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Received: 21 December 2021 | Accepted: 3 July 2022

Running head: YAHN ET AL.

ARTICLE

Sexually dimorphic characteristics of short-finned pilot whales, false killer whales, pygmy killer whales, and melon-headed whales assessed using fin and body morphometrics from photographs taken at sea

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Abstract

Adults of many free-ranging delphinid species cannot be reliably sexed at sea. Sexually mature, known-sex adult short-finned pilot, pygmy killer, melon-headed, and false killer whales were profiled from at-sea photos to assess proportional fin and body dimorphism. Males of all four species had larger dorsal fins proportional to anterior body length. False killer whales showed no further dimorphism, while melon-headed whales showed subtle dimorphism in dorsal fin overhang. Pygmy killer whales showed subtle dimorphism in lateral positioning of the top-most point and overhang. Lastly, short-finned pilot whales showed strong dimorphism in the leading edge, lateral positioning of the top-most point, and height of the overhang. Generalized linear models showed strong predictive accuracy for pilot and false killer whales, and moderate accuracy for pygmy killer and melon-headed whales. Results indicate that adult short-finned pilot and false killer whales can be accurately sexed in the field or via morphometrics. Adult pygmy killer and melon-headed whales have subtle sexual dimorphism that can be detected using morphometrics. The presence of dimorphism gives insight into potential reproductive strategies and social structure. Further analysis is needed to explore morphometric differences between inshore and pelagic populations of these species, as well as ontogenetic growth between life stages.

KEYWORDS

dorsal fin, *Feresa attenuata*, generalized linear model, *Globicephala macrorhynchus*, Globicephalinae, Hawai‘i, morphometry, *Peponocephala electra*, *Pseudorca crassidens*, sexual dimorphism

1 | INTRODUCTION

The sex and sexual maturity of individuals within a population are crucial demographic features necessary for developing robust population models and making accurate life history assessments. Current methods of identifying delphinid sex and sexual maturity are generally restricted to invasive skin biopsies (Winn et al., 1973), intrusive skin swabbing (Harlin et al., 1999), infrequent necropsy investigation, or limited opportunistic observations of genitalia, postanal hump or keel (Jefferson et al., 1997; Neumann et al., 2002), head or rostrum enlargement in some species (Mesnick & Ralls, 2018), mating behaviors, or recurring calf association. Some species of dolphins can be sexed using behavior-related physical differences, such as competitive male scarring in common bottlenose dolphins (*Tursiops truncatus*) (Currey et al., 2008; Tolley et al., 1995) and pigmentation loss in Australian humpback dolphins (*Sousa sahulensis*; Brown et al., 2016), but adults of many species cannot be reliably sexed at sea.

Delphinid fin and body morphometric analysis has been a useful tool in discriminating between similar-appearing species (Rone & Pace, 2012; Yahn et al., 2019) and ecotypes (Costa et al., 2021; Simões-Lopes et al., 2019). Adults of some delphinid species have sexually dimorphic differences in fin and body proportions that can be used to determine sex, including spinner dolphins (*Stenella longirostris*; Perrin et al., 1991), Fraser's dolphins (*Lagenodelphis hosei*; Jefferson et al., 1997), and North Pacific Shiho and tropical Atlantic Naisa short-finned pilot whales (*Globicephala macrorhynchus*; Kritzler, 1952; Yonekura et al., 1980), or can be indicators of sex in species such as striped dolphins (*Stenella coeruleoalba*; Carlini et al., 2014). Other species exhibit no apparent sexual dimorphism as adults in fin shape, including short-beaked common dolphins (*Delphinus delphis*; Murphy & Rogan, 2006) and common bottlenose dolphins (Rowe & Dawson, 2009; Tolley et al., 1995). Yet other species, such as long-finned pilot whales (*Globicephala melas*) in the North Atlantic, have conflicting reports of dorsal fin sexual dimorphism (Augusto et al., 2013; Sergeant, 1962a, b).

The presence of sexually dimorphic features may serve as visual signals to potential mates or male competitors (Mesnick & Ralls, 2018; Perrin, 1972), provide greater maneuverability for corralling females and intrasexual competition (Mesnick & Ralls, 2018; Ngqulana et al., 2017), or enhance thermoregulation (Tolley et al., 1995). Sexually dimorphic features can therefore serve as indicators of social structure and mating systems. Poor environmental conditions can also have an epigenetic influence on the presence and extent of dimorphism (Eirin-Lopez & Putnam, 2019; Feil & Fraga, 2012), with less exaggerated male features seen in low productivity areas (Amano & Miyazaki, 1996; Bell et al., 2002).

In species that have sexually dimorphic fin characteristics, the emergence of these traits could be used to determine the onset of sexual maturity (Rowe & Dawson, 2009). For killer whales (*Orcinus orca*; Cagnolaro et al., 1983; Heimlich-Boran, 1986) and spectacled porpoises (*Phocoena dioptrica*; Brownell & Clapham, 1999), fin height is a secondary sexual characteristic and can be used to indicate both sex and maturity of adult males (Durban & Parsons, 2006). Conversely, sexually mature long-finned pilot whales have proportionally larger dorsal fins (Sergeant, 1962b) but are thought to have otherwise indistinguishable fin characteristics (Augusto et al., 2013). Sexual dimorphism has not been examined in Hawaiian populations of four species of the subfamily Globicephalinae, including short-finned pilot whales, false killer whales (*Pseudorca crassidens*), pygmy killer whales (*Feresa attenuata*), and melon-headed whales (*Peponocephala electra*). This study measured relative fin and body proportions from photographs taken at sea to quantify sexual dimorphism in these four species, and determine whether morphometrics taken from photos can be used to determine the sex of adult individuals.

