Kotik Chloe Meghan (Orcid ID: 0000-0002-1918-313X)
Fearnbach Holly (Orcid ID: 0000-0002-4599-3339)

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ARTICLE

Morphometrics of mammal-eating killer whales from drone photogrammetry, with comparison to sympatric fish-eating killer whales in the eastern North Pacific

Chloe Kotik[1,2] | John W. Durban[2,3] | Holly Fearnbach[2] | Lance G. Barrett-Lennard[4]

[1]University of California San Diego, La Jolla, California

[2]SR3 SeaLife Response, Rehabilitation, and Research, Des Moines, Washington

[3]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, California

[4]Ocean Wise Conservation Association, Vancouver, British Columbia, Canada

Correspondence

Chloe Kotik, 102 Florence Avenue, Arlington, MA 02476.

Email: chloe.kotik@gmail.com

Abstract

Aerial photogrammetry has provided increased power for monitoring the health of individuals in the endangered population of Southern Resident killer whales (SRKW, *Orcinus orca*) in the eastern North Pacific. These data have shown evidence of nutritional stress, with individual growth and body condition correlating with the availability of their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*). We used drones to derive similar but novel photogrammetry measurements from a sympatric population of mammal-eating Bigg's killer whales (BKWs) that has been increasing in abundance in recent decades. From 2014 to 2019 we photographed 95 individual BKWs in Canadian waters off Vancouver Island and US waters in the Salish Sea; we estimated asymptotic lengths of 6.4 m for adult females and 7.3 m for adult males, both longer than corresponding length estimates for SRKWs. As a proxy for body condition, we measured head width at a standardized distance behind the blowhole, expressed as proportion of the length between the blowhole and dorsal fin, and estimated that on average, all age/sex classes of BKWs were more robust than corresponding classes of SRKWs. These differences likely reflect divergent adaptive selection in these prey-specialist ecotypes, but may also partially indicate recent impacts of differential prey availability.

KEYWORDS

Bigg's killer whale, body condition, drone, growth, length-at-age, *Orcinus orca,* Resident killer whale, Transient killer whale, UAS, UAV

1 | **INTRODUCTION**

Data on the individual size and body condition of cetaceans provide insight on the most fundamental aspects of life history. Morphometric data can be used to estimate growth trends (Fearnbach et al., 2011; Read et al., 1993; Stewart, Durban, Knowlton, et al., 2021), energetic requirements (Fahlman et al., 2018; Fortune et al., 2013; Noren, 2011), and individual health (Christiansen et al., 2020; Fearnbach et al., 2018; Miller et al., 2012; Stewart, Durban, Fearnbach, et al., 2021). Historically, assessments of body size and condition in free-ranging cetaceans were dependent upon captures or strandings, however, in recent years drones have become a field standard for their applicability towards noninvasive aerial photogrammetry (Durban, Fearnbach, et al., 2015; Fiori et al., 2017).

Aerial photogrammetry, the derivation of measurements from aerial photographs, has previously been performed using conventional piloted aircraft (Fearnbach et al., 2011; Miller et al., 2012; Perryman & Lynn, 2002; Pitman et al., 2007), but drones are considerably smaller, quieter, and less expensive, allowing high resolution images to be collected from lower altitudes without disturbing study subjects. Additionally, drones may be safely flown from vessels in remote regions that are inaccessible to other aerial platforms (Dawson et al., 2017;

Durban, Fearnbach, et al., 2015). As such, drones provide safe, cost-effective, and powerful tools that are increasingly used to measure the growth and body condition of free-ranging cetacean populations (e.g., Christiansen et al., 2016, 2018, 2020; Dawson et al., 2017; Durban, Fearnbach, et al., 2015, 2021; Fearnbach et al., 2020; Groskreutz et al., 2019; Soledade Lemos et al., 2020; Stewart, Durban, Fearnbach, et al., 2021; Stewart, Durban, Knowlton, 2021).

Drone photogrammetry was first applied to cetaceans in a study of killer whales (*Orcinus orca*) off Vancouver Island, British Columbia, Canada (Durban, Fearnbach, et al., 2015), where two sympatric ecotypes exist: fish-eating "Resident" and mammal-eating "Bigg's" killer whales (BKWs), also known as "Transient" killer whales (Ford & Ellis, 1999). Although these ecotypes overlap in distribution, they exhibit pronounced ecological (Baird & Dill, 1995; Barrett-Lennard et al., 1996; Riesch et al., 2012) and genomic (Foote et al., 2016; Moura et al., 2014; Parsons et al., 2013) differences related to their dietary specializations, and may represent separate species (Morin et al., 2010). Within the Resident ecotype, two populations occupy the waters surrounding Vancouver Island: "Northern" and "Southern" Residents, which have historically aggregated in summer around northern and southern Vancouver

Island, respectively (Ford et al., 1996) to feed primarily upon Chinook salmon (*Oncorhynchus tshawytscha*; Ford & Ellis, 2006). The Southern Resident killer whale (SRKW) population, numbering 74 individuals as of July 15, 2022 (Center for Whale Research, https://whaleresearch.com), is listed as "Endangered" in both the United States and Canada. The availability of Chinook salmon has been identified as a key correlate with SRKW survival and fecundity (Ford et al., 2009a; Ward et al., 2009; Wasser et al., 2017), but remaining uncertainty over if and when SRKWs are nutritionally stressed (Hilborn et al., 2012) has constrained management actions.

Photogrammetry data have improved SRKW assessments by providing a greater sample of metrics compared to the small number of births and deaths observed each year, resulting in greater statistical power for detecting changes (Stewart, Durban, Fearnbach, et al., 2021). Specifically, declines in adult length (Fearnbach et al., 2011) and body condition (Stewart, Durban, Fearnbach, et al., 2021a) derived from aerial photogrammetry have been correlated with the decreased abundance of Chinook salmon and are hypothesized to represent the long- and short-term effects, respectively, of nutritional limitation. Groskreutz et al. (2019) further used drone-based photogrammetry to document correlated declines in adult length for the more

numerous Northern Resident killer whales. Here we extend this comparative approach by using drone photogrammetry to estimate the length, growth trends, and current body condition of BKWs for the first time. These data allow enhanced morphometric comparisons between the sympatric Resident and Transient ecotypes and may provide further context for interpreting the nutritional status of SRKWs.

