A protocol for photo-identification catalog-based age estimation: An application to endangered Hawaiian false killer whales (*Pseudorca crassidens*)

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ABSTRACT

Age is essential for studying population dynamics yet is challenging to estimate for individuals in wild populations. While methods exist for aging dead animals, it is difficult to obtain reasonably accurate age estimates of free-ranging animals, especially for cetaceans. We developed a protocol for deriving age estimates using information commonly curated in marine mammal photo-identification catalogs and applied the approach to biopsy-sampled false killer whales (*Pseudorca crassidens*) from the endangered main Hawaiian Islands insular population. The protocol integrates qualitative lines of evidence into a quantitative framework for deriving age point estimates and plausible ranges. Confidence ratings reflecting the strength of supporting evidence were developed to account for uncertainty in age estimates. These estimates were then translated to a statistical distribution that can be used in further analyses. Age point estimates of biopsy-sampled false killer whales ranged from three to 40 years (minimum range: 2-33; maximum range: 5-65) and were strongly influenced by the estimated age when first seen and span of years since first seen. Overall, this method provides a useful approach for aging individuals with common metrics from photo-identification catalogs and for which other aging methods of biological samples are not yet feasible or available.

INTRODUCTION

Age is a critical metric for understanding the dynamics of wildlife populations, such as life history (e.g., age at first reproduction, age-specific birth, death, and growth rates), post-reproductive phase (i.e., age when last documented giving birth and extent of post-reproductive lifespan), social organization (e.g., age of dispersal), and for assessing population trends (e.g., age structure to determine if populations are growing or shrinking) (Clapham, 1992; Gerber et al., 2020; Photopoulou et al., 2017; Skalski et al., 2010; Raum-Suryan et al., 2004; Wolf et al., 2007). This is an especially important metric for marine mammals, as many species are long-lived and/or exhibit complex social structure, thus playing a particularly influential role in both group and population dynamics (Wade, 2018; Whitehead, 2008). Importantly, having estimates of age provides a basis for applied research that can further common management goals. Studies on age-based relationships of cetaceans have informed risk of overlap with anthropogenic activities (e.g., vessel strike, Stepanuk et al., 2021), identified demographic characteristics related to risk of exposure to activities or substances (e.g., environmental contaminants, Krahn et

al., 2009; Kratofil et al., 2020), and documented reduced body size/growth linked to increased rates of harmful human-related interactions or environmental conditions (e.g., entanglements, Stewart et al., 2021; reduced prey availability, Fearnbach et al., 2011; Groskreutz et al., 2019). Changes in life history traits, such as those related to age, are expected to increase in the future as a result of climate change (Gardner et al., 2011; Issac, 2009), thus emphasizing the need for methods that can robustly estimate the age of individuals in wild populations.

Despite the importance of age in marine mammal science and conservation, estimating the age of live individuals in wild populations is challenging. Most quantitative studies on life history in wildlife populations have occurred post-mortem (i.e., from data collected from mass strandings, whaling landings, or drive fisheries as in Photopoulou et al., 2017). However, in limited cases, free-ranging individuals that have been live captured have had teeth extracted for aging (e.g., Hohn et al. 1989), and for some long-term studies where individuals are extensively photo-identified each year (e.g., Fearnbach et al., 2011; Groskreutz et al., 2019; Wells, 2014), age of most individuals in the population may be known based on the year they are first seen. Herman et al. (2008) also presented a potential method for aging free-ranging cetaceans through an assessment of fatty acid composition in blubber biopsies of known-age killer whales (*Orcinus orca*). More recently, epigenetic aging methods have been developed for a few species either using samples available from dead individuals for which age can be independently determined (Bors et al., 2021) or based on populations with concurrent age information from photo-identification (e.g., Beal et al., 2019; Polanowski et al., 2014). However, for many populations and species of cetaceans, there are insufficient known-age individuals to develop epigenetic aging models. Further, epigenetic aging methods require analyses of tissue samples that can be difficult to obtain from rare and elusive species (e.g., Baird et al., 2022).

As part of a collaborative effort to develop an epigenetic age estimation model for an endangered population of false killer whales in Hawaiian waters (Martien et al., In Prep), we developed a method to estimate the age of individual false killer whales using information available from a long-term photo-identification catalog (see Baird et al., 2008) in conjunction with sex information from biopsy samples (Martien et al., 2014), given sex differences in asymptotic length (Ferreira et al., 2014), as well as relative position of the dorsal fin on the back (Yahn et al., 2022), and a previously undescribed trait that appears to indicate physical maturity in male false killer whales. Although originally developed to inform the epigenetic aging work, this approach is of value for estimating age of false killer whales for a variety of other purposes, including informing the interpretation of results from aerial photogrammetry, assessment of age of animals acquiring evidence of fishery interactions, interpreting results of diving behavior studies, assessing age-related changes in social structure including philopatry, dispersal patterns and relatedness, investigating evidence of a prolonged post-reproductive lifespan, and understanding association patterns based both on photo-identification and on simultaneous satellite tag deployments. Here, we detail the methods of this approach and provide a summary of its application on a sample population of Hawaiian false killer whales, as they may be relevant for age estimation of other marine mammals for which similar lines of evidence are available. We provide metrics of uncertainty in age estimates to explicitly reflect the various strengths and weaknesses of supporting evidence, and give an example of how these estimates can be translated to statistical age probability distributions so that the full range of uncertainty for each individual can be quantified for subsequent downstream age-related analyses.

METHODS

The age estimation protocol described herein was developed on a subset of false killer whales (n=81 unique individuals) included in Cascadia Research Collective's (CRC's) long-term photo-identification catalog (photographs spanning 1985-2022) for which biopsy samples were available for inclusion in the epigenetic aging study (n=97 biopsy samples); see Baird et al. (2008) for details on field and photo-identification methodologies. The goal of the photo-identification based age estimation process applied in the epigenetic aging study was to estimate the age of individuals at the time of biopsy sampling (henceforth "sampling", whereas "seen" is used for photo-identification) for samples used in the study, using all available evidence from the photo-identification work. The lines of evidence (Table 1) utilized include the years in which the individual was first seen ($Year_F$) and last seen ($Year_L$), the year the individual was sampled ($Year_S$), the sex (from genetic analyses; see Martien et al. 2014), and several qualitative assessments such as the relative size of the individual to other individuals in photos (when available), the extent of markings on the dorsal fin when first seen (since markings accumulate with age; Baird et al., 2008), presence and degree of prominence of a leading edge hump at the base of the dorsal fin (Figure 1; indicative of physically mature males; CRC unpublished) and field estimates of age class when sampled (or tagged, as some individuals sampled for this study were also tagged at some point in their sighting history) by CRC (Table 1). For some individuals, information on genetic parentage was also incorporated into the age estimation process when parentage ordinality was confident (i.e., high confidence that individual X is the parent of individual Y, or vice versa; Martien et al., 2019). For each individual in the study, the age estimation process produced four values: a minimum (Age_{min}) and maximum (Age_{max}) age at the time of sampling (i.e., ages that we are 100% confident that the individual was no younger than or older than, respectively), a "best" age estimate (Age_{best}), and a confidence rating (CR) on the best age estimate.

