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Conception, fetal growth, and calving seasonality of harbor porpoise (*Phocoena phocoena*) in the Salish Sea waters of Washington, USA, and southern British Columbia, Canada

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Abstract: We evaluated harbor porpoise (*Phocoena phocoena* (Linnaeus, 1758)) strandings in the Salish Sea to determine calving seasonality (1980–2015). A total of 443 strandings were analyzed, of which 134 were calves and 53 were neonates. Stranded calves were reported every month, but peaked in July, August, and September. Based on fetal size and an estimated fetal growth rate of 80 mm/month, mean (±SD) conception date (and range) was back-calculated to 11 October ± 30 days (16 August – 31 December) and was later than in most other studies. Using mean (±SD) length at birth (80 ± 5.8 cm), gestation was estimated to be approximately 10.8 months. Estimated birthing period was 16 July – 27 November, with a mean (±SD) birth date of 10 September (±30.7 days) and a birth length of 80.0 cm. Estimated pregnancy rate (0.28–0.29) is lower than reported in other areas and is likely an underestimate due to missed early embryos, poor postmortem condition of a large proportion of the stranded adult females, and potential biases related to the animals that strand and are available. This study of harbor porpoise reproduction and calving in the Salish Sea is the first assessment of calving seasonality for this species in the northeast Pacific Ocean.

Key words: calving, harbor porpoise, *Phocoena phocoena*, Salish Sea, seasonality, strandings.

Résumé : Nous avons évalué les échouages de marsouins communs (*Phocoena phocoena* (Linnaeus, 1758)) dans la mer des Salish pour déterminer la saisonnalité de la mise bas (1980–2015). Un total de 443 individus échoués ont été analysés, dont 134 bébés et 53 nouveau-nés. Des bébés échoués ont été signalés chaque mois, atteignant toutefois un maximum aux mois de juillet, août et septembre. Sur la base des tailles des fœtus et d'un taux de croissance fœtal estimé de 80 mm/mois, la date de conception moyenne (±ÉT) (et sa fourchette) est établie au 11 octobre ± 30 jours (16 août – 31 décembre) et est plus tardive que dans la plupart des autres études. En utilisant la longueur moyenne (±ÉT) à la naissance (80 ± 5,8 cm), il est estimé que la durée de la gestation est d'environ 10,8 mois. La période de mise bas estimée va du 16 juillet au 27 novembre, la date de mise bas moyenne étant le 10 septembre (±30,7 jours) et la longueur à la naissance de 80,0 cm. Le taux de conception estimé (0,28–0,29) est plus faible que ce qui est rapporté pour d'autres régions et constitue probablement une sous-estimation en raison de la sous-représentation d'embryons précoces, du piètre état après la mort d'une proportion élevée des femelles adultes échouées et de biais potentiels associés aux animaux qui s'échouent et sont disponibles. La présente étude sur la reproduction et la mise bas des marsouins communs dans la mer des Salish est la première évaluation de la saisonnalité de la mise bas pour cette espèce dans le nord-est de l'océan Pacifique. [Traduit par la Rédaction]

Mots-clés : mise bas, marsouin commun, *Phocoena phocoena*, mer des Salish, saisonnalité, échouages.

Introduction

Reproductive seasonality and calving intervals in mammals are generally highly synchronized in higher latitudes due to shorter periods of high productivity compared with low-latitude populations where reproduction may be less synchronized and more prolonged (Bronson 1989). Variation in reproductive seasonality is often the result of (or attributed to) fluctuation in seasonal prey availability, predation pressure, ambient temperature, or anthro-

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Fig. 1. Map of the Salish Sea study area (dark grey) consisting of marine waterways of southwestern British Columbia, Canada, and northwestern Washington, USA.
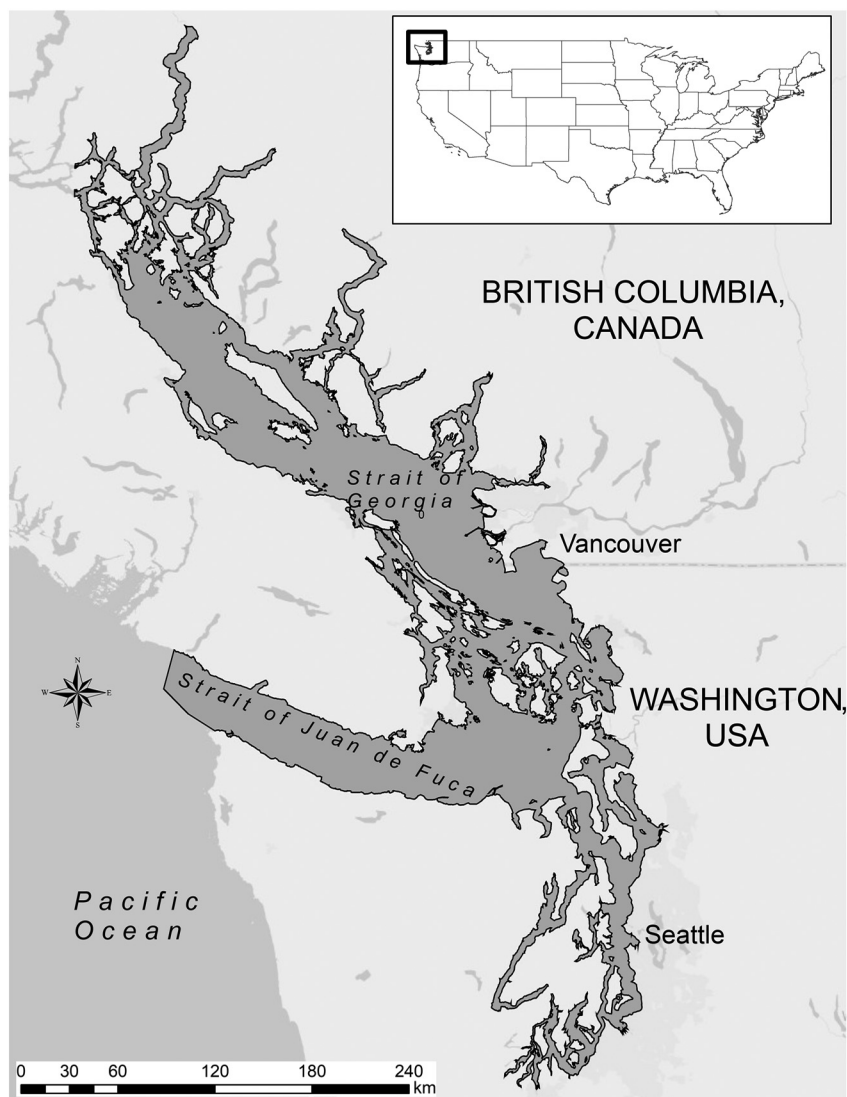
pogenic stressors (Thayer et al. 2003; McGuire and Aliaga-Rossel 2007). Knowledge of a species' birthing seasonality and time of conception are one of several life-history parameters that are crucial for species conservation.

