





Sighting patterns reveal unobserved pupping events to revise reproductive rate estimates for Hawaiian monk seals in the main Hawaiian Islands

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Abstract

We used sighting reports, including decades of citizen-reported Hawaiian monk seal (*Neomonachus schauinslandi*) sightings, to describe female breeding biology and reproductive success in the main Hawaiian Islands. We first used this data set to describe the timing of events in the female reproductive cycle. We then conducted an expert review of patterns in sighting histories to detect unobserved pupping events. Finally, we estimated the age-specific reproductive curve for female monk seals in the main Hawaiian Islands. Charting reproductive cycles showed indications of the robust condition of female monk seals in the main Hawaiian Islands; they nursed pups 12% longer than their counterparts in the Northwestern Hawaiian Islands and regained condition to molt more quickly after weaning a pup. By examining sighting histories, we were able to infer 25 unobserved pupping events that had previously gone uncounted. We accounted for additional uncertainty with a randomization procedure. After accounting for unobserved pupping events, the age-specific reproductive rate of main Hawaiian Islands monk seals exceeded 0.70 for prime aged females (8–18 years). This is the highest reproductive rate reported for any of the Hawaiian monk seal breeding sites,

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illustrating the important role of the main Hawaiian Islands population in Hawaiian monk seal recovery.

KEYWORDS

citizen science, Hawaiian monk seal, *Neomonachus schauinslandi*, reproductive cycle, reproductive rate, sightings

1 | INTRODUCTION

Marine mammal research often relies on brief onshore or at-surface sightings of animals that live otherwise elusive lives underwater. Although limited sighting opportunities can leave important gaps in observations, the long-term pattern of sightings can be exploited to describe many aspects of marine mammal biology. Animal sightings provide the basis for standard methods of estimating marine mammal population abundance and condition (Hammond, 1995), as well as determining their distribution and conservation status (Bundone et al., 2019). Given sufficient numbers of sightings, researchers can achieve high statistical power for tracking vital rates and abundance trends (Embling et al., 2015). Here we examine patterns in Hawaiian monk seal (*Neomonachus schauinslandi*) sightings data to infer unobserved pupping events and improve reproductive rate estimates.

Hawaiian monk seals are among the world's most endangered marine mammals, with only around 1,400 remaining as of 2017 (Carretta et al., 2019). The majority of the population (~1,100) inhabits remote islands and atolls of the Northwestern Hawaiian Islands (NWHI), and the remainder (~300) occur in the heavily human populated main Hawaiian Islands (MHI) (Figure 1). Although the monk seal population had a many-decades history of decline and remains well below historic levels, recent trends have shown encouraging growth (Baker et al., 2016). An important part of the monk seals' potential for recovery has been an increase in monk seal abundance in the MHI over the past two decades (Baker et al., 2011). The MHI contained a negligible portion of the species total population until this segment of the monk seal population began expanding in the late 1980s (Baker & Johanos, 2004; Baker et al., 2011).

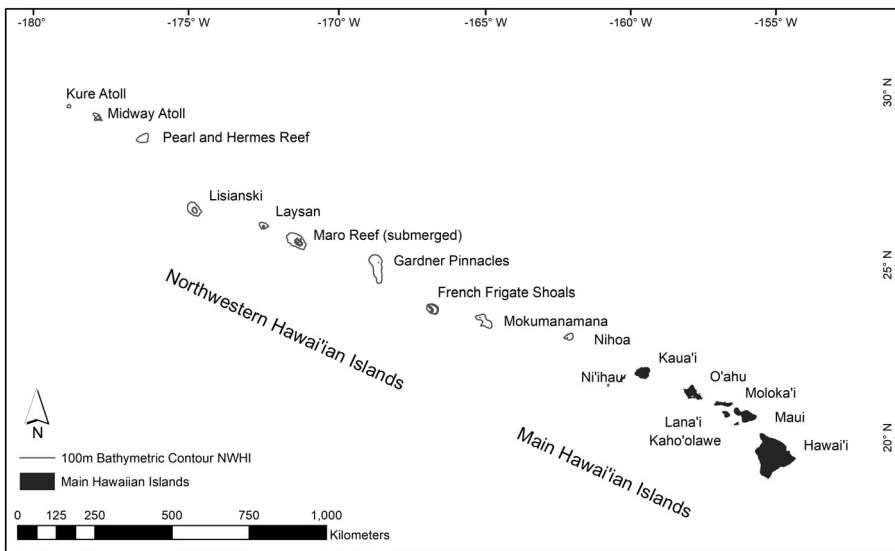


FIGURE 1 This study took place in the main Hawaiian Islands. The range of Hawaiian monk seals extends throughout the Hawaiian Archipelago (including main and northwestern islands).