Age class determination

A schematic overview of the protocol and an example with one individual in our study (HIPc114) is presented in Figure 2. The protocol starts by determining the age class of the focal individual (e.g., "adult", "older adult", "juvenile") when first seen and at the time of sampling (if first seen before the sampling event), which relies on qualitative information documented in the field and from photographs, as well as the sex. A field assessment of combined age/sex class was often but not always made at the time of sampling or tagging by CRC based on size of the individual and the presence or absence of sexually-dimorphic characteristics. Common field assessment age/sex class categories included: adult male, adult-female sized (which could be an adult female or a sub-adult male for false killer whales), sub-adult, juvenile, or calf. If an animal was considered "adult-sized" in the field but was not assigned a sex, we subsequently used genetic results and supporting qualitative data to consider it either an adult (if female) or sub-adult (if male). Field assessments by CRC were considered to be reliable estimates of age class and sex in most cases (see below), and were often used as reference points when assigning age/sex classes to other sightings within an individual's sighting history. The individual(s) responsible for the field assessments had substantial prior field experience with cetaceans in addition to false killer whales. Field assessments of age/sex class for samples collected by NOAA Fisheries were not used.

If an individual was only seen once, the age class determination relied heavily on the field assessment. Cases where individuals were sampled subsequently to when they were first seen involved estimating age when first seen and adding the time period from this first estimate to when the animal was sampled for this study, provided this number didn't conflict with the field assessment. The age class of individuals that were seen more than once was determined by first noting whether one or more field assessments for age and/or sex were recorded. For field assessments where both age class and sex were recorded, the field classification of sex and the sex obtained from genetic analysis of the sample were compared; if the genetic results were the same as the field assessment, the age class was considered highly reliable and was accepted unless there was a gross discrepancy when reviewing photos. However, if genetic results differed from the field assessment for sex, the age class assessment was also questioned, as there is significant overlap in the sizes of adult females and sub-adult males (Ferreira et al., 2014). If a field assessment for age class but not sex was recorded, the age class assessment was reviewed using the sex from genetic analyses and the aforementioned series of qualitative assessments.

Assigning age ranges

After an age class was determined for the year first seen and for the sampling year, a reference range of ages was assigned to the individual to serve as the basis for the age estimate calculation. Reference ranges for age classes were generated separately for male and female false killer whales (Table 2; Mahaffy et al., unpublished): for females, a minimum age of 10 (i.e., the age at sexual maturity; Ferreira et al., 2014) was assigned for adults, followed by 6-9 for sub-adults, and 3-6 for juveniles (juvenile = non-adult that is no longer nursing but still strongly associated with its' mother; Mahaffy et al., unpublished). For males, a minimum age of 15 was assigned for sexually-mature adults (Ferreira et al., 2014) and 25 for physically-mature adults (the latter was determined either by the presence of a leading edge hump in photographs, through field assessment, or for those in the catalog ≥25 years), with sub-adults ranging from 9-14 years, and juveniles 3-9 years (Mahaffy et al., unpublished). Although calves are seldom biopsied, calves for both sexes were assumed to be within 0-3 years of age (Mahaffy et al., unpublished).

Age at time of sampling

Best age (in years; Age_{best}) at the time of sampling was estimated by first considering the lower age within the range for the individual's assigned age/sex class when the animal was first seen ($Age_{C,F}$), and then adding the number of years between when it was first seen ($Year_F$) and when it was sampled ($Year_S$) to derive a starting point for the best age estimate (Eq.1; Figure 2).

Eq. (1)

$$Age_{best} = Age_{C,F} + (Year_S - Year_F) \pm Aux$$

Auxiliary data sources were incorporated into Age_{best} estimates when available by adding an adjustment (*Aux*) to the age point estimate (Eq.1; Figure 2). Types of auxiliary data sources included evidence from photographs (e.g., relative size, markings, dorsal fin shape), genetic parentage (e.g., offspring or parent of another individual, see Martien et al., 2019), and age estimates from tooth sectioning on five stranded whales (tooth sectioning estimates provided by K. West/University of Hawai'i). The exact value of the adjustment, *Aux*, was primarily determined based on the assessor's qualitative judgement rather than a strict quantitative rule. For example, if an individual was classified as a juvenile in the field, but photographs revealed

that it was likely an older juvenile (e.g., based on markings, relative size to other individuals in photographs, etc.), the *Aux* would be set to a value (e.g., 2 or 3 years) that moves the individual's age estimate closer to the top of the corresponding age class range (Table 2). For adult males with leading edge humps on their dorsal fins, *Aux* was chosen so as to move the best age estimate closer to the age of physical maturity (25 years). Thus, a male with a leading edge hump whose Age_{best} was 16 based on other factors would receive an *Aux* of 9, resulting in Age_{best} equalling 25. *Aux* adjustments derived from genetic parentage information were typically more quantitative due to the ages that would be required for an individual to have offspring (i.e., ages at sexual maturity; Table 2). For example, if an adult female sampled in year A had a calf in year B, then the best age estimate would be adjusted through *Aux* so that she was a minimum of 10 years old in year B. It should be noted that genetic parentage was only used in the age estimation process if the parent/offspring ordinality was resolved with high confidence; ordinalities that were resolved with less confidence (i.e., individual X could be the parent or the offspring of individual Y with similar confidence) were only included in the process if other sources of information supported the ordinality (e.g., individual X was much younger than individual Y, so unlikely the parent of Y; see details on analytical methods in Martien et al., 2019). Lastly, for stranded individuals with tooth sectioning estimates, *Aux* years were added to the best estimate to equate to the tooth sectioning estimate, as the latter estimate is more precise.

Confidence Rating

A confidence rating (1-5: 1 = low, 5 = high) was determined for each best age estimate based on the quantity and quality of information supporting the estimate. General examples of criteria for assigning confidence ratings are listed in Table 3. Primary factors affecting uncertainty in age estimates involve the span of years the individual was seen prior to being sampled, the age class when the individual was first sighted, and whether more definitive lines of evidence, such as genetic parentage, were available to inform the estimate. For example, if an animal assessed in the field as an adult male or adult female was biopsied during the same encounter when it was first sighted and no other information was available to guide a plausible age range (i.e., older or younger adult), then we chose 30 years as the best age, with a confidence rating of 1. In contrast, some individuals sampled were first documented when young (i.e., a juvenile or sub-adult), and as such, the range of plausible ages is narrow and we can be more precise in deriving a best age estimate (confidence = 4 or 5). In several cases, it was known that an individual was sexually mature, either based on known parent-offspring relationships (from Martien et al., 2019) or presumed in the case of sexually mature females from photographs documenting small calves in close association earlier in their sighting history. In these cases, this information was used to back-calculate a plausible age based on age at sexual maturity and relative age of the offspring.

