

# Variability in Body Condition and Growth Rates for Rehabilitated Harbor Seal (*Phoca vitulina*) Pups

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## Abstract

In the United States, Canada, and Europe harbor seal (*Phoca vitulina*) pups are commonly rehabilitated after stranding and then released. Size at release is likely important to post-release survival; however, data have not been compiled to track the body condition of rehabilitated harbor seals at release across the U.S. To better understand spatiotemporal variations in harbor seal morphometrics during rehabilitation and at release, this study retrospectively analyzed body conditions, weights, lengths, and growth rates of rehabilitated harbor seal pups in the U.S. Body condition index (BCI) was calculated, and weight and BCI were modeled regionally and temporally. There was significant variation in weight, length, BCI, and growth rate for rehabilitated and released seals between the East and West Coasts of the U.S. and among different years. Growth rates during rehabilitation were slower than reported for wild pups from birth to weaning. Length at release was not a strong predictor of weight. Because animals of similar weights can have different lengths, weight alone might not be the best criterion for pre-release body condition. A body condition score incorporating weight, length, and possibly other variables such as age or axillary girth could be more informative; however, data on post-release survival are needed to evaluate these options.

**Key Words:** body condition index, growth, harbor seal, *Phoca vitulina*, length, rehabilitation, weight

## Introduction

In the United States, Canada, and Europe, harbor seal (*Phoca vitulina*) pups that strand are commonly rehabilitated and then released (Lander et al., 2003; Frouin et al., 2013; Salazar-Casals

et al., 2019). The goal of rehabilitation is to release healthy animals that survive and behave like wild animals. The accumulation of significant subcutaneous fat prior to weaning allows seal pups to sustain themselves while they learn to successfully forage in the wild (Harding et al., 2005; MacRae et al., 2010). The same is true for rehabilitated seals such that facilities aim to release harbor seal pups at optimal body condition (highest relative fat reserves) to provide the best chance for survival. However, release facilities do not use standard metrics to assess body condition nor do they have standard body condition criteria for release.

Weight is a commonly used proxy for fat reserves in pinnipeds. As summarized by MacRae et al. (2010), a positive association between weaning weight and survival has been documented in pinnipeds, including northern fur seals (*Callorhinus ursinus*; Baker & Fowler, 1992), southern elephant seals (*Mirounga leonina*; McMahon et al., 2000), and grey seals (*Halichoerus grypus*; Hall et al., 2001). For harbor seal pups, greater mass at weaning may prevent subsequent emaciation and malnutrition—primary threats to first-year survival (Steiger et al., 1989; Huggins et al., 2013; Ashley et al., 2020). Fat reserves help to counteract the effects of a post-wean fast as wild harbor seal pups lose 21% of their body mass by 5 weeks post-weaning while they learn to forage (Muelbert & Bowen, 1993). Loss of body mass may be greater for rehabilitated harbor seals post-release as they spend more time in the water (Lander et al., 2002), travel more, and disperse farther than their wild counterparts (Gaydos et al., 2012; Sangster et al., 2020). Harding et al. (2005) found that wild, 4-month-old harbor seals in Sweden that weighed 32 kg by their first autumn had a 96% chance of surviving the winter, while a pup weighing 17 kg at 4 months of age only had a 63% chance of survival. Greig et al. (2019) found that, in central California, increased mass was correlated

with greater survival probability for both wild and rehabilitated, recently weaned harbor seal pups; for rehabilitated pups specifically, mass at the time of release was the best predictor of survival. Using duration of satellite transmission post-release as a proxy for survival, Sangster et al. (2020) found that the annual cohort of rehabilitated pups in the Salish Sea with the greatest release weights had the longest post-release survival, although there was no overall interannual correlation between mass and duration of transmission. Also in the Salish Sea, Horning et al. (2017) recorded transmission durations (indicating survival) of at least 9 months for four rehabilitated harbor seals weighing at least 30 kg at release, which is larger than the minimum release weight recommendation of 22 kg that has been established for some rehabilitation facilities in this region (Gaydos et al., 2012; Sangster et al., 2020).

While weight influences post-release survival, considering weight alone might not provide an ideal approximation of fat reserves because it does not incorporate the skeletal dimensions of a seal. Seals of similar weights but different lengths may have different quantities and distributions of fat reserves. Estimating body condition, or relative energy storage, may be a more reliable proxy to assess a seal's nutritional condition. Various body condition indices have been applied to phocids such as the body condition index (BCI) calculated by  $(\text{mass} \times 100)/\text{length}$  (e.g., Lander et al., 2003) or  $\text{mass}/\text{length}$  (e.g., Boveng et al., 2020). Other studies have incorporated axillary girth to measure body condition—for example,  $(\text{axillary girth} \times 100)/\text{length}$  (McLaren, 1958; Ryg et al., 1990). Similarly, Smirnov (1924) defined the degree of fatness of harp seals (*Pagophilus groenlandicus*) as maximum girth divided by body length. Blubber depth has also been incorporated into condition indices of harbor seals (Trumble & Castellini, 2002; Mellish et al., 2007)—for instance, Rosen & Renouf (1997) calculated the ratio of blubber depth to body radius. Ryg et al. (1990) estimated blubber content with the “LMD index” that incorporated standard length (L), body mass (M), and xiphosternal blubber thickness (d). Neale et al. (2004) described a condition index which assumes that harbor seal body mass, a three-dimensional parameter, increases proportionally to the cube of straight length (SL) to avoid age-related differences between juveniles and adults.

It is possible that harbor seals in rehabilitation are released at body conditions that differ from their wild, weaned counterparts. In the Salish Sea, wild harbor seal pups gain on average  $0.394 \pm 0.026$  kg/d and are weaned at a mean of  $23.6 \pm 1.2$  kg (Cottrell et al., 2002). In the same region, rehabilitated harbor seal pups gain less weight on average, with estimates ranging from 0.18 kg/d (Cole & Fraser, 2021) to 0.043 to 0.123 kg/d

(MacRae et al., 2010) to 0.21 kg/d (Briese et al., 2012). Seals in this region are released after meeting a variety of criteria which, for some facilities, includes reaching a minimum weight of 22 kg (Gaydos et al., 2012; Sangster et al., 2020). However, because seals in rehabilitation gain weight slower and therefore take longer to achieve this minimum weight, but continue to gain length with age, rehabilitated seals being released at weights close to those of wild, weaned seals could be longer and, therefore, in lesser body condition (e.g., weight to length ratio). Closely examining the body condition of rehabilitated harbor seals at the time of release is the first step before rehabilitation facilities can consider pre-release body condition criteria.

Marine mammal rehabilitation facilities in the U.S. are authorized to respond to and provide care for marine mammals through an agreement with the National Marine Fisheries Service (NMFS) under the Marine Mammal Protection Act. Day-to-day activities in rehabilitation centers, including feeding, handling, and husbandry, are conducted following nationally standardized minimum criteria for rehabilitation facilities (Whaley & Borkowski, 2009). Additionally, there are national standardized criteria that animals must meet prior to release (Whaley & Borkowski, 2009). The national criteria require an assessment by the attending veterinarian that the animal is releasable and meets the outlined developmental, behavioral, and medical clearance standards, including the ability to self-feed, an absence of significant physical deformities, and normal parameters of blood counts and serum chemistry. In some locations, additional criteria need to be met (Gaydos et al., 2012). The national criteria do not include a minimum weight or body condition; however, many individual facilities have their own standards for release (Gaydos et al., 2012; Fonfara et al., 2016; Sangster et al., 2020).

Despite the importance of size and condition at release to post-release survival, the morphometrics for rehabilitated and released harbor seals in the U.S. have not been studied in detail. This information is critical to provide rehabilitation facilities with reference data necessary to maximize post-release survival. In this study, we retrospectively examine metrics of rehabilitated and released harbor seal pups in the U.S. with the goals to (1) identify interannual and interregional changes in intake and release weights, body conditions, and growth rates; (2) compare the morphometrics of rehabilitated seals to their wild counterparts; and (3) determine whether two commonly used metrics of nutritional status—weight and BCI—could be more informative for optimizing release condition. We hypothesized that the size and condition

of harbor seals at release varies by year and region, and might differ from their wild counterparts. This investigation was conducted to improve our understanding of variability in harbor seal size and condition at release to inform potential future efforts in creating standardized body condition metrics that would optimize post-release survival.

