



How to tell them apart? Discriminating tropical blackfish species using fin and body measurements from photographs taken at sea

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ABSTRACT

The misidentification of species and populations is a hindrance to effective cetacean management. We devised a method of species identification using 10 fin and body measurements obtainable from at-sea photographs, and demonstrated its ability to distinguish four species of Hawaiian “blackfish”: pygmy killer, melon-headed, short-finned pilot, and false killer whales. Measurements from photos of 382 known individuals were converted into 14 ratios and reduced using nonmetric multidimensional scaling and principal component analysis. The first three components of the PCA explained 81% of variance among species. Ratios indicated by PCA and NMDS were tested using analysis of variance, and results identified three fin ratios that had distinct means across all four species: height/base, depth (from anterior insertion) at trailing edge apex/depth at topmost point, and width (from leading edge) at posterior point/base. Dual analysis of adults and all age classes showed near-identical sources of variance, 90% similarity in interspecies ratio relationships, and overlapping ratio means and ranges. Results suggest similar ontogenetic growth across these four species, and confirm the efficacy of this discrimination technique for all age classes. This study established a reliable means of distinguishing these cetacean species, which will improve the efficacy of management in areas with sympatric distributions.

Key words: species identification, morphometry, blackfish, Hawai‘i, PCA, dorsal fin, *Feresa attenuata*, *Peponocephala electra*, *Globicephala macrorhynchus*, *Pseudorca crassidens*.

Appropriate and effective cetacean management is contingent upon the ability to identify animals at the species, population, and individual levels. Misidentification can lead to misattributed descriptions of group structure, behavior, habitat use, and anthropogenic interactions. Targeted management is particularly challenging for similar-appearing

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species and subgroups with sympatric distributions (Caldwell and Caldwell 1989, Segura *et al.* 2006).

With specimens or genetic samples in hand, or with good quality photos that show pigmentation patterns, identification of species (or populations) of cetaceans is a relatively straightforward task (*e.g.*, Duffield *et al.* 1983, Natoli *et al.* 2004, Wang *et al.* 2008). However, in many cases, lighting conditions, the research platform used, or the behavior of the animals themselves preclude obtaining even good quality photos, so species identification often relies on silhouettes of individuals from sometimes distant photographs. We sought to develop a means of species identification using simple fin and body measurements that could be garnered from such photos, using four similar-appearing and sympatric species of delphinids.

In Hawaiian waters there are four species of delphinids, known collectively as “blackfish” (Baird 2016), that sometimes form multispecies aggregations (Migura and Meadows 2002, Baird *et al.* 2008, McSweeney *et al.* 2009). These tropical blackfish species are the pygmy killer whale (*Feresa attenuata*) (PKW), melon-headed whale (*Peponocephala electra*) (MHW), short-finned pilot whale (*Globicephala macrorhynchus*) (SFPW), and the false killer whale (*Pseudorca crassidens*) (FKW), all of which share characteristics of gray-black coloration, falcate dorsal fin, and bulbous head without a beak (Fig. 1). Tropical blackfish species are difficult to distinguish at sea, and peer-reviewed literature occasionally misidentifies them (*e.g.*, Watkins *et al.* 1997, Castro 2004, Marigo and Giffoni 2010, Baird 2010, Siciliano and Brownell 2015), highlighting a need for reliable means of discriminating among them. We used these four tropical blackfish species to examine the efficacy of using fin and body morphometrics to distinguish similar cetacean species.

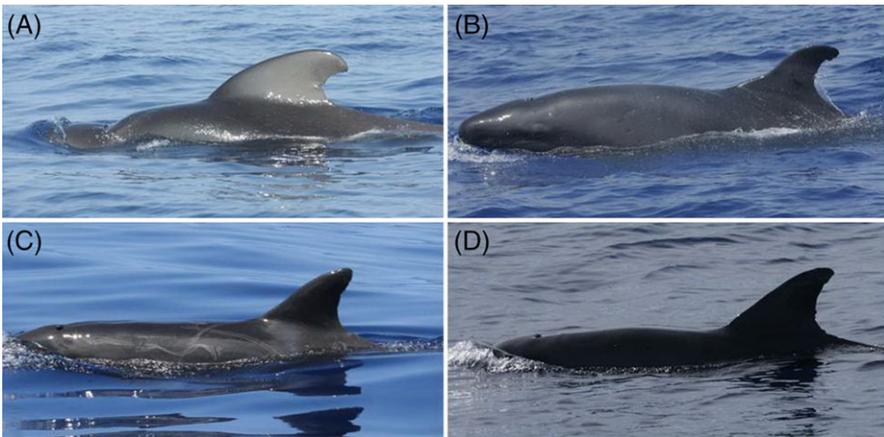


Figure 1. At-sea photographs of four tropical blackfish species in Hawaiian waters: short-finned pilot whale (A), false killer whale (B), pygmy killer whale (C), and melon-headed whale (D). All animals shown are adult males, and meet the photo-selection criteria of full visibility and perpendicular angle.