While seals in the MHI face a number of anthropogenic threats (Barbieri et al., 2016; Gobush et al., 2017), seals in this region appear to be free of some of the ecological limitations facing seals in the NWHI (Baker, 2008). Seals in the main islands are generally observed in good body condition, pups wean at large girths and have favorable survival rates, and females, on average, pup at younger ages than those in the NWHI (Baker & Johanos, 2004). All of these observations are consistent with a high reproductive rate for main islands females. However, estimates based on direct observation of nursing pairs are likely to be biased low, leading to underestimating the recovery potential of this population. Monk seal pupping events are likely to be particularly subject to detection bias, as these seals pup asynchronously, typically haul out and pup in solitude (unlike many pinniped species with concentrated breeding colonies), and often select remote locations where observations are less likely. However, previous research (Johanos et al., 1994) suggests that, on the individual level, female monk seals follow well-defined timing patterns in pupping and molting that may aid the detection of these unobserved pupping events. Additionally, many (22%; NMFS, unpublished data) of the females in the main islands were first identified as adults. Due to assigning these females a minimum adult age (5 years), standard reproductive curves (Harting et al., 2007) would likely be skewed toward younger ages. A more accurate accounting of maternal age and pup production is necessary to better estimate the reproductive rates of this important component of the monk seal population.

Accurate estimation of reproductive rates is crucial to conservation management and setting reasonable recovery goals (Lalas & Bradshaw, 2003). Further, changing trends in birth rates can be indicative of either recovery or decline, thus it is important to eliminate bias based on low detection at remote locations (Holmes et al., 2007). Better characterizing the reproductive biology of female monk seals in the MHI will be crucial in tracking population trends and managing the recovery of this population.

In the effort to monitor Hawaiian monk seals across the remote reaches of numerous islands within the MHI, the United States National Oceanographic and Atmospheric Administration's Hawaiian Monk Seal Research Program (NOAA HMSRP) has supplemented data collected by professional biologists with sightings from large networks of volunteers and public hotlines. While in the NWHI, HMSRP has used long-established seasonal camps where professional biologists complete dozens of systematic surveys per season, sometimes achieving full enumeration of all individuals (Baker et al., 2006; Johanos & Baker, 2002), it would be impractical/impossible to routinely survey all beaches along the >1,000 km of coastline in the MHI. Thus, HMSRP relies on public reports and volunteer citizen scientists to collect data on seals in the MHI. Citizen science (the involvement of members of the public or amateur scientists in the collection of scientific data) has a long and increasingly recognized role in wildlife conservation science (Follett & Strezov, 2015). The use of volunteer citizen scientists often provides cost savings that can vastly increase the capacity for wildlife research (Newman et al., 2003).

Here we used HMSRP's rich data set, including decades of citizen-reported Hawaiian monk seal sightings, to better understand female breeding biology and reproductive success in the MHI. We first used this data set to better determine the temporal patterns of the female reproductive cycle. We then used patterns in sighting histories to detect unobserved pupping events, which allowed us to fill gaps and incorporate uncertainty in estimated reproductive output. Finally, we estimated age-specific reproductive curves for female monk seals in the MHI.

2 | METHODS

2.1 | Sources of sightings data

For this study, we used all sighting reports (from 1962 to 2017) of individually identified adult female seals compiled by biologists from HMSRP or partner agencies, volunteer citizen scientists, and public hotlines. Citizen science efforts have increased concomitant to the growth of the MHI monk seal population since the 1990s. Monk seal volunteer organizations had more than 250 members as of 2018, with effort concentrated on the islands of O'ahu and Kaua'i. The structure of volunteer citizen science groups has been tailored to specific islands throughout the

MHI chain, but data reporting has been standardized (reporting key biological and geographical variables in consistent format) to ensure compatibility with HMSRP databases. HMSRP liaisons have played a key role in ensuring the quality of volunteer data collection. HMSRP staff have provided regular training, including methods of identifying individual seals (including applied alpha-numeric identification flipper tags, codes bleached into seal hair, natural markings such as pigment irregularities or scars), describing the molt status of individuals (monk seals molt their hair in a catastrophic molt each year). Trained volunteers monitored the public reporting hotlines and typically followed up on hotline reports to verify animal identification and data such as sex, size, and molt status. Sighting reports from the public were often accompanied by digital photographs, allowing HMSRP biologists to further confirm the data's quality and accuracy.

2.2 | Describing reproductive cycles

Previous research based on intensive observations (where nearly all pupping events were observed) at seasonal field camps in the NWHI found that there were discernible patterns in the time intervals a pup nursed, the female molted, and the next pup was born (Johanos et al., 1994). The interpup interval of approximately 12.5 months leads to a characteristic staggered pattern in the year-to-year timing of an individual female's pupping and molting. Here we describe the timing of reproductive events for seals in the MHI and report any differences from those in the Northwest Hawaiian Islands.