## Methods

Data on harbor seal weight and length during rehabilitation were obtained from the National Oceanic and Atmospheric Association (NOAA)'s Marine Mammal Health and Stranding Response database (requested data were extracted from the database on 12 February 2021). This query resulted in 2,404 cases of harbor seals that were admitted into rehabilitation as pups between 1 January 2005 and 31 December 2020, were alive from admission until release, were rehabilitated and released on the East Coast (Connecticut, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, North Carolina, Rhode Island, and Virginia) or continental West Coast (Washington, Oregon, and California), and had complete data. Complete data included date admitted into rehabilitation, date released from rehabilitation, straight length (cm) at admission and release, and weight (kg) at admission and release. Other measures of size or body composition (e.g., girth, blubber depth, percent fat) are not reported in this database and, thus, were not considered. The start date for rehabilitation (hereinafter referred to as "intake") was the date an animal was admitted to a care facility, including triage facilities. Dates when animals were transferred to other facilities were included as part of the duration of time in rehabilitation, consolidating intake and release morphometrics for transferred seals into a single case report (removing 663 duplicate records). Cases were removed in which seals had a lower weight or length at release than at intake or had a weight gain of 0 kg during rehabilitation because these cases did not inform growth in rehabilitation, and data may have been erroneous (120 records). Cases in which seals had a length gain of 0 cm during rehabilitation were not removed due to the challenges in measuring an accurate straight length as seals tend to retract or extend their necks during measurement. For each animal, average daily weight gain (total weight gain [kg]/number of days in rehabilitation), average daily length gain (total length gain [cm]/number of days in rehabilitation), and BCI (weight (kg)  $\times$  100/length [cm]) were calculated (Lander et al., 2002).

We attempted to limit analyses to pups that were pre-weaned at intake, meaning pups that were less than 6 weeks old and were maternally dependent (requiring nursing and not consuming fish) as

determined by morphometrics, presence of umbilicus, number of teeth erupted, and/or presence of lanugo coat (Muelbert & Bowen, 1993; Cottrell et al., 2002; Cole & Fraser, 2021). For some cases, data about umbilicus, teeth, and/or lanugo were provided and confirmed the pre-weaned age class; but for many cases, morphometrics were the only data available. Because the database query for harbor seals admitted at age class "pup" could not discern between pre-weaned or weaned pups, multiple methods were used to maximize the number of pre-weaned pups in the dataset. First, 15 cases were removed whose additional notes indicated they were admitted as weaned pups. Next, 48 cases were removed that were released older than the target age class "pup" (e.g., yearling, juvenile, subadult). Then, each seal's intake date was compared to its region's corresponding harbor seal pupping season, excluding 191 cases that were admitted outside of pupping season, indicating they were unlikely to be pre-weaned pups (Temte et al., 1991; Skinner, 2006; Zier & Gaydos, 2014). Harbor seals that were admitted within 1 month prior to the start of the pupping season, and that may have been premature pups, were included. Harbor seals that were admitted up to 6 weeks after the end range of pupping season were also included. It is possible that this dataset contains some recently weaned pups that were unable to be separated from pre-weaned admissions. Next, two cases that were in rehabilitation for less than 1 week and 140 cases that were in rehabilitation for longer than 4 months (122 days) were removed. Then, with the remaining 1,225 cases, the median absolute deviation (MAD) method as described by Leys et al. (2013) was used to detect and exclude outliers for these variables: weight gain in rehabilitation, length gain in rehabilitation, release weight, release length, and average daily weight gain. For each variable, the MAD was computed using the constant 1.4826 and calculated the median plus or minus three absolute deviations around the median. Boxplots for each variable were compared to the range produced by the MAD method to assess if the range appropriately captured the distribution and excluded outliers. Finally, after determining that each range was appropriate, cases that fell within the MAD range for each variable were included (removing 101 cases; Table S1; the supplementary tables for this article are available in the "Supplemental Material" section of the *Aquatic Mammals* website: [https://www.aquaticmammalsjournal.org/index.php?option=com\\_content&view=article&id=10&Itemid=147](https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147)).

Rehabilitated harbor seals were divided into two geographic regions as they represent unique subspecies (*P. v. concolor* on the East Coast and *P. v. richardii* on the West Coast of North

America) and face unique environmental drivers (Reid, 1961; Douglass et al., 2013). Further, there is a lack of intraregional data comparing growth rates of wild harbor seals within each coast. Between 2005 and 2020, there were 11 facilities on the East Coast and 10 on the West Coast that provided long-term rehabilitation for releasable harbor seals, including facilities that were only operational for a subset of that period (Table S2). Comparisons by facility were omitted due to the numerous network changes that occurred during these years and the high quantity of animals that were transferred between facilities. Data were not evaluated regarding reason for stranding, any treatments for illness or injury, or type of clinical care received during rehabilitation as these data are maintained by the individual facilities and not available from the national stranding database.

Histograms, quantile-quantile plots, and residuals vs fits plots assessed the normality for each morphometric. Two-sample *t* tests and the Wilcoxon rank sum test compared differences in the means between the East and West Coasts. Welch's correction was applied to two-sample *t* tests when samples had unequal variances. Differences were considered significant at  $p \leq 0.05$ . Linear regression models investigated the relationship between weight and length of rehabilitated harbor seals by coast, as well as in comparison to wild seals, using *RStudio*, Version 1.4.1106 (R Core Team, 2020). Specifically, models included weight at intake and release (kg), length at intake and release (cm), daily weight gain, daily length gain, and BCI at intake and release. Data were plotted with lines of best fit and 95% confidence intervals (CIs) using the package 'ggplot2' (Wickham, 2016). Interannual trends in weight and BCI were investigated using linear models, with year as a categorical explanatory variable, and were visualized using box-and-whisker plots.

Since the parameter estimates from these models were in relation to a reference year, the earliest year from the database query was used as the reference. However, because not all facilities from California had uploaded their 2005 data into the national stranding database by the time of the query, 2006 was used as the reference year for the West Coast and 2005 as the reference year for the East Coast. Still, 2005 data were retained from the West Coast for two-sample *t* tests because these tests did not consider year, and these cases informed growth during rehabilitation.

Morphometrics of rehabilitated harbor seals were compared to their wild, recently weaned counterparts using previously published data from both coasts (Table 1). East Coast seals were compared to wild seals on Sable Island, Canada, a 31 km<sup>2</sup> island located 300 km southeast of Halifax, Nova Scotia; and West Coast seals were compared to wild seals in the Salish Sea, a 16,925 km<sup>2</sup> inland sea shared by Washington State and British Columbia. Means and standard deviations of wild seals were obtained from previous studies. Data points ( $n = 100$  for each coast) were generated and normally distributed around the reported means and standard deviations. Two sample *t* tests compared the data that were generated for wild seals to the measurements from rehabilitated seals.

## Results

There were 1,124 rehabilitated harbor seal pups that fit the study criteria, including 237 cases from the East Coast and 887 from the West Coast. East Coast seals spent a longer time in rehabilitation than West Coast seals (East:  $84.33 \pm 2.55$  d; West:  $70.74 \pm 1.27$  d;  $p < 0.001$ ; Table 2). East Coast seals were admitted at a greater mean weight and length ( $8.84 \pm 0.21$  kg;  $75.06 \pm 0.73$  cm) than West Coast seals ( $8.57 \pm 0.11$  kg;  $74.00 \pm 0.40$

**Table 1.** Morphometrics of wild harbor seals (*Phoca vitulina*) from Sable Island (East Coast) and the Salish Sea (West Coast) as reported in previous studies. \*Mean was calculated from reported values in the referenced study. Standard deviation was not reported and was estimated as 1.0 for use in our study.