Tropical blackfish species are typically distinguished at sea using subtle and often unreliable behavioral and biological characteristics. One such trait is average group size (PKW ~10, FKW ~15, SFPW ~20, MHW ~250), though each species can also occur in pairs or alone (Baird *et al.* 2013), or in much larger groups than is typical (*e.g.*, Reeves *et al.* 2009). While average adult length differs among the species (SFPW 5.5–7.2 m, FKW 5–6 m, PKW 2.6 m, and MHW 2.8 m (Jefferson *et al.* 2015), all the species overlap in length, and size can be difficult to determine at sea (Baird 2010). Pigmentation along the mouthline and cape can differentiate species, but only when the animal is at close range, in good lighting conditions, and enough of the body is visible. In the case of short-finned pilot whales, adult males have a distinctly enlarged dorsal fin (Jefferson *et al.* 2015, Olson 2017), but this trait is not present in females or immature animals (Leatherwood *et al.* 1982). Behavioral and biological characteristics are useful to distinguish tropical blackfish species when in close proximity, under ideal sighting conditions, and when they are in their typical group sizes, but the species can be difficult to distinguish in many circumstances.

We used photographs taken as part of a long-term multispecies study in Hawai'i (Baird *et al.* 2013, Baird 2016), and identified ratios that distinguish all four species regardless of age. Also presented are other useful ratios that distinguish just one or two species. This technique should reduce instances of their misidentification, as well as provide general body proportion characteristics of value in species identification even when no photographs are available.

METHODS

Study Area and Data Set

This study utilized photographs collected throughout the Hawaiian Archipelago *via* dedicated small boat surveys beginning in 2000 (Baird *et al.* 2013), and opportunistic vessel encounters for false killer whales and pygmy killer whales extending back to 1986 (Baird *et al.* 2008, McSweeney *et al.* 2009). The data set consisted of known, individually distinctive animals from a number of different populations: the pelagic and main Hawaiian Islands insular population of false killer whales (Martien *et al.* 2014), insular and pelagic populations of short-finned pilot whales, both of the *naisa* form (Mahaffy *et al.* 2015, Baird 2016, Van Cise *et al.* 2016), both Hawaiian Islands and Kohala resident populations of melon-headed whales (Aschettino *et al.* 2011, Martien *et al.* 2017), and the Hawai'i Island resident population of pygmy killer whales (McSweeney *et al.* 2009). Killer whales (*Orcinus orca*) are another blackfish species that occur around Hawai'i, but they are encountered very infrequently (Baird *et al.* 2006), and there was insufficient data to include them in this study.

Age and Sex Classification

Of the 225 adults measured for this study, 88 (39.1%) were sexed *via* genetic analyses of biopsy samples, undertaken at the Southwest

Fisheries Science Center. Sex and age class was also determined for 55 adult females (24.4% of adults) based on photos at some point in their sighting history that included close proximity to a neonate or small calf. Two short-finned pilot whales (1%) were deemed adult males because they displayed obvious sexually dimorphic features, including larger relative size in photos (Kasuya and Matsui 1984, Mahaffy *et al.* 2015), more anteriorly positioned dorsal fin (Heimlich-Boran 1993), thickened leading edge of the dorsal fin (Heimlich-Boran 1993, Mahaffy *et al.* 2015), and squarer-shaped melon (Olson 2017). The remaining 80 adults (35.5%) were unsexed. Known sexual dimorphism in short-finned pilot whale dorsal fin shape and potential sexual dimorphism in other species likely increases the variability associated with morphometric analysis, although since the sex of animals of unknown species identity are typically not known, including both sexes in our analyses was warranted.

Aside from the sexual maturity qualifiers listed above which designate adults, age classes were based on factors of relative body size (when more than one individual was in the same photo), extent of association with an adult, and sighting history. Modifying the age classifications in Mahaffy (2012) to include the span of years seen, animals that were of adult length and had 10+ yr of sighting history were considered adults. It should be noted that most individuals with sighting histories exceeding 10 yr were likely several years old when first documented. Individuals in close association with an adult that were <66% of adult length were considered calves, and those that were 66%–75% of adult length were considered juveniles. Although Mahaffy (2012) classified subadults as individuals slightly smaller than adults, all individuals (including juveniles) who were classified as calves when first seen with a sighting history spanning 4–9 yr were grouped together as subadults for this study.

Image Processing

While some original photographs were black and white negatives or color slides, these were scanned and all images were analyzed as JPEG files. A variety of criteria were necessary for images to be used in analyses. Animals could not be angled more than $\sim 10^\circ$ from the camera in the horizontal plane (Rone 2009, Rone and Pace 2011), photographs had to be of sufficiently high resolution, had to have unobstructed views of the dorsal fin, and the subject animal did not have severe dorsal fin disfigurements (Fig. 1). Photos of porpoising animals were not used, as the arched bodies may have distorted features. Selected photos were cropped and leveled in *ACDSee Pro 7* and measured using *ImageJ* (1.48 V).