Minimum age

Minimum age was estimated by starting with the minimum age for one age/sex class lower than the age classified when first seen ($Age_{C-1,F}$), and adding the number of years prior to being biopsied ($Year_S - Year_F$) to derive an overall minimum age estimate at the time of sampling (Eq.2; Figure 1).

Eq. (2)

$$Age_{min} = Age_{C-1,F} + (Year_S - Year_F) \pm Aux$$

For example, if a biopsied individual was classified as an adult female at the time of biopsy but was first seen five years earlier, we would assume it could be no younger than six years old (sub-adult range 6-10 years) when first seen and thus a minimum of 11 years when biopsied. For younger individuals, a lower minimum age was set either based on the number of years seen or set at two years, since no calves thought to be younger than two (based on size) have been biopsied.

Maximum age

Maximum age estimates were calculated in two ways. The first approach determined maximum age through a set of rules that consider the age/sex classification of the individual at the time of sampling and the confidence rating associated with the individual's best age estimate at the time of sampling (Age_{CmaxCR}; Table 4, detailed below). With this approach, the confidence rating is used to scale the range of plausible maximum age estimates by the quantity and quality of supporting information available on each individual, such that individuals with strong supporting information have maximum estimates closer to their best age and those with poor supporting information have maximum estimates farther from their best age. Rules for determining maximum age estimates based on confidence ratings are as follows (Table 4): For adults (both sexes) with confidence ratings of 1 or 2 (poor support), the maximum age estimate at the time of biopsy sampling was set to 65[1]. Maximum age estimates for adults with best age confidence ratings of 3 (intermediate support), 4 (moderate support), and 5 (high support) were calculated as the best age point estimate plus 20 years, 15 years, and 10 years, respectively. The rules for sub-adults and juveniles followed a similar approach, albeit with a shorter scale and smaller range of years added to best age estimates, as the range of plausible ages for younger individuals is much narrower than that for adults. Maximum age estimates for sub-adults (both sexes) were calculated as follows: for confidence ratings of 2, maximum age was the best age point estimate plus 10 years; if the confidence rating was 3, maximum age was the best age point estimate plus 5 years; lastly, if the confidence rating was 4 or 5, the maximum age was the best age point estimate plus 3 years. The maximum age estimate rules for juveniles (both sexes) were on the same scale of confidence rating intervals as sub-adults, with the number of years added to the best age point estimate set to 5 years, 3 years, and 2 years for confidence ratings of 2, 3, and 4-5, respectively. Note that in our example on false killer whales, a confidence rating of 1 could not be assigned to individuals classified as juveniles or sub-adults, as we can have some level of confidence (greater than CR = 1) in the plausible range of ages for younger individuals.

The second maximum age calculation was based on the last year the animal was seen after sampling and was only applied to adults. Here, we assume that adult whales can be no older than 65[1] at any point during their sighting history. Thus, if an adult was seen several years after sampling, then the maximum age at sampling would be less than 65 (specifically, 65 minus the years between last seen and sampling, Table 4). Therefore, a maximum age estimate based on the confidence rating (Age_{CmaxCR}) and a maximum age estimate based on the last year seen ($Year_L$; assuming maximum possible age of 65 years at last year seen) were calculated for adults, and the

[1] Sixty-five was chosen as the maximum age attainable, based on Ferreira et al., (2014), with a sample size of 65 aged males and 121 aged females. It should be noted that it is possible that false killer whales may live longer than 65 years of age.

estimate that was lower was assigned as the overall maximum age estimate for adults (Eq. 3; Figure 2; Table 4).

Eq. (3)

Maximum age, non-adults:

$$Age_{max} = Age_{C_{maxCR}}$$

Maximum age, adults:

If:

$$Age_{C_{maxCR}} < (65 - (Year_L - Year_S))$$

Then:

$$Age_{max} = Age_{C_{maxCR}}$$

Else:

$$Age_{max} = (65 - (Year_L - Year_S))$$

With this approach, we accommodate situations that may include individuals with strong supporting evidence leading up to sampling (i.e., maximum age estimate closer to best age estimate), and also those with more limited histories prior to sampling but that have post-sampling sightings that provide enough information to warrant a lower maximum age estimate.

Age probability distributions

We fit three different distributions to the estimates generated for each individual as examples of how this type of data could be used in a quantitative modeling framework: a Uniform distribution, a Skew-Normal (SN) distribution, and composite distribution that is the weighted average of uniform and SN distributions. Examples of these three distributions are illustrated in Figure 3, fit to three different individuals which were selected to span a range of estimated ages and confidence ratings.

The uniform distribution (Figure 3, gray line) only uses Age_{min} and Age_{max}, and is therefore useful in studies where there are not sufficient data to estimate Age_{best}. To fit an SN distribution (Figure 4, dashed black line) to the age estimates for each individual, we estimated the location (χ), scale (ω), and shape (ρ) parameters of each SN distribution by setting the mode equal to Age_{best}, while Age_{min} and Age_{max} were used as the 0.025 and 0.975 percentiles of the distribution. The SN parameters were estimated using Nelder-Mead optimization as implemented in the R *optim()* function along with the *qsn()* function of the *sn* v.2.0.2 package (Azzalini, 2022). Because Age_{min} and Age_{max} were estimated such that there is zero probability of the true age being less than or greater than them, respectively, we truncated the distribution at Age_{min} and Age_{max}.

Finally, to reflect the confidence rating of the estimate of Age_{best} for an individual, we generated a composite distribution (Figure 3, solid black line) that is a weighted average of the Uniform and SN distributions at each point between Age_{min} and Age_{max}, with the weights based

on the confidence rating. For individuals with a confidence rating of 5, the uniform distribution was given zero weight, so the composite distribution was the same as the fitted SN distribution. To determine the weights assigned to confidence categories 1 through 4, the two researchers who made the age and confidence rating estimates were asked to adjust the weights (between 0.05 and 0.95) assigned to the Uniform distribution for each confidence category so that the resulting composite distributions reflected their intended meaning when assigning confidence. The researchers each developed their own mapping without consulting each other, then the resulting weight mappings were compared and reconciled.

Principal Components Analysis

We conducted a principal components analysis (PCA) in the statistical programming language R version 4.2.0 (R Core Team, 2022) to quantify the correlations between variables and their impact on confidence ratings. The variables we included in the PCA were best age at time of sampling (Age_{best}), best age when first seen ($Age_{best,F;}$ detailed below), age class when first seen ($Class_F$), age range ($Age_{max} – Age_{min}$), the length of the sighting history ($Year_L – Year_F$), and the presence/absence of well-resolved genetic parentage information and age estimates from tooth sectioning. Best age when first seen ($Age_{best,F}$) was calculated by subtracting the number of years between when an individual was first seen ($Year_F$) and when it was sampled ($Year_S$) from Age_{best} (note: this value is different from the age value based on age classification when first seen ($Age_{C,F}$) that is used to calculate the best age estimate (Table 1)). Parentage and tooth age were each coded as 0/1 to indicate whether or not data were available. Because 24% of females have information from one of these two data types while only 6% of males do, we performed separate PCAs for each sex. We also ran a PCA for females without presence/absence of tooth age and genetic parentage as variables and excluded from it all individuals for which those data types are available. We used the R package *psych* (Revelle, 2021) to visualize the correlations between variables and the package *ggbiplot* (Vu, 2011) to generate a biplot of the first and second components of the PCA and look for clustering by confidence rating.