Knowing when high numbers of newborns typically occur can help mitigate against anthropogenic threats that preferentially affect neonates. Additionally, knowing seasonality of breeding and conception can help minimize disturbance during this important reproductive period, especially if breeding locations are discrete and known. For example, just as noise from road traffic can decrease survival of young Amur tigers (*Panthera tigris altaica* Temminck, 1844) due to maternal abandonment (Kerley et al. 2002), increased vessel traffic or fisheries interaction could impact seasonal cetacean reproduction or neonatal survival (e.g., Noren 2013).

Relatively little is known about the natural history or threats facing harbor porpoises in the Salish Sea. Suspected pressures include takes from incidental fishery bycatch (Williams et al. 2008), disease (Huggins et al. 2015), disturbance from noise (Dyndo et al. 2015), predation by transient killer whales (*Orcinus orca* (Linnaeus, 1758)) (Dahlheim and White 2010), and pollution (Calambokidis and Barlow 1991; Pierce et al. 2008), the latter of which may particularly interfere with reproductive success (Murphy et al. 2015). Information on the reproductive biology of

harbor porpoises is known primarily from stranded specimens. In the western North Atlantic, reproduction is considered seasonal with yearly peak parturition occurring in mid-May in the Bay of Fundy, late spring – early summer in the Gulf of Maine (Read and Hohn 1995; Börjesson and Read 2003), and in the eastern North Atlantic in May through July (Learmonth et al. 2014). However, in California, USA, females appear to be on a 2 year calving cycle (Read 1999). In British Columbia, Canada, births supposedly occur from May through September (Baird and Guenther 1995); in inland Washington, USA, waters, they are suspected to occur within a similar temporal window, though more specific timing is less understood.

The Salish Sea is a 17 000 km² inland sea shared by Washington state and British Columbia and consists of Puget Sound, the Strait of Juan de Fuca, and the Strait of Georgia (Gaydos et al. 2008) (Fig. 1). Within the Salish Sea, harbor porpoises (*Phocoena phocoena* (Linnaeus, 1758)) are one of the most commonly sighted cetaceans and are observed year-round (Osborne et al. 1988; Calambokidis et al. 1997). They are also the most reported stranded cetaceans in these waters (Norman et al. 2004; Huggins et al. 2015). Harbor porpoises were abundant in the Salish Sea through the 1940s (Scheffer and Slipp 1948), after which time sightings of the species declined and almost completely ceased for the Puget

Sound basin and adjacent areas (south of Admiralty Inlet) through the 1990s (Calambokidis et al. 2004; Carretta et al. 2014). Recent aerial and vessel surveys, as well as anecdotal reports of sightings, indicate harbor porpoises are frequenting Puget Sound and can be found throughout the Salish Sea in greater numbers than were previously recorded during 1970–2000 and growing at >9% annually, suggesting high local recruitment coupled with immigration (Evenson et al. 2016; Jefferson et al. 2016).

Although seasonal movement patterns are incompletely understood in Washington and British Columbia, distinct seasonal changes in abundance and strandings have been noted throughout this region and may be due to shifts in distribution to deeper waters off the outer coasts during the latter portion of winter (Barlow 1988; Raum-Suryan and Harvey 1998). The timing of conception and births has always been assumed to occur during the summer months; however, no formal studies have clearly defined this.

A comprehensive assessment of stranding records, combined with temporal sighting data of neonates, can aid in delineating calving dates in inland waters (Fearnbach et al. 2012). Estimating calving seasonality will allow for better prediction of periods of vulnerability to anthropogenic and environmental pressures, as well as provide insight into harbor porpoise habitat-use patterns within the Salish Sea (Lusseau and Higham 2004; Tougaard et al. 2009; Kastelein et al. 2013; Thompson et al. 2013). Our goal for this study was to analyze harbor porpoise stranding data from the Salish Sea from 1980 to 2015 to determine if distinct seasonal calf stranding patterns and birthing periods exist by estimating the distribution of conception dates from fetal growth rates and sizes, as well as estimating duration of gestation, dates, size at birth, and pregnancy rates. We hypothesized the distribution of conception and calving of Salish Sea harbor porpoises would be within the ranges observed in other studied populations such as the Bay of Fundy and Scottish eastern North Atlantic. Definitively delineating calving seasonality is the first step in identifying and mitigating potential impacts of anthropogenic stressors on reproductive behavior or neonate survival for harbor porpoise in the Salish Sea.

Materials and methods

The study area included inland waters of Washington state and British Columbia from Campbell River in the north to the south end of Puget Sound (the Salish Sea). The Marine Mammal Health and Stranding Response Program, coordinated by the National Marine Fisheries Service (National Oceanic and Atmospheric Administration (NOAA) Fisheries), was formalized in 1992. A majority of the strandings are reported to federally authorized marine mammal stranding network responders by local citizens and tourists, with additional specimens encountered during scientific activities or beach patrols by park staff (Norman et al. 2004). The British Columbia harbor porpoise data were obtained from the British Columbia Response Network, which consisted of Fisheries and Oceans Canada, the Province of British Columbia, nongovernment agencies, and volunteers.