Fin and Body Measurements

Existing fin terminology was used when available, including the fin base (distance from anterior to posterior fin insertion) and foil (curvature of the fin's leading edge) (Weller 1998, Morteo *et al.* 2017). Fin depth (horizontal distance from anterior fin insertion to trailing edge)

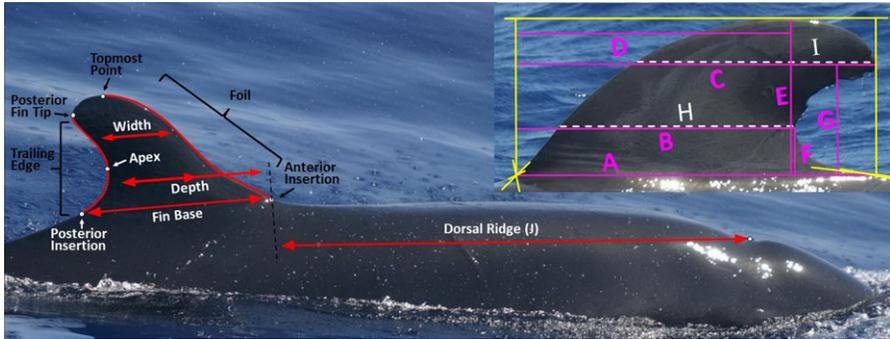


Figure 2. General terminology and positions of the reference points used to orient measurements for this study, marked on a false killer whale. Inset photo shows nine of the ten measurements, A–I, conducted on a short-finned pilot whale fin. Not shown in inset is measurement J, the length of the dorsal ridge. See Table 1 for detailed descriptions of fin and body measurements.

and width (horizontal distance from foil to trailing edge) were also used (Fig. 2).

Six reference points and one reference line were marked along the dorsal fin and body to anchor measurements (Fig. 2). One reference point each was placed at the fin's anterior insertion point, where the lower foil contour changed, and posterior insertion point, where the posterior dorsal ridge contour changed. The placement of insertion points differed from Durban and Parsons (2006) and Rone (2009) who used the midpoint of the fin's curvature located between reference lines drawn along the fin and back axes. Additional reference points were placed at the fin's topmost point, posterior point of the tip, and apex of the trailing edge, as well as at the animal's blowhole. If reference points occurred on nicked or notched segments of fin, the points were placed on existing portions of the fin, rather than inferring the original contour. A reference line was constructed vertically through the anterior insertion point, perpendicular to the fin base, to anchor depth measurements.

Ten lateral and vertical lengths were measured between the reference points or to the reference line (Fig. 2 inset). Besides the fin base (A) between the fin insertion points, three depth measurements were made from the reference line to the trailing edge apex (B), posterior point (C), and topmost point (D). In contrast, two width measurements were made from the foil edge of the fin to the trailing edge apex (H) and posterior point (I). The three vertical height measurements were made from the fin base to the topmost point (fin height [E]), trailing edge apex (F), and posterior point (G). The final measurement of the anterior dorsal ridge (J) was the distance between the reference line and blowhole.

Dimensions were measured in pixels and compared as relative measurements. Absolute measurements were not available for analysis because many of the photographs used for this study predated the inclusion of scale references, such as laser dots (Durban and Parsons 2006).

Table 1. Description of the 10 measurements taken from each photograph, and their contribution to the 14 ratios examined in this study. Ratios were found by dividing one measurement of interest by another, such as the fin height divided by the fin base (E/A). Depth measurements are from the anterior insertion while width measurements are from the leading edge (foil) of the fin.

Measurement	Measurement description	Associated ratios
A	Fin base	E/A, J/A, B/A, D/A, C/A, H/A, I/A
B	Depth at trailing edge 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 trailing edge apex	F/E, F/G
G	Height at posterior point	G/E, F/G
H	Width at trailing edge apex	H/A, I/H
I	Width at posterior point	I/A, I/H
J	Anterior dorsal ridge	J/A

Additionally, these photographs were not collected using arrays of multiple cameras to provide 3-dimensional information from which absolute measurements could be made (Bräger and Chong 1999, Waite *et al.* 2007). Ratios were calculated by dividing two measurements of interest (Table 1), and described features such as the relative height of the dorsal fin (E/A), the overhang of the fin tip (C/D), and the relative width of the fin (I/A), among others.

Statistical Analysis and Visualization

We used a combination of principal component analysis (PCA) and non-metric multidimensional scaling (NMDS) to reduce the 14 ratios to those with the highest variance and greatest dissimilarity across the four species. PCA reoriented the ratios into factorial planes of components that decreasingly explained the variance between the species (Pearson 1901). Individual loadings for each component's ratios were multiplied by the proportion of variance explained by its component, providing a scaled "weight" of each variable in terms of the overall variance observed between species.