While overlapping in distribution with Resident killer whales, BKWs in the eastern North Pacific do not feed on fish but instead consume a variety of marine mammal species, including both pinnipeds and cetaceans (Baird & Dill, 1995; Ford et al., 1998, 2007; Saulitis et al., 2000; Trites et al., 2007). Feeding at a higher trophic level exposes BKWs to extremely high levels of bioaccumulating anthropogenic pollutants (Ross, 2006) and they are listed as "Threatened" by the Department of Fisheries and Oceans in Canada (DFO, 2007). Nevertheless, the BKW population occupying the coastal waters of Southeast Alaska, British Columbia, and Washington State (designated as the "West Coast Transients") has been increasing in abundance by approximately 4% per year since the 1970s as a result of high recruitment and low mortality (Ford et al., 2007; Towers et al., 2019). This consistent population growth has contributed to relatively high abundances of BKWs in the region (currently

~350; Towers et al. 2019), contrasting with the small and declining population of SRKWs.

Morphometric measurements of length and weight were derived from four captured individuals of the West Coast Transient population of BKWs during live-capture events in the 1970s (Hoyt, 1981). However, the utility of these measurements is limited for inferring patterns of growth and body condition because precise age data were not available for this small sample. In contrast, we used aerial photogrammetry of BKWs to estimate length and body condition for a much larger sample of free-swimming whales and linked these measurements to whales of known age and sex in an established photo-identification catalog (Towers et al., 2019) to parameterize length-at-age relationships, describe patterns of growth, and estimate body condition for each age/sex class to provide a baseline for future monitoring. We compared these parameter estimates to those generated from corresponding data from SRKWs (Fearnbach et al., 2011, 2018) to directly compare the morphology of these populations, and herein discuss these differences in the context of evolutionary divergence and potential recent nutritional effects.

2 | METHODS

Aerial photographs of BKWs were collected during 13 3-week field

efforts from August 2014 to December 2019 (Table 1). Drone

flights were conducted in two regions: the coastal waters off

northern Vancouver Island, British Columbia, and the Salish Sea

region off Washington State (Figure 1). Flights followed the

methods described in Durban, Fearnbach, et al. (2015) and were

conducted from three different boat platforms: (1) an 8.2 m

fiberglass cabin cruiser (Durban, Fearnbach, et al., 2015) from

2014 to 2017; (2) a 9.4 m aluminum catamaran from 2018 to 2019;

and (3) a 7.3 m rigid-hulled inflatable boat in November 2019.

Two different models of drones were flown: the 22 in. (0.56 m)

wingspan Aerial Photographic Hexacopter (APH-22) and the 42 in.

(1.1 m) wingspan Aerial Photographic Octocopter (APO-42), both

from Aerial Imaging Solutions

(https://aerialimagingsolutions.com). Both drones were equipped

with mirrorless digital cameras and lenses of fixed focal length

sufficient to ensure no wide-angle distortion and water-level

pixel resolution of 2 cm or better (Durban, Fearnbach, et al.,

2015). Prior to 2017, the altitude of the aircraft was recorded

at 1 s intervals by an onboard pressure altimeter (Durban,

Fearnbach, et al., 2015); beginning in 2017 a more precise laser

altimeter was used (Dawson et al., 2017).

Each aerial image was examined by the author (CK) on a 27-

inch high-definition LED flat panel monitor using the ACDSee

photo management program (ACD Systems International Inc., Victoria, Canada). Photographed BKWs were matched to preexisting identifications in an established photo-identification catalog (Towers et al., 2019) via congenital differences in saddle patch pigmentation and acquired scar patterns. All photographs of identified BKWs were subsequently assessed for measurement quality; only photographs depicting individuals in flat and elongate surfacing orientation were selected. The freely available image processing program ImageJ (https://imagej.nih.gov/ij/) was used to generate length measurements in pixels (Figure 2). The steep surfacing angle of BKWs does not typically permit a single accurate measurement of total length; we instead collected two separate measurements of length: a snout to dorsal fin (SNDF) measurement from the tip of the rostrum to the anterior insertion of the dorsal fin, and a dorsal fin to fluke (DFFL) measurement from the anterior insertion of the dorsal fin to the central margin of the fluke notch (Figure 2). These measurements were typically from separate but sequential images when each respective body segment was flat and parallel to the water's surface. Total length (TL) estimates were derived by adding the maximum SNDF and DFFL values of an individual whale collected within a sampling period, as this could be assumed to represent the flattest

description of an individual (Groskreutz et al., 2019).

To estimate body condition, fatness behind the cranium was quantified by taking a measurement of head width (HW) at 15% of the longitudinal distance between the blowhole and the dorsal fin (BHDF). We expressed HW as a proportion of the BHDF, with both measured in pixels and taken from the same image, to standardize for differences in individual size. This same HW/BHDF index of condition has been measured for SRKWs, with data available from Fearnbach et al. (2018). The area behind the head has been shown to be a sensitive indicator of nutritional stress in cetaceans, which are known to mobilize postcranial adipose tissue when in poor condition (Bradford et al., 2012; Pettis et al., 2004); losses in the region cause emaciated killer whales to develop what is referred to as "peanut head" (Fearnbach et al., 2018, 2020). The HW/BHDF index was designed to quantify tissue loss in this region, and significant declines have been detected in emaciated SRKW individuals prior to death (Fearnbach et al., 2018). This measure is not as sensitive for detecting changes within individuals as the "eye patch ratio," which measures the divergence of the white eyepatches of killer whales (Fearnbach et al., 2020), but Residents and BKWs are known to have small phenotypic variations in eye patch pigmentation that could impact the eye patch ratio (Emmons et

al., 2019). The HW measure does not depend on pigmentation and has previously been used to compare killer whale ecotypes with known eye patch differences (Durban et al., 2021).

Pixel measurements of length were converted to the scale of the camera sensor using their ratio to the known size of the sensor (our micro 4/3 sensor was 4,608 pixels and 0.0173 m wide) and then scaled to real lengths using the altitude of the drone and the known focal length of the lens (scale = altitude/focal length). The average growth trends of BKWs were then estimated by fitting the Richard's growth curve model (Richards, 1959) to length-at-age data of males and females separately (following Fearnbach et al., 2011). Ages of individual BKWs were determined from the birth years provided in the most recent photo-identification catalog (Towers et al., 2019), which details over 60 years of birthing and sighting records. Ages were standardized by setting all birth dates to February 1 in the first year of life based on the established calving trends of Resident killer whales, with whom BKWs share many aspects of life history (Ford & Ellis, 1999; Olesiuk et al., 2005; Towers et al., 2019). Individual sex was also reported by Towers et al. (2019) and determined by the visual identification of secondary sexual characteristics in males (dorsal fin elongation and enlarged pectoral fins; Robeck & Monfort, 2006), genital

pigmentation patterns, or the birth of a calf. Additionally, the sexes of four younger animals were determined for the first time based on genital pigmentation patterns documented in our aerial images.