Study population

Stranding records included in this study covered the years 1980–2015, during which time beach cast harbor porpoises were reported to stranding response organizations throughout the Salish Sea region. In most cases, attempts were made to collect data such as length, sex, and state of decomposition. When feasible, full examinations were performed to assess reproductive status, presence of disease or injuries, and to determine cause of death (Huggins et al. 2015) as

(1) Adults: ≥140 cm (males) and ≥155 cm (females);
(2) Subadults: 106–139 cm (males) and 106–154 cm (females). Yearlings were included with subadults because it was difficult to differentiate a 1-year-old from a 2-year-old by length;

(3) Calves: ≤105 cm (with a further distinction of neonates when possible);
(4) Neonates: animals with length greater than or equal to the smallest animal confirmed not to be an aborted fetus (65 cm) — i.e., presence of aerated lungs — and ≤87 cm, or presented with an unhealed umbilicus, rostral hairs in the bristle pits, or nonerupted teeth (following Lockyer 1995), and are likely 0–2 months old;
(5) When feasible, a further distinction was made between calves and neonates using the presence of fetal folds and hair in neonates.

Age determination was not uniformly performed using tooth growth layer groups (GLG), so age-class assignments were made based on standard (i.e., straight) lengths. Length measurements were grouped into age-class range cutoffs that were developed using morphometric data from known-age harbor porpoises incidentally caught in fisheries in Washington state (Gearin et al. 1994), as well as cutoffs used in other regional harbor porpoise studies (Huggins et al. 2015). Six porpoises, reported during autumn months, were larger than 105 cm (120–127 cm) and had only a portion (front) of their teeth erupted or milk in their stomach or proximal small intestine (duodenum). Fresh or partially digested milk was presumed to be present in these cases based on the finding of one or more of the following: a large amount of thick white fluid, milk curd, or flecks of undigested milk in the stomach and (or) proximal small intestine or duodenum. However, because the age of these animals was not confirmed by GLG (Gaskin and Blair 1977) and to maintain a conservative definition of a calf according to the published literature (Gearin et al. 1994), these animals were not categorized as calves for this study, but rather as subadults. They likely represent calves that nurse longer than the mean 8 months or calves that may continue to periodically nurse while transitioning to a completely solid food diet (Lockyer 2003).

Determining reproductive seasonality

Parametric and nonparametric methods were used to estimate the calving seasonality, which included duration of gestation, conception date and period, and birthing period. To assess monthly and seasonal variability in calving rates, calves were assigned to a calendar month using straight length. Monthly totals were grouped into four seasons (December–February = winter; March–May = spring; June–August = summer; September–November = autumn). To standardize for irregular discovery or reporting of stranded calves and the degree to which these specimens represented sampling of the true harbor porpoise population, the number of calves was represented as a proportion of the total stranded porpoises reported each month and season, combined across all study years. We combined strandings across years after 2001 since there were no significant temporal shifts in births over the study period after that time when tested by negative binomial regression (likelihood ratio χ^2 = 3.22, P = 0.073), as presented by calf and neonate strandings. The year 2001 was selected because this is when the John H. Prescott Marine Mammal Rescue Assistance Grant Program was formed (NOAA 2016a). This program provided an influx of funding to support stranding response capabilities, resulting in an initial perceived increase in reported porpoise strandings that persisted over the next decade as stranding response effort caught up and became more consistent.

Due to small monthly sample sizes and variability of reported strandings, the proportion point estimates were likely to vary in how well they corresponded to the same point estimates from the true population. Therefore, Bayesian modeling was used to estimate the proportions in the form of probability distributions to help account for this variation (after Fearnbach et al. 2012). The number of stranded calves each month (and season) was modeled as being binomially distributed from all reported harbor porpoise strandings that month (and season), resulting in an estimate of

Table 1. Descriptive statistics for harbor porpoise (*Phocoena phocoena*) calf body lengths used to calculate birth size.

Age class	n	Mean (cm)	Standard deviation (cm)	Range (cm)
Fetus	15	34.5	26.7	2–81
Calves	134	89.1	8.7	65–104

the proportion of stranded calves that was assigned a prior distribution between 0 and 1, subsequently updated with the data to estimate the posterior distribution.

Length of gestation was estimated from fetal growth rate and mean length at birth, taking into account the initial lag period or nonlinear phase (t_0). Estimating birth length in wild cetaceans most often relies on assuming neonates (i.e., newborns) are distinguishable from near-term fetuses or older calves (Perrin and Reilly 1984; van Waerebeek and Read 1994). However, this is not always feasible, so to delineate likely birth lengths, an overlap criterion was used to define and estimate birth length as the mean of overlapping in utero fetal (n = 15) and calf (n = 134) straight lengths that contained the largest nonoverlapping fetus and the smallest nonoverlapping calf (body length ranges in Table 1).

An individual fetal porpoise's conception date was estimated from its corresponding length (n = 15 total fetuses). The conception date was calculated by subtracting the estimated fetal age (defined as t days) from the date on which the animal was first reported stranded (Julian date) (Börjesson and Read 2003; Learmonth et al. 2014). Therefore, fetal age at birth (i.e., length of gestation) is defined as (L_t/u)·30.5 + t_0, where u is the fetal growth rate (equal to the slope of the linear regression of fetal length (mm) on month), L_t is the mean length at birth (mm), 30.5 is the mean number of days in a month, and t_0 is the estimated duration of the lag phase. Lag phase duration (t_0) was then estimated utilizing the equation: $t_0 = 7.25 \cdot m_{birth}^{0.19}$, where m_{birth} is mean birth mass (g) (Calder 1982). Other studies (Börjesson and Read 2003; Learmonth et al. 2014) calculated mean birth mass by using the mean mass overlap of the smallest neonates with the largest fetuses; however, in the present study most fetuses were not weighed so the mean of the 10 smallest neonates was used to estimate mean birth mass. Probable dates of birth for fetuses were estimated from calculated conception dates and gestation period, assuming growth rate is the same for all fetuses.

