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Common bottlenose dolphins (*Tursiops truncatus*) in California waters: Cranial differentiation of coastal and offshore ecotypes

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ABSTRACT

Coastal and offshore bottlenose dolphins in California waters are currently assessed and managed as separate stocks. Recent molecular studies (of mtDNA haplotypes and microsatellites) have shown the two populations to be genetically differentiated. This study investigated cranial osteological differentiation of the forms. The sample analyzed included 139 skulls from live captures, direct takes, fishery bycatch, and strandings; the skulls were assigned to form based on collection locality or mtDNA haplotype. The coastal form differs from the offshore form mainly in features associated with feeding: larger and fewer teeth, more robust rostrum, larger mandibular condyle, and larger temporal fossa. This suggests that it may feed on larger and tougher prey than the offshore form. Differences between the forms in other features of the skull may reflect differences in diving behavior and sound production. Approximately 86% of the stranded specimens were estimated to be of coastal origin; based on relative estimated sizes of the two populations and assuming similar mortality rates, this suggests that a coastal carcass is about 50 times more likely to beach than an offshore one. The morphological differences between the two

ecotypes indicate evolutionary adaptation to different environments and emphasize the importance of conserving the relatively small coastal population and its habitat.

The taxonomic history of bottlenose dolphins in the eastern North Pacific is long and confused. *Tursiops gillii* was described from Monterey Bay (Dall 1873) based on a dolphin taken by Scammon (1874). *T. nuuanu* was described from the far-offshore eastern tropical Pacific, at 12°N, 120°W (Andrews 1911). Hershkovitz (1966) synonymized the latter with *Tursiops truncatus*, assigning it to a subspecies *T. t. aduncus*, but recognized the former. More recent workers have considered all the bottlenose dolphins in the eastern Pacific, including the nominal species *T. gillii* and *T. nuuanu*, to belong to *T. truncatus* (Rice 1998, Perrin *et al.* 2009). *Tursiops aduncus* is now recognized as a separate species restricted to the western Pacific and Indian Oceans (Wang and Yang 2009).

Norris and Prescott (1961) first noted that bottlenose dolphins occur in both shallow inshore waters and bays and in deeper offshore waters of California. Based on experiences while capturing dolphins for exhibit, Walker (1975) suggested that these were separate populations. The existence of two populations or ecotypes has been widely recognized since he presented the results of a study of osteology, parasites, and stomach contents in an unpublished contract report (Walker 1981), and subsequent studies of distribution, behavior, ecology, physiology, population dynamics, and population size and status have proceeded on that assumption (Duffield *et al.* 1983; Hansen 1983, 1990; Wells *et al.* 1990; Barlow 1995; Forney *et al.* 1995; Carretta *et al.* 1998, 2009; Defran and Weller 1999; Defran *et al.* 1999; Dudzik 1999; Ward 1999). The coastal range extends from near San Francisco to south of the border along the coast of Baja California, Mexico and is thought to be restricted to within about 1 km of the mainland coast (Hansen 1990, Hansen and Defran 1990, Carretta *et al.* 1998, Defran and Weller 1999), with the animals typically encountered in water <10 m deep (Ward 1999). These dolphins are not highly philopatric, being found at different times nearly anywhere within their linear range (Hansen and Defran 1990, Hanson and Defran 1993, Carretta *et al.* 1998, Defran *et al.* 1999). Presumed offshore bottlenose dolphins occur in deeper water beyond 1 km from the coast, around the Channel Islands, and as far north as 41°N (Carretta *et al.* 2009). The coastal population off California is most recently estimated at 450–500 animals and the offshore population at 3,495 (CV = 0.43) (Dudzik *et al.* 2006).

Walker's (1981) sample of specimens included dolphins known to have been captured from around the Channel Islands and stranded dolphins recovered from mainland beaches and from the Gulf of California. Two clusters were evident in multivariate analyses of skull measurements, one containing the known offshore animals and the other the stranded specimens (including those from the Gulf of California), suggesting that all of the stranded dolphins were of coastal origin. The coastal animals had on the average larger teeth, greater proximal ramus height, and larger mandibular condyles. Walker also found differences in parasite faunas and stomach contents, with only the offshore dolphins containing mesopelagic prey.