In cases where individuals were encountered more than once during the study period, length data were taken from the most recent period of sampling so that each individual was only represented once in the growth curve. This also preferentially selected later measurements that were associated with laser rather than pressure altimetry, as the error associated with the pressure altimeter (<1%) exceeded that associated with the laser (~0.1%; Dawson et al., 2017; Durban, Fearnbach, et al., 2015a). Individual length measurement variability is largely attributed to foreshortening of whales photographed when not elongating to maximum length (Fearnbach et al., 2011), therefore the data were further constrained to the maximum values associated with each length metric (SNDF and DFFL) for each individual in its most recent sampling period.

We used a formulation of Richard's growth curve implemented in package *drm* (Ritz & Strebig, 2016) in the R software environment for statistical computing (R Core Team, 2019). This describes length-at-age (*L*) as a function of an intercept (*c* = length at birth, age 0), asymptotic adult length (*d*), age in

years (*t*), the position of an inflection point relative to the asymptote (*e*), and free parameters adjusting the slope and inflection point, *b* and *f* (Richards, 1959):

$$L = c + \left(\frac{d-c}{1+\exp\{b[\log(t)]-\log(e)\}} \right)^{f}$$

The model was fitted separately to length-at-age data for each sex. To facilitate model fitting for males in the absence of measurements of younger individuals (minimum age >4 years), the intercept parameter *c* was fixed at the smallest length measured for a neonatal female calf in this study. The parameters of the model, specifically the asymptotic length and inflection point, were compared to estimates of the same parameters derived from SRKW length data presented by Fearnbach et al. (2011).

In order to assess body condition, the mean HW/BHDF ratio was calculated for each suitably photographed whale in each sampling period. Recognizing that this index of body condition can change with growth (Fearnbach et al., 2018), measured individuals were divided into the following age/sex classes based on reproductive and growth trends established herein as well as those already known (Fearnbach et al., 2011; Olesiuk et al., 2005; Towers et al., 2019): calf (0-3 years old), juvenile (3-10 years old), subadult (10-15 years old), adult female (15-

45 years old), adult male (15+ years), and senescent female (45+ years old). Unlike length-based metrics that are negatively biased by foreshortening and failure to elongate fully during surfacing, relative width measurements are affected by the degree of flexion in the individual. We therefore presented the HW/BHDF measurements as average values, both within individuals and for entire age/sex classes. Many whales were resighted during multiple sampling periods; if an individual was sampled multiple times within the age brackets of an age/sex class, HW/BHDF measurements were only represented from the most recent encounter, but individuals sampled across multiple age/sex classes were represented once in each. Individual HW/BHDF values for SRKWs presented in Fearnbach et al. (2018) were grouped into the same age and sex classes, allowing direct comparison to the BKW measures.

3 | RESULTS

A total of 97 drone flights were conducted over BKWs from 2014 to 2019 in the coastal waters off northern Vancouver Island, British Columbia, and in the Salish Sea region off Washington State (Table 1, Figure 1). Average flight duration was 12.2 min (maximum = 24.1 min, total 19.7 hr); average altitude during image capture was 37.6 m. BKWs were encountered on 30 different days in groups ranging from 1 to 25 individuals. These flights

yielded a total of 3,179 photogrammetry images from which 1,651 were deemed of sufficient quality for measurement of an identified individual whale. A total of 95 individuals were photographed. All were matched to known individuals in the existing BKW photo-identification catalog (Towers et al., 2019) and 91 of these were photographed in orientation and quality suitable for measurement. Forty-one (43%) of the animals were imaged during multiple sampling periods across the study. Both SNDF and DFFL measurements were available from flat images for 86 whales (39 estimated using pressure altimetry data, 47 using laser altimetry data). Sex was known for 67 of the measured individuals. SNDF and DFFL measurements were typically taken multiple times in the most recent sampling period of each animal (which was selected for growth curve modeling): median number of SNDF measurements per animal = 6, range 1–18; median number of DFFL measurements per animal = 2, range = 1–13.

Total length (TL) estimates (Table 2) of confirmed females ranged from 2.4 m for a first-year calf (T65A6) to 7.1 m for a 33-year-old (T123); TL of confirmed males ranged from 4.8 m for a 4-year-old (T49A4) to 8.3 m for a 38-year-old (T11A). Individuals of unknown sex were typically younger and smaller (photographed prior to the development of sexually diagnostic characteristics at the onset of maturity) and ranged from 2.9 m

(first-year calf T75B2) to 5.7 m (11-year-old T65A3). Adult female (ages 15+) BKW lengths ranged from 5.5 to 7.1 m (n = 26, median = 6.4 m) and adult male (ages 15+) BKW lengths ranged from 6.3 to 8.3 m (n = 12, median = 7.2 m). The fitted Richard's growth curve estimated asymptotic adult lengths of 6.4 m (standard error [SE] = 0.10) for females and 7.3 m (SE = 0.22) for male BKWs (Figure 3), for which a Z-test of differences yielded p < .0001. In contrast, SRKW adults measured in Fearnbach et al. (2011) only reached an asymptotic adult length of 6.0 m (SE = 0.1) in females and 6.9 m (SE = 0.2) in males. The estimated asymptotic lengths for both sexes of BKWs were longer than those of SRKWs (female Z-test, p = .003; male Z-test, p = .093).

BKW males reached asymptotic growth later than females; the Richards model estimated the age of physical maturity (at which growth begins to slow, indicated by a clear inflection point) at 14.2 years (SE = 2.8) in females and 18.4 years (SE = 2.3) in males (Figure 3; Z-test, p = .12). These estimates are consistent with established growth trends for SRKWs, which previously reported inflection points at 15 years (SE = 1.8) in females and 18 years (SE = 4.7) in males (Fearnbach et al., 2011). The ages of inflection for both males and females were similar between BKWs and SRKWs (Z-test, p = .53 for males, p =

.45 for females). Additionally, the estimated TL in the youngest
BKW measured (2.4 m in 0.3-year-old neonate T65A6) was
consistent with estimates of neonate length in SRKWs (2.7 m in
0.5-year-old neonate reported by Fearnbach et al., 2011).