Pregnancy rate

To generate a pregnancy rate, the effects of reproductive seasonality need to be considered. The rate was defined as the proportion of females with a detectable fetus on necropsy examination (i.e., pregnant) of the sample of mature (adult) females. As stranded adult females were not further classified as to their sexual maturity, we assumed for the purposes of this study that an adult female (≥155 cm) was sexually mature based on Gearin et al. (1994). Following steps taken in other studies, samples from the period of conception were excluded from this calculation to avoid missing the existence of early embryos (Read 1990; Read and Hohn 1995; Learmonth et al. 2014). To determine the amount of bias that could result from missing early embryos, the calculation was repeated using mature females from the whole year (i.e., not excluding the conception period females).

Data analysis

Stranding data were screened for implausible values of date, length, and age. Suspect values were checked against original data and the NOAA Fisheries National Marine Mammal Stranding database, referring to necropsy notes when feasible. Recording or copying errors were corrected and any remaining suspect values were deleted from the subsequent analysis. Data exploration and regression statistical modeling were performed using Stata version 12.0 (StataCorp LLC, College Station, Texas, USA) and WinBUGS (Lunn et al. 2000) was used to determine monthly and seasonal variability in calving rates.

Results

Stranding seasonality

Over the study period (1980–2015), a total of 510 (405 in the inland waters of Washington state; 105 in British Columbia) stranded harbor porpoises of all age classes were recorded. Of the 510 reported strandings, 443 had a confirmed straight-length measurement and age-class categorization and were used for the analyses (133 adults, 175 subadults, and 134 calves). Of the 134 calves, 53 were considered neonates. Seasonal patterns of strandings showed some degree of variation. Strandings peaked in the spring and mid- to late summer with strandings dominated by animals <1 year of age (Fig. 2). The proportion of adult females examined internally that were either lactating with signs of a recent pregnancy (e.g., unilaterally distended uterine horn or histological evidence), pregnant, or both was 21% (7/33) in spring, 5% (1/20) in summer, 50% (8/16) in autumn, and 44% (4/9) in winter. The smallest confirmed pregnant female was 161 cm. Although calves (including neonates) stranded every month, the majority were recorded during 3 months in mid- to late summer and early autumn (July–September) (Fig. 2). The proportion of calf strandings peaked during August (n = 41), with a median date of 13 August, 19 days after the median date of 25 July for neonates. Moreover, stranded non-neonate calves were recorded as early as 17 January (95 cm), which suggests births could theoretically occur as late as mid-November. The number of calves and neonates stranded showed a significant trend over time for the years 2001–2015 (Spearman's rank correlation, $r_S = 0.580$, $P = 0.022$) (Fig. 3), which coincided with the period of rapid porpoise population growth and implementation of the Prescott Program.

In spite of uncertainty related to sample sizes, there were differences in the proportion of individuals of all age classes stranded across months (Fig. 4). Calf strandings peaked in August, with a posterior median for the proportion of individuals that were calves of 0.66 (95% probability interval (PI) = 0.53–0.77) and was lowest in April (posterior median = 0.07, 95% PI = 0.03–0.14) (Fig. 4). Greater than half the number of the calves (79/137 or 58%) stranded during the summer season (June–August), resulting in a discernible difference in the monthly mean calf proportion between seasons (Fig. 5). The proportion of calves stranding during the summer out of all age classes (posterior median = 0.54, 95% PI = 0.46–0.62) was significantly greater than that in the other seasons (winter posterior median = 0.23, 95% PI = 0.14–0.35; spring posterior median = 0.08, 95% PI = 0.05–0.14; autumn posterior median = 0.38, 95% PI = 0.28–0.48), with no overlap of the posterior distributions and therefore a high probability ($P = 1$) that the proportions of stranded calves in the summer were different from the proportions in the other seasons.

Fetal growth

The fetal body length range was 2.4–81.0 cm (n = 15). A linear regression of fetal length on month (treating October as the first month) provided a good fit, with month significantly explaining 91.4% of the observed variation in fetal length ($P < 0.001$) (Fig. 6). The slope of the regression line indicates a fetal growth rate of 83.6 mm/month.

Duration of gestation and conception dates

Based on a mean birth mass of 7.7 kg or 7700 ± 122 g (n = 10 neonates for which body mass was recorded), the fetal growth lag phase (t_0) would be at least 39.7 days. Using the figure of 39.7 days and applying the fetal growth rate (83.6 mm/month) and mean length of 800 ± 58 mm, gestational duration is estimated to be 331.6 days (10.8 months). Confirmed fetuses were observed between mid-April and late December, with the smallest fetus re-