The three events used to characterize a female's reproductive cycle were nursing, weaning, and molting. A birth date was recorded as the first day a female was observed with a nursing pup. The weaning date was recorded as the first day after which the pup was consistently observed without its mother. As such, the weaning date indicates the end of female investment in nursing the pup, whether the pup successfully weaned, was abandoned, or died. We limited our examination to pups that were nursed and weaned alive and excluded pups that were stillborn, died before weaning, or were abandoned before reaching size to survive independently (<17 days, consistent with Johanos et al., 1994). The date of molt beginning was recorded as the date a female was observed with >10% of her hair molting or sloughing off. Molt beginning dates frequently go unrecorded (often unnoticed by less skilled observers), but the molt records from trained observers that are entered into the database are highly accurate, as verified with photos by HMSRP biologists.

Following the methods previously used in the NWHI (Johanos et al., 1994), we took several measures to ensure data quality; we excluded data for sighting reports with pupping, nursing, and molting dates coded as uncertain (date completely unknown or estimated over a range of >4 days). Because our analysis relied on the recreation of individual sighting histories, we excluded seals with uncertain identities and those only observed on Ni'ihau Island (where access was limited and surveillance was insufficient for tracking events in the reproductive cycle). This data filtering resulted in a smaller data set. However, the increased accuracy was essential to calculate the duration of intervals between key reproductive events.

2.3 | Inferring unobserved pupping events

Previously described patterns in female reproductive and molting cycles suggest that there are discernible differences in the timing of events for females that have given birth and nursed a pup in a given year than those that have not (Johanos et al., 1994). We exploited these telltale patterns to assess the number of pupping events that may be missed based on observed nursing alone. We plotted a timeline of all sightings of adult female seals in the MHI, including the date and island of the report, lactation, and molting status. We calculated the length of gaps between sightings, highlighting gaps approaching the length of a normal lactation period (≥ 35 days), indicating that a female

could have given birth and nursed a pup undetected between sightings. All plots were constructed in R (R Core Team, 2013).

A team of three experienced NOAA HMSRP monk seal biologists examined plots and reached consensus for coding each breeding year for each female seal (hereafter “seal-year”) with one of four sighting history codes.

1. Pup observed: the female was observed with a nursing pup.
2. Pup ruled out: sighting reports were sufficient to say that a female could not have given birth and nursed a pup without detection, i.e., there were no sighting gaps of ≥ 35 days, and/or sighting gaps were either postmolt or more than 90 days prior to molt, indicating they were unlikely to be associated with pupping (note: in relying on sighting gaps related to healthy nursing periods, it would be possible to miss miscarriages, stillbirths, or births followed by neonatal mortality).
3. Pup inferred: the year-to-year pattern of observed nursing and/or molting suggests that a nursing event took place during a noted sighting gap, i.e., sighting gaps ≥ 35 days exist preceding molt and in staggered pattern from year to year.
4. Pup status unknown: not enough sightings to confirm or rule out a pup (note: this could be the norm for seldom-seen animals since pattern detection requires sequences of years with pupping and/or molting data).

2.4 | Recalculating reproductive rates

We used a Monte Carlo (MC) simulation process account for unknown maternal age and unobserved pupping events to produce a reliable age-specific reproductive curve for MHI female monk seals. The first step in each MC iteration ($N = 10,000$ simulations) was to assign a random starting age and birth year to females first observed as adults (hereafter referred to as minimum-aged seals) consistent with the estimated survivorship schedule of main island seals (Baker et al., 2011). Also, it is constrained to fall between the minimum age for adult-sized seals (age 5) and a maximum of age 32 (the age of the oldest known monk seal in the wild) at the seal's last sighting.

The next step was to limit the impact of detection bias by supplementing the observed pupping with the estimates of unobserved pupping. First, because seal-years were only coded 3 if sightings patterns strongly supported inference of an undetected pup, we treated each seal-year coded as either 1 or 3 (observed and inferred pups, respectively) as a pupping year. Next, we added pups to the estimate to account for some amount of unobserved pupping that went undetected in those seal-years with pup status unknown (insufficient data to confirm or rule out pupping). We know that any seal-year in which we cannot rule out a pup, a birth could have occurred. However, because it would likely produce an overestimate to directly add all code 4 seal-years to the pup total, these cases were probabilistically allocated to pupping or nonpupping using binomial sampling. For each code 4 seal-year, a random number was sampled (uniform distribution in the interval $[0,1]$) and tested against the corresponding age-specific rate for seals at Laysan Island. Laysan was selected because it is the site having the most complete reproductive data set, where the estimated rates are believed to be the most reliable, and, because this Northwestern site is likely to have lower reproductive rates than the MHI, it is likely to provide a conservative estimate (Harting et al., 2007). Each MC iteration thereby provided one possible age structure and one possible reproductive rate for each age class.