The measured index of body condition (HW/BHDF; see Figure
2) was available for 81 Bigg's killer whales: 41 females, 27
males, and 13 of unknown sex. The average number of HW/BHDF
measures per whale was 3 (range = 1–12), and individual
measurement variability was low, with an average coefficient of
variation 3.5% (median 3.0%) for repeated measurements of the
same individual within a sampling period. Individuals were only
represented once, using the most recent encounter, within each
age/sex class, but five individuals were sampled and represented
in two age/sex classes. We found that HW/BHDF values of BKWs
differed across age/sex classes (ANOVA, p < .0001). Calves had
the highest average HW/BHDF values and adult females the lowest
(Table 3, Figure 4). The same pattern was evident in SRKWs
(ANOVA, p < .05, excluding senescent females with n = 1,
Fearnbach et al., 2018). Comparison between BKWs and SRKWs found
higher mean HW/BHDF values in all classes of BKWs (Z-test, p <
.0001 for all; Table 3); the difference was greatest when
comparing calves and least when comparing adult females.

4 | **DISCUSSION**

This is the first study estimating size, growth, and body condition of free-swimming Bigg's killer whales, an increasingly abundant apex predator in the eastern North Pacific. Prior to this study, morphometrics were only available from limited numbers of strandings and live captures (Bigg & Wolman, 1975; Hoyt, 1981; Raverty et al., 2020). We used aerial images taken using noninvasive drones to identify and collect photogrammetric measurements of 95 individual BKWs. Our sample represents over 27% of the known population of coastal West Coast Transient BKWs (Towers et al., 2019) and includes individuals ranging in age from neonate calves to mature adults of both sexes. As such, our data on length and body condition represent important baselines for future monitoring of individual health.

BKWs are listed as "Threatened" under the Species at Risk Act by the Department of Fisheries and Oceans in Canada, and they are subject to significant anthropogenic pressures in their coastal environment including habitat loss, acoustic and physical disturbance, and high levels of persistent bioaccumulating contaminants (DFO, 2007). Among these, polychlorinated biphenyls (PCBs) and polybrominated diphenyl ethers (PBDEs) occur at potentially dangerous levels in BKWs due to their feeding at the highest trophic levels (Ross, 2006; Ross et al., 2000). BKWs have been increasing in abundance since the

1970s (Ford et al., 2007; Towers et al., 2019), but we may expect the population to respond as it approaches carrying capacity, or as carrying capacity changes due to the impacts of environmental variation on BKW prey (Feddern et al., 2021). Photogrammetry measures of body condition for a large sample of individuals can provide greater power for detecting changes in population health compared to limited observation of births and deaths (Stewart, Durban, Fearnbach, et al., 2021) or uncertain estimates of demographic rates (Durban et al., 2022). Length estimates can also reveal sublethal effects on growth (Fearnbach et al., 2011; Groskreutz et al., 2019) that may have prolonged implications for individual survival and reproduction. As such, continued application of drone-based photogrammetry has utility for future monitoring of individual and population health.

A comparative approach to photogrammetry can be a useful framework to infer contrasting nutritional and/or energetic stress (Christiansen et al., 2020) as well as the effects of adaptive divergence between ecotypes or species (Durban et al., 2021). However, separating the two poses a challenge. Our study demonstrates that fundamental aspects of growth are similar between BKWs and SRKWs, including the length of neonates (Table 1; Fearnbach et al., 2011) and the estimated age of physical maturity (indicated by slowing growth) in both males and females

(Figure 3; Fearnbach et al., 2011). However, BKWs were longer than SRKWs, with female BKWs growing to an estimated asymptotic adult length of 6.4 m compared to 6.0 m in SRKWs, and adult male BKWs reaching an asymptotic length of 7.3 m compared to 6.9 m in SRKWs (Figure 3; Fearnbach et al., 2011). These differences confer large disparities in energetic requirements (Noren, 2011): a 7.3 m male BKW is projected to weigh 673 kg more than a 6.9 m male SRKW (Bigg & Wolman, 1975). Furthermore, even these calculations are based on a length versus mass relationship of Resident and Bigg's killer whales in a live-capture sample (which in turn was biased towards keeping smaller individuals), and do not necessarily account for the differences in body condition that we infer from our measurements of head width (HW) as a proportion of blowhole to dorsal fin length (BHDF). We found that average HW/BHDF values of every age/sex class of BKW measured were greater than corresponding values for SRKW reported in Fearnbach et al. (2018).

It is likely that the morphometric differences we detected between BKWs and SRKWs reflect diverging ecological selection in these ecotypes. Greater agility and smaller body sizes may be advantageous in fish-eating SRKWs, while BKWs may benefit from larger body sizes as they hunt larger and more formidable marine mammals. Phenotypic differences in the pigmentation of the

saddle patch and eye patch regions and the shape of the dorsal

fin (Baird & Stacey, 1988, Emmons et al., 2019) have previously

been reported for these ecotypes. Similarly, genomic signatures

of diet adaptation have been revealed between Resident and BKWs,

notably relating to differences in digestive requirements for

diets of different protein content (Foote et al., 2016). Most

relevant are differences in dentary bone and skull morphology of

the two ecotypes (Fung, 2016; Fung & Barrett-Lennard, 2004),

which are plausibly inferred to be the result of selection on

BKWs for efficient capture and processing of larger prey with

denser bones. The resultant differences in cranial shape may

explain some of the differences in our measurements of head

width; while the standardized measurement site at 15% of the

distance between the blowhole and the dorsal fin was designed to

measure variable width of soft adipose tissue deposits behind

the cranium (Fearnbach et al., 2018) rather than reflecting

cranial morphology, the differences in HW/BHDF we estimated

between these ecotypes may partially reflect differences in

cranial shape, structure, and musculature.