RESULTS

Age estimates

Derived best age estimates for the sample population of false killer whales (81 individuals (42 males, 39 females), 97 samples/time points) at the time of biopsy sampling ranged from three to 40 years old, with a range of two to 33 years old, and five to 65 years old for minimum and maximum categories, respectively. Confidence ratings were variable among individuals, with younger individuals generally having higher confidence ratings and corresponding lower minimum and maximum age values (Figure 4); no individual was assigned a confidence rating of 1, reflecting that other lines of evidence were usually available. Mean “best” age estimates by confidence rating were as follows: 13.3 years (CR = 2), 17.1 years (CR = 3), 20.6 years (CR = 4), and 11.8 years (CR = 5).

Approximately one third (35 of 97) of the samples included in this study had auxiliary information that warranted inclusion in the age estimate calculations (i.e., years added/subtracted to age estimates based on auxiliary information, hereafter “auxiliary years”.) Just over half (18 of 35) of the auxiliary years were associated with within-age-class distinctions (e.g., younger adult, older juvenile) identified through photographs or a combination of photographs and field assessments. The number of years added to the best age estimate for within-age-class distinctions

ranged from 1-8 years. Nine of the 35 cases with auxiliary years were attributed to parentage information, and included individuals with high confidence in genetic parentage ordinality as well as individuals with lower confidence in parentage ordinality, but with adequate sightings/photographic evidence to support the ordinality. Five of the 35 samples were from individuals who had stranded (three females, two males) and had more precise age estimates from tooth sectioning methods, so auxiliary years were added to the best estimate to equate to the tooth sectioning estimate. The remaining cases (3) were driven by uncertainty, such as conflicting evidence from field assessments and photographs/sightings (e.g., classified in the field as a juvenile, but documented over a period longer than the age of most juveniles).

Age probability distributions

Nonlinear optimization fits of the Skew-Normal model location, scale, and shape parameters to Age_{best}, Age_{min}, and Age_{max} showed successful convergence for all individuals. The two authors who made the age and confidence estimates (MAK and SDM) independently mapped the confidence scores to the same relative weights for the composite distribution (Table 5). Examples of the effects of these weights on the composite distribution can be seen in Figure 3 as described above.

Principal Components Analysis

The PCA revealed strong correlations between all of the age-related variables ($Age_{best,F}$, Age_{best}, $Class_F$, and age range), all of which have high positive loading on the first principal component (Figure 5 a and b, Table 6). The second principal component is strongly negatively correlated with length of the sighting history in both sexes, though the correlation is stronger for males than females. Conversely, the second principal component has a strong positive correlation with the presence of tooth age data for females, but a weaker correlation for males (Table 6).

The biplot for males shows clustering of animals by confidence rating (Figure 5a). The highest confidence rating (CR = 5) is seen primarily in younger males (low values of PC1) due to the narrower range of possible ages associated with the age classes of juvenile and sub-adult. As animal age increases (i.e., PC1 increases), the strongest influence on confidence rating is the length of the sighting history, with animals seen over a long period of time (low values of PC2) tending to have higher confidence ratings than those seen only a few times. The biplot for females, in contrast, does not exhibit notable clustering by confidence rating (Figure 5b). However, when individuals with tooth age estimates or genetic parentage information were excluded from the PCA, females exhibit the same clustering by confidence as seen for males (Figure S1).

Males exhibit a stronger correlation between $Age_{best,F}$ and $Class_F$ than do females (Figures 5, S2, S3). This is due in part to the fact that adult males have separate age classes for sexually- and physically-mature adults, while there is only a single adult female age class. The female data set showed a weak correlation between length of the sighting history and the presence of tooth age data due to the fact that one of the animals with the shortest sighting histories was a non-distinctive female with a tooth age estimate that was only seen once, when it stranded (this individual's assignment to the study population confirmed by mitochondrial haplotype).

DISCUSSION

The methodology presented here provides a comprehensive and straightforward approach towards estimating the age of photo-identified individuals. Importantly, this methodology is structured to incorporate a variety of age-related information while also accounting for uncertainty associated with the lines of supporting evidence (or lack thereof) used to derive age point estimates. The amount of information available on a given individual can be highly variable across sample populations, especially for extensive photo-identification catalogs curated over several decades, as demonstrated with our sample of Hawaiian false killer whales. This protocol allows for such case-by-case variability (e.g., confidence ratings and scaled age estimates) while also maintaining a consistent and pragmatic approach that can be applied to an entire sample population.

The application of this protocol to a sample population of Hawaiian false killer whales highlighted variability among individuals and levels of supporting information but also revealed general trends in the age estimation process. In general, younger individuals, especially males, had higher confidence ratings and corresponding narrower ranges of plausible age values (Figure 4 and 5). Higher confidence ratings in adults were primarily driven by increased numbers in the years since first seen; if an individual has been sighted over a span of 20 years, then we have high support for that individual's older age estimate.

The differences in the PCA results for males and females illustrate the relative weight that the different variables had in the confidence rating assigned to estimates of Age_{best}. Both of the males with tooth age estimates had relatively long sighting histories (10 and 13 years) and sufficient auxiliary information that they would have been assigned a high confidence rating even without the tooth age estimate. The three females with tooth age estimates, in contrast, had less auxiliary information and shorter sighting histories, including one that had never been sighted prior to stranding. Thus, the tooth age data resulted in the animals being assigned much higher confidence ratings than they would have based on sighting data alone. Similarly, eight of the nine animals with parentage data are females, which again resulted in them receiving higher confidence ratings than they otherwise would have. Because of the strong influence of tooth age and genetic parentage information on confidence ratings, including them in the PCA obscures the relationship between the age estimates and confidence rating. These findings can help inform data collection efforts in a manner that would maximize age-related information (i.e., confidence ratings) for individuals in this endangered population, such as targeted field efforts in poorly sampled areas (i.e., obtaining photographs and sampling rarely encountered individuals), biopsy sampling adult females (or adult female-sized whales) for various age-related biomarker analyses (e.g., hormone chemistry for pregnancy status, parentage), and obtaining historical photographs of individuals that may exist within the community of researchers and community scientists in Hawai‘i (i.e., potentially extending sighting histories for individuals already in the catalog).