Fig. 2. Total number of stranded harbor porpoises (*Phocoena phocoena*) (n = 512) and calves (≤105 cm) (n = 137) reported from the Salish Sea (1980–2015).
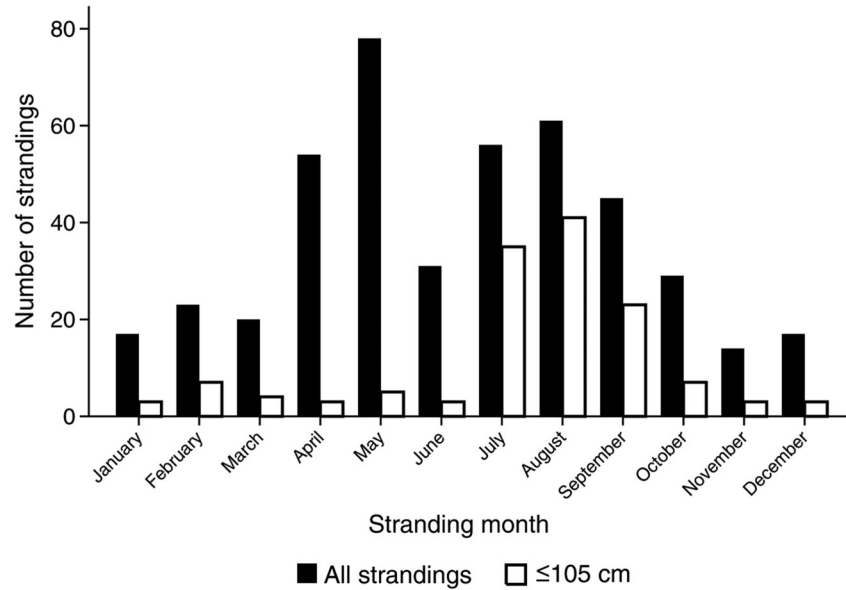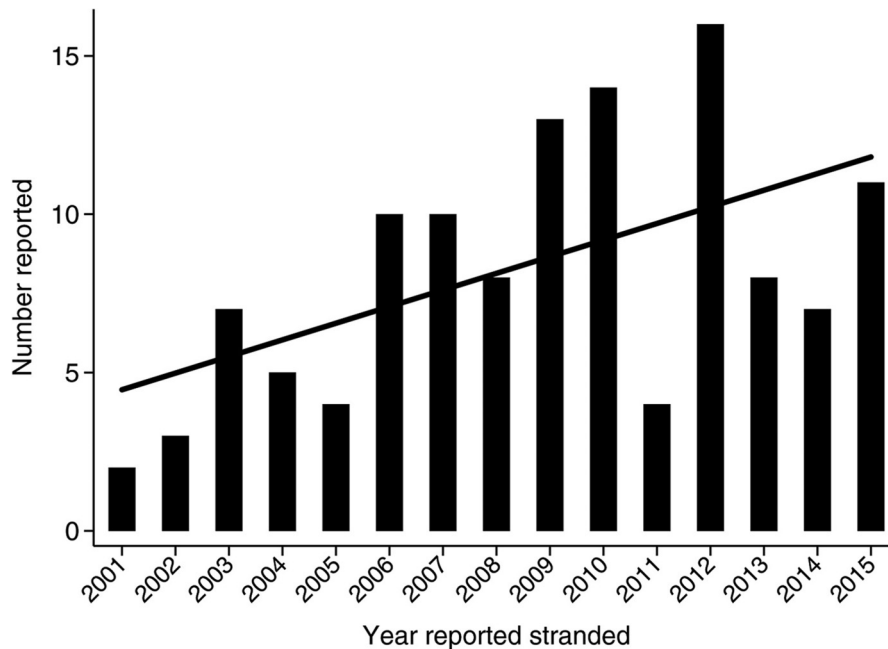

Fig. 3. Number of calves (animal ≤105 cm) reported stranded per year since implementation of the John H. Prescott Marine Mammal Rescue Assistance Grant Program in 2001 when stranding response began to receive federal financial support.

corded in October (2.4 cm) and the largest fetus (81 cm) recorded in mid-May, suggesting conception typically occurs prior to October (when the smallest fetus was recorded). The range of estimated conception dates was 16 August (for the 74 cm fetus reported in May 2013) to 31 December (30.5 cm fetus found April 1995). Of the other 13 fetuses, conception likely occurred in September (n = 3), October (n = 9), and November (n = 1).

Timing of calving

To help determine timing of calving, the occurrence of calf strandings was examined first. Calf strandings (n = 134) were recorded during every month; however, most (n = 96; 71.6%) were reported between the end of July through September. In addition, 53 of the calves were neonates (i.e., 65–87 cm) (39.6%) and were reported stranded from 5 January to 23 November, with the ma-

jority (n = 39; 75%) occurring during July and August. Thus, the approximate birth dates of the 15 fetuses, based on estimated conception dates, duration of gestation (331.6 days), and fetal growth rate (83.6 mm/month), would have ranged from 16 July to 27 November, with a mean date of 10 September (SD = 30.7 days). If the lone July birth date is removed, then the mean birth date would shift later to 14 September (SD = 27.4 days).

Neonatal size

Neonates (n = 53) had a minimum body length of 65 cm with the smallest measuring 65 and 66 cm in length. Mean length for this group was 80 cm (95% CI = 78.6–81.9 cm). Neonatal individuals, although represented in every month except December, were reported stranded almost exclusively during July and August. Of those neonates displaying traits such as fetal folds, unhealed