At the conclusion of all simulations, the mean rate and associated 5/95 percentiles were calculated for the distribution of age-specific observations, and a 5-parameter reproductive function was fit to the mean values as described in Harting et al. (2007). This function defines a typical reproductive pattern in which there is a gradual increase in fecundity as seals approach maturity, peak fecundity for mature seals, and a gradual senescent decline in fecundity as females' age. To assess the impact of adjusted reproductive rates on population dynamics, we compared the relative effect of each sighting history code on the population growth rate (λ). We calculated λ using reproductive rates based

(1) solely on observed pups (code 1), (2) adding inferred (codes 1 + 3) pups, (3) adding a randomized portion of pups to account for unknown events (codes 1 + 4), and (4) incorporating all possible pupping events (codes 1 + 3 + 4).

3 | RESULTS

3.1 | Sources of sightings data

Citizen-reported seal sightings made a notable contribution to monk seal science, making up the vast majority (87.2%) of HMSRP's monk seal data records in the MHI (Figure 2). Though sightings were rare and sporadic prior to the 2000s ($n = 1,522$ from 1962 to 1999), a growing monk seal population and increased public awareness led to greater engagement and increasing sighting reports ($n = 98,347$ sightings from 2000 to 2017; Figure 2).

A 2003 O'ahu pupping event marked the beginning for one "super volunteer," D. B. Dunlap, who dedicated much of his time to reporting seals and developed great skill in seal identification and observation. In these early years Dunlap's reports accounted for as many as 47% of all seal sightings reported. Active from his first seal pup experience in 2003 until his death in 2017, Dunlap was responsible for a total of 21% of all seal sighting reports during this time (Figure 2). We highlight the contribution of this individual volunteer to demonstrate both the impact that a single citizen scientist can have and the importance of growing a citizen science program beyond the few super-dedicated participants.

3.2 | Describing reproductive cycles

Based on extensive sighting reports, we were able to describe the reproductive cycle of MHI female monk seals (Figure 3). Pupping occurred throughout the year, with peak pupping season from April through July (Figure 4). Lactation occurred for a mean of 43.7 ($SD = 4.7$) days after pupping. Females molted an average of 54.0 ($SD = 10.1$) days after weaning a pup. Subsequent pups were born an average of 288.8 ($SD = 10.6$) days after a female began molting. For females pupping in consecutive years, the mean pup to pup interval was 381.7 ($SD = 9.9$) days. In confirming that

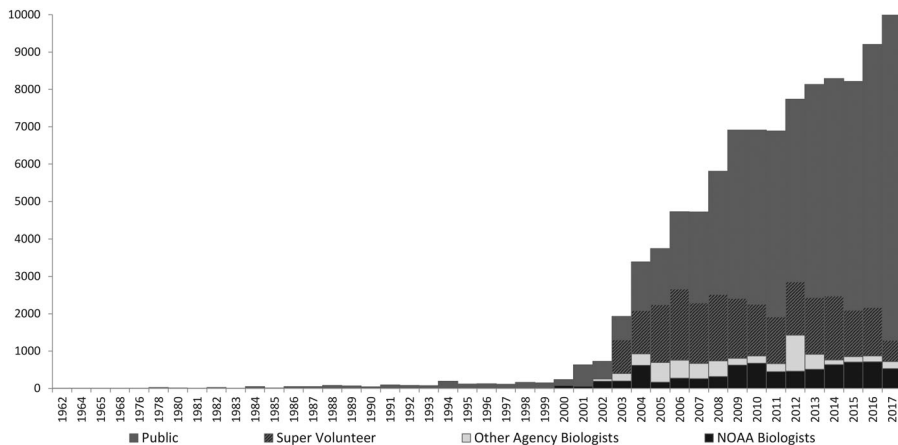


FIGURE 2 Trends in Hawaiian monk seal sightings reports in the main Hawaiian Islands, 1962–2017. While agency efforts remained relatively stable, citizen involvement in reporting monk seal sightings grew rapidly over time. Note, some seal occurrences may be reported by more than one member of the public, so this graph reflects sighting effort, but not necessarily number of individual seals reported.