It is also plausible that the greater adult length and

HW/BHDF of BKWs may partially reflect differential prey

availability and body condition. SRKWs are specialized hunters

of salmon with a demonstrated preference for larger Chinook

salmon (Ford & Ellis, 2006; Ford et al., 2009b; Hanson et al., 2010). Declines in the availability of Chinook have been linked to decreased survival (Ford et al., 2009a), reproduction (Ward et al., 2009), body length (Fearnbach et al., 2011), and body condition (Stewart, Durban, Fearnbach, et al., 2021) in SRKWs over recent decades. Conversely, populations of marine mammal prey favored by BKWs have increased in abundance since protective laws were introduced in the US and Canada in the 1970s: harbor seal (*Phoca vitulina*), harbor porpoise (*Phocoena phocoena*), and California sea lion (*Zalophus californianus*) abundances have all increased throughout the range of the West Coast Transient BKWs (Ashley et al., 2020; Jefferson et al., 2016, 2021; Laake et al., 2018; Magera et al., 2013; Trites et al., 2007) and migrating gray whales (*Eschrichtius robustus*) have doubled in abundance over the same period (Durban, Weller, et al., 2015). We therefore suggest that the disparities in adult lengths of BKWs and SRKWs partially represent the longer-term impacts of differential prey availability, while the differences detected in body condition via HW/BHDF may represent short-term and current impacts. Notably, the adult lengths of male and female BKWs were both 0.4 m greater than those of SRKWs, corresponding with recent 0.4 m and 0.3 m declines in the adult lengths of Northern and Southern Resident killer whales,

respectively (Fearnbach et al., 2011; Groskreutz et al., 2019),

which were in turn correlated with declining Chinook salmon

availability in recent decades. Our comparisons of body

condition between age/sex classes may also offer a plausible

link to nutritional status: in both BKWs and SRKWs the leanest

condition was measured in adult females, while calves were the

most robust. While the comparatively poorer condition of adult

females to adult males may be indicative of potential sexual

dimorphism in the cranial region, it is also likely

representative of the bioenergetic demands of reproduction and

lactation on females, while the better condition of calves may

reflect the benefit of lactation (Fearnbach et al., 2018). The

variation of condition within each ecotype and the similar

trends of condition between the ecotypes provide some evidence

that the HW/BHDF estimate may be interpreted in the context of

nutrition. Future monitoring of the growth and body condition of

BKWs relative to indices of prey availability will help

elucidate the extent to which these morphological features are

determined in the short- and medium-term by nutrition relative

to the longer-term effects of their adaptation as prey

specialists (Stewart, Durban, Fearnbach, et al., 2021), but the

novel data presented herein provide a foundation for continued

morphological assessment and comparison of killer whale ecotypes

in the eastern North Pacific Ocean.

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TABLE 1 Details of drone flights conducted over Bigg's killer whales in two main regions: the coastal waters off northern Vancouver Island (NVI), British Columbia, Canada, and the Salish Sea (SS) off Washington State (see Figure 1).

Year	Month	Location	Flights	Whales	Flight time (min)	Mean altitude (m)	Drone
2014	8	NVI	3	6	39.38	36.73	APH 22
2015	8	NVI	21	21	218.47	39.52	APH 22
2015	9	SS	1	6	9.92	40.09	APH 22
2016	5	SS	20	22	258.57	43.30	APH 22
2016	8	NVI	8	16	101.07	36.08	APH 22
2016	9	SS	4	7	42.52	37.43	APH 22
2017	5	SS	10	10	92.93	33.44	APH 22
2017	8	NVI	9	15	101.73	33.21	APH 22
2017	9	SS	7	12	69.27	32.96	APH 22
2018	5	SS	10	29	169.25	38.60	APO 42
2018	9	SS	1	5	23.75	36.20	APO 42
2019	5	SS	2	8	33.02	38.34	APO 42
2019	9	SS	1	4	23.32	43.69	APO 42

TABLE 2 Sampling details of 86 individual Bigg's killer whales (41 females, 26 males, 19 of unknown sex), all taken from each individual's most recent sampling period. Maximum total length (TL) was derived by combining the maximum snout to dorsal fin (SNDF) and dorsal fin to fluke (DFFL) values measured within that sampling period.

Whale ID	Year	Month	Sex	Altimeter type	Age (years)	Max TL (m)	*N* SNDF	*N* DFFL
T65A6	2018	6	F	Laser	0.3	2.4	6	5
T124A2B	2017	5	F	Laser	1.3	4	2	2
T49A5	2018	6	F	Laser	1.3	3.4	4	1
T86A4	2018	5	F	Laser	2.3	4.1	2	1
T60F	2015	8	F	Pressure	3.5	4	2	1
T36A2	2016	5	F	Pressure	4.3	4.2	3	2
T123C	2018	5	F	Laser	6.3	4.9	11	7
T86A3	2018	5	F	Laser	7.3	5	3	1
T65A4	2018	6	F	Laser	7.3	4.9	15	2
T90C	2019	5	F	Laser	9.3	5.6	7	2
T137B	2016	8	F	Pressure	10.6	5.9	5	6
T100E	2019	9	F	Laser	10.6	5.4	6	3
T36A1	2016	5	F	Pressure	11.3	6	5	1
T124A3	2017	5	F	Laser	11.3	5.9	11	7
T69D	2015	8	F	Pressure	14.5	5.9	1	2
T124A2	2019	5	F	Laser	18.3	6.4	11	3
T59A	2015	8	F	Pressure	20.5	5.7	7	1
T75B	2015	9	F	Pressure	20.6	5.5	4	2
T124A1	2017	5	F	Laser	21.3	6.6	10	8
T65B	2017	9	F	Laser	24.6	6.4	7	3
T49B	2017	9	F	Laser	25.7	6.5	3	3
T36A	2016	5	F	Pressure	26.3	6.1	12	8
T41A	2016	8	F	Pressure	28.6	6.9	2	2
T69A	2017	8	F	Laser	28.6	6.3	11	9
T86A	2018	5	F	Laser	30.4	6.3	7	2
T99	2016	5	F	Pressure	32.3	6.4	9	2
T65A	2018	6	F	Laser	32.4	6.7	18	2
T49A	2018	6	F	Laser	32.4	6.4	5	2
T137	2016	8	F	Pressure	32.6	6.1	8	6
T123	2018	5	F	Laser	33.3	7.1	7	5