2 | MATERIALS AND METHODS

2.1 | Study area and data set

All analyzed images were taken from uniquely identifiable individuals in a long-term data set within the Hawaiian Archipelago, spanning 2003–2019. Just over 70% of individuals were photographed during dedicated small boat surveys undertaken by Cascadia Research Collective (Baird, 2016; Baird et al., 2013), with the remaining images provided by citizen scientists (17.7%) or other researchers (11.9%). This study analyzed images of individuals across multiple populations within the archipelago, including: short-finned pilot whales from insular and pelagic populations (Mahaffy et al., 2015; Van Cise et al., 2016), false killer whales from the main Hawaiian Islands insular, Northwestern Hawaiian Islands insular, and pelagic populations (Martien et al., 2014), melon-headed whales from the Hawaiian Islands and Kohala resident populations (Aschettino et al., 2011; Martien et al., 2017), and pygmy killer whales primarily from the insular population (McSweeney et al., 2009) (Table S1). The short-finned pilot whales in the Hawaiian Archipelago are of the Naisa type (Van Cise et al., 2016), which differ morphometrically from the Shiho type that inhabit the Eastern Pacific and Northern Japan (Van Cise et al., 2019).

2.2 | Sex and age classifications

A total of 328 sexed, adult individuals were measured for this study. Sexes were ascribed through one of three methods (Table 1): (1) genetic sex determination from biopsy samples undertaken by the Southwest Fisheries Science Center, following the methods described in Morin et al. (2005), and Martien et al. (2014, 2017) (52%); (2) in the case of nongenetically sexed females, by at least two encounters with a calf or neonate in calf position (43%) (Karenina et al., 2010); or (3) in the case of males, using the presence of a postanal keel (5%), which is a sexually dimorphic trait observed within many delphinid species (Mesnick et al., 2019). The latter sex determination method was used only for pygmy killer whales to increase sample size of sexed males. Although underwater photos to assess the presence or absence of a postanal keel are limited, two genetically sexed mature male pygmy killer whales in our photoidentification catalog had postanal keels and one genetically sexed mature female did not have a postanal keel, which lent further support to sexing adult pygmy killer whales using the postanal keel.

Age classification was determined using recurring calf presence for females throughout their sighting histories, adult body size matching physically mature adult conspecifics, or duration of sighting history exceeding 10 years (Yahn et al., 2019). Ten years of age does not fully encompass the range of sexual maturity in all species (short-finned pilot whales 7–17 years, Kasuya & Marsh (1984); false killer whales 8–11 years, Ferreira et al. (2014); melon-headed whales 11.5 years, Miyazaki et al. (1998); pygmy killer whales unknown), but animals are most likely older than the minimum 10 years, since distinct individuals are often identified when they are at least several years old. Immature individuals were excluded from analysis to avoid measurements skewed by allometric growth during ontogeny (e.g., killer whales, Clark & Odell, 1999; long-finned pilot whales, Sergeant, 1962b), and to better identify sex-specific traits that could be secondary sex characteristics emerging after maturity (Durban & Parsons, 2006).

2.3 | Image processing

Digital JPEG images were selected for high resolution, minimal angle deviation from the camera, and unobstructed view between the blowhole and posterior insertion of the dorsal fin. Fins were also rejected for analysis if the fin marker positions were altered or absent due to disfiguration (e.g., injuries at the leading or trailing edge base of the fin). Images were light-balanced and reoriented in ACDSee Pro 7 XE (ACD Systems International Inc., Fort Lauderdale, FL) so that the anterior dorsal ridge was horizontal in the frame. All images exceeding ~10° deviation from the camera were excluded from the data set to assure measurement accuracy (Rone, 2009; Rone & Pace, 2012). For consistency, only one researcher manually measured the fin and body lengths using ImageJ 1.52V (Schneider et al., 2012). Traces of dorsal fins were generated in Inkscape 1.1 (Inkscape Project, 2020).

2.4 | Morphometric measurements

Fin and body measurements were made following the methodology of Yahn et al. (2019), using five anchor points along the dorsal fin and one bisecting the blowhole to make 10 fin and body measurements. The ten raw measurements were made in pixels, since absolute measurements cannot be made without a scale reference, such as laser dots (Durban & Parsons, 2006). The fin measurements were made vertically or horizontally across the 2-dimensional fin surface, from the sides of a perimeter rectangle connecting four of the fin markers, or directly on the fin between anterior and posterior contours (Figure 1). The raw pixel measurements were put into 14 relative ratio terms to quantify fin and body dimensions (Figure 1). Anchor points were placed by hand and measurements were made on multiple photos of the same individual during an encounter, when possible, to check for consistency in ratios.