The nature of the data involving multiple species, age classifications, and sexes caused ratios to have inconsistent distributions and variances, and be resilient to data transformations. Traditionally PCA is performed on data with Gaussian distributions, but this assumption is not required when using PCA as a descriptive tool for exploratory analysis (Jolliffe and Cadima 2016), and non-Gaussian ratio data have been successfully analyzed using PCA (*e.g.*, Marina *et al.* 2018). It is also possible that because resultant principal components are linear functions of 14 random variables with large sample sizes ($n = 382$ for all-animal analysis and $n = 225$ for adult-only analysis), the central limit theorem (CLT) can be applied to assume approximate normality even though the ratios are not normally distributed (Jolliffe 2002). Performing PCA on non-Gaussian data with

many dimensions but too few points to apply the CLT still produces consistent eigenvalues and eigenvectors, but can limit their distributions (Yata and Aoshima 2009, Jung *et al.* 2012).

Scaling was also conducted using NMDS to corroborate the high variance ratios suggested by the PCA. Unlike PCA, NMDS does not require linear (Phillips 1978) or Gaussian (Prentice 1977) distributions, and calculates pairwise Euclidean distances between data point coordinates, which are regressed and fitted by least squares (Kruskal 1964, Takane *et al.* 1977, Shepard 1980). NMDS was plotted along two axes and the test repeated with 500 iterations to avoid the issue of local minima and produce the truest ordinations. NMDS was conducted in *Primer 7*, and its ordinations were compared with the PCA ordinations. This process was repeated twice, once with all individuals and again with a subset containing just adults, to explore if age had an effect on any ratio's interspecies comparisons.

The results of the PCA and NMDS were used to select ratios that showed the highest weighted variance and greatest dissimilarity between species, and these were further subjected to significance testing. The selected ratios were tested for normal distribution (Shapiro-Wilk test) and equal variance (Breusch-Pagan test), and the appropriate parametric or nonparametric analysis of variance (ANOVA) tests were used to compare the selected ratios across all species.

Ratios with normal distribution and homoscedasticity were analyzed using one-way ANOVA and a Tukey honest significant difference *post hoc* test, which controls for familywise Type 1 errors (Tukey 1949). Those with normal distribution but heteroscedasticity were analyzed using Welch's ANOVA and a Games-Howell test, a *post hoc* extension of the Welch's ANOVA, neither of which assumes homoscedasticity (Games and Howell 1976). A Benjamini-Hochberg correction was added to the Games-Howell test to control for multiple pairwise comparisons influencing the false discovery rate (Benjamini and Hochberg 1995).

Ratios with nonnormal distribution but homoscedastic variance were analyzed using the Kruskal-Wallis test, with a Dunn's multiple comparisons *post hoc* test and Benjamini-Hochberg correction. Those with neither normal distribution nor equal variance were analyzed using the Brown-Forsythe test, which examines the absolute values of the deviations from the median in heteroscedastic populations (Brown and Forsythe 1974, O'Brien 1981). A Games-Howell *post hoc* test was performed following the Brown-Forsythe test, which is robust to data with non normal distribution when sample sizes are over 20 (Games *et al.* 1979).

The PCA and ANOVA statistical analyses were conducted in *R* (3.1.1), utilizing the packages of *car*, *userfriendlyscience*, *FSA*, *vGWAS*, *dunn.test*, and *lmtest*. Select ratios were visualized across species, age classifications, and sexes using box, bar, and scatter plots in *R* and Microsoft Excel 2010.

RESULTS

Data Overview and Variable Reduction

Fin and body measurements were made on 94 short-finned pilot whales, 102 false killer whales, 82 pygmy killer whales, and 104 melon-headed

whales of all age classifications and sexes, including 225 sexually mature adults (Table 2). Two distinct variable reduction techniques, NMDS and PCA, were conducted to indicate which ratios were the most dissimilar across species. Their ordination plots were compared to support the selection of reduced ratios, and vectors of both methods suggested J/A, E/A, H/A, and B/A to be ratios of interest, while PCA suggested the additional ratios of C/D, I/A, and G/E (Fig. 3).

Eigenvalues extracted from the PCAs indicated that the first three components largely summarized the data, explaining 81.3% and 80.8% of the overall variance in the full data set and adult subset, respectively (Table 3). The weight of each ratio within the first three components was visualized to better determine how they contributed to the overall variance between species (Fig. 4).

The first component described the position of horizontal fin features (B, C, D, I, H) in relation to the fin base (A) or each other, and indicated its inverse relationships with both height (E, F, G) and dorsal ridge length (J). The second component described the vertical (F) and horizontal (B) position of the trailing edge apex, and showed an inverse relationship with the topmost (D) and posterior-most (C) points on the fin. The final component described the length between the trailing edge apex (B) and fin's topmost point (D), and showed an inverse relationship with positions of the apex and topmost point (C/B, I/H).