For individuals with auxiliary information available, the vast majority of auxiliary years added to estimates were in a manner that increased precision, while there were a select few cases where auxiliary years were added to recognize uncertainty. The exact value for auxiliary years was primarily determined in consideration of the range of years of the focal age class, and as such fewer years were typically added for younger individuals and more years for older individuals. For example, one individual classified as an adult male when first seen had a field assessment indicating physical maturity at sampling 2 years later. The calculated age based on

the age/sex class when first seen and years since first seen was 17 years old, and 8 years were added to achieve the approximate age where sexually dimorphic features become obvious (25 years). In a few select cases, there was conflicting information that created uncertainty in the individuals' age classifications (e.g., field assessment not in agreement with photographic assessment) that subsequently affected the age estimates (e.g., lower confidence or including auxiliary years to account for uncertainty.) This type of discrepancy may arise due to individual variability in asymptotic length (e.g., Fearnbach et al., 2011; Ferreira et al., 2014). Additional lines of evidence that would help refine this approach for this specific population of false killer whales could include comparisons of age estimates of future stranded individuals that had pre-stranding protocol-derived age estimates and formal evaluations of relative size and growth rates for young individuals (i.e., progression from calf to sub-adult as growth generally ceases during adulthood; Ferreira etal., 2014).

Although a number of types of supporting information were used to derive our age estimates, this general protocol could be easily modified to involve metrics that may be more specific to a particular population or photo-identification catalog with more or less available information. For example, for species that have more distinguishable sexually-dimorphic features (e.g., killer whales), genetic sex information may not be necessary, at least for adults. While genetic information was a strength in our example on biopsied false killer whales (e.g., to inform minimum age values for different sexes), this protocol is not structured to exclusively estimate the age of individuals with such genetic information. Ages could be estimated for individuals who have not been biopsied, with lower confidence ratings assigned as needed if genetic information on sex would be a strong determinate for minimum age values, as is the case for false killer whales. Photogrammetric information (e.g., total length) could also be a potential line of evidence to incorporate into this protocol if relevant to the species of interest. Here, we did not include such information for the select individuals with drone images available due to a temporal mismatch between when most of the individuals were biopsy sampled (i.e., from 2000 through 2019) and when drone images were available (i.e., 2018-2022). In addition, given growth slows with age and ceases by ~25-30 years for both sexes (Ferreira et al., 2014), metrics on length would not be informative for generating age estimates for older adults.

Researchers employing this method may also wish to modify some aspects of the age estimate equations to better meet the needs of their study species and research questions. For example, when estimating the maximum age for individuals through confidence rating rules (Table 4), the number of years added for each confidence rating/age class rule were chosen based on our perspective of the relative span of years that each confidence rating represents, and also considering the known age ranges for each age class specific to false killer whales (e.g., adding 15 years to the best age estimate of a juvenile would not be a realistic maximum age for false killer whales as they are only juveniles for a short period of time). Researchers implementing this approach may wish to adjust the number of years added to the best age estimate corresponding to each confidence rating rule as appropriate for their study species and expertise. Further, the criteria that define each confidence rating (Table 3) may need to be tailored to the specific species and corresponding datasets that researchers have available for age estimation, with the general scale remaining the same (i.e., CR of 1 for very low confidence to CR of 5 for high confidence).

We highlight particular relevance of this method for quantitative applications. For example, using the minimum, best, and maximum age estimates, age probability distributions can be constructed for each individual (Figure 3). These are ideal for use as prior probability distributions in quantitative modeling approaches that incorporate age-related information. Further, the confidence ratings can be factored into the probability distribution by scaling the shape of the distribution curve, with higher confidence ratings being reflected by more informative, or peaked, distributions, while lower confidence ratings are broader, nearing a uniform, or non-informative, distribution. Collectively, the protocol presented here generates estimates that can be directly integrated into both quantitative and qualitative analyses.

Future studies implementing this method could benefit from an evaluation of variability in estimates and confidence ratings among multiple researchers. For our application on false killer whales, two of us derived the estimates: one (SDM) summarized qualitative information and assigned age classifications while the other (MAK) computed age estimates using the qualitative information and other lines of evidence from the photo-identification catalog (Figure 2). We worked closely to review estimates and inform outputs of any complex cases (e.g., those involving auxiliary information). While the most reliable age estimates may result from having a few key individuals with extensive experience on the data/species derive the estimates, future users of this method may wish to employ a number of researchers with varying experience levels to estimate ages of their sample population (e.g., for large photo-identification catalogs). In such cases it would be important to assess consistency in the more subjective or qualitative components of the protocol (e.g., age classification, auxiliary years, confidence ratings) among individuals prior to any formal analyses and inference on the outputs. While we strived to structure the protocol in a manner that would limit the degree of variation associated with subjective input, this method does involve qualitative assessments that are more likely to vary among individuals compared to the qualitative metrics.

ACKNOWLEDGMENTS

Funding for photo-identification catalog development was provided by grants from the Pacific Islands Fisheries Science Center and contracts from the State of Hawaiʻi (supported by NOAA Section 6 grants). Funding for field efforts during which samples were collected was received from NOAA Fisheries (PIFSC, SWFSC, NWFSC, Ocean Acoustics Program), the U.S. Navy (LMR, ONR, Pacific Fleet), and the Wild Whale Research Foundation. Biopsy samples were collected under NMFS Scientific Research Permits No. 774-1437, 774-1714, and 14097 issued to Southwest Fisheries Science Center, 15240 and 20311 issued to Pacific Islands Fisheries Science Center, and 20605 issued to Cascadia Research Collective. We are grateful for all individuals and organizations who have contributed photographs to CRC's false killer whale photo-identification catalog, which are invaluable to the work and results presented here, especially Wild Dolphin Foundation, Pacific Whale Foundation, PIFSC, Hawaiʻi Whale Research Foundation, Daniel J. McSweeney (Wild Whale Research Foundation), Chuck Babbitt, Colin Cornforth, Captain Zodiac, Cynthia Hankins, Mark Deakos, Dolphin Excursions, Paul Johnson, Lynn Opritoiu, Doug Perrine, Deron Verbeck, and Kimberly Wood. We thank Katy Frey and Suzanna Mickey for feedback on visualizations, and Uko Gorter for providing his false killer whale illustrations. We appreciate Kristi West (University of Hawaiʻi) for providing age estimates from tooth sectioning on stranded whales. We thank Stephanie Stack, and Jens Currie for feedback on this approach, and Alexandra Curtis for a review of the manuscript.

AUTHOR CONTRIBUTIONS

Michaela A. Kratofil: conceptualization; formal analysis; methodology; visualization; writing – original draft; writing - review & editing. **Sabre D. Mahaffy:** data curation; formal analysis; methodology; writing – original draft; writing – review & editing. **Karen K. Martien:** formal analysis; visualization; writing-original draft; writing – review & editing. **Frederick I. Archer:** formal analysis; visualization; writing – review & editing. **Robin W. Baird:** conceptualization; data curation; funding acquisition; investigation; project administration; supervision; methodology; writing – original draft; writing – review & editing.

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Table 1. Variable names and descriptions for values incorporated and calculated in the catalog-based age estimation protocol.