Region	Birth weight (kg)	Birth length (cm)	Nursing period (d)	Mean daily weight gain (kg/d)	Mean daily length gain (cm/d)	Weight at weaning (kg)	Length at weaning (cm)
Sable Island (East Coast)	$10.9 \pm 0.06^\dagger$	$76.6 \pm 1.0^{*\ddagger}$	$23.9 \pm 0.24^\ddagger$	$0.6 \pm 0.015^\ddagger$	$0.1 \pm 0.02^§$	$24.8 \pm 0.26^\ddagger$	$90.4^\ddagger$
Salish Sea (West Coast)	$11.2 \pm 0.31^1$	$78.0 \pm 1.90^1$	$32.0 \pm 1.5^1$	$0.394 \pm 0.026^1$	$0.33 \pm 0.027^1$	$23.6 \pm 1.2^1$	$87.15 \pm 2.54^§$

**Sources:** <sup>‡</sup>Boulva & McLaren, 1979; <sup>§</sup>Bowen et al., 2001; <sup>§</sup>Muelbert et al., 2003; <sup>1</sup>Cottrell et al., 2002; <sup>§</sup>Gaydos et al., 2012

**Table 2.** Morphometrics of rehabilitated and released harbor seal pups on the East ( $n = 237$ ) and West ( $n = 887$ ) Coasts of the United States, including  $t$  scores, mean estimates for each coast, 95% confidence interval (CI) for the differences in the means, and  $p$  values

	East Coast mean and SD	West Coast mean and SD	$t$	95% CI	$p$
Time in rehabilitation (d)	84.33 $\pm$ 2.55	70.74 $\pm$ 1.27	9.395	10.742-16.429	< 0.001
Length (cm) at intake	75.06 $\pm$ 0.73	74.00 $\pm$ 0.40	2.522	0.234-1.893	0.012
Length (cm) at release	91.70 $\pm$ 0.74	89.15 $\pm$ 0.40	5.995	1.713-3.385	< 0.001
Weight (kg) at intake	8.84 $\pm$ 0.21	8.57 $\pm$ 0.11	2.240	0.033-0.510	0.026
Weight (kg) at release	23.42 $\pm$ 0.45	22.92 $\pm$ 0.28	1.892	-0.020-1.034	0.059
Daily weight gain (kg/d)	0.181 $\pm$ 0.007	0.213 $\pm$ 0.005	-7.826	-0.041- -0.024	< 0.001
Daily length gain (cm/d)	0.202 $\pm$ 0.011	0.223 $\pm$ 0.007	-3.160	-0.033- -0.008	0.002
Body condition index at release (weight $\times$ 100/length)	25.58 $\pm$ 0.48	25.67 $\pm$ 0.28	-0.310	-0.640- -0.466	0.757

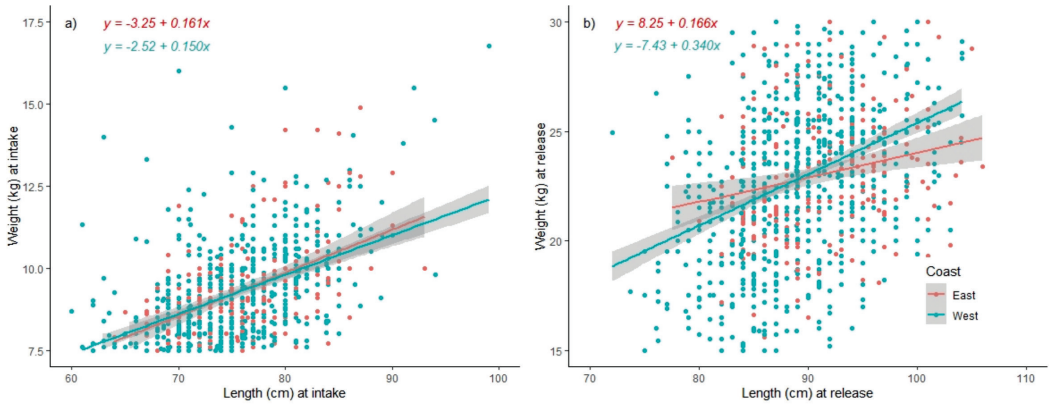
cm) ( $p = 0.026$  and  $p = 0.012$ , respectively) and released at greater lengths (East: 91.70  $\pm$  0.74 cm; West: 89.15  $\pm$  0.40 cm;  $p < 0.001$ ). East and West Coast seals were released at similar weights (East: 23.42  $\pm$  0.45 kg; West: 22.92  $\pm$  0.28 kg;  $p = 0.059$ ) and BCIs (East: 25.58  $\pm$  0.48; West: 25.67  $\pm$  0.28;  $p = 0.757$ ). West Coast seals had a higher mean daily weight gain (0.213  $\pm$  0.005 kg/d;  $p < 0.001$ ) and length gain (0.223  $\pm$  0.007 cm/d;  $p < 0.002$ ) compared to East Coast seals (0.181  $\pm$  0.007 kg/d; 0.202  $\pm$  0.011 cm/d).

Across all years, there was a similar linear relationship between weight and length at intake for East Coast harbor seals ( $\beta = 0.161$ , adjusted  $R^2 = 0.310$ , 95% CI [0.130 to 0.192]) and West Coast harbor seals ( $\beta = 0.150$ , adjusted  $R^2 = 0.276$ , 95% CI [0.134 to 0.166]) (Figure 1; Table 3). At release, the relationship between West Coast seals' weight and length ( $\beta = 0.340$ , adjusted  $R^2 = 0.232$ ,  $p < 0.001$ , 95% CI [0.300 to 0.381]) was greater than East Coast seals ( $\beta = 0.166$ , adjusted  $R^2 = 0.071$ ,  $p < 0.001$ , 95% CI [0.091 to 0.240]) (Figure 1; Table 3). The West Coast model explained more of the variability in weight plotted against length at release (adjusted  $R^2 = 0.232$ ) than the East Coast model (adjusted  $R^2 = 0.071$ ). However, while the  $p$  values indicated that the relationship between weight and length at release was significant, both  $R^2$  values were low, indicating that length was not a strong predictor of weight. West Coast seals had a higher rate of daily weight gain compared to daily length gain ( $\beta = 0.241$ ,  $p < 0.001$ , 95% CI [0.199 to 0.283]) than East Coast seals ( $\beta = 0.160$ ,  $p < 0.001$ , 95% CI [0.083 to 0.238]) (Figure 2; Table 3).

The number of days in rehabilitation for East (84.33  $\pm$  2.55) and West (70.74  $\pm$  1.27) Coast harbor

seals was longer than the nursing period for wild seals on Sable Island (23.9  $\pm$  0.24;  $p < 0.0001$ ) and in the Salish Sea (32.0  $\pm$  1.5;  $p < 0.001$ ; Tables 2 & 3) such that animals at release were two to three times older at release than wild pups at weaning. At release, rehabilitated East Coast seals were lighter (mean weight: 23.42  $\pm$  0.45 kg) and longer (mean length: 91.70  $\pm$  0.74 cm) than wild Sable Island seals at weaning (mean weight: 24.8  $\pm$  0.26 kg; mean length: 90.4 cm) ( $p < 0.001$  and  $p < 0.001$ , respectively). Rehabilitated West Coast seals at release were also lighter (22.92  $\pm$  0.28 kg) and longer (89.15  $\pm$  0.40 cm) than wild Salish Sea seals at weaning (23.6  $\pm$  1.2 kg; 87.15  $\pm$  2.54 cm) ( $p = 0.002$  and  $p < 0.001$ , respectively; Tables 2 & 3). Mean daily weight gain during rehabilitation was much lower (East: 0.181  $\pm$  0.007 kg/d; West: 0.213  $\pm$  0.005 kg/d) than from birth to weaning in wild seals (Sable Island: 0.600  $\pm$  0.015 kg/d; Salish Sea: 0.394  $\pm$  0.026 kg/d;  $p < 0.001$ ; Tables 2 & 3). On the East Coast, rehabilitated seals had a greater mean daily length gain (0.202  $\pm$  0.011 cm/d) than wild Sable Island seals (0.100  $\pm$  0.020 cm/d;  $p < 0.001$ ) (Tables 2 & 3); however, on the West Coast, wild seals had a greater mean daily length gain (0.330  $\pm$  0.027 cm/d) than rehabilitated seals (0.223  $\pm$  0.007 cm/d;  $p < 0.001$ ) (Tables 2 & 3).