Fig. 4. Number of calves as a proportion of the total number of individual harbor porpoises (*Phocoena phocoena*) stranded during each month. The boxes represent the central 75% interquartile range, the vertical lines represent the intervals encompassing 95% of the distribution, and the horizontal lines represent the posterior medians.
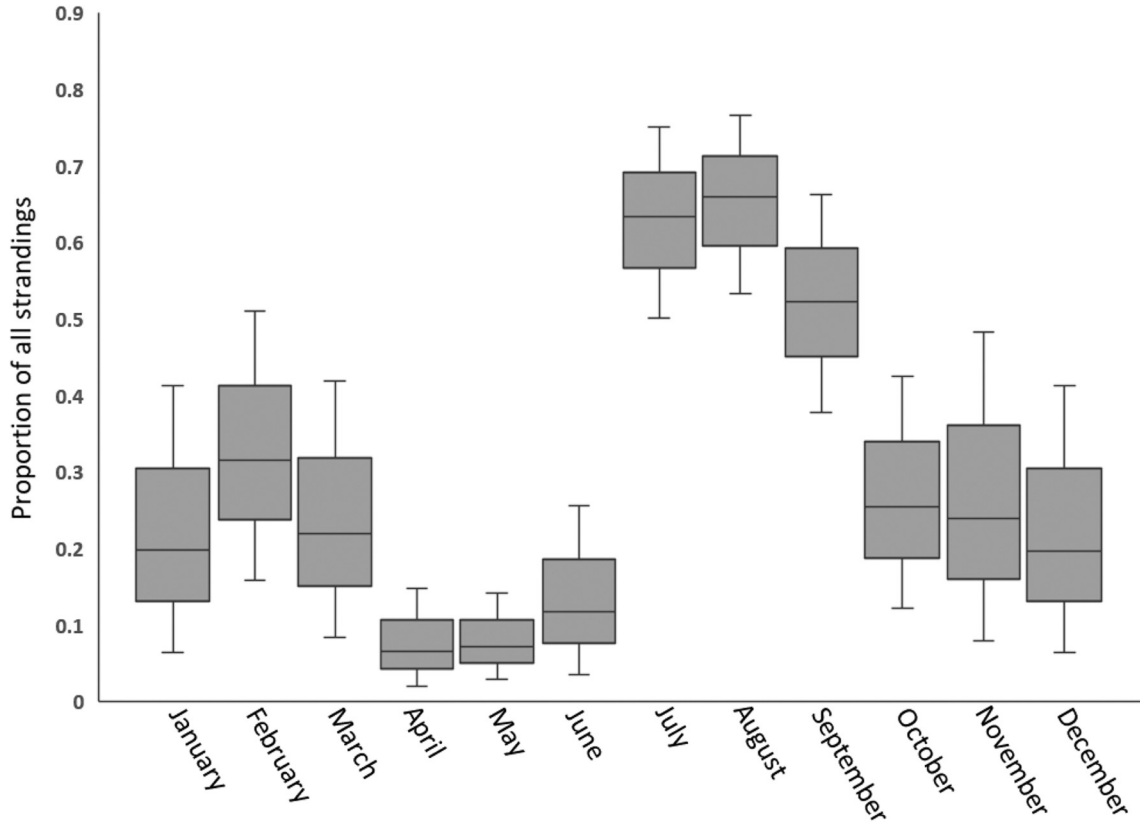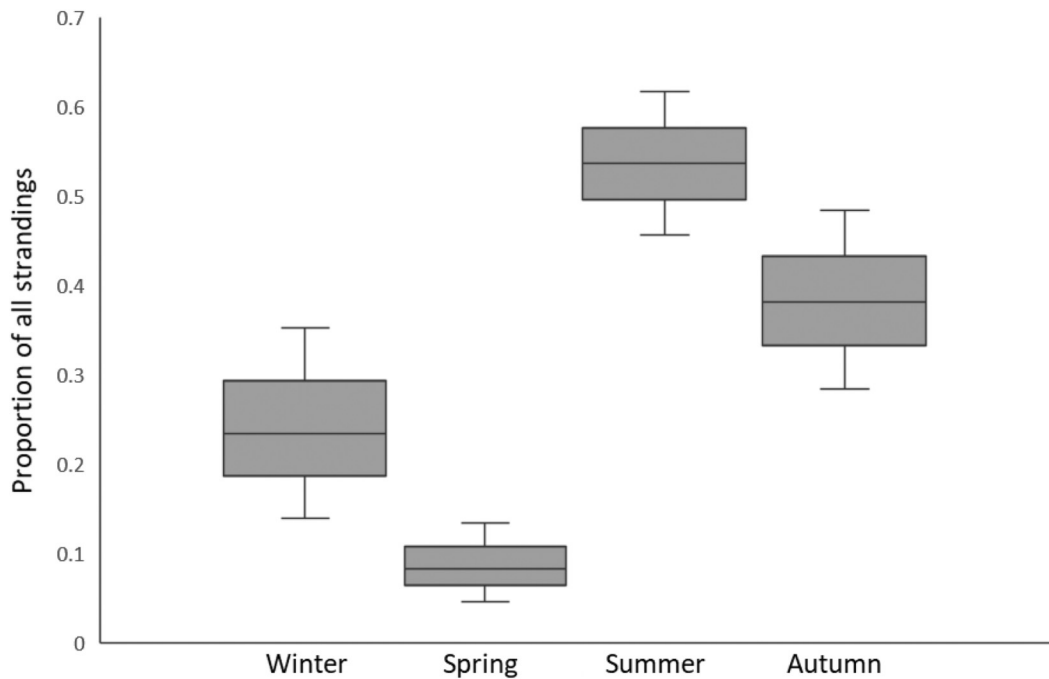

Fig. 5. Number of calves as a proportion of the total number of individual harbor porpoises (*Phocoena phocoena*) stranded during each season. The boxes represent the central 75% interquartile range, the vertical lines represent the intervals encompassing 95% of the distribution, and the horizontal lines represent the posterior medians.

Fig. 6. Relationship of fetal length (mm) and month first reported stranded for harbor porpoises (*Phocoena phocoena*) from the Salish Sea, in southern British Columbia, Canada, and Washington, USA ($n = 15$). $R^2 = 0.914$.
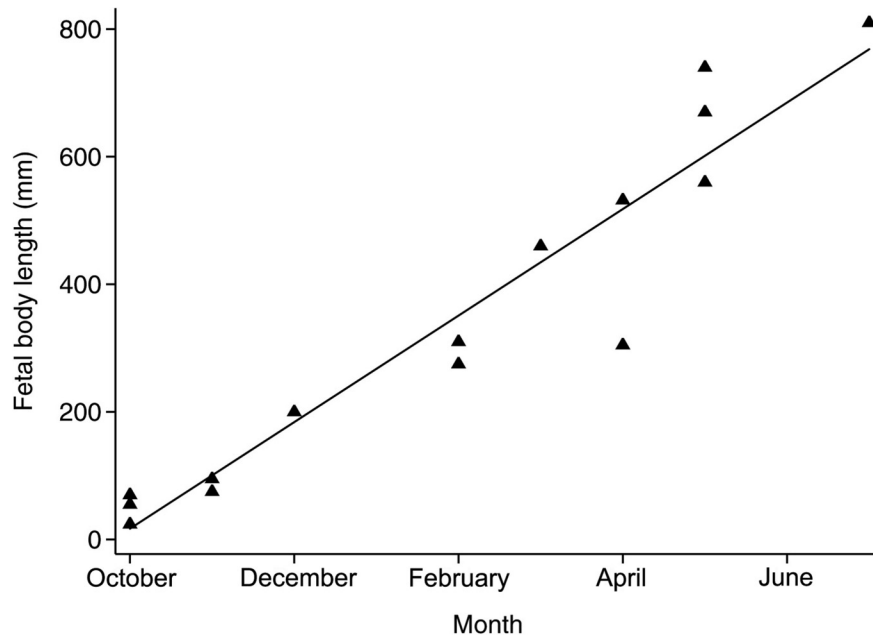
umbilicus, or bristles on the snout ($n = 6$), lengths ranged from 70 to 87 cm (mean = 81.0 cm).