Variable name	Description
$Year_F$	Year first (*F*) seen
$Year_S$	Year sampled (*S*)
$Year_L$	Year last (*L*) seen
CR	Confidence rating associated with the individual's resulting age estimates (1-5); see Table 3 for details
$Age_{C,F}$	Age value when first seen, based on minimum age value for age classification, *C*, (adult, sub-adult, juvenile, or calf)
$Age_{C-1,F}$	Age value based on one age class lower than that assessed when first seen (i.e., if C = adult, then C-1 = sub-adult)
$Age_{C,maxCR}$	Maximum age estimate based on the age classification and adjusted by CR; see Table 4 for details
Age_{best}	Best age estimate at the time of sampling
Age_{min}	Minimum age estimate at the time of sampling
Age_{max}	Maximum age estimate at the time of sampling; for non-adults, this is the same value as $Age_{C,maxCR}$; for adults, this is the lowest of the two maximum values computed (see methods for details)
Aux	Adjustment value added to or subtracted from age point estimates (best, min, max) in consideration of auxiliary information (e.g., parentage)
$Class_F$	Age class when first seen (not age value)
$Age_{best,F}$	Best age estimate when first seen; this value is derived from the best age estimate

Table 2. Minimum age values associated with each age/sex class category for false killer whales used in age point estimate calculations. Note that physical maturity in adult males is indicated either by the presence of a leading-edge hump (Figure 1) in photographs, through field assessment, or for those in the photo-identification catalog at least 25 years.

Age/sex class	Minimum age value
Adult Female (i.e., sexually mature)	10
Adult Male, sexually mature	15
Adult Male, physically mature	25
Sub-adult Female	6
Sub-adult Male	9
Juvenile (both sexes)	3
Calf (both sexes)	0

Table 3. Confidence rating criteria used for the false killer whale age estimation assessment.

Confidence rating	Criteria
1	First seen when sampled (no prior sighting history) and age classification was adult; no other auxiliary information
2	Limited sighting history, but one level of auxiliary information available (e.g., physically mature male)
3	Sighting history and/or auxiliary information provide reasonable evidence for age estimate, although precision may be low (e.g., seen as adult over long sighting history, with age when first seen more uncertain)
4	Sighting history and/or auxiliary information provide strong evidence for age estimate (e.g., long-term sighting history/span of years seen, genetic parentage information, younger individual so range of plausible ages narrower)
5	Extensive sighting history and/or genetic parentage; age from tooth sectioning (stranded animals only); younger individual so range of plausible ages is narrower (especially when sighting several times)

Table 4. Maximum age estimate rules based on age class and confidence ratings. Note that in our example here, a confidence rating of 1 cannot be assigned to individuals classified as juveniles or sub-adults, as we can have some level of confidence in the plausible range of ages for younger individuals.

Age class	Confidence Rating (CR)	Max age based on CR
Adult	1 or 2	65 years
Adult	3	Age_{best} + 20 years
Adult	4	Age_{best} + 15 years
Adult	5	Age_{best} + 10 years
Sub-adult	2	Age_{best} + 10 years
Sub-adult	3	Age_{best} + 5 years
Sub-adult	4 or 5	Age_{best} + 3 years
Juvenile	2	Age_{best} + 5 years
Juvenile	3	Age_{best} + 3 years
Juvenile	4 or 5	Age_{best} + 2 years

Table 5. Weights applied to the Uniform distribution to compute the composite age probability distribution as the weighted average of a Uniform (0) and a Skew-Normal (1) for each confidence rating.

Confidence Rating	Weight
1	0.05
2	0.2
3	0.55
4	0.75
5	1.0

Table 6. Loading of variables on the first and second principal components (PC1 and PC2, respectively) for males and females.

Variable	Males		Females	
	PC1	PC2	PC1	PC2
Years in catalog	0.215	-0.778	0.329	-0.590
Age_{best}	0.462	-0.259	0.474	0.012
Age_{F}	0.507	0.161	0.464	0.258
$Age_{C,F}$	0.497	0.234	0.524	0.137
Age range	0.454	0.265	0.415	-0.086
Parentage data available	-0.173	0.210	-0.035	0.209
Tooth age available	0.013	0.364	0.057	0.718

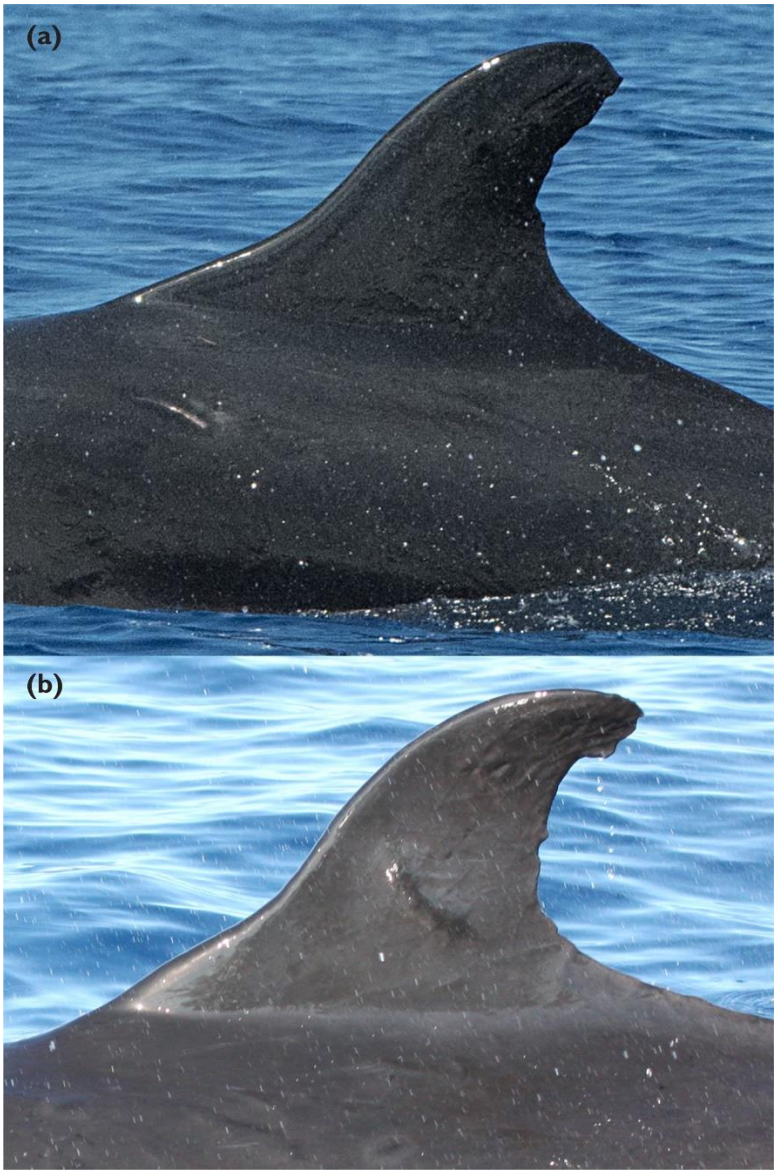

Figure 1. Two examples of an adult male false killer whale showing the hump at the leading-edge base of the dorsal fin indicative of older, physically mature males: (a) is HIPc205 with an emerging leading-edge hump and who was estimated to be 23 years old at the time this photo was taken in 2021 and is the approximate age we would expect to see the leading-edge hump (estimated age when biopsied in 2010 = 12 years old based on protocol detailed herein); (b) is HIPc114 representing an example of a fully developed leading-edge hump, and who was estimated to be 36 years old (see Figure 2 for full details) at the time this photograph was taken which aligns with our expectation to see a fully developed leading-edge hump for physically mature males. Top photograph taken by © Doug Perrine and bottom photograph taken by Katrina Tritz/© Cascadia Research Collective (both used with permission).