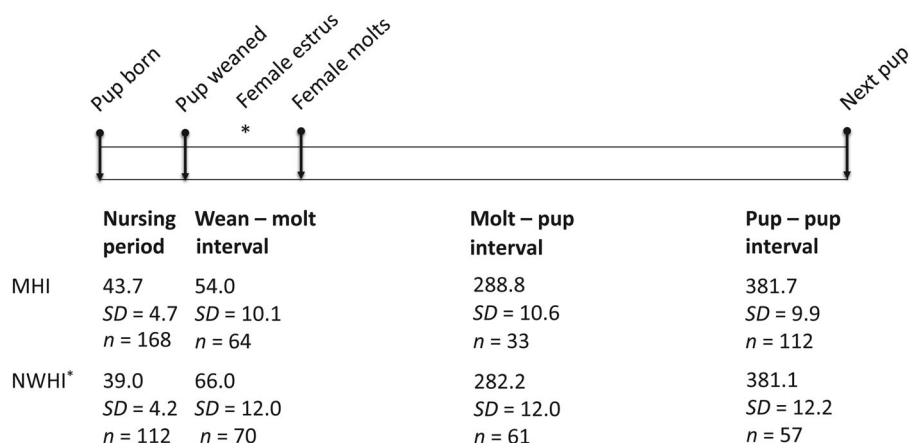


FIGURE 3 Data from the current study of main Hawaiian Islands (MHI) monk seals is displayed in comparison to results from an earlier study employing similar methods in the Northwestern Hawaiian Islands (NWHI).

* Data from Johanos et al. (1994). Their NWHI research inferred that estrus occurred between weaning and molting, based on mating wounds observed on females. Observations of mating wounds were not recorded in the current MHI study.

main islands seals had a regular inter pup interval longer than 1 year, we could be confident that the pattern of nursing and molting dates should stagger in postpupping years, aiding our effort to detect the signal of unobserved pupping events in the sightings histories.

3.3 | Inferring unobserved pupping events

We plotted sightings for all adult female monk seals (total 79) sighted in the MHI from Hawai'i Island to Kaua'i Island from 1962 through 2017. Most plots revealed sufficient information to determine reproductive histories. A total of 57 females (72.15%) had sufficient sighting reports to confirm, rule out or infer a pup in all or most years of their reproductive history. The other 22 females (27.85%) had insufficient observations to make conclusions regarding pupping; thus, most or all years were coded as pup status unknown (code 4).

Examples of all codes used in describing female reproductive histories can be seen in the plot for one seal, R010 (Figure 5a). Of the 14 years that R010 was sighted as an adult (2001–2013), it was observed nursing in 5 years. However, after examining its annual sighting histories for gaps and patterns in the timing of observed pupping and molting, we inferred that it likely had four additional pups during that timeframe.

Across all seal-years, 55 mothers were observed with 245 pups and inferred pups added another 10% to the observed pup numbers ($n = 25$). Three females for which unobserved pupping events were inferred would have otherwise been considered nonparous (for example R303; Figure 5b). While pups could be ruled out for 91 seal-years, the pup status was unknown for 131 seal-years. Accounting for unobserved pupping events that could have occurred during those code 4 years added another 24% to potential pup count (mean number estimated through 10,000 MC replicates with binomial randomizations = 60.83).

3.4 | Recalculating reproductive rates

The estimated reproductive rates were markedly different based on whether the data were supplemented with the unobserved pupping events. When reproductive rates were estimated using only observed pupping, the fitted