2.5 | Statistical analysis

All statistical analyses and graphical output were conducted in

R using RStudio v.1.4.1717 (R Core Team, 2021; RStudio Team, 2020). Shapiro-Wilk tests conducted on the male and female ratios for each species indicated a non-Gaussian distribution, so ratios were normalized with a log10 transformation in Microsoft Excel v.2110 (Microsoft Corporation, 2018). *F*-tests were used to test for unequal variance between sexes, and the null hypothesis of equal variance was rejected for *F*-scores between 0.75 and 1.25. Two-tailed student *t*-tests were used to test for significant differences between male and female ratios of each species, accounting for equal or unequal variance as indicated by the *F*-test.

Ratios were also modeled to examine the predictive power of ratio combinations in determining sex. Collinearity of variables can bias models to overemphasize related variables (Mackinnon & Puterman, 1989), so correlation coefficients were used to identify collinearity. Coefficients exceeding 0.75 were further quantified using Variance Inflation Factors (VIFs). Those ratios with VIFs ≥ 10.0 were considered problematic (Hair et al., 1995) and potentially weakening to the model’s predictive ability. To determine which of the correlated ratios to reject from the generalized linear model (GLM), related ratios were put into linear models and those with the lowest resulting Akaike information criterion (AIC) values were retained (Bozdogan, 1987). The remaining unrelated ratios were put into a GLM as independent variables with sex as the dependent variable. A backwards stepwise regression was performed on the GLM, which progressively removed ratios based on the resulting AIC values. The resulting ratios in the GLM were considered the most predictive of the differences between adult males and females for each species.

The predictive power of each species' GLM was then tested. The data set for each species was randomized within the data frame to avoid positional bias, and was assigned to a training group (66.6%) or testing group (33.3%). The accuracy of the predicted sex was determined with a threshold of 0.9 and averaged following 100 repetitions of randomized data. The area under the receiver operating characteristics curve (AUC of the ROC) was also calculated to determine the overall predictive power of the GLM when accounting for unequal female bias in the data set.

A priori power tests were used to determine if pygmy killer whales sexed using only genetics (n = 12) and recurring calf presence (n = 17) had sufficient data to produce meaningful analyses without intolerable levels of Type I and Type II errors (Kyonka, 2019). A priori power analyses required an estimate of effect size for each ratio (Cohen, 2013), which is the expected magnitude of difference between males and females. The effect sizes of melon-headed whale ratios were calculated and used to approximate those of pygmy killer whales, as the two species are morphometrically similar and likely to have comparable effect sizes.

3 | RESULTS

3.1 | Variable significance and collinearity

All four species showed significant dimorphism in the ratio of the anterior dorsal ridge to fin base length (J/A from Figure 1), and short-finned pilot whales, pygmy killer whales, and melon-headed whales showed further fin dimorphism (Table 2). Pilot whales had the most sexually differentiated fin ratios (10 of 13), and pygmy killer whales and melon-headed whales both had minor dorsal fin differentiation (2 of 13 ratios). A priori power analyses on pygmy killer whales sexed without using postanal keels (n = 29, α = 0.05) showed E/A, J/A, and B/A had power below the recommended 0.80 (Cohen, 2013) and were considered unreliable in the inferential statistics, therefore analyses were conducted including those sexed using postanal keels.

Significant ratios can be used independently to indicate sex, but collinearity between ratios may bias predictive models that incorporate multiple ratios. Collinearity coefficients flagged nine ratio pairs in short-finned pilot whales, seven pairs in false killer whales, five pairs in pygmy killer whales, and four pairs in melon-headed whales for collinearity. Variance inflation factors, linear models, and resulting AIC values determined which ratio in each collinear pair was discarded from the model, resulting in B/A, F/E, I/H, C/D, and C/B removed from short-finned pilot whale, B/A, D/A, B/D, I/H, and F/G removed from false killer whale, D/A, B/D, B/A, I/A, and G/E removed from pygmy killer whale, and C/A, B/A, B/D, I/A, and G/E removed from melon-headed whale GLMs.

3.2 | Final generalized linear models and predictive ability

Predictive models were generated using backwards stepwise logistic regression of each species' reduced GLM. Stepwise model selection with a backwards reduction of independent variables calculated the AIC value after each variable was removed in order to determine which, if any, variable should be removed next. The resulting reduced model had the lowest possible AIC with the fewest variables, indicating which variables accounted for the greatest effect on the dependent factor of sex. The following models were selected for each species, and all models with an AIC ≤ 2.0 of the top model were considered substantially supported and highly competitive (Burnham & Anderson, 2002) (Table S2):

$$SFPWsex = 7.78 + 27.65\,(E/A) - 24.04\,(J/A) - 59.95(D/A) + 23.48(H/A); AIC = 67.46$$

$$PKWsex = 6.09 - 17.91\,(J/A) + 18.51\,(C/A);\ AIC = 55.86$$

$$FKWsex = 13.11 - 36.84\,(J/A) + 23.05\,(C/A);\ AIC = 119.50$$

$$MHWsex = 15.23 - 55.33\,(J/A) + 103.74\,(C/D) + 19.19\,(H/A);\ AIC = 29.98$$

In order to test the model accuracy in predicting sex from the selected ratios, the data set was randomized and split into 2/3 training and 1/3 testing group. On a scale of 50% being entirely random prediction and 100% being perfect prediction, the model based on the training group with a threshold of 0.9 correctly predicted 88.2% of pilot whale, 46.8% of pygmy killer whale, 66.1% of false killer whale, and 54.9% of melon-headed whale sex in the testing group after 100 randomized repetitions (Figure 2). A further assessment of model predictive ability was calculated using the AUC of the receiver operating characteristics curve to account for all model thresholds and unequal sample sizes of males and females in the data set, and gave a value between 0 (no fit) and 1 (perfect fit). The AUC indicated strong to moderate model predictive ability, with pilot whale = 0.948, pygmy killer whale = 0.713, false killer whale = 0.810, and melon-headed whale = 0.710 (Figure 2).