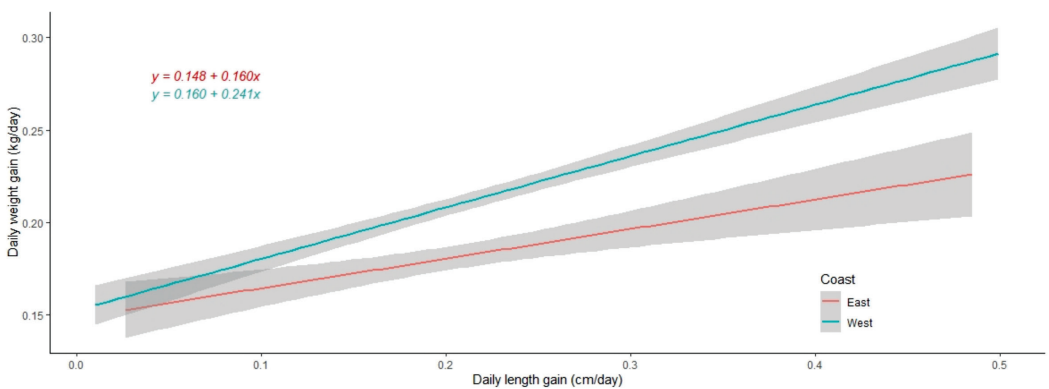
Size at intake was compared to size at release. There was no strong relationship between intake weight and release weight for the East Coast (adjusted  $R^2 = 0.087$ ,  $\beta = 0.64 \pm 0.13$ ,  $p < 0.001$ ) or the West Coast (adjusted  $R^2 = 0.025$ ,  $\beta = 0.40 \pm 0.08$ ,  $p < 0.001$ ). Similarly, there was no strong relationship between intake BCI and release BCI for the East Coast (adjusted  $R^2 = 0.048$ ,  $\beta = 0.47 \pm 0.13$ ,  $p < 0.001$ ) or West Coast (adjusted  $R^2 = 0.0006$ ,  $\beta = 0.09 \pm 0.07$ ,  $p < 0.222$ ).



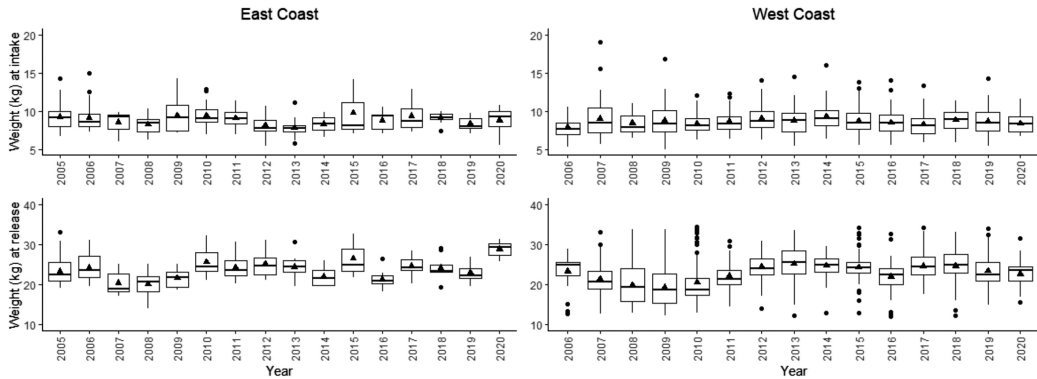
**Figure 1.** Weight plotted against length for rehabilitated and released harbor seals (*Phoca vitulina*) on the East and West Coasts at intake (a) and release (b), represented by linear models with 95% confidence intervals (CIs) shaded in grey

**Table 3.** Results of linear regression models, including estimates for coefficients ( $\beta$ ),  $p$  values, adjusted  $R^2$ , and 95% CIs; lengths are in centimeters and weights are in kilograms.

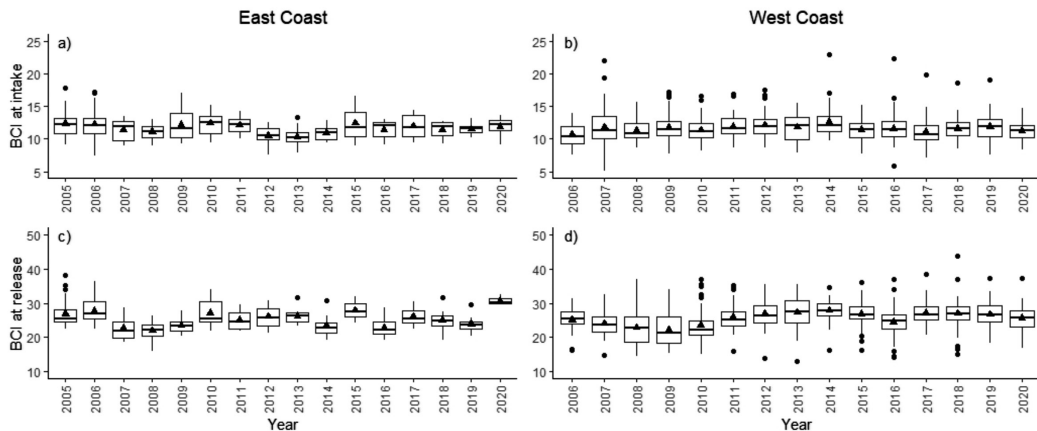
Coast	Predictor	Response	$\beta$	$p$	Adjusted $R^2$	95% CI
East	Length at intake	Weight at intake	0.161	< 0.001	0.310	0.130-0.192
East	Length at release	Weight at release	0.166	< 0.001	0.071	0.091-0.240
East	Daily length gain	Daily weight gain	0.160	< 0.001	0.062	0.083-0.238
West	Length at intake	Weight at intake	0.150	< 0.001	0.276	0.134-0.166
West	Length at release	Weight at release	0.340	< 0.001	0.232	0.300-0.381
West	Daily length gain	Daily weight gain	0.241	< 0.001	0.125	0.199-0.283



**Figure 2.** The relationship between daily weight gain (kg) and daily length gain (cm) for East and West Coast harbor seals, with 95% CIs shaded in grey



**Figure 3.** Weights at intake and release by year for East and West Coast harbor seals from 2005 to 2020; the triangles represent the means.



**Figure 4.** Body condition index (BCI; weight  $\times$  100/length) by year for East and West Coast harbor seals at intake and release from 2005 to 2020; the triangles represent the means.

Interannual variability in weight (Figure 3) and BCI (Figure 4) at release were evaluated from 2005 to 2020. For East Coast harbor seals, release weight and BCI had overall more interannual variation than intake weight and BCI. For East Coast seals, release weight and BCI decreased from 2006 to 2007, 2013 to 2014, and 2015 to 2016. West Coast harbor seals also had more variation in release weight and BCI over time than intake weight and BCI. For West Coast seals, release weight and BCI decreased from 2006 to 2009, increased from 2010 to 2014, and decreased from 2015 to 2016 (Figures 3 & 4). In relation to the reference year (2005 for the East Coast; 2006 for the West Coast), there was significant statistical variation ( $p < 0.05$ ) in intake and release weight and BCI by year. Notably, East Coast intake weight and BCI declined in 2008 and 2012 to 2013; East Coast release weight and BCI declined in

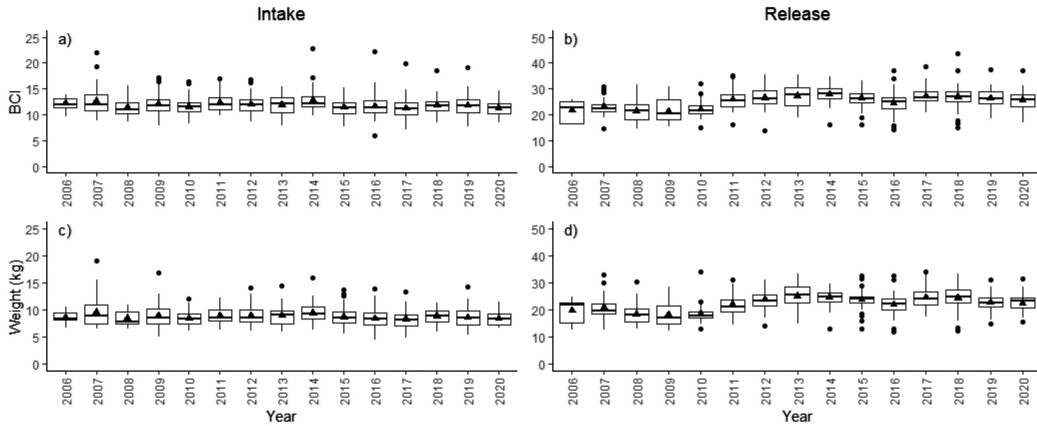
2007 to 2008 and increased in 2020; and West Coast release weight and BCI declined in 2008 to 2009 (Table 4). Adjusted  $R^2$  values helped to determine if weight or BCI might be a more informative metric for interannual changes in pre-release criteria. While adjusted  $R^2$  values for all the annual models were low, indicating there was not a strong linear relationship, we found that the BCI model had a higher adjusted  $R^2$  for the East Coast release model, while the weight model had a higher adjusted  $R^2$  for the West Coast release model (Table 4).