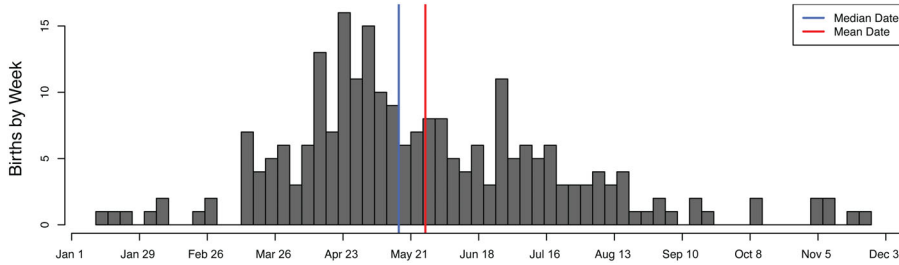
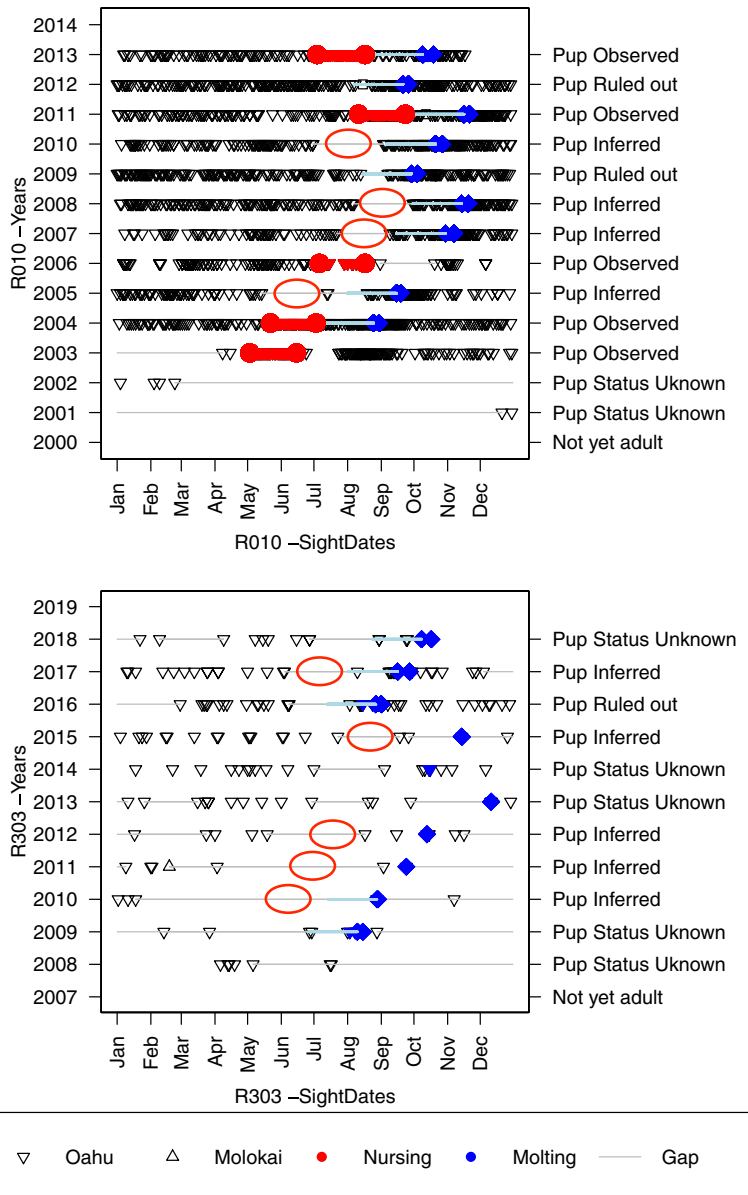


FIGURE 4 Distribution of pupping dates (by week) for female monk seals in the main Hawaiian Islands.

FIGURE 5 (a) The sightings plot of R010 illustrates years in which all codes were applied to describe this seal's reproductive history: Pup Observed (code 1), Pup Ruled Out (code 2), Pup Inferred by patterns of sighting history (code 3), and Pup Status Unknown because sightings were too sparse (code 4). (b) The sightings plot for R303 shows occasional sightings on O'ahu punctuated by frequent gaps in sightings. Because its molts were often observed, we could use the staggered pattern in its year-to-year molt dates to infer that it nursed several pups without detection.



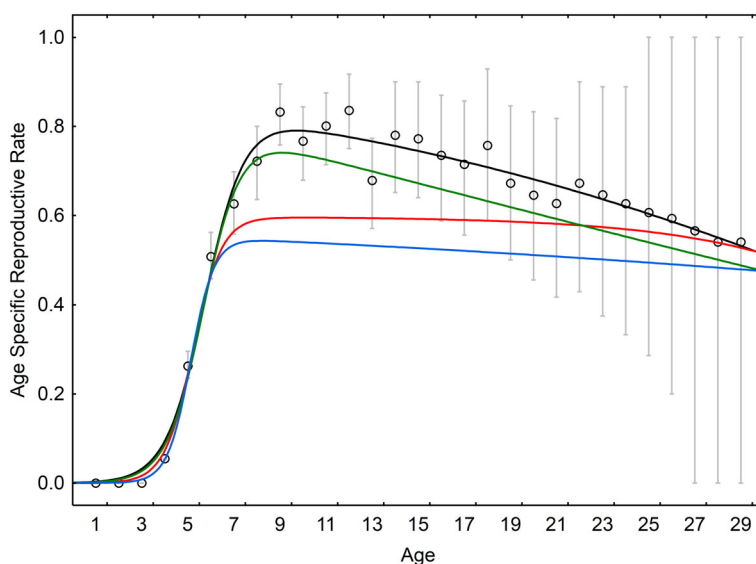


FIGURE 6 Estimated age-specific reproductive rates for the main Hawaiian Islands as derived from Monte-Carlo simulations ($N = 10,000$) with and without the addition of supplementary data to account for unobserved pupping. Lines represent the fitted 5-parameter reproductive function (Harting et al., 2007) for the following scenarios: blue = observed pupping only (baseline); red = observed + inferred (code 3) pupping; green = observed + status unknown (code 4) pupping, and black = observed + both types of supplementary reproductive data (codes 3 and 4). Points and vertical bars represent the mean age-specific rate and 5/95 percentiles when all data types are included.