T124A	2017	5	F	Laser	33.3	6.6	14	9
T7B	2016	8	F	Pressure	34.6	6.1	9	3
T2B	2014	8	F	Pressure	35.6	6.6	3	3
T60	2016	9	F	Pressure	36.6	6	8	6
T90	2019	5	F	Laser	39.3	6.8	10	3
T58	2015	8	F	Pressure	39.6	5.5	6	2
T100	2019	9	F	Laser	40.7	6.3	3	2
T69	2017	8	F	Laser	43.6	6.7	12	2
T59	2015	8	F	Pressure	45.6	6.1	5	2
T11	2016	5	F	Pressure	52.3	6.3	8	6
T10	2016	8	F	Pressure	52.6	6	2	2
T49A4	2018	6	M	Laser	4.3	4.8	6	4
T65A5	2018	6	M	Laser	4.3	4.7	3	2
T65B1	2016	5	M	Pressure	5.3	4.2	4	1
T124A2A	2019	5	M	Laser	6.3	5	10	2
T49A3	2018	6	M	Laser	7.3	5.6	5	2
T60E	2016	9	M	Pressure	8.6	4.3	7	5
T49A2	2018	6	M	Laser	11.3	5.8	7	3
T7B3	2016	8	M	Pressure	11.5	6.3	6	1
T69A2	2017	8	M	Laser	11.6	5.6	2	2
T60D	2016	9	M	Pressure	12.6	4.5	11	7
T90B	2018	9	M	Laser	12.6	7	10	4
T60C	2014	8	M	Pressure	13.6	7.4	4	1
T65A2	2018	6	M	Laser	14.3	7	10	5
T137A	2016	8	M	Pressure	14.6	6.5	2	2
T10C	2015	8	M	Pressure	16.5	6.7	8	5
T49A1	2018	6	M	Laser	17.3	7.1	4	1
T100C	2019	9	M	Laser	17.6	7.2	2	2
T123A	2018	5	M	Laser	18.3	7.5	11	1
T77A	2017	5	M	Laser	21.3	7.2	3	2
T101A	2018	5	M	Laser	25.3	7.6	4	2
T10B	2015	8	M	Pressure	32.5	6.7	6	1
T97	2016	5	M	Pressure	36.3	6.3	8	3
T11A	2016	5	M	Pressure	38.3	8.3	12	3
T54	2015	8	M	Pressure	43.6	7.4	8	3
T93	2016	5	M	Pressure	52.3	7.5	11	1
T87	2019	5	M	Laser	57.3	7.1	3	2
T75B2	2015	9	U	Pressure	0.6	2.9	2	2
T99D	2016	5	U	Pressure	1.3	3.8	4	1
T69A4	2017	8	U	Laser	1.6	3.8	6	10
T7B5	2016	8	U	Pressure	2.1	3.9	7	6
T90D	2019	5	U	Laser	2.3	4.1	4	5
T59A3	2015	8	U	Pressure	2.5	3.5	3	1

T100F	2018	5	U	Laser	4.3	3.9	5	5
T137D	2016	8	U	Pressure	4.6	4.2	7	5
T49B3	2017	9	U	Laser	4.6	4.2	2	3
T59A2	2015	8	U	Pressure	6.5	3.9	3	3
T7B4	2016	8	U	Pressure	6.5	4.8	4	2
T69A3	2017	8	U	Laser	6.6	4.6	6	1
T124A4	2017	5	U	Laser	7.3	5.3	12	13
T69F	2017	8	U	Laser	7.6	5.4	3	1
T49B2	2017	9	U	Laser	7.6	4.7	2	2
T99B	2016	5	U	Pressure	9.3	4.6	2	6
T59A1	2015	8	U	Pressure	9.5	5	9	5
T65A3	2018	6	U	Laser	11.3	5.7	3	3
T69E	2017	8	U	Laser	13.6	5.5	10	8

TABLE 3 Mean (*M*) HW/BHDF values (with standard deviation, *SD*) for six age/sex classes of Bigg's killer whale (BKW) and Southern Resident killer whale (SRKW, data from Fearnbach et al., 2018). Also displayed are the number of individuals measured in each class (*N*) and *p*-values (*p*) for *Z*-tests of difference in HW/BHDF between corresponding age/sex classes of the two populations (excluding senescent females, as only a single SRKW from this class was measured).

| Class	Age (years)	BKW *N*	BKW *M* HW/BHDF (*SD*)	SRKW *N*	SRKW *M* HW/BHDF (*SD*)	*p*
Calf	0–3	10	0.55 (0.03)	6	0.47 (0.02)	<.0001
Juvenile	3–10	23	0.53 (0.04)	13	0.46 (0.03)	<.0001
Subadult	10–15	13	0.51 (0.04)	14	0.46 (0.03)	<.0001
Adult male	15+	14	0.52 (0.02)	9	0.46 (0.02)	<.0001
Adult female	15–45	21	0.48 (0.02)	21	0.44 (0.02)	<.0001
Senescent female	45+	5	0.48 (0.02)	1	0.41 (NA)	NA

FIGURE 1 Locations of drone flights over Bigg's killer whales in the coastal waters off Vancouver Island, British Columbia, Canada, and the Salish Sea region off Washington State.

FIGURE 2 Aerial images of Bigg's killer whale T36A showing pixel length measurements for snout to dorsal insertion (SNDF), dorsal insertion to fluke notch (DFFL), head width (HW), and blowhole to dorsal fin (BHDF).

FIGURE 3 Total length (TL, in meters) estimates of 41 confirmed female (red) and 26 confirmed male (blue) Bigg's killer whales plotted against known age of individual. The fitted Richard's growth curves are plotted for each sex (females in red, males in blue), with shaded regions representing 95% confidence intervals for the model fit.