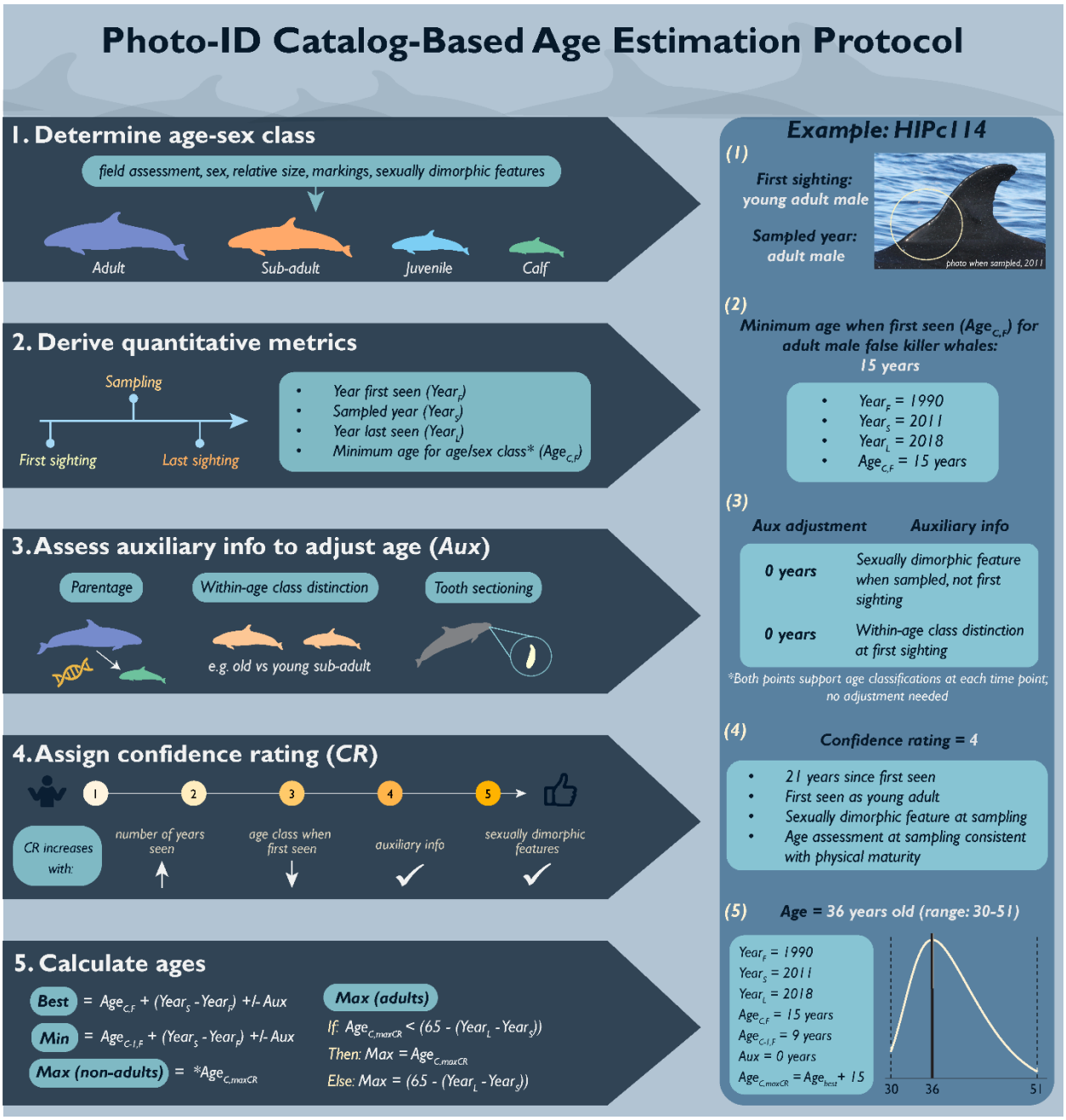

Figure 2. Overview of the photo-ID catalog-based estimation protocol (left side of figure), including an example (right side of figure) accompanying each step for one individual (HIPc114). Variables with asterisks indicate those that are set by the researcher and based on the biology of the species (e.g., age at sexual maturity) and range of available information (e.g., criteria for confidence ratings). False killer whale illustrations were provided by Uko Gorter; HIPc114 photograph taken by Jessica M. Achettino/© Cascadia Research Collective.