reproductive function attained an asymptotic peak of 0.54 (blue line in Figure 6). In contrast, when rates were estimated from data supplemented with the inferred pups and randomized additions to account for seal-years with pup status unknown, and starting ages were randomly assigned to minimum-aged females, the mean rate for mature females exceeded 0.70 for all ages 8–20 (black line in Figure 6). Given that many seal-years had unknown pupping status, the randomized additions produced the largest increase in estimated reproductive rate (green line in Figure 6). As expected, the 5/95 percentiles for the MC simulations became progressively broader with age due to the small sample for older age seals. For many simulations, $n = 1-2$ seals for one or more ages ≥ 25 years, leading to a preponderance of rate estimates of 0.0 or 1.0 for those ages. The increase in reproductive rates subsequently impacted the estimated population growth rate (λ) for the MHI monk seal population (Table 1). The baseline λ of 1.022 increased to 1.029 with the addition of the inferred code 3 pups, equating to an approximate increase of 31% in the instantaneous rate of growth, r . Inclusion of both the code 3 and code 4 categories yielded $\lambda = 1.045$, an approximate doubling of r as compared to the baseline.

4 | DISCUSSION

In this study, we are able to produce a detailed description of the reproductive cycle and estimate age-specific reproductive rates of Hawaiian monk seals in the MHI by incorporating inferred as well as observed reproductive events based on multiyear sighting histories. This was largely possible thanks to the contribution of volunteer citizen scientists. This massive public participation in seal monitoring vastly extended the coverage that agency biologists could have accomplished alone. Citizen science can often be most beneficial in situations like that of the Hawaiian monk seal, where animals are rare and sightings are sporadic (Farhadinia et al., 2018). The amount of data from large volunteer networks can improve data quality despite the amateur status of those collecting the data (Schmeller et al., 2009).

TABLE 1 Increase in pup count, peak reproductive rate, and population growth rate (λ) when unobserved pups (codes 3 and 4) supplement the sample of observed (code 1) pups.

Sighting history code	Number of females ^a	Number of seal-years	Pups counted (per MC simulation)	Peak reproductive rate	Population growth rate
1: Pup observed	55	245	245	0.54	1.022
2: Pup ruled out	38	91	NA	—	—
3: Pup inferred	9	25	Code 1 + 25	0.60	1.029
4: Pup status unknown	49	131	Code 1 + 60.83 ^b	0.74	1.040
All possible pups			Codes 1 + 3 + 4	0.79	1.045

^aBecause an individual female may have different codes in different years (e.g. observed pup in some years and inferred pups in other years), the number of females represented by each code does not sum to the number of females in the study.

^bMean number of additional pups added per simulation in Code 4 seal-years.

In comparing the current data to the previous findings from the NWHI, we saw several important differences as well as similarities (and comparison is facilitated by similar numbers of individuals observed and similar levels of precision found by Johanos et al., 1994; Figure 3). While the intervals between pups were nearly identical, the main Hawaiian Island females had longer lactation periods than those in the NWHI, thus offsetting the intervals observed between weaning and molting or between molting and subsequent pupping. Perhaps the most biologically important difference noted was that females in the MHI nursed their pups for an average of 4.7 days (12%) longer than NWHI females. This increase in lactation period would give a significant benefit to main islands pups, providing more nutritional resources. This is consistent with previous observations that MHI pups tend to be larger at weaning, grow more rapidly postweaning, and on average, enjoy higher first-year survival than NWHI pups (Baker & Johanos, 2004; Baker, Johanos, Wurth, & Littnan, 2014). Girth at weaning is known to be a key factor impacting juvenile survival (Baker, 2008). The capacity of main islands females to invest more resources into nursing their pups suggests favorable foraging conditions for the females (commensurate with positive trends in MHI population; Baker & Johanos, 2004), and is a likely factor underlying the higher average juvenile survival observed in main compared to northwestern islands. Similar patterns have been seen in other pinniped species, with mothers in more favorable environments investing more into their pups, positively impacting population dynamics (McMahon, Harcourt, Burton, Daniel, & Hindell, 2017; McMahon, Hindell, Burton, & Bester, 2005).

Molt timing also differed in the two regions; with MHI females molting closer to the time of weaning their pups (54 days postweaning/98 days postpupping vs. 66/105 days for NWHI females). This may be an additional indicator of positive resource availability in the MHI. Nursing significantly depletes female reserves, and molt represents another large physiological investment. It appears that seals in the MHI have greater physiological resources to transfer to their pups, and also regain condition and are ready to molt more quickly than those in the NWHI.