Pregnancy rate

Taking the range of conception dates to be 16 August – 31 December and excluding mature females recorded between these dates to reduce error due to missing early-term fetuses, there were 55 adult (i.e., ≥155 cm) females of which 16 displayed signs of pregnancy (presence of a fetus, actively lactating, etc.), giving a pregnancy rate of 0.29 ± 0.46 (mean ± SD). Excluding adult females from the entire August to December period leaves 53 adult females of which 15 showed signs of a current or recent pregnancy, giving a pregnancy rate of 0.28 ± 0.45 (mean ± SD).

Discussion

Harbor porpoise calving within the Salish Sea is seasonal as demonstrated by analysis of stranded specimens over 30 years. Animals classified as calves (≤105 cm) are most commonly reported in the late spring and summer months. Corresponding to this is the finding of a significant trend of fetal growth rate over the calendar year, resulting in maximum fetal length at the approximate beginning of the main calving season (May – late July). Based on the approximate length of gestation (10.8 months), estimated conception dates range between mid-August and the end of December. This is the first time a comprehensive assessment of calving seasonality has been evaluated for this population of harbor porpoise. However, it must be kept in mind that stranded animals may not be entirely representative of the population from which they originate compared with fishery bycatch animals. The former are individuals that are often unhealthy or fail to thrive and thus die prematurely, whereas the latter are presumed to be healthy and are more representative of the overall population.

Although there was relatively constant stranding response effort from 2001 to 2015 (Fig. 3), the increasing annual calf strandings recorded during this time period were likely due to population growth associated with changes in prey availability or habitat (Urian et al. 1996; Nichol et al. 2013; Meyer-Gutbrod et al. 2015). However, stranding increases from other causes such as changing disease or contaminant burden patterns have not been ruled out,

as detailed data on these factors are currently limited for this region and the youngest age classes.

The estimated rate of fetal growth, approximately 83.6 mm/months, is in very close range to rates estimated in harbor porpoises in Scottish waters (84 mm/months) (Learmonth et al. 2014), the Kattegat and Skagerrak seas (Börjesson and Read 2003), and from historic data from the North (Grieg 1897) and Black (Tsalkin 1940 cited in Tomilin 1967) seas (83 mm/months). The use of multiple data sets afforded Grieg (1897) and Tsalkin (1940) the opportunity to check the assumption that fetal growth rate is constant and species-specific. Having detected no differences in rate between the three geographic data sets (North, Black, and Kattegat and Skagerrak seas), this suggests gestation duration is relatively constant in harbor porpoises as in other mammals (Ricklefs 2010).

Although fetal growth rates remain relatively constant within species, the length of gestation may vary under certain conditions (Boyd 1996), but variation is not expected to be large among individuals or within geographic regions. In the Salish Sea, conception (11 October) peaks approximately 3, 2, and 1.5 months later than the Bay of Fundy – Gulf of Maine (6 July), the Kattegat, Skagerrak, and North seas (25 July), and the Baltic Seas (18 August), respectively (Börjesson and Read 2003) and 2 months later than harbor porpoise in Scottish waters (4 August) (Learmonth et al. 2014). Peak conception dates have not been determined for this species in California; however, a 5 cm fetus was observed in August in a study of 332 harbor porpoises from central California waters (Hohn and Brownell 1990), indicating conception in that animal occurred no later than late July or early August.

As with fetal growth, duration of gestation is not expected to vary considerably between individuals or geographic areas. Duration of gestation in the Salish Sea (10.5–11 months) is consistent with that estimated in other regions (10.6–10.8 months) (Read 1990, 1999; Sørensen and Kinze 1994; Börjesson and Read 2003). Therefore, if the estimates of length of gestation and conception are accurate for the Salish Sea, most calving probably occurs between August and October when water temperatures are higher and prey availability is abundant for the mother (Hohn and Brownell 1990; Read 1990, 1999; Börjesson and Read 2003). As Börjesson and Read (2003) noted, given the relatively small size of newborn calves and their high surface to volume ratio, it is ex-

pected reproduction would be timed so that birth occurred during the most favorable environmental conditions. In the Salish Sea, timing of peak calving (early September) corresponds with the warmest months of the year to benefit neonate thermoneutrality (Börjesson and Read 2003), whereas calmer weather increases calf survival and reduces energy expenditure (Whitehead and Mann 2000). The relatively high number of strandings observed in July may be driven by premature births or weaned calves from the previous season, as demonstrated by specimens ranging from 66 to 104 cm documented during this month. Sea surface temperatures here are highest during the months June through October (mean 11–12 °C) with the first 2 weeks of September averaging 12 °C (NOAA 2016b).

Mean length at birth may vary within and between populations and ideally should be estimated separately for each geographic population. The range of birth sizes in this study was not as great when compared with other studies, although this could be due to a smaller sample size. Other studies suggest that a wide range of harbor porpoise birth sizes is common. The estimated mean birth length in this study (80.0 cm) is similar to, and at times slightly larger than, values reported in other populations where researchers give sizes within the range of 70–85 cm, including central California (77.3 cm) (Hohn and Brownell 1990), Scotland (76.4 cm) (Learmonth et al. 2014), British waters (70.0 cm) (Lockyer 1995), and the Kattegat and Skagerrak seas (76.2 cm) (Börjesson and Read 2003). A much wider range was reported in Denmark (63–86 cm) (Sørensen and Kinze 1994), which suggests a wide range of birth lengths is characteristic for this species.