Interannual differences in morphometrics were also examined for harbor seals, specifically from California, the state with the greatest number of cases ( $n = 725$ ; Table S3). Intake weight and BCI remained relatively stable over the years (Figure 5), supported by the low adjusted  $R^2$  values which showed there was not a strong change by

**Table 4.** Results from linear regression models comparing year to weight (kg) and body condition index (BCI) for East and West Coast harbor seal pups. 2005 is the intercept for the East Coast, and 2006 is the intercept for the West Coast.

Response	Adjusted $R^2$ for overall model	Estimate of intercept $\pm$ standard error	$p$ value for overall model	Significant years ( $p < 0.05$ )	Estimate of year $\pm$ standard error	$p$ value for year
East Coast intake weight	0.039	9.26 $\pm$ 0.24	0.07	2008	-1.04 $\pm$ 0.40	0.010
				2012	-1.16 $\pm$ 0.52	0.027
East Coast intake BCI	0.080	12.31 $\pm$ 0.26	0.003	2013	-1.49 $\pm$ 0.48	0.002
				2008	-1.24 $\pm$ 0.43	0.004
				2012	-1.86 $\pm$ 0.56	0.001
East Coast release weight	0.255	23.33 $\pm$ 0.45	< 0.001	2013	-1.95 $\pm$ 0.51	< 0.001
				2014	-1.35 $\pm$ 0.66	0.043
				2007	-2.93 $\pm$ 1.31	0.026
				2008	-3.23 $\pm$ 0.75	< 0.001
East Coast release BCI	0.283	26.84 $\pm$ 0.47	< 0.001	2010	2.34 $\pm$ 0.84	0.006
				2020	5.51 $\pm$ 1.22	< 0.001
				2007	-4.19 $\pm$ 1.37	0.002
				2008	-4.84 $\pm$ 0.79	< 0.001
				2009	-3.42 $\pm$ 0.92	< 0.001
				2014	-3.34 $\pm$ 1.21	0.006
				2016	-3.98 $\pm$ 1.06	< 0.001
West Coast intake weight	0.019	7.83 $\pm$ 0.29	0.008	2019	-2.93 $\pm$ 1.06	0.006
				2020	3.80 $\pm$ 1.28	0.003
				2007	1.08 $\pm$ 0.37	0.004
				2009	0.93 $\pm$ 0.36	0.010
				2011	0.83 $\pm$ 0.39	0.034
				2012	1.18 $\pm$ 0.36	0.001
				2013	0.96 $\pm$ 0.38	0.012
				2014	1.44 $\pm$ 0.39	< 0.001
				2015	0.88 $\pm$ 0.34	0.009
				2018	0.97 $\pm$ 0.39	0.012
West Coast intake BCI	0.026	10.67 $\pm$ 0.33	0.001	2019	0.81 $\pm$ 0.36	0.024
				2007	1.15 $\pm$ 0.42	0.006
				2009	1.13 $\pm$ 0.41	0.006
				2011	1.25 $\pm$ 0.45	0.005
				2012	1.42 $\pm$ 0.41	< 0.001
				2013	1.10 $\pm$ 0.44	0.012
				2014	1.97 $\pm$ 0.44	< 0.001
				2015	0.76 $\pm$ 0.39	0.048
				2016	0.92 $\pm$ 0.39	0.018
				2018	0.94 $\pm$ 0.44	0.034
West Coast release weight	0.168	23.27 $\pm$ 0.67	< 0.001	2019	1.17 $\pm$ 0.41	0.005
				2007	-1.81 $\pm$ 0.85	0.034
				2008	-3.44 $\pm$ 0.93	< 0.001
				2009	-3.98 $\pm$ 0.83	< 0.001
				2010	-2.75 $\pm$ 0.81	< 0.001
West Coast release BCI	0.138	25.05 $\pm$ 0.68	< 0.001	2013	1.91 $\pm$ 0.88	0.030
				2008	-2.24 $\pm$ 0.95	0.018
				2009	-2.71 $\pm$ 0.85	0.001
				2012	1.74 $\pm$ 0.85	0.041
				2013	2.22 $\pm$ 0.90	0.014
				2014	2.83 $\pm$ 0.91	0.002
				2015	1.88 $\pm$ 0.79	0.018
				2017	2.07 $\pm$ 0.83	0.013
				2018	1.89 $\pm$ 0.91	0.039
2019	1.72 $\pm$ 0.85	0.043				





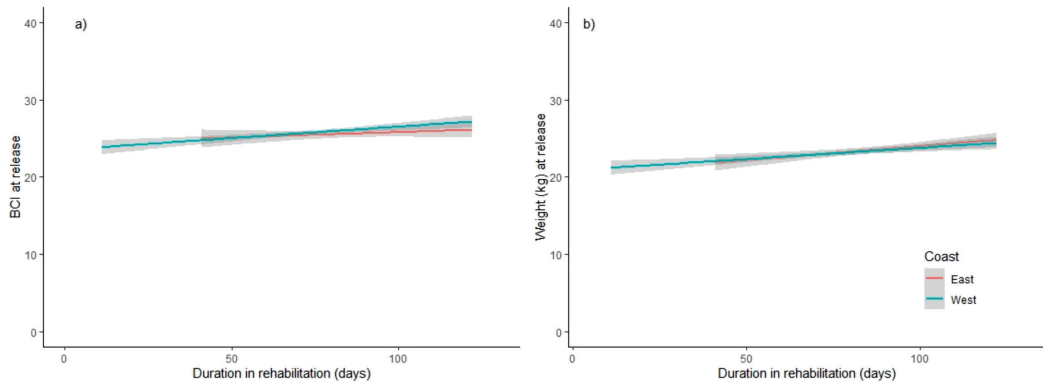
**Figure 5.** BCI (weight × 100/length) and weight by year for California harbor seals from 2006 to 2020; the triangles represent the means.

**Table 5.** Results from linear regression models comparing weight (kg) and BCI for California harbor seal pups by year, using 2006 as the intercept

Response	Adjusted $R^2$ for overall model	Estimate of intercept ± standard error	$p$ value for overall model	Significant years ( $p < 0.1$ )	Estimate of year ± standard error	$p$ value for year
Intake weight	0.022	$8.59 \pm 0.47$	0.009	N/A	--	--
Intake BCI	0.031	$12.16 \pm 0.53$	< 0.001	N/A	--	--
Release weight	0.276	$19.76 \pm 0.98$	< 0.001	2011	$2.39 \pm 1.16$	0.040
				2012	$4.11 \pm 1.09$	< 0.001
				2013	$5.32 \pm 1.13$	< 0.001
				2014	$4.96 \pm 1.13$	< 0.001
				2015	$4.02 \pm 1.05$	< 0.001
				2016	$2.16 \pm 1.05$	0.040
				2017	$4.78 \pm 1.08$	< 0.001
				2018	$4.63 \pm 1.14$	< 0.001
				2019	$2.90 \pm 1.08$	0.008
				2020	$2.86 \pm 1.16$	0.014
Release BCI	0.229	$21.58 \pm 1.05$	< 0.001	2011	$4.41 \pm 1.25$	< 0.001
				2012	$4.82 \pm 1.17$	< 0.001
				2013	$5.72 \pm 1.21$	< 0.001
				2014	$6.29 \pm 1.21$	< 0.001
				2015	$4.86 \pm 1.13$	< 0.001
				2016	$2.97 \pm 1.13$	0.009
				2017	$5.56 \pm 1.16$	< 0.001
				2018	$5.37 \pm 1.22$	< 0.001
				2019	$4.71 \pm 1.16$	< 0.001
				2020	$4.17 \pm 1.25$	< 0.001