Despite the differences in lactation and molting intervals, we found no difference in the intervals between consecutive pups in the current study of MHI females compared to the previous study of NWHI females. Our estimate of 381.7 days between pups matched previous research in which the interpup interval has been recorded with remarkable consistency across a wide temporal range (381.1 days in Johanos et al., 1994; 382 days in Wirtz, 1968). Although availability of resources and body condition may give main islands females the flexibility to nurse longer or regain condition to molt sooner, it appears that the key factors of the reproductive cycle such as estrus and gestation are less flexible. This finding may suggest that female monk seals in their natural habitat are more constrained in their reproductive

cycling than previously suggested based on a captive seal study (Pietraszek & Atkinson, 1994). Further research of monk seals under natural conditions will be valuable to clarify our understanding of female reproductive capacity.

The dependable patterns that can be observed in the female monk seal reproductive cycles with over a year between pups, lactation period of over a month, and molting nearly 2 months after nursing, allowed us to confidently rely on sighting patterns to detect unobserved pupping events. While citizen scientists could not access all areas of the MHI at all times, the heavy effort in many areas created telltale gaps in sighting histories when seals went to unmonitored areas to have their pups. The 25 inferred pupping events identified in this study constitute a meaningful addition to observed reproductive events (10%). Further, our randomization procedure added up to 24% beyond the observed pups, suggesting that reproductive estimates would indeed be biased low if it were assumed that all unseen females failed to pup.

There are, of course, limitations in inferring the unseen. By inferring missed pups from the gaps in sighting patterns, we constrain our ability to detect only events that result in the live birth of a pup that is nursed for at least the majority of an average lactation period. We have observed cases of fetal loss which would not be captured with the current method (for example female RI37 routinely lost fetuses early in gestation, presumably due to some inability to carry a full-term pup, possibly related to injury early in life; HMSRP, unpublished). Neonatal mortality has been observed, typically <10% at most sites (Harting et al., 2020). Thus, our analysis may still underestimate the total reproductive cycling and pregnancy rates, but the measurement of successfully birthed and weaned pups is likely to be the most meaningful in considering population recovery potential.

Our estimates of MHI age-specific reproductive rates are consistent with other observations of MHI body condition and intrinsic population growth rates (Baker et al., 2011). The female reproductive rate reported here for the MHI is the highest of any of the Hawaiian monk seal breeding sites (Harting et al., 2007). This is a marked change from previous estimates based only on observed nursing, and with small sample sizes over limited ages when the MHI population was earlier in its recovery (Baker et al., 2011). The high reproductive rates seen after correcting for unobserved pupping events underscore the importance of the MHI population in the species' recovery. While ecology and vital rates in the MHI appear favorable, it remains important to focus on other factors that could constrain population recovery, including anthropogenic threats such as intentional killings or injuries from fishing gear, or disease impacts such as toxoplasmosis (Barbieri et al., 2016; Gobush et al., 2017; Harting et al., 2020).

In addition to using monk seal sighting information to refine reproductive rate estimates in the current analysis, what we learned about the gaps in the sighting data will help to guide future research efforts. For example, we found that records of molt timing were very important in discerning reproductive patterns and facilitating the detection of unobserved pupping events. This has informed training needs to help citizen scientists identify molting animals. Further, in examining each female's sighting history, we could see that several of the animals with frequent gaps between sightings were females typically sighted on Kaua'i, and suspected to spend part of their time (and likely pup) on Ni'ihau. Future monitoring efforts will benefit from additional survey efforts, or cultivation of greater citizen science involvement on the seldom visited island of Ni'ihau.

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AUTHOR CONTRIBUTIONS

Stacie Robinson: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing-original draft; writing-review and editing. **Albert Harting:** Conceptualization; formal analysis; investigation; methodology; validation; visualization; writing-original draft; writing-review and editing. **Tracy Mercer:** Data curation; investigation; methodology; validation; writing-review and editing. **Thea Johanos:** Data curation; investigation; methodology; validation; writing-review and editing. **Jason Baker:**

Investigation; methodology; validation; writing-review and editing. **Charles Littnan**: Funding acquisition; supervision; writing-review and editing.

DATA ACCESSIBILITY STATEMENT

Data to recreate this analysis are available through HMSRP's data repository at the U.S. National Oceanographic Data Center: Johanos T.C. (2020b) Hawaiian Monk Seal Research Program Hawaiian monk seal master identification records (seal) collected in the Hawaiian Archipelago, 1962–2019: <https://inport.nmfs.noaa.gov/inport/item/5677>

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