The smallest neonate seen in this study measured 65 cm, but it cannot be confirmed as being full term because a complete necropsy was not performed. The next smallest were 66 and 68 cm long. A necropsy was not performed on either of the two 66 cm porpoises (one was a live stranding pushed back out to the water), but a necropsy was performed on the 68 cm animal where an internal exam revealed its lungs had been aerated. The largest fetus was an 81 cm long specimen recorded in mid-July and the next largest specimen was 53–74 cm long. However, the smallest neonate lengths may represent premature births, whereas the largest fetuses may be abnormally large (Learmonth et al. 2014).

There were six porpoises longer than 105 cm (one measured 127 cm), with partially erupted teeth or milk in the stomach. These animals were not aged by GLGs, so they were classified as subadults for the purposes of this study. Calves as large as 120 cm have been reported in the Bay of Fundy – Gulf of Maine, from specimens killed during the months of July through September (Read and Tolley 1997), whereas in Scotland, maximum recorded length was 88 cm (Learmonth et al. 2014). For porpoises in the Pacific Northwest, there may be individual variability in length at birth and tooth eruption within the Salish Sea that might also fluctuate by region, time of year, and timing of birth, as noted in the Sea of Azov and Black Sea (Gol'din 2004). Furthermore, Salish Sea calves measuring between 105 and 127 cm may represent individuals approaching the end of their first year, but who have not completed tooth eruption nor weaning. Aging of these animals by GLGs would help better define age for large calves with partially erupted teeth or milk in their stomach.

In this study, the estimated pregnancy rate was 0.29, slightly lower than the lowest published rates that were observed in harbor porpoises in Scottish waters (0.34–0.40) (Learmonth et al. 2014) and the North Sea (0.32) (Hasselmeier et al. 2004). The rate of 0.28 is equivalent to mature females becoming pregnant, on average, once every 3.0–3.5 years and is lower than estimates for northwest Washington state (0.77), Denmark (0.73), Bay of Fundy (0.74), Gulf of Maine (0.93), or Iceland (0.98) (Read 1990; Gearin et al. 1994; Sørensen and Kinze 1994; Read and Hohn 1995; Ólafsdóttir et al. 2002), all of which were based on bycaught porpoises. In a study of stranded specimens only, the pregnancy rate along the east coast of the United States was 0.72 (Polacheck et al.

1995). It is likely, however, that our figure of 0.28–0.29 is underestimated. This study was based only on stranded animals, some of which may have been mature females that presented outside the implantation period calculated for this population (16 August – 31 December) when small embryos or fetuses could be missed. In addition, the number of corpora lutea was not used to determine presence of a pregnancy, so very early pregnancies may have been missed. Additionally, early pregnancies may have also been missed due to postmortem decomposition, lack of necropsy, or examiner inexperience.

Despite the relatively low pregnancy rate calculated in the present study, the population growth rate observed in the Washington state portion of the study area, and overlapping a similar time period as this study, was around 10%, approaching twice that rate through the late 1990s (Evenson et al. 2016). Within Puget Sound, the growth rate was 33.8% for 2000–2014 during which time harbor porpoises were observed every year. The results of aerial surveys conducted over 20 years documented increasing population growth trends, followed by stabilization of the harbor porpoise in the waters of the Salish Sea (Evenson et al. 2016), further highlighting the pregnancy rate in the present study is an underestimate.

The presence of four pregnant and actively lactating females in our sample suggests that porpoises in Salish Sea waters can give birth annually (fetal size range: 2.4–9.5 cm). An annual breeding cycle has been reported for porpoises in the Bay of Fundy, West Greenland, and Iceland (Read and Hohn 1995; Ólafsdóttir et al. 2002; Lockyer 2003). In Learmonth et al. (2014), the authors found that 10 of the pregnant females (n = 21) for which cause of death could be determined died from poor health or pathological conditions (n = 5) and dystocia (n = 5). These findings highlight two possible issues: (1) the birth rate can be artificially low because of abortions and deaths of pregnant females or (2) strandings can include a high proportion of animals that are in poor health and females that are less healthy may experience lower pregnancy rates and fewer successful pregnancies than healthy mature females. Therefore, pregnancy rates calculated from stranded porpoises are likely underestimates (Learmonth et al. 2014). The low pregnancy rate in the Salish Sea should be further explored and revised as additional stranding data become available.

Using fetal size to back-calculate conception dates is a relatively new approach (Börjesson and Read 2003; Learmonth et al. 2014) that holds promise for providing data on reproduction and life history of cetaceans. The results of this work highlight the value of continuing to collect biological (i.e., stranding) data and using the results to analyze the status of Salish Sea harbor porpoises, as well as other species found within the region such as the endangered Southern Resident killer whales. Harbor porpoises may serve as a sentinel for killer whale health and environmental monitoring. The results of this study represent the first comprehensive effort to examine calving seasonality for harbor porpoises in the Pacific Ocean apart from the study by Hohn and Brownell (1990) who examined harbor porpoises from central California. They determined calving occurred primarily in May and in early June, earlier than the estimate for the Salish Sea.

The use of stranded specimens to calculate life-history parameters presents caveats during interpretation given that the study sample may not accurately reflect characteristics of the overall population from which the animals originated (Peltier et al. 2012). Carcass condition, currents, or other factors may result in inaccurate sex and age class ratios resulting in biased life-history rates. Although there may be biases using life-history data obtained from strandings, cetacean stranding data nonetheless play an important role in providing the main biological information on which vital rates such as calving can be estimated and represent a valuable research resource.

Potential contributors to porpoise mortality in the Salish Sea (disease, contaminants, fishery bycatch, killer whale attacks, star-

vation, and separation of calves from mothers due to anthropogenic disturbance) could threaten these animals at a population level (Calambokidis and Barlow 1991; Gearin et al. 2000; Gaydos et al. 2005; Noren 2013; Norman et al. 2017). Parameters such as conception and calving rates can help researchers assess and model these threats and their impact on this population.

Acknowledgements

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