**Table 6.** Results of linear regression models comparing the number of days in rehabilitation to release weight (kg) and release BCI for East and West Coast harbor seals

Response	Intercept $\pm$ standard error	Slope estimate $\pm$ standard error	<i>p</i> value	Adjusted $R^2$
East Coast release weight	20.37 $\pm$ 0.97	0.036 $\pm$ 0.011	0.001	0.039
East Coast release BCI	24.41 $\pm$ 1.05	0.014 $\pm$ 0.012	0.253	0.001
West Coast release weight	20.87 $\pm$ 0.54	0.029 $\pm$ 0.007	< 0.001	0.016
West Coast release BCI	23.52 $\pm$ 0.54	0.030 $\pm$ 0.007	< 0.001	0.017

**Figure 6.** BCI and weight at release based on the number of days in rehabilitation for East and West Coast harbor seals, with 95% CIs shaded in grey

year (intake weight  $R^2_{\text{adj}} = 0.022$ ; intake BCI  $R^2_{\text{adj}} = 0.031$ ; Table 5). Meanwhile, variation in release weight and BCI may be partially explained by year (release weight  $R^2_{\text{adj}} = 0.276$ ; release BCI  $R^2_{\text{adj}} = 0.229$ ; Table 5). Release weight and BCI increased from 2011 to 2014 (Table 5) and declined from 2015 to 2016 before increasing again (Figure 5).

To understand if longer duration in rehabilitation resulted in greater release sizes, the number of days in rehabilitation was compared to release weight or BCI. For both East and West Coast harbor seals, an increase in the number of days in rehabilitation did not result in a notable increase in weight or BCI at release (Table 6; Figure 6).

### Discussion

The results of this study demonstrate that there has been spatiotemporal variation in body condition, weight, length, and growth rate for rehabilitated and released harbor seal pups in the U.S. This variation may be a function of variables that we were not able to explore such as differences in age at intake, differences in rehabilitation practices between facilities or over time, or differences in the morphometrics or growth curves of the harbor

seal subspecies. Intake weight and BCI may be dependent on interannual environmental factors that affect harbor seal pups before they are admitted to rehabilitation. These same factors may affect survival during rehabilitation such that the animals that lived to release may not be the best dataset to address annual variation in size and body condition. It is unknown why intake weight and BCI decreased for East Coast seals in 2008, 2012, and 2013. It may have been related to the phocine distemper virus epizootic in pinnipeds in the northeast Atlantic from 2006 to 2007 (Duignan et al., 2014) and/or the avian influenza outbreak in the same region beginning in 2011 (Anthony et al., 2012). It is possible that these disease outbreaks decreased the fitness of survivors and resulted in smaller pups in the years following the outbreaks. Alternatively, it is possible that older females were killed and the remaining younger females produced smaller pups as maternal reproductive experience and age can influence offspring birth mass (Ellis et al., 2000). Additionally, it is unknown why release weight and BCI fluctuated for both coasts from 2005 to 2020, although it may have been related to numerous network and rehabilitation protocol changes that occurred during these years. Along the central California coast in 2009,

uncharacteristically warm sea surface temperatures coincided with increased mortality of starving California sea lion (*Zalophus californianus*) pups, likely caused by changes in prey availability (Melin et al., 2010). While there was no evidence for a significantly lower intake BCI or weight in 2009 and 2010 for harbor seals in California, unusual oceanic conditions may have indirectly contributed to the lower release BCI during those years as California facilities dealt with a high influx of patients and may have lowered their internal (facility) weight threshold for release. Additionally, the harbor seal pups that stranded but did not survive rehabilitation were not examined as part of this study.

Harbor seals that remained in rehabilitation for longer periods of time were not released at a greater BCI or weight than seals that remained in rehabilitation for shorter time periods after excluding outliers (seals held in rehabilitation for less than 1 week or greater than 4 months). Although treatment and clinical data were not evaluated here, generally animals may be held longer in rehabilitation due to medical complications that required longer rehabilitation time. Underlying conditions for which animals were admitted into rehabilitation may have influenced growth rates; however, the data to assess this are not submitted to the national stranding database. Additionally, some seals may require a longer transition from tube-feeding to eating fish, leading to lower weight gain and a possible longer rehabilitation period. Thus, even if harbor seals are released at a standard weight or BCI, a greater length of time spent in rehabilitation (as a proxy for age) may decrease their survival (Greig et al., 2019).

Rehabilitated harbor seals were released at different weights and lengths than their wild counterparts at weaning. Mimicking the normal weaning size and body condition of wild seals at the time of release could give rehabilitated pups the best chance at survival. However, this strategy is confounded by the length of time necessary to achieve weaning weight in rehabilitation compared with wild seals. The mean daily weight gain for rehabilitated seals was significantly less than that of wild animals during nursing until weaning, which is consistent with results from previous studies (MacRae et al., 2010; Briese et al., 2012; Trumble et al., 2013; Fonfara et al., 2016; Cole & Fraser, 2021).

When determining optimum morphometrics for release criteria, rehabilitation centers should continue to work to safely increase mean daily weight gain for harbor seals in rehabilitation. However, merely adopting a higher minimum weight criterion that mimics wild seals (24.8 kg on the East Coast [Bowen et al., 2001] and 23.6 kg on the West Coast [Cottrell et al., 2002]) does not come without trade-offs. Keeping animals in rehabilitation longer to achieve higher weights can increase

the costs of rehabilitation (e.g., limited resources such as space, personnel, and funding) and increase the chance that seals could become acclimated to humans during care. Longer stays in rehabilitation may also work against the pup's natural postweaning fast (Muelbert & Bowen, 1993). This fast could be related to seals learning to forage or to some innate physiologic mechanism that has not been described. Additionally, the timing of weaning may have evolved to take advantage of local conditions as it has been hypothesized in other locations that harbor seal pupping phenology can shift in response to food availability (Jemison & Kelly, 2001; Bowen et al., 2003; Osinga et al., 2012). It is possible that a delayed release from a long rehabilitation could result in a mismatch between pup foraging skills and prey availability.

Our analyses highlight the value of and limits to the routinely reported morphometrics (weight and length) for evaluating harbor seal body condition for release. There was a weak linear relationship between weight and length, the two components of the BCI used in this study. It is possible that the observed variation in length and BCI resulted from challenges in measuring an accurate straight length as seals can retract or extend their necks during measurement. Still, BCI might be more informative than weight alone. For instance, seals with slower weight gain are likely to be kept in rehabilitation longer to reach a minimum weight criterion such that they are older and possibly longer at the same release weight. This could translate to a lesser body condition at the time of release suggesting that longer animals may have less body fat and possibly a lower chance at post-release survival.

BCIs with other variables might be worth investigating (e.g., age, girth, blubber thickness) and compared to survival. In grey seals, Boyd (1984) found that the body weight of adult females could be predicted from the body length and axillary girth. For Hawaiian monk seals (*Neomonachus schauinslandi*), axillary girth of pups at weaning is strongly correlated with their survival to 2 years of age (Craig & Ragen, 1999; Baker, 2008; Baker et al., 2021). While Greig et al. (2019) did not find a similar correlation between girth and survival in harbor seals, further research is necessary to understand this potential relationship. Ultrasound measurements of blubber depth also could be incorporated into a BCI (Rosen & Renouf, 1997; Trumble & Castellini, 2002; Mellish et al., 2007).

When possible, rehabilitation facilities should pursue post-release monitoring of rehabilitated harbor seals to assess their survival and compare how different metrics of body condition influence post-release survival, with the goal of developing pre-release body condition criteria for harbor seal pups. It is recommended that rehabilitation facilities

in the U.S. continue to evaluate the ideal release body condition and weight for harbor seals, considering data about comparable wild conspecifics or data from successfully rehabilitated and released stranded pups (Whaley & Borkowski, 2009).