FIGURE 4 Head width (HW) at 15% of the distance between the blowhole and the dorsal fin (BHDF), expressed as a proportion of BHDF, for 81 individual Bigg's killer whales: 41 females (ranging in age from 0.3 to 52.6 years, in red), 27 males (ranging in age from 1.3 to 57.3 years, in blue), and 13 of unknown sex (ranging in age from 1.5 to 13.6 years, in gray). Points represent the mean values of each individual in each sampling period. Vertical lines delineate age/sex classes: 0–3 years (calf), 3–10 years (juvenile), 10–15 years (subadult), 15+ years (adult male), 15–45 years (adult female), and 45+ years
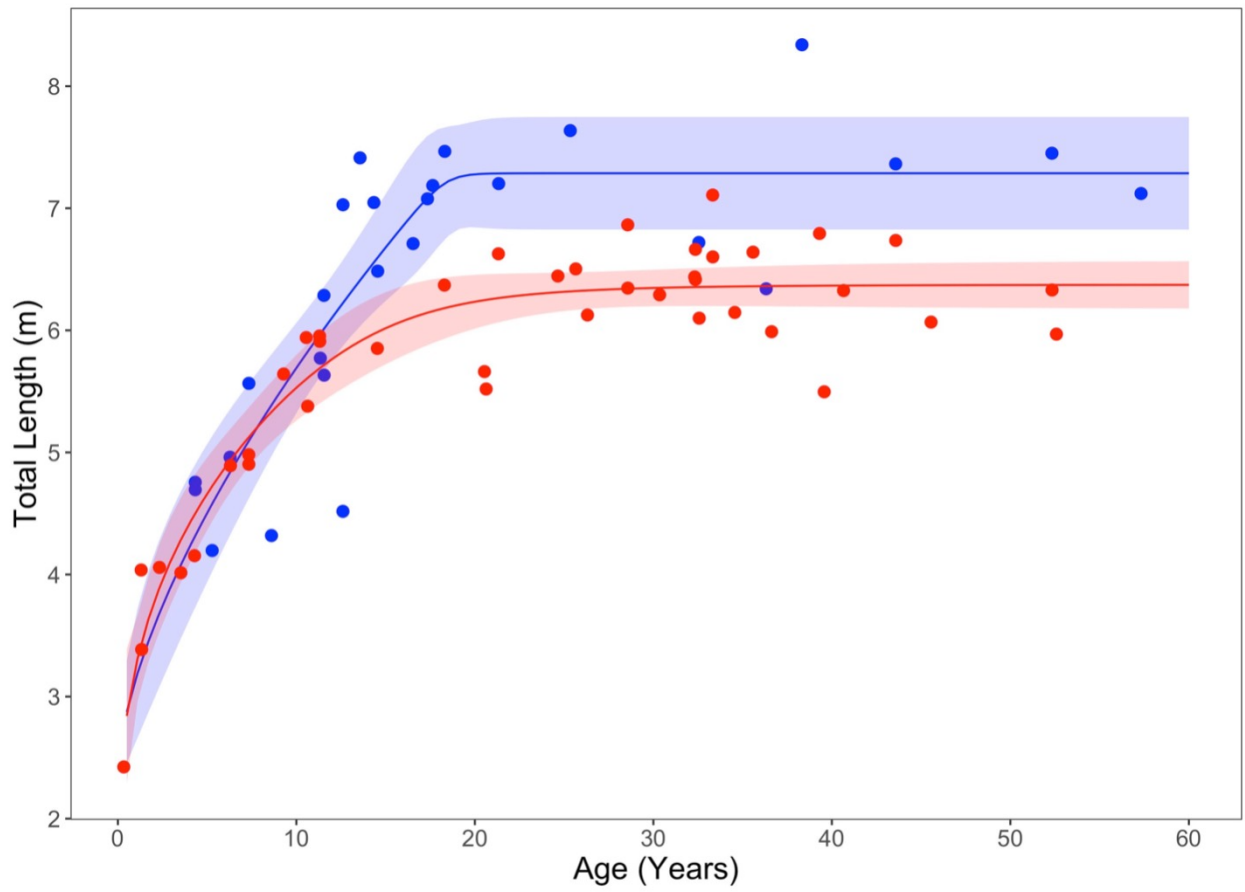
(senescent female) (Fearnbach et al., 2011; Olesiuk et al.,
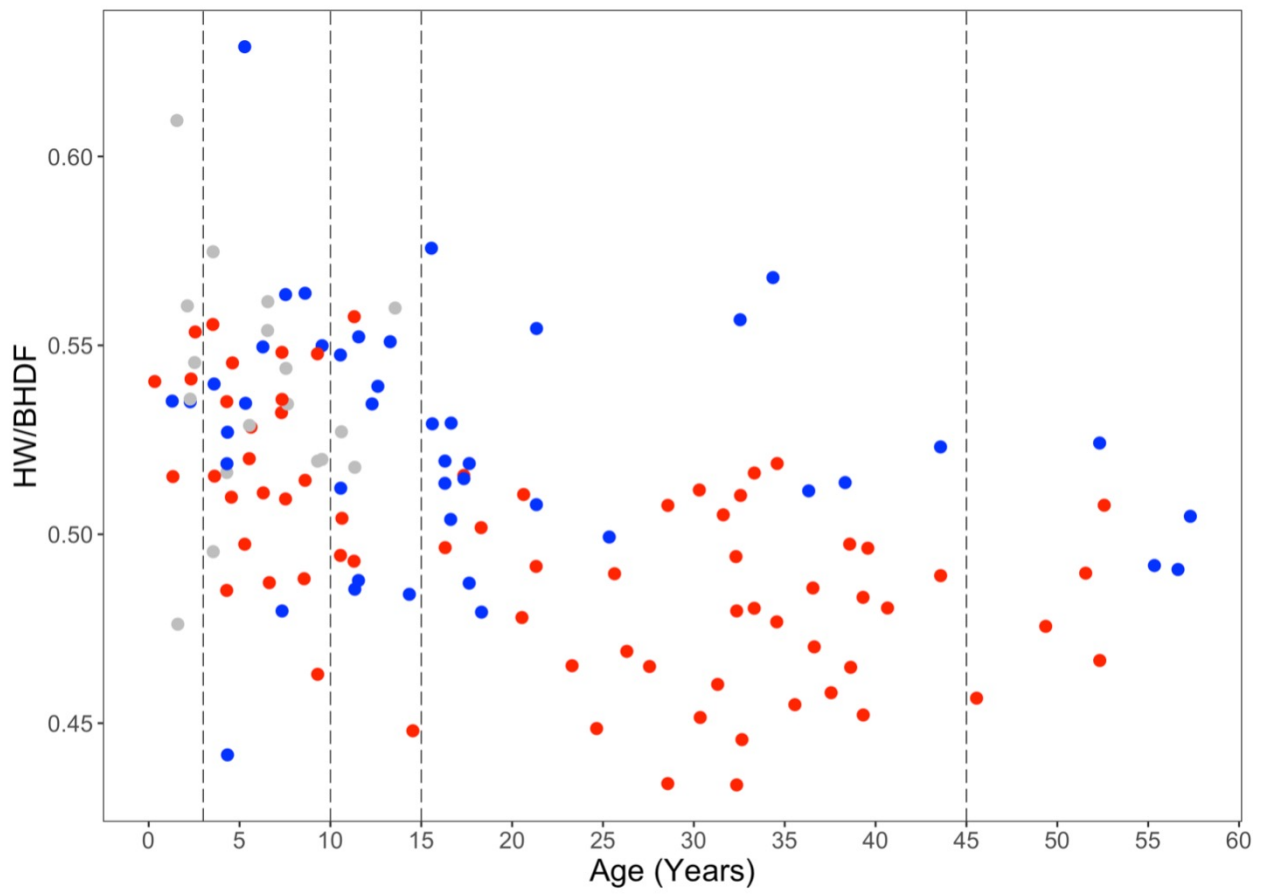2005; Towers et al., 2019).
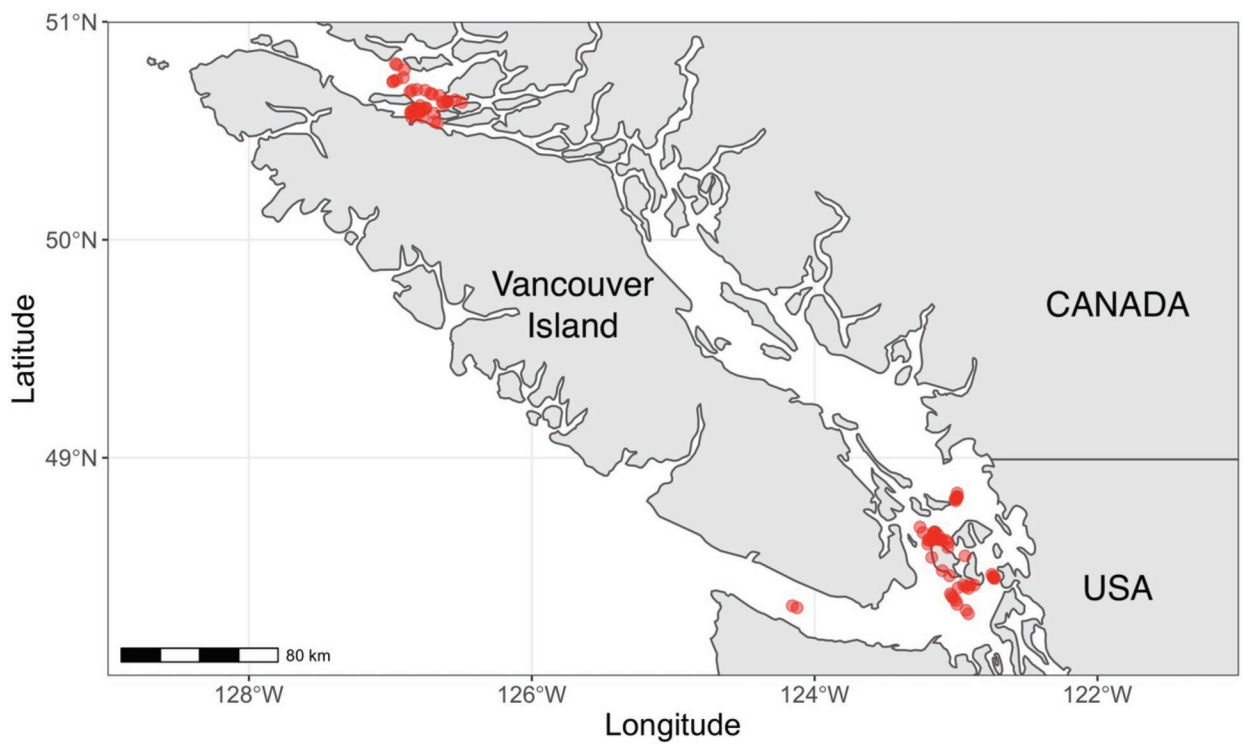
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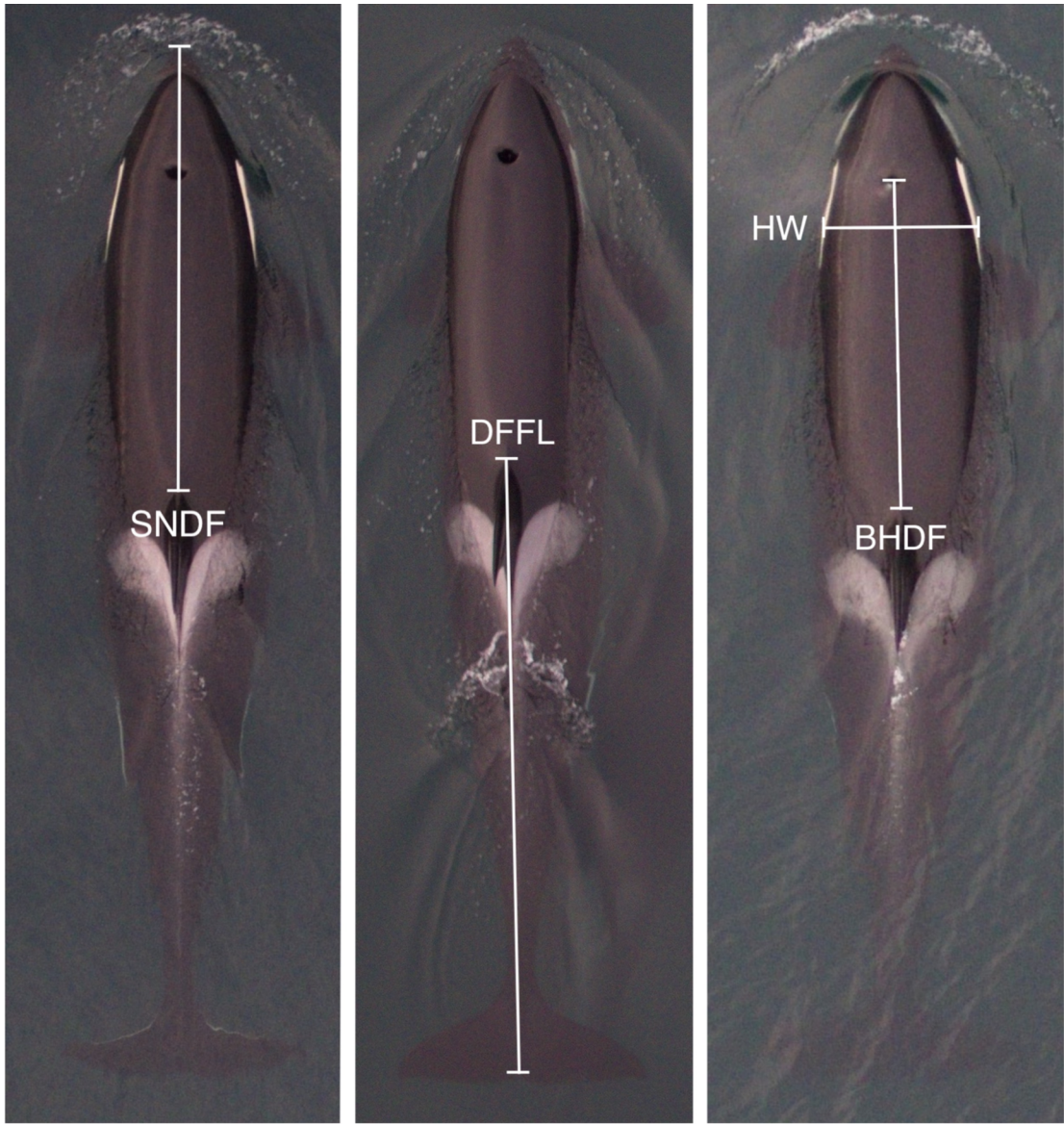
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