4 | DISCUSSION

4.1 | Species dimorphism

Short-finned pilot whales had the most sexually dimorphic fin and body features of all four species. Adult male short-finned pilot whales have a broader and steeper leading edge of the dorsal fin, a more anterior topmost point, a lower overhang, and a shorter anterior dorsal ridge (Figure 3). The three insignificant ratios indicate that overall fin depth and height, as well as falcation height, are not consistent dimorphic features. The pilot whale generalized linear model also had the highest predictive ability of any species (Figure 2) using the combined features of dorsal ridge, fin height, and locations of the topmost point and falcation apex. Size dimorphism has previously been documented in short-finned pilot whales, with adult males having larger bodies and associated larger dorsal fins (Olson, 2009), and Naisa type males off Japan being 25% larger than females (Yonekura et al., 1980). The number and extent of ratios that differ between sexually mature adults, high predictive accuracy of sex-associated features, and obvious size difference between males and females lends support to field sexing adult short-finned pilot whales using fin and body features.

Sexual dimorphism has been documented in false killer whale body length and skull morphology (Kitchener et al., 1990; Purves & Pilleri, 1978). The results of our analyses confirm the presence of sexual dimorphism in body proportion along the anterior dorsal ridge of false killer whales (Table 2). The model showed relatively high accuracy in predicting sex using the dorsal ridge and fin depth (Figure 2). A highly competitive model indicated that falcation apex position may also be a predictive trait (Table S2). Female false killer whales from Japan and South Africa were measured to be approximately 83%–84% of male total body length (Ferreira et al., 2014) and our results measured anterior dorsal ridge/fin base to be approximately 10% larger in females, indicating adult females have a more posterior-positioned dorsal fin and/or a smaller dorsal fin (and likely body length, given allometric growth) than adult males. These consistencies in body proportions indicate that the sex of sexually mature animals can be ascertained from photographs or potentially in the field, using the relative length of the dorsal fin in relation to the dorsal ridge.

There is evidence of slight but significant sexual dimorphism in melon-headed whales, with males being 4% longer than females (Perryman, 2009), and having larger fin width, height, and base length (Best & Shaughnessy, 1981; Miyazaki et al., 1998). Our findings support that melon-headed whales had indicators of larger fin depth in males and a significantly smaller anterior dorsal ridge (Table 2, Figure 3). The models agreed that these features, as well as the position of the falcation apex and fin height (in a competitive model), were important predictors of sex (Table S2), though the models performed only slightly better than random sex assignment (Figure 2). Our study found the length of the dorsal ridge relative to the dorsal fin is approximately 10% smaller in adult males than in adult females, which is similar to false killer whales. Like false killer whales, this difference is detectable when analyzing photographs, but likely difficult to identify by eye in the field except by very experienced observers.

Most morphological records of pygmy killer whales come from observations of single animals, and only two mass strandings of five or six individuals (Clua et al., 2014; Mignucci-Giannoni et al., 2000) have been recorded, making male and female dimorphic characteristics difficult to compare. There is no documented body size dimorphism between male and female pygmy killer whales (Baird, 2018; Ross & Leatherwood, 1994), but the results of our study show that mature males have a significantly shorter dorsal ridge and slightly larger fin depth around the overhang (Table 2; Figure 3). The pygmy killer whale model also identified these features as predictors of sex, but it performed only slightly better than random sex assignment (Figure 2). These results indicate that the extent of the dorsal fin overhang is a small but important characteristic that can be used in addition to the dorsal ridge to determine pygmy killer whale sex using morphometrics.

This study used the presence of postanal keels to identify additional male pygmy killer whales for analysis. Of the four species, pygmy killer whales had the smallest sample of genetically confirmed males in the data set. Using the postanal keel to confirm males is common in several dolphin species (Mesnick & Ralls, 2018) and were observed in two of the genetically sexed male pygmy killer whales used in this study, but using this characteristic is inherently more subjective than genetic confirmation of sex, potentially introducing error into the analyses. Without the inclusion of individuals sexed using postanal keels, the sample size was insufficient to detect a significant difference between sexes. Future investigation of sexual dimorphism in these species could be bolstered by including males that are identified using postanal keels, particularly for melon-headed whales, which are also somewhat data-deficient and have keel sexual dimorphism in adults (Miyazaki et al., 1998; Cascadia Research Collective, unpublished data).

4.2 | Drivers of dimorphism

Despite these four species having recent phylogenetic divergence

(McGowen et al., 2020), the presence and extent of their sexual dimorphism ranges from many pronounced differences in short-finned pilot whales, to a few subtle differences in melon-headed and pygmy killer whales, to a prominent single relative trait differing in false killer whales (Table 2). The presence and extent of sexual dimorphism may relate to mating strategy, where larger dimorphic males compete with other males or are able to sequester females, while minimal presence or absence of sexually dimorphic traits may indicate a strategy of sperm competition, as evidenced by enlarged testes in relation to body size (Heimlich-Boran, 1993; MacLeod, 2010). Dines et al. (2015) compared testes mass per body length of 58 cetacean species, and noted that the testes of false killer, short-finned pilot, and melon-headed whales were slightly above average size, and the testes of pygmy killer whales were slightly below average size, but none of the four species deviated significantly enough to indicate sperm competition as the exclusive mating strategy. Given their anatomies, we postulate that all four of the examined species engage in some form of mating display or physical competition.