Fundamental Ratios

There was very high similarity in the composition of principal components for both analyses (Fig. 4). Still, to eliminate any possible effect of age on interspecies differences, analysis of variance was performed on the seven ratios reduced from the NMDS and PCA for only the adult subset. The parametric and nonparametric ANOVAS revealed three of the original 14 ratios were significantly different in all *post hoc* cross comparisons: the relative height (*i.e.*, height by base length, E/A), the overhang of the fin tip (*i.e.*, depth at posterior by depth at topmost point, C/D), and the relative width of the fin (*i.e.*, width at posterior point by base length, I/A) (Table 4). These fundamental ratios were visualized for both data sets and again showed high similarity (Fig. 5). The other 11 ratios were not significantly different between all species, but some could distinguish one or two of the species in a cross comparison (Table 5). The one additional

Table 2. Sample size for each species by age class and sex.

Age/sex class	SFPW	PKW	FKW	MHW	Total
Adult male	21	8	20	10	59
Adult female	21	21	23	21	86
Adult unknown sex	12	16	19	33	80
Total adults	54	45	62	64	225
Subadult and juvenile	20	20	20	20	80
Calf	20	17	20	20	77
Total all age classes	94	82	102	104	382

Table 3. Eigenvalues and the percentage of accumulated variance for the first three components of the principal component analysis. The all-individual data set and adult-only subset were organized into similarly proportional components in the PCA. The remaining components are detailed in Table S1.

Component	All ages eigen-value	Adult eigen-value	All ages percentage of variance	Adult percentage of variance	All ages accumulation of variance (%)	Adult accumulation of variance (%)
1	6.142	6.42	43.9	45.9	43.9	45.9
2	3.148	2.954	22.5	21.1	66.4	67.0
3	2.02	2.007	14.4	14.3	80.8	81.3

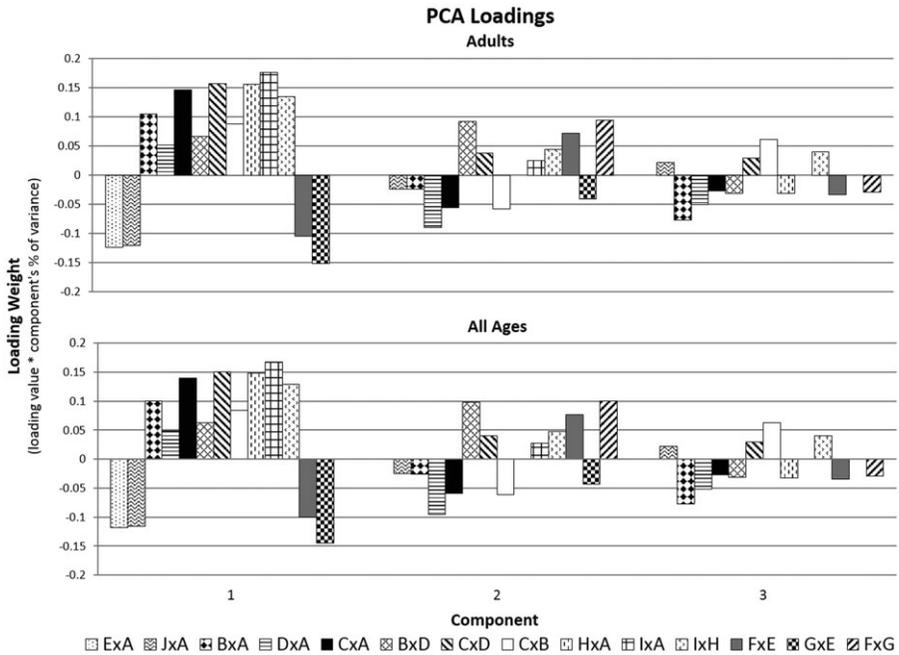


Figure 4. Relative weights of ratios on the overall variance observed among species. Weights were calculated by multiplying the loading values of the top three components' ratios by each component's proportion of variance. Negative ratios indicate an inverse relationship with positive values within that component. The vectors and relative weights of the ratios largely overlapped between dual analyses of adults and all individuals.

Table 4. Mean (SD) fin dimensions of each species for the three ratios that distinguish all four species in adults. Also listed are the types of ANOVA used for that particular ratio's analysis based on how it met statistical assumptions (see methods section for details).