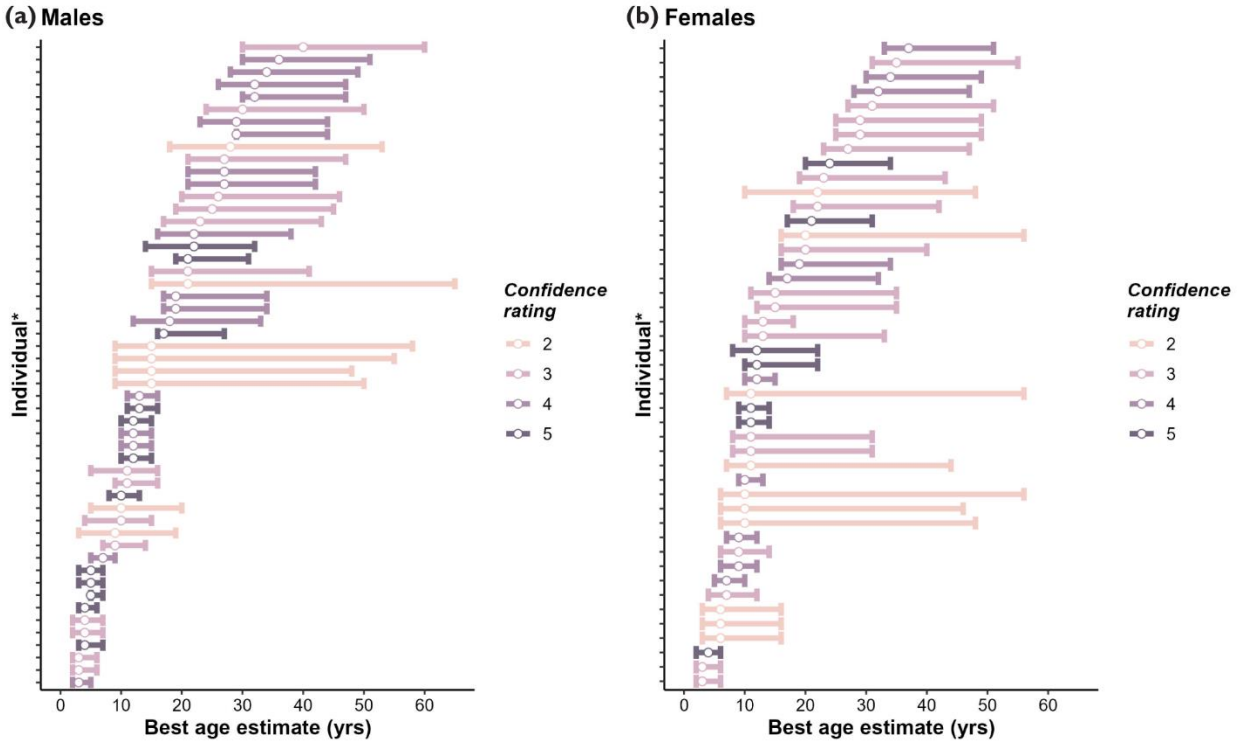

Figure 3. Age estimates (x-axis) for individual Hawaiian false killer whales at the time of biopsy sampling (y-axis; individual IDs not included on the axis for clarity); white circles represent the "best" age estimate and the bar lengths span the minimum and maximum age estimates. (a) Age estimates for males colored by confidence rating (1-5); (b) Age estimates for females colored by confidence rating (1-5). Note: no individuals were assigned a confidence rating of 1, so only confidence ratings 2 through 5 are shown here.

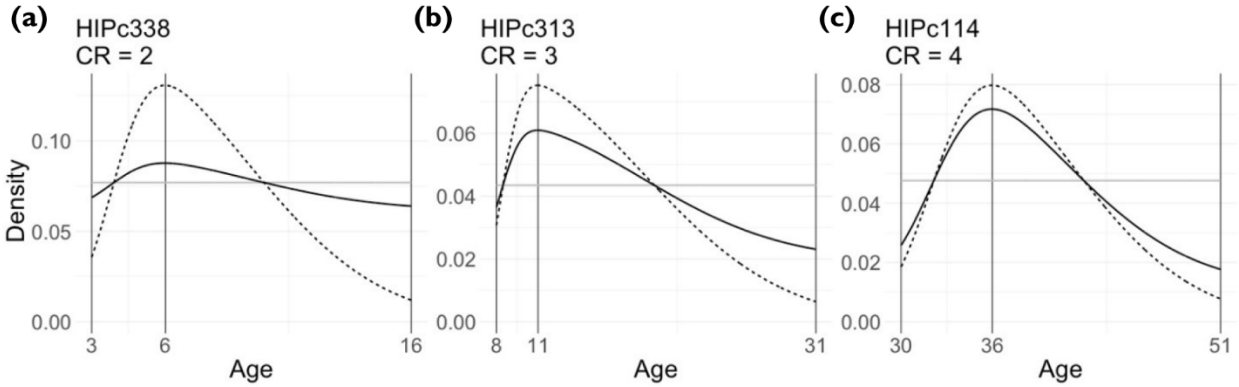

Figure 4. Age probability distributions for three example individuals. The horizontal gray line shows the Uniform distribution, the black dotted line shows the Skew-Normal distribution, and the solid black line shows a composite distribution that is a weighted average of the Uniform and SN distributions, with weights based on confidence rating (CR; see Table 5 for weight values). For animals with CR = 5, zero weight is given to the uniform distribution, resulting in a composite distribution that is identical to the Skew-Normal (black dotted line). Note that the x- and y-axis scales differ across the plots.

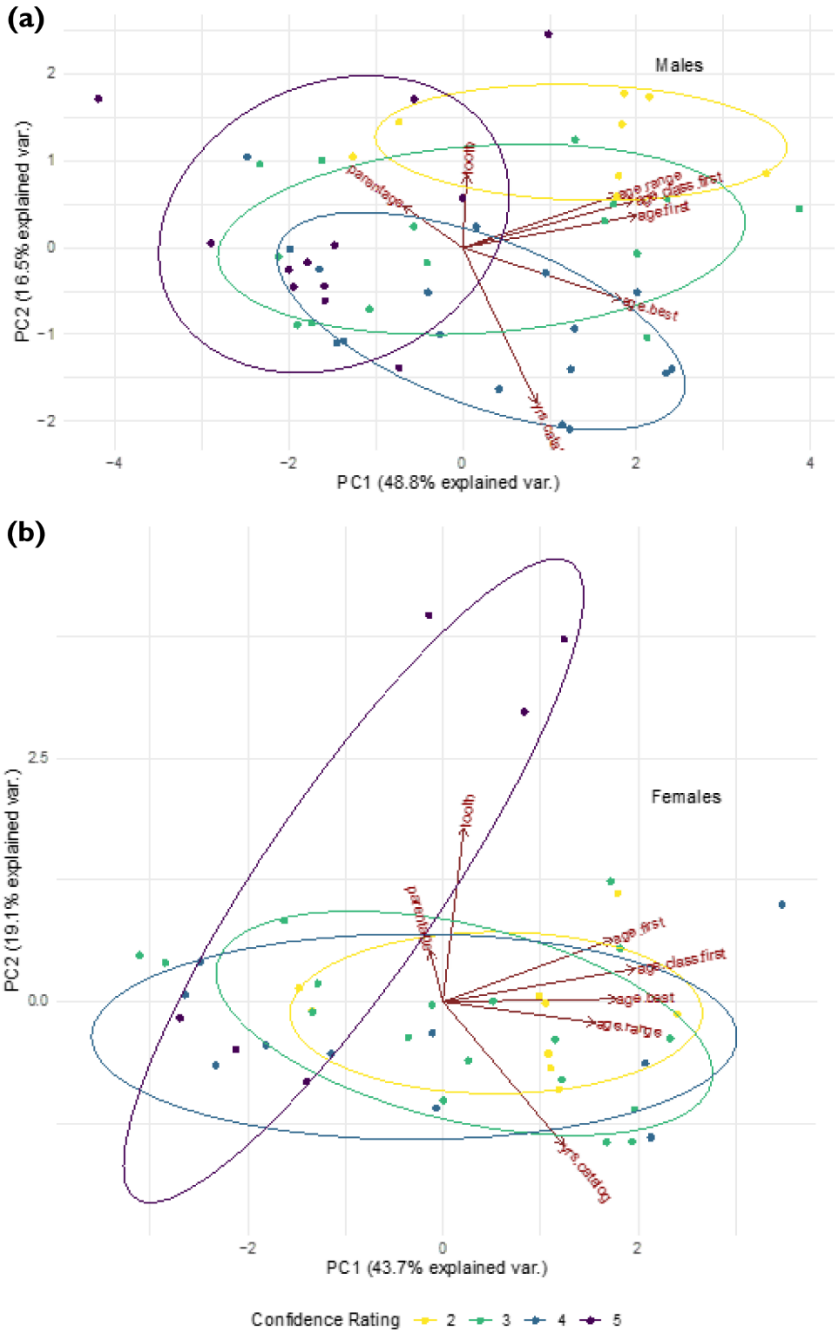

Figure 5. Biplots of first and second principal components of PCA analysis for males (a) and females (b).