There were certain limitations to this study. First, the wild groups used for comparisons (Sable Island and Salish Sea) were at the north end of the range of rehabilitated animals in this study, and it is possible that there are latitudinal differences in body condition. While Skinner (2006) studied the morphometrics of harbor seal pups from birth to weaning in Maine, our study based East Coast comparisons on Sable Island pups because they were of known age at birth and weaning (Muelbert & Bowen, 1993; Bowen et al., 1994). Second, it is possible that East Coast seals had higher intake weights and lengths because they came into rehabilitation relatively older than their West Coast counterparts or because of unknown differences between the two subspecies. Third, variation in morphometrics according to facility could not be examined due to the numerous network changes that occurred during these years, the number of animals that were transferred between facilities, and the difficulty associated with prescribing the relative impact of each facility on the animal's overall release conditions. It is possible that interannual changes in morphometrics were due to changes in protocols at facilities (e.g., formulas fed to pups have changed over the time span of our study) and network changes. Fourth, and finally, despite efforts to only include pre-weaned pups in analyses, it is possible that some weaned pups were included as they are indistinguishable from pre-weaned pups by morphometrics. Despite these limitations, this study provides critical baseline data about the morphometrics of harbor seals released from rehabilitation in the U.S.

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### Literature Cited

- Anthony, S. J., St. Leger, J. A., Pugliares, K., Ip, H. S., Chan, J. M., Carpenter, Z. W., Navarrete-Macias, I., Sanchez-Leon, M., Saliki, J. T., Pedersen, J., Karesh, W., Daszak, P., Rabadan, R., Rowles, T., & Lipkin, W. I. (2012). Emergence of fatal avian influenza in New England harbor seals. *mBio*, 3(4), e00166-12. <https://doi.org/10.1128/mBio.00166-12>
- Ashley, E. A., Olson, J. K., Adler, T. E., Raverty, S., Anderson, E. M., Jeffries, S., & Gaydos, J. K. (2020). Causes of mortality in a harbor seal (*Phoca vitulina*) population at equilibrium. *Frontiers in Marine Science*, 7, 319. <https://doi.org/10.3389/fmars.2020.00319>
- Baker, J. D. (2008). Variation in the relationship between offspring size and survival provides insight into causes of mortality in Hawaiian monk seals. *Endangered Species Research*, 5, 55-64. <https://doi.org/10.3354/esr00122>
- Baker, J. D., & Fowler, C. W. (1992). Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology*, 227(2), 231-238. <https://doi.org/10.1111/j.1469-7998.1992.tb04819.x>
- Baker, J. D., Barbieri, M. M., Johanos, T. C., Littnan, C. L., Bohlander, J. L., Kaufman, A. C., Harting, A. L., Farry, S. C., & Yoshinaga, C. H. (2021). Conservation translocations of Hawaiian monk seals: Accounting for variability in body condition improves evaluation of translocation efficacy. *Animal Conservation*, 24, 206-216. <https://doi.org/10.1111/acv.12622>
- Boulva, J., & McLaren, I. (1979). *Biology of the harbor seal, Phoca vitulina*, in Eastern Canada (Bulletin 200). Bulletin of the Fisheries Research Board of Canada. 24 pp.
- Boveng, P. L., Ziel, H. L., McClintock, B. T., & Cameron, M. F. (2020). Body condition of phocid seals during a period of rapid environmental change in the Bering Sea and Aleutian Islands, Alaska. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 181-182, 104904. <https://doi.org/10.1016/j.dsr2.2020.104904>
- Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2001). Maternal effects on offspring growth rate and weaning mass in harbor seals. *Canadian Journal of Zoology*, 79(6), 1088-1101. <https://doi.org/10.1139/z01-075>
- Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2003). Maternal and newborn life-history traits during

- periods of contrasting population trends: Implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology*, 261, 155-163. <https://doi.org/10.1017/S0952836903004047>
- Bowen, W. D., Oftedal, O. T., Boness, D. J., & Iverson, S. J. (1994). The effect of maternal age and other factors on birth mass in the harbour seal. *Canadian Journal of Zoology*, 72, 8-14. <https://doi.org/10.1139/z94-002>
- Boyd, I. L. (1984). The relationship between body condition and the timing of implantation in pregnant grey seals (*Halichoerus grypus*). *Journal of Zoology*, 203(1), 113-123. <https://doi.org/10.1111/j.1469-7998.1984.tb06048.x>
- Briese, A. A., Gaydos, J. K., Harner, P., Bildfell, R., & Robinson, D. (2012, May). Growth rates of harbor seal (*Phoca vitulina*) pups in rehabilitation. *Proceedings of the 43rd Annual Conference on the International Association for Aquatic Animal Medicine*, Atlanta, GA.
- Cole, J., & Fraser, D. (2021). Sink or swim: Risk stratification of preweaning mortality in harbor seal pups (*Phoca vitulina richardii*) admitted for rehabilitation. *Marine Mammal Science*, 37(3), 807-825. <https://doi.org/10.1111/mms.12777>
- Cottrell, P. E., Jeffries, S., Beck, B., & Ross, P. S. (2002). Growth and development in free-ranging harbor seal (*Phoca vitulina*) pups from southern British Columbia, Canada. *Marine Mammal Science*, 18(3), 721-733. <https://doi.org/10.1111/j.1748-7692.2002.tb01069.x>
- Craig, M. P., & Ragen, T. J. (1999). Body size, survival, and decline of juvenile Hawaiian monk seals, *Monachus schauinslandi*. *Marine Mammal Science*, 15(3), 786-809. <https://doi.org/10.1111/j.1748-7692.1999.tb00843.x>
- Douglass, E. M., Kwon, Y.-O., & Jayne, S. R. (2013). A comparison of North Pacific and North Atlantic subtropical mode waters in a climatologically-forced model. *Deep-Sea Research II: Topical Studies in Oceanography*, 91, 139-151. <https://doi.org/10.1016/j.dsr2.2013.02.023>
- Duignan, P. J., Van Bresseem, M-F., Baker, J. D., Barbieri, M., Colegrove, K. M., De Guise, S., de Swart, R. L., Di Guardo, G., Dobson, A., Duprex, W. P., Early, G., Fauquier, D., Goldstein, T., Goodman, S. J., Grenfell, B., Groch, K. R., Gulland, F., Hall, A., Jensen, B. A., Lamy, K., . . . Wellehan, J. F. X. (2014). Phocine distemper virus: Current knowledge and future directions. *Viruses*, 6, 5093-5134. <https://doi.org/10.3390/v6125093>
- Ellis, S. L., Bowen, W. D., Boness, D. J., & Iverson, S. J. (2000). Maternal effects on offspring mass and stage of development at birth in the harbor seal, *Phoca vitulina*. *Journal of Mammalogy*, 81(4), 1143-1156. [https://doi.org/10.1644/1545-1542\(2000\)081<1143:MEOOMA>2.0.CO;2](https://doi.org/10.1644/1545-1542(2000)081<1143:MEOOMA>2.0.CO;2)
- Fonfara, S., Sundermeyer, J., Casamian Sorrosal, D., Weber, C., & Rosenberger, T. (2016). Usefulness of serum cardiac troponin I concentration as a marker of survival of harbor seal (*Phoca vitulina*) pups during rehabilitation. *Journal of the American Veterinary Medical Association*, 249(12), 1428-1435. <https://doi.org/10.2460/javma.249.12.1428>
- Frouin, H., Haulena, M., Akhurst, L. M. F., Raverty, S. A., & Ross, P. S. (2013). Immune status and function in harbor seal pups during the course of rehabilitation. *Veterinary Immunology and Immunopathology*, 155(1-2), 98-109. <https://doi.org/10.1016/j.vetimm.2013.06.011>
- Gaydos, J. K., Vilchis, L. I., Lance, M. M., Jeffries, S. J., Thomas, A., Greenwood, V., Harner, P., & Ziccardi, M. H. (2012). Postrelease movement of rehabilitated harbor seal (*Phoca vitulina richardii*) pups compared with cohort-matched wild seal pups. *Marine Mammal Science*, 29(3), E282-E294. <https://doi.org/10.1111/mms.12002>
- Greig, D. J., Gulland, F. M. D., Harvey, J. T., Lonergan, M., & Hall, A. J. (2019). Harbor seal pup dispersal and individual morphology, hematology, and contaminant factors affecting survival. *Marine Mammal Science*, 35(1), 187-209. <https://doi.org/10.1111/mms.12541>
- Hall, A. J., McConnell, B. J., & Barker, R. J. (2001). Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*, 70(1), 138-149. <https://doi.org/10.1111/j.1365-2656.2001.00468.x>
- Harding, K. C., Fujiwara, M., Axberg, Y., & Harkonen, T. (2005). Mass-dependent energetics and survival in harbour seal pups. *Functional Ecology*, 19, 129-135. <https://doi.org/10.1111/j.0269-8463.2005.00945.x>
- Horning, M., Haulena, M., Rosenberg, J. F., & Nordstrom, C. (2017). Intraperitoneal implantation of life-long telemetry transmitters in three rehabilitated harbor seal pups. *BMC Veterinary Research*, 13, 139. <https://doi.org/10.1186/s12917-017-1060-1>
- Huggins, J. L., Leahy, C. L., Calambokidis, J., Lambourn, D., Jeffries, S. J., Norman, S. A., & Raverty, S. (2013). Causes and patterns of harbor seal (*Phoca vitulina*) pup mortality at Smith Island, Washington, 2004-2010. *Northwestern Naturalist*, 94, 198-208. <https://doi.org/10.1898/12-14.1>
- Jemison, L. A., & Kelly, B. P. (2001). Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Marine Mammal Science*, 17(3), 585-600. <https://doi.org/10.1111/j.1748-7692.2001.tb01006.x>
- Lander, M. E., Harvey, J. T., & Gulland, F. M. D. (2003). Hematology and serum chemistry comparisons between free-ranging and rehabilitated harbor seal (*Phoca vitulina richardsi*) pups. *Journal of Wildlife Diseases*, 39(3), 600-609. <https://doi.org/10.7589/0090-3558-39.3.600>
- Lander, M. E., Harvey, J. T., Hanni, K. D., & Morgan, L. E. (2002). Behavior, movements, and apparent survival of rehabilitated and free-ranging harbor seal pups. *The Journal of Wildlife Management*, 66(1), 19-28. <https://doi.org/10.2307/3802867>
- Lays, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Biology*, 49(4), 764-766. <https://doi.org/10.1016/j.jesp.2013.03.013>
- MacRae, A. M., Haulena, M., & Fraser, D. (2010). The effect of diet and feeding level on survival and weight gain