Species	E/A (relative height)	C/D (fin tip overhang)	I/A (relative width)
Pilot whale	0.427 (0.032)	1.211 (0.086)	0.460 (0.150)
False killer whale	0.557 (0.057)	1.127 (0.036)	0.284 (0.062)
Pygmy killer whale	0.653 (0.073)	1.078 (0.032)	0.199 (0.055)
Melon-headed whale	0.605 (0.048)	1.105 (0.033)	0.249 (0.060)

Significance test: Welch's ANOVA $F(3,185.26) = 257.88$, $P < 0.001$; Brown-Forsythe $F(3,195.95) = 20.18$, $P < 0.001$; Brown-Forsythe $F(3,194.45) = 20.38$, $P < 0.001$.

ratio examined the relative width of the fin as it tapered from the base (I/A). Pertaining to this measure, pygmy killer whales had the greatest tapering from the base, followed by melon-headed whales, then false

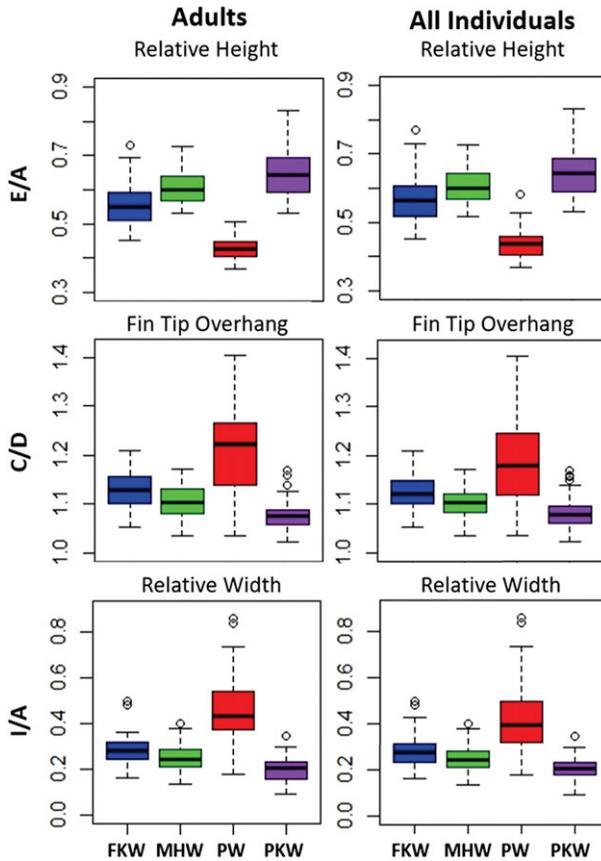


Figure 5. Boxplots of the three fundamental ratios for both the adult-only and combined-ages data sets. There is high correlation between the two analyses, indicating the interspecies ratio relationships were largely unaffected by age, and that fundamental ratios can distinguish species regardless of age classification.

killer whales, and finally short-finned pilot whales had the least tapering. The latter two ratios are occasionally used to discriminate between coastal and offshore ecotypes of cetaceans (*e.g.*, Félix *et al.* 2018), and highlight differences between these four blackfish species.

Other Ratios and Species Discrimination

Several ratios with large PCA weights and strong NMDS vectors were not significantly different across all four species, but illuminated distinctive characteristics for certain blackfish species, and can therefore be used to confirm species designations (Table 5). One such ratio is the dorsal ridge to fin base (J/A). The data confirms that this metric can strongly distinguish short-finned pilot whales ($M = 0.918$, $SD = 0.159$) and false killer whales ($M = 2.183$, $SD = 0.302$) from other blackfish

Table 5. The mean (SD) of 10 adult fin ratios that showed significant differences between at least two species, not including the three fundamental ratios.

Ratio	J/A (fin location)	B/A (depth of apex)	C/A (depth of fin tip)	B/D (topmost and apex alignment)	C/B (depth of overhang)	H/A (width of apex)	I/H (fin tapering)	F/E (height of apex)	G/E (height of posterior tip)	F/G (height of overhang)
Short-finned pilot whale (*)	0.918 ^{‡‡} ~ (0.159)	0.799 ^{‡‡} ~ (0.041)	0.941 ^{‡‡} ~ (0.067)	1.027 ^{‡‡} ~ (0.043)	1.179 ^{‡‡} ~ (0.061)	0.597 ^{‡‡} ~ (0.076)	0.760 ^{‡‡} ~ (0.182)	0.400 ^{‡‡} ~ (0.068)	0.810 ^{‡‡} ~ (0.084)	0.495 [‡] (0.077)
False killer whale (†)	2.183 ^{*‡} ~ (0.302)	0.714 ^{*~} (0.054)	0.854 ^{*~} (0.076)	0.944 ^{*~} (0.047)	1.197 [‡] ~ (0.063)	0.419 ^{*~} (0.053)	0.679 [‡] ~ (0.128)	0.400 [‡] ~ (0.064)	0.886 ^{*~} (0.035)	0.452 ^{*‡} ~ (0.075)
Pygmy killer whale (‡)	1.879 ^{*†} (0.205)	0.737 ^{*~} (0.055)	0.833 ^{*~} (0.068)	0.956 ^{*~} (0.063)	1.132 ^{*†} (0.067)	0.412 ^{*~} (0.064)	0.485 ^{*†} (0.119)	0.476 ^{*†} (0.084)	0.909 ^{*~} (0.051)	0.526 [†] (0.095)
Melon-headed whale (~)	1.846 ^{*†} (0.179)	0.753 ^{*†} (0.041)	0.858 ^{*~} (0.049)	0.970 ^{*†} (0.050)	1.142 ^{*†} (0.060)	0.470 ^{*†} (0.061)	0.531 ^{*†} (0.114)	0.467 ^{*†} (0.068)	0.909 ^{*†} (0.036)	0.514 [†] (0.075)

