRKWs measured in 2008, when adult whales <30 yr of age were shorter on average than older adults (Fearnbach et al. 2011). These changes were documented at different ages (10 yr apart) for the 2 populations, which suggests this is unlikely to reflect continued somatic growth through life (see Fearnbach et al. 2011), which is further supported by evidence of asymptotic growth in captive killer whales (Williams et al. 2011). Rather, these shorter NRKWs were actually growing at the same time period as the shorter SRKWs, as the 2 sets of measurement data were collected 10 yr apart. This

supports the hypothesis of correlated food limitation in both NRKWs and SRKWs and highlights the significant long-term effects of nutritional stress in salmon-eating killer whales in the coastal eastern North Pacific. These photogrammetry measurements of free-ranging killer whales demonstrate that the aforementioned effects are not only acutely lethal (Ford et al. 2010) but also impact a larger number of individuals in the population. Non-lethal effects on condition and growth may help explain recent evidence of low reproductive success (Wasser et al. 2017) that—at least for the smaller SRKW population—is constraining recovery.

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