Concerning body size, Dines et al. (2015) further postulates that without evidence of severe injury resulting from competition, it is unlikely any of these species have monopolized access to females, and enlarged features of pilot whales and killer whales are used for ornamentation or a sign of fitness to attract mates (Amano & Miyazaki, 1996; Bell et al., 2002). That said, short-finned pilot whales have a high frequency of mandibular fractures in both males and females, thought to be associated with mating (Oremland et al., 2010), and all four species show evidence of tooth rakes from intraspecific interactions, indicating that competition and aggression does occur. Postanal keels are present in pygmy killer whales, melon-headed whales, and short-finned pilot whales, and are thought to be a visual signal to receptive females and competing males (Mesnick & Ralls, 2018), indicating that these three species likely employ this reproductive technique. False killer whales, which have no dorsal fin dimorphism but dorsal ridge and overall length dimorphism, engage in communal prey sharing (Baird et al., 2008), and may use behavioral displays like hunting success or acrobatics to demonstrate fitness and attract mates.

Most members of the subfamily Globicephalinae have strong social cohesion with long-term bonds (Aschettino, 2010; Baird et al., 2008; Mahaffy et al., 2015; Martien et al., 2017; McSweeney et al., 2009) and some have hierarchies (Ford et al., 2002; Mahaffy et al., 2015; Servidio, 2014), so it may be that increased body size determines mate choice through minor competitions without lasting injury to conspecifics, which would otherwise weaken the health of the group. When mating occurs outside of natal groups, the presence of sexual dimorphism may be driven by communal benefits to kin rather than mate choice (Ralls & Mesnick, 2009), which could be the case in these species. Increased body size in males likely improves their ability to defend a group against threats, such as interspecies harassment and predation by sharks (Baird, 2016; Cascadia Research Collective, unpublished observations). Larger males may also be physiologically capable of diving deeper or longer than females, potentially reducing competition for food within groups. Short-finned pilot whales off North Carolina exhibit different dive patterns with males performing the deeper dives than females, lending support to foraging niches between sexes in at least one population (Quick et al., 2017). Sex-based prey differentiation was also preliminarily detected from a small sample of skin stable isotopes in false killer whales off Chile, indicating that females had higher trophic niches than males (Haro et al., 2019). The presence of foraging niches would further support the benefits of prey sharing seen in false killer whales (Baird, 2009). Foraging niches have not yet been examined in melon-headed whales.

4.3 | Study limitations and significance

The age of sexual maturity (i.e., when individuals are capable of reproduction) and physical maturity (i.e., the full extent of physical development) normally occurs many years apart in cetaceans. Off central Japan, the Naisa type short-finned pilot whales reach sexual maturity between ages 7 and 12 in females and 7 and 17 in males (Kasuya, 2017), with testes size increasing the most between ages 14 and 17 (Kasuya & Marsh, 1984), but individuals do not stop growing until age 22 in females and 27 in males (Kasuya & Matsui, 1984). Similarly, false killer whales from two different populations reach sexual maturity around age 8–11, when they are roughly 83%–85% of their asymptotic length, but do not attain full length until around 25–30 years (Ferreira et al., 2014). Melon-headed whales reach sexual and physical maturity temporally close, with females achieving them at 11.5 years and 13 years, respectively, and males achieving them at 15–16.5 years and 15 years, respectively (Miyazaki et al., 1998; Perryman, 2009). Information on pygmy killer whale life history is limited given their rarity, so it is unknown how their development compares to the other three species. While all animals analyzed for this study were sexually mature adults (Table 1), it is possible that some individuals were not yet physically mature. It is suspected that sexually dimorphic features would be more pronounced in fully grown, physically mature animals, and unclear if they are present in immature animals. Further exploration is needed into the ontogenetic growth of dorsal fins between the immature, sexually mature, and physically mature stages of life in these species before this technique is used to sex immature animals.

Another potential source of error with this data set comes from grouping animals from multiple social groups and clusters around the Hawaiian Archipelago, including insular and pelagic populations (Table S1). Some species have morphometric adaptations between inshore and offshore populations to optimize their foraging success, predator avoidance, and energetic expenditure, e.g., common bottlenose dolphin, Felix et al. (2018); *Kogia* sp., Barros (1998); harbor porpoise (*Phocoena phocoena*), Galatius et al. (2012); and short-beaked common dolphins, Bell et al. (2002). Morphometric differences between insular and pelagic populations of our study species are unknown, but the exclusive nature of their groupings and tendency toward natal group breeding in false killer and short-finned pilot whales (Martien et al., 2019; Van Cise et al., 2016) promotes divergent characteristics and specialization between groups.