Note: The symbols following the means represent which species they were significantly different from: * are short-finned pilot whales, † are false killer whales, ‡ are pygmy killer whales, and ~ are melon-headed whales. Ratios are defined in Table 1, and marked on a fin in Figure 2.

(Baird 2010, Jefferson *et al.* 2015), but cannot be used to distinguish melon-headed whales ($M = 1.846$, $SD = 0.179$) from pygmy killer whales ($M = 1.879$, $SD = 0.205$).

Two other weighted ratios included the depth and height of the posterior point compared to the fin's base (C/A) and height (G/E). These are both distinctive characteristics of short-finned pilot whales, which have a larger and lower overhang beyond the fin base than the other three blackfish species.

The remaining ratios that were heavily weighted and most dissimilar pertain to the width of the fin as it tapers to a hook: H/A and B/A, the width and depth of the trailing edge apex to the fin base, respectively, and I/H, the width at the posterior point to the width at the trailing edge apex. A wider fin with a convex foil are the primary distinguishing features of melon-headed whales when compared to pygmy killer whales. The mean width at the trailing edge apex is 47.0% of the base length ($SD = 6.1\%$) in melon-headed whales (H/A), compared to 41.2% ($SD = 0.064\%$) in pygmy killer whales, and their posterior point width is 53.1% ($SD = 11.4\%$) of the trailing edge apex width (I/H) compared to 48.5% ($SD = 11.9\%$) in pygmy killer whales (Table 5). Besides the three fundamental ratios, the ten ratios presented in Table 5 had a significant difference between at least two species, and can therefore aid in species designation within Hawaiian waters.

Dissimilar Ratios and Growth Rates

The composition of the PCA components highlighted fin and body features where the greatest variance occurred between species. The ratios that highlighted the largest differences between species were the least Gaussian in nature, while those ratios that followed more normal distribution had greater overlap between species, making them less useful as distinguishing features. As previously stated, non-Gaussian data used in PCAs produce relatively consistent eigenvalues and eigenvectors (Yata and Aoshima 2009, Jung *et al.* 2012), but their limiting distributions shorten the boundaries and muddle the strength of the vectors presented in the ordination plots. This is likely the basis for the differences observed between the PCA and NMDS ordination plots (Fig. 3); PCA highlighted the same four strongest vectors of the NMDS plot, and also indicated three additional ratios as having great variance. The similar results between the two distinct variable reduction techniques, with PCA using degree of variance and NMDS using Euclidean distance of dissimilarity, lends validation to PCA's ability to explore non-Gaussian ratio data.

The positive and inverse relationships between fin features identified by the PCA components (Fig. 4) were also grossly observed as trends in fin shape. Animals with wider fins had relatively shorter dorsal fins and smaller dorsal ridges, which was indicated in component 1. Similarly, those with wider fins had lower, more anteriorly positioned trailing edge apices, as was indicated by component 2. Finally, animals with more expansive overhang of their fin also had lower trailing edge apices and more anteriorly positioned topmost points, as indicated by component 3. The three

fundamental ratios, those distinct for all species, were all strongly present in component 1.

We conducted dual analyses, once with individuals of all age classifications and again with only confirmed mature adults, to determine if the same morphometric ratios could distinguish species regardless of age class. This situation is representative of typical photos of blackfish taken at sea, where age classification is difficult to ascertain. The components of the PCAs showed strong similarity between the data sets (Fig. 4), indicating that the ratios which contributed the greatest variance between species were largely unaffected by age classification. The three fundamental ratios were plotted for each data set (Fig. 5), which indicated that age class had minimal effect on the ranges of these ratios or their interspecies ratio relationships. This trend was also true for the remaining ratios, which together showed 90% consistency in interspecies relationships between the dual analyses.

These results indicate either that fin growth in Hawaiian blackfish is isometric where features develop at a rate directly proportional to body size, or else that body and fin features develop at the same rate across all four species, which maintains their interspecies relationships. It is common for cetaceans to have allometric growth, *e.g.*, common bottlenose dolphin, *Tursiops truncatus* (Félix *et al.* 2018) and killer whale (Clark and Odell 1999), or a combination of feature-specific allometric and isometric growth, *e.g.*, long-finned pilot whale, *Globicephala melas* (Sergeant 1962); Dall's porpoise, *Phocoenoides dalli* (Amano and Miyazaki 1993); dusky dolphin, *Lagenorhynchus obscurus* (Van Waerebeek 1993); and vaquita, *Phocoena sinus* (Torre *et al.* 2014). It is possible animals were assigned to age classes that could not adequately detect allometric growth rates because they spanned multiple growth phases or did not encompass a growth phase in its entirety. Bloch *et al.* (1993a) suggested long-finned pilot whales undergo four distinct growth periods, including early postnatal, juvenile, young adult, and prephysically mature adult phases, which were grouped together into calf and subadult classifications for this analysis. Further investigation is needed to better classify growth characteristics of body and fin features, but the results of this study indicate that fin ratios can be used to identify species regardless of age.