- of hand-raised harbor seal pups (*Phoca vitulina*). *Zoo Biology*, 30, 532-541. <https://doi.org/10.1002/zoo.20356>
- McLaren, I. (1958). The biology of the ringed seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic. *Bulletins of the Fisheries Research Board of Canada*, 118.
- McMahon, C. R., Burton, H. R., & Bester, M. N. (2000). Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, 12(2), 149-153. <https://doi.org/10.1017/S0954102000000195>
- Melin, S. R., Orr, A. J., Harris, J. D., Laake, J. L., DeLong, R. L., Stoudt, S., & Gulland, F. M. D. (2010). Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. *California Cooperative Oceanic Fisheries Investigations Reports*, 51, 182-194.
- Mellish, J.-A. E., Horning, M., & York, A. E. (2007). Seasonal and spatial blubber depth changes captive harbor seals (*Phoca vitulina*) and Steller's sea lions (*Eumetopias jubatus*). *Journal of Mammalogy*, 88(2), 408-414. <https://doi.org/10.1644/06-MAMM-A-157R2.1>
- Muelbert, M. M. C., & Bowen, W. D. (1993). Duration of lactation and post-weaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. *Canadian Journal of Zoology*, 71, 1405-1414. <https://doi.org/10.1139/z93-194>
- Muelbert, M. M. C., Bowen, W. D., & Iverson, S. (2003). Weaning mass affects changes in body composition and food intake in harbour seal pups during the first month of independence. *Physical and Biochemical Zoology*, 76(3), 418-427. <https://doi.org/10.1086/375427>
- Neale, J. C. C., Gulland, F. M. D., Schmelzer, K. R., Harvey, J. T., Berg, E. A., Allen, S. G., Greig, D. J., Grigg, E. K., & Tjeerdema, R. S. (2004). Contaminant loads and hematological correlates in the harbor seal (*Phoca vitulina*) of San Francisco Bay, California. *Journal of Toxicology and Environmental Health, Part A*, 68, 617-633. <https://doi.org/10.1080/15287390590921748>
- Osinga, N., Pen, I., Udo de Haes, H. A., & Brakefield, P. M. (2012). Evidence for a progressively earlier pupping season of the common seal (*Phoca vitulina*) in the Wadden Sea. *Journal of the Marine Biological Association of the United Kingdom*, 92(8), 1163-1168. <https://doi.org/10.1017/S0025315411000592>
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Reid, J. L., Jr. (1961). On the temperature, salinity, and density differences between the Atlantic and Pacific Oceans in the upper kilometre. *Deep Sea Research*, 7(4), 265-275. [https://doi.org/10.1016/0146-6313\(61\)90044-2](https://doi.org/10.1016/0146-6313(61)90044-2)
- Rosen, D. A. S., & Renouf, D. (1997). Seasonal changes in blubber distribution in Atlantic harbor seals: Indications of thermodynamic conditions. *Marine Mammal Science*, 13(2), 229-240. <https://doi.org/10.1111/j.1748-7692.1997.tb00630.x>
- Ryg, M., Lyderson, C., Markussen, N. H., Smith, T. G., & Øritsland, N. A. (1990). Estimating the blubber content of phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1223-1227. <https://doi.org/10.1139/f90-142>
- Salazar-Casals, A., Arriba-Garcia, A., Mignucci-Giannoni, A. A., O'Connor, J., & Rubio-Garcia, A. (2019). Hematology and serum biochemistry of harbor seal (*Phoca vitulina*) pups after rehabilitation in the Netherlands. *Journal of Zoo and Wildlife Medicine*, 50(4), 1021-1025. <https://doi.org/10.1638/2018-0098>
- Sangster, S., Haulena, M., Nordstrom, C., & Gaydos, J. K. (2020). Interannual differences in postrelease movements of rehabilitated harbor seal pups (*Phoca vitulina richardii*) in the Salish Sea. *Marine Mammal Science*, 37(1), 64-79. <https://doi.org/10.1111/mms.12739>
- Skinner, J. P. (2006). *Physical and behavioral development of nursing harbor seal (Phoca vitulina) pups in Maine* (Unpub. Master's thesis). University of Maine, Orono. <https://digitalcommons.library.umaine.edu/cgi/view-content.cgi?article=1655&context=etd>
- Smirnov, N. (1924). On the eastern harp seals *Phoca (pagophoca) groenlandica* var. *oceanica* Lepechin. *Tromsø Museums Årshefter*, 47(2), 1-11.
- Steiger, G. H., Calambokidis, J., Cubbage, J. C., Skilling, D. E., Smith, A. W., & Gribble, D. H. (1989). Mortality of harbor seal pups at different sites in the inland waters of Washington. *Journal of Wildlife Diseases*, 25(3), 319-328. <https://doi.org/10.7589/0090-3558-25.3.319>
- Temte, J. L., Bigg, M. A., & Wiig, Ø. (1991). Clines revisited: The timing of pupping in the harbour seal (*Phoca vitulina*). *Journal of Zoology*, 224, 617-632. <https://doi.org/10.1111/j.1469-7998.1991.tb03790.x>
- Trumble, S. J., & Castellini, M. A. (2002). Blood chemistry, hematology, and morphology of wild harbor seal pups in Alaska. *The Journal of Wildlife Management*, 66(4), 1197-1207. <https://doi.org/10.2307/3802953>
- Trumble, S. J., O'Neil, D. O., Cornick, L. A., Gulland, F. M. D., Castellini, M. A., & Atkinson, S. (2013). Endocrine changes in harbor seal (*Phoca vitulina*) pups undergoing rehabilitation. *Zoo Biology*, 32, 134-141. <https://doi.org/10.1002/zoo.21036>
- Whaley, J. E., & Borkowski, R. (2009). *Final policies and best practices: Marine mammal stranding response, rehabilitation, and release* (NOAA Institutional Repository ID #14917). U.S. Department of Commerce, National Oceanic and Atmospheric Administration. <https://repository.library.noaa.gov/view/noaa/14917>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. <https://ggplot2.tidyverse.org/>; <https://doi.org/10.1007/978-3-319-24277-4>
- Zier, J. C., & Gaydos, J. K. (2014). Harbor seal species profile. In *Encyclopedia of Puget Sound* (pp. 1-55). Puget Sound Institute at the University of Washington.