This study is unique because it had access to 35 years of life history information for some of these populations (Baird, 2016; Baird et al., 2008, McSweeney et al., 2009). This study took a conservative approach to determining female sex, requiring multiple encounters with a smaller animal alongside it in “calf position.” Some cetacean species exhibit alloparental care, meaning calves and subadults are not always alongside their mothers, e.g., long-finned pilot whales, Augusto (2017) and sperm whales (*Physeter macrocephalus*), Whitehead (1996). Analyses of photographs and video footage from a drone indicates that short-finned pilot and false killer whales in Hawaiʻi at least occasionally pass calves between adults (Cascadia Research Collective, unpublished data), so it is possible there were animals incorrectly assigned as female within this data set despite having been encountered more than once with an animal in calf position. An ideal data set would sex all animals through genetic confirmation alone to reduce this potential for error.

Our study was the first to employ this system of length and width-based measurements on delphinid dorsal fins to identify dimorphic features between sexes without having the animal in-hand. The benefit to using this detailed profiling technique is that it detects subtle and multifaceted dimorphic features which single-feature assessments of height/basal length may not detect. This technique could be used to expand upon dorsal fin and body dimorphism in other delphinid species inside and outside of the subfamily Globicephalinae, including species such as long-finned pilot where there is some disagreement regarding sexual dimorphism (Augusto et al., 2013; Bloch et al., 1993; Sergeant, 1962a, b).

4.4 | Conclusions

The life history of all four species included in this study can benefit from this noninvasive technique to sex individuals in the field and from photographs taken at sea, using fin and body proportions. All four species have sexually dimorphic anterior dorsal ridges, and three have dimorphic fin dimensions. Short-finned pilot whales had the most dimorphic characteristics and high model predictability of sex, melon-headed and pygmy killer whales had a few dimorphic features with moderate model predictive accuracy, and false killer whales had one body dimorphic feature with moderately high model predictive accuracy. The presence of these physical traits and size dimorphism lends support to sexing short-finned pilot and false killer whales in the field, while the sex of melon-headed and pygmy killer whales is not readily distinguishable by sight but can be ascertained using morphometrics. The identification of sexually dimorphic characteristics also provides insights into these species’ social structure and reproductive strategies.

Future investigation is needed to determine if insular and pelagic populations of any of these species possess more pronounced dimorphic traits. Ontogenetic research is also needed to pinpoint when these dimorphic traits develop in each species, and explore the efficacy of using this technique on immature animals.

ACKNOWLEDGMENTS

Funding for fieldwork was provided by NOAA Fisheries (Southwest Fisheries Science Center, Pacific Islands Fisheries Science Center, Bycatch Reduction Engineering Program), the State of Hawaiʻi (through a NOAA Section 6 grant), and the U.S. Navy (Office of Naval Research and Commander, Pacific Fleet). Funding for photo processing for catalogs was provided by the Pacific Islands Fisheries Science Center and a contract from the State of Hawaiʻi. For assistance during Cascadia Research Collective field operations we thank Daniel Webster, Colin Cornforth, Kimberly Wood, Brittany Guenther, Jordan Lerma, and Greg Schorr, and we extend thanks to Jim Ault, Chuck Babbitt, Colin Cornforth, Tori Cullins, Jens Currie, Mark Deakos, Alicia Franco, Kimberly Jeffries, Paul Johnson, Brett LeMaster, Dan McSweeney, the Pacific Islands Fisheries Science Center, Adam Pack and The Dolphin Institute, Dan Salden, the Southwest Fisheries Science Center, Stephanie Stack, Deron Verbeck, Jim

Ward, and Kimberly Wood for contributing additional photos used in the analyses. We also thank Jessica Aschettino, Annette Harnish, Annie Gorgone, and Alex Vanderzee for work with our photo-ID catalogs. We extend our gratitude to Karen Martien, Sarah Mesnick, and two anonymous reviewers for their helpful comments on the manuscript. Cascadia Research Collective work was undertaken under NMFS Permits 731-1509, 731-1774, 15330, and 20605. Photos were also collected under Permits No. 15240 and 20311 (issued to PIFSC), 774-1714 and 14097 (issued to SWFSC), 107-1770 (issued to The Dolphin Institute), and 21321 (issued to Pacific Whale Foundation).

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TABLE 1 Demographics of data indicating the number of individuals sexed using genetic sampling (g), recurring calf association (c), and postanal keel morphometry (m) for each species.

Species	**Male (g)**	**Male (m)**	**Female (g)**	**Female (c)**	**Total**
Short-finned pilot whale	33	0	20	73	126
Pygmy killer whale	6	17	6	17	46
False killer whale	40	0	50	35	125
Melon-headed whale	10	0	3	18	31
Total	91	17	78	142	328