Observed Variance in Ratios

Despite the statistical significance of the fundamental ratios' means and medians, many ratios share overlapping ranges between species (Fig. 5), highlighting individual variations between animals. Therefore, it is suggested that all three of the fundamental ratios are calculated on Hawaiian blackfish species to produce the most compelling evidence for species designation. Ratio ranges may overlap between species for a variety of reasons, including natural variation in fin shape or sexually dimorphic fin features.

Fin and flipper features are adapted to meet habitat or foraging demands, as observed in off-shore and coastal bottlenose dolphin populations (Hersh and Duffield 1990, Morteo *et al.* 2017, Félix *et al.* 2018).

The Hawaiian Archipelago has both coastal and deep-ocean habitat, and supports insular and offshore populations of false killer whales (Baird *et al.* 2008), and island-specific populations of short-finned pilot whales (Mahaffy *et al.* 2015) and melon-headed whales (Aschettino *et al.* 2011). It is possible that these blackfish populations have different foraging demands and endure different environmental conditions, which has led to adapted fin features over time. We measured individuals from multiple populations for three of the four species, so the data includes any natural variation between groups.

This study intentionally disregarded sex in analysis of adult ratios to simulate the realistic situation of encountering unidentified, unsexed blackfish at sea. The only dorsal fin features previously examined for sexual dimorphism in short-finned pilot whales are the base length and height, which were found to be monomorphic (Bloch *et al.* 1993b), but there has been speculation of adult males having a more prominent overhang (Leatherwood *et al.* 1982). There are conflicting reports of sexual dimorphism in dorsal fins of the close-related long-finned pilot whale (Sergeant 1962, Rumage 1983, Bloch *et al.* 1993b, Augusto *et al.* 2013), which may be present in short-finned pilot whales. Sexual dimorphism in the other three tropical blackfish species is largely uninvestigated. Consequently, no sexually dimorphic characteristics were accounted for in the data and may have contributed to some of the ratios' overlapping distribution between species.

Applicability to Other Populations and Species

This study demonstrated the efficacy of using fine scale morphometrics to discriminate between four similar cetacean species in Hawaiian waters. This was done using relative measurements rather than absolute measurements, which is an established method of analysis in morphometry (*e.g.*, Rone and Pace 2011, Morteo *et al.* 2017, Félix *et al.* 2018). One benefit to analyzing relative measurements is that data can be collected remotely and noninvasively, without requiring animals to be stranded, captured, landed, or otherwise in-hand. This method of analysis can also incorporate historic and citizen science photographic data, allowing for greater sample sizes and more powerful statistical conclusions. We suspect that analysis of absolute measurement data would corroborate the results presented in this study.

While we have included multiple populations for three of the four species studied, the morphometric differences exhibited in these species may be specific to the populations we analyzed within the Hawaiian Archipelago. All four species studied are known to exhibit large-scale population structuring (Martien *et al.* 2014, 2017; Hancock-Hanser *et al.* 2015; Van Cise *et al.* 2016), and in the case of short-finned pilot whales this includes at least two different morphological forms, and thus phenotypic variation among more widely separated populations may muddle some of the differences documented here. This morphometric approach should be applied to other blackfish populations before making any gross generalizations about the four species' distinguishing features worldwide.

The full potential of this approach has not been explored for other sympatrically-distributed species or populations, and ecotypes of marine mammals. For instance this tool could help distinguish short-finned from long-finned pilot whales which have overlapping ranges in the Northwest Atlantic (Rone and Pace 2011), or killer whale ecotypes which show genetic divergence despite sympatry (Moura *et al.* 2015). This approach could also be used to better understand genetic distinctiveness and distributions of bordering morphotypes, such as the *shibo* and *naisa* forms of SFPW in the Pacific. The ten measurements may be directly applied to nonblackfish species, or adapted to better assess features such as triangular fin shape. This technique also has potential to illustrate differences between cetacean populations, highlight sexually dimorphic characteristics, map growth rates, or categorize stages of ontogeny, making it a valuable research tool.

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SUPPORTING INFORMATION

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Table S1. Eigenvalues and the percentage of accumulated variance for each component of the principle component analysis. Eigenvalues dropped substantially after component 3 in both data sets, indicating successive components weakly contributed to the overall variance, and were therefore not examined further.