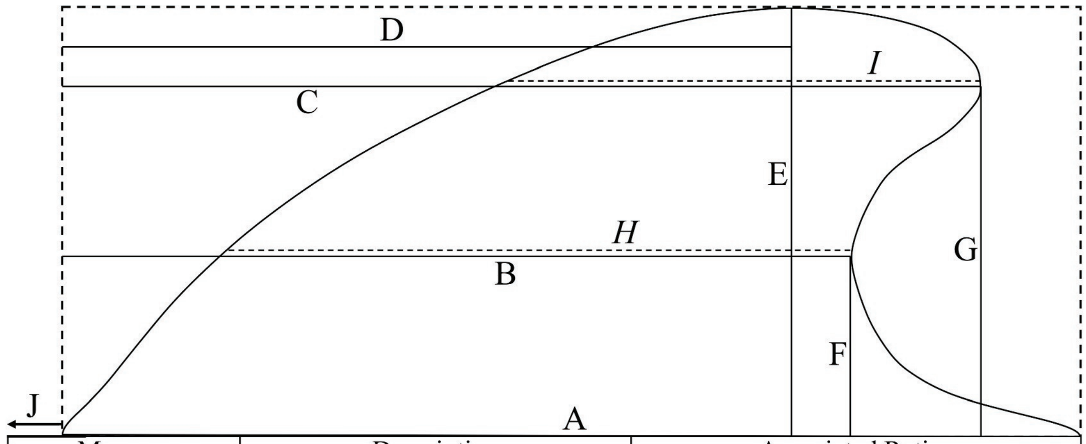
TABLE 2 Two-tailed student *t*-tests comparing males and females for each ratio, with * indicating tests with equal variance, and all significant ratios (*p* < .1) noted in bold. Short-finned pilot whales (SFPW) had 11 significantly dimorphic ratios, melon-headed whales (MHW) and pygmy killer whales (PKW) had three, and false killer whales (FKW) had one. Ratios E/A and F/E were not significant for any species and were not included in this table.

Species	**JA**	**BA**	**DA**	**CA**	**BD**	**CD**	**CB**	**HA**	**IA**	**IH**	**GE**	**FG**
SFPW	***p* < .001** *F*(1,125) = 0.336	***p* = .019** *F*(1,125) = 0.643	***p* < .001** *F*(1,125) = 0.266	*p* = .658 *F*(1,125) = 0.247	***p* < .001** *F*(1,125) = 0.016	***p* < .001** *F*(1,125) = 0.175	***p* = .003** *F*(1,125) = 0.102	***p* = .002** *F*(1,125) = 0.859*	***p* < .001** *F*(1,125) = 0.061	***p* < .001** *F*(1,125) = 0.162	***p* < .001** *F*(1,125) = 0.000	***p* = .009** *F*(1,125) = 0.351
PKW	***p* = .040** *F*(1,45) = 0.213	*p* = .147 *F*(1,45) = 0.056	***p* = .081** *F*(1,45) = 0.136	***p* = .087** *F*(1,45) = 0.072	*p* = .476 *F*(1,45) = 0.653	*p* = .872 *F*(1,45) = 0.064	*p* = .468 *F*(1,45) = 0.686	*p* = .389 *F*(1,45) = 0.165	*p* = .586 *F*(1,45) = 0.111	*p* = .389 *F*(1,45) = 0.171	*p* = .605 *F*(1,45) = 0.767*	*p* = .898 *F*(1,45) = 0.180
FKW	***p* < .001** *F*(1,135) = 0.482	*p* = .714 *F*(1,135) = 0.019	*p* = .749 *F*(1,135) = 0.097	*p* = .739 *F*(1,135) = 0.188	*p* = .958 *F*(1,135) = 0.992*	*p* = .963 *F*(1,135) = 0.554	*p* = .986 *F*(1,135) = 0.673	*p* = .358 *F*(1,135) = 0.014	*p* = .992 *F*(1,135) = 0.804*	*p* = .424 *F*(1,135) = 0.169	*p* = .630 *F*(1,135) = 0.002	*p* = .522 *F*(1,135) = 0.020
MHW	***p* = .002** *F*(1,30) = 0.163	*p* = .667 *F*(1,30) = 0.959*	*p* = .985 *F*(1,30) = 0.952*	*p* = .148 *F*(1,30) = 0.077	*p* = .713 *F*(1,30) = 0.222	***p* = .050** *F*(1,30) = 0.692	*p* = .524 *F*(1,30) = 0.505	*p* = .205 *F*(1,30) = 0.101	***p* = .092** *F*(1,30) = 0.723	*p* = .229 *F*(1,30) = 0.515	*p* = .582 *F*(1,30) = 0.908*	*p* = .667 *F*(1,30) = 0.954*

FIGURE 1 Schematic of the 10 measurements (labeled A through J) made on each individual, with J starting at the anterior fin insertion and extending to the bisection of the blowhole. The table describes each of the measurements and lists the analyzed ratios that include them.

FIGURE 2 Boxplots of top model performance for each species following 100 repetitions of the test groups. The accuracy of sex prediction (left) has a broader distribution than the area under the receiver operating characteristics curve (AUC) (right) that accounts for female bias in the data.

FIGURE 3 Overlayed traced outlines of dorsal fins showing average proportions in males (solid outline with white background) and females (dashed outline with grayed background) for the three species that showed fin dimorphism, with measurement A having the same value for visual comparability between the sexes. Letter markers indicate the location of measurements on the fin, with * indicating significant differences between males and females.



Measure	Description	Associated Ratios
A	Fin base	E/A, J/A, B/A, D/A, C/A, H/A, I/A
B	Depth at falcation apex	B/A, B/D, C/B
C	Depth at posterior point	C/A, C/D, C/B
D	Depth at topmost point	D/A, B/D, C/D
E	Fin height	E/A, F/E, G/E
F	Height at falcation apex	F/E, F/G
G	Height at posterior point	G/E, F/G
H	Width at falcation apex	H/A, I/H
I	Width at posterior point	I/A, I/H
J	Anterior dorsal ridge	J/A

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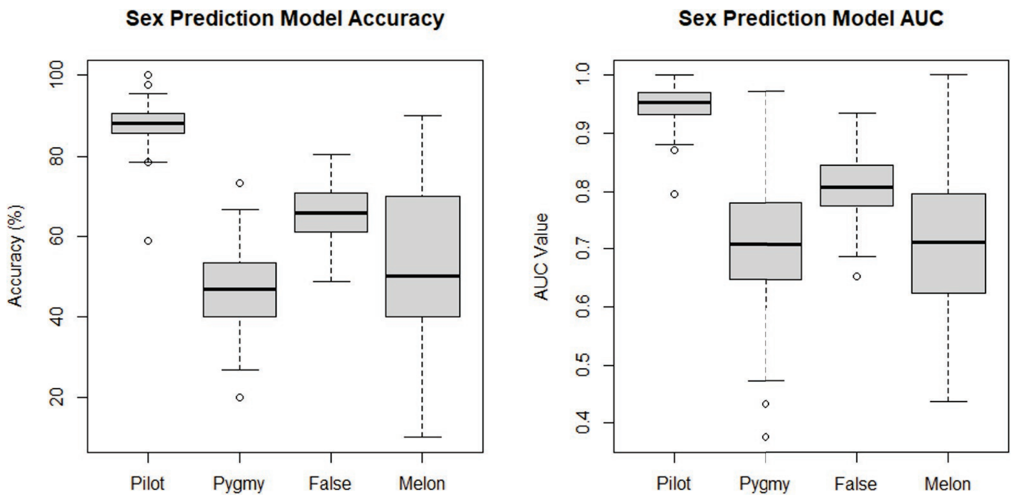

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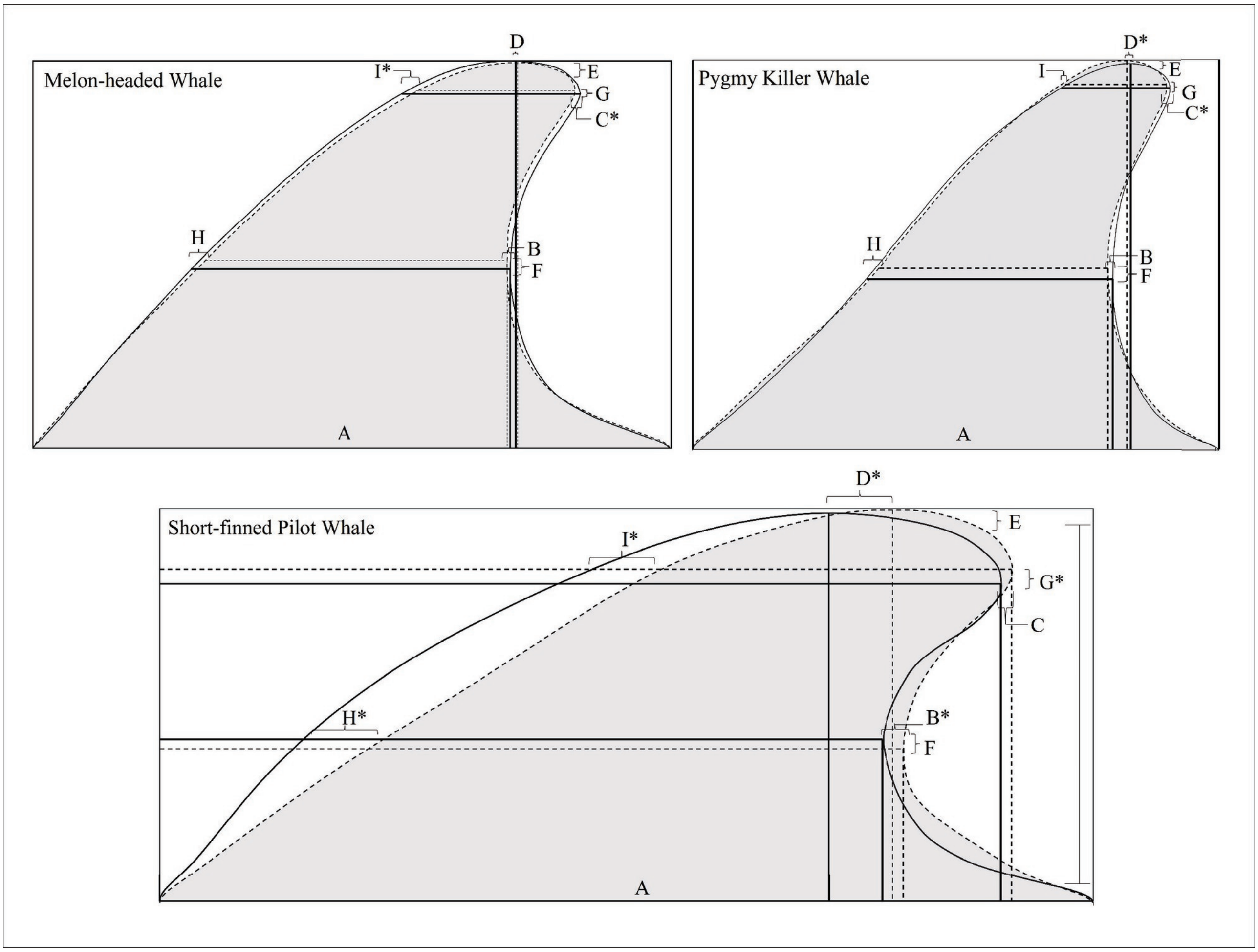

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