Most recently, Lowther [Thieleking] (2006) found nonoverlapping mtDNA control-region haplotypes and differences in microsatellite frequencies for biopsy samples taken close to the coast (within 1 km) *vs.* farther offshore. She also found
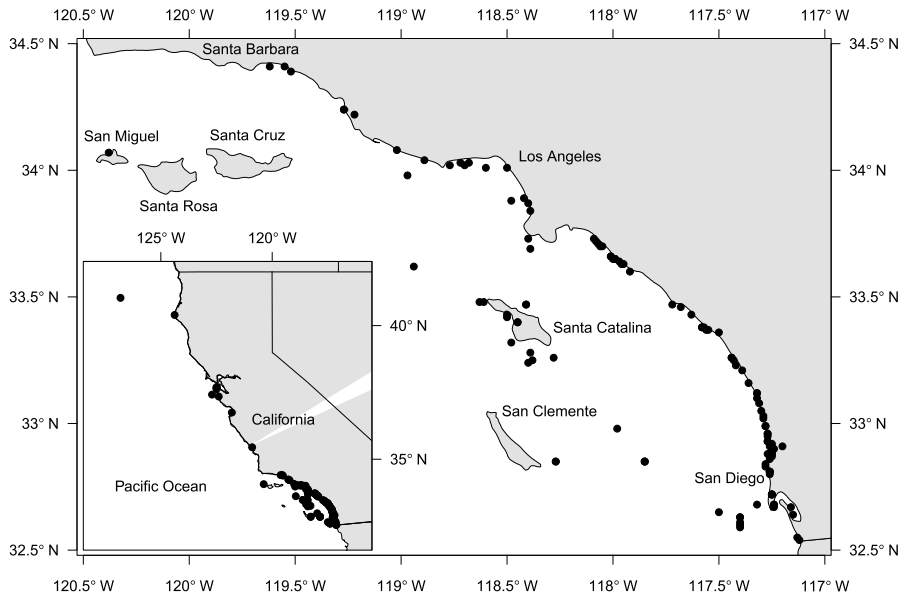
Figure 1. Map of localities of specimens and biopsy samples used in this study. Main map shows enlargement of Southern California Bight; inset shows entire distribution of sample localities. One symbol may represent more than one specimen. In addition, the sample included two dolphins captured from imprecisely recorded localities in the vicinity of the Channel Islands.

differentiation between coastal samples from California and samples from the Gulf of California, suggesting that they should not be considered to be from the same population.

In the present study, we extended the genetic analysis to include additional biopsies, dolphins live-captured for exhibit, a dolphin bycaught in an offshore fishery, and stranded dolphins. We also measured the much larger series of osteological specimens now available in U.S. museums. Based on the overall genetic patterns in the larger series, we examine morphology of the two ecotypes and estimate population membership for the adult specimens stranded on the mainland and lacking molecular assignments (not making the assumption that all were coastal dolphins). We discuss the ecologies of the forms in light of their morphological differences and estimate stranding rates for carcasses of the coastal and offshore ecotypes.

METHODS

The Sample

We examined 139 osteological specimens in museums and private collections that were collected between the 1850s and 2006 (Appendix 1) from the border with Mexico north to Cape Mendocino (~40°N) in California (Fig. 1). We excluded specimens from the Gulf of California because of Lowther's (2006) finding of genetic difference from California specimens. We excluded the few specimens available from

the outer coast of Baja California because of uncertainty about the southern limit of the range of the population in California waters and the logistical difficulties of obtaining samples from those specimens for genetic analysis. Most of the specimens examined were from strandings (all but two that stranded on the Channel Islands were from the mainland). Sixteen were from dolphins live-captured offshore (in the vicinity of the Channel Islands) for exhibit at Marineland of the Pacific, and two were from dolphins live-captured in San Diego Bay. Seventy-four of the 139 California specimens were cranially adult, evidenced by the approximate criterion of distal fusion of the premaxillae and maxillae of >1 cm (Mead and Potter 1990, Perrin and Heyning 1993); 65 were cranially juvenile. We collected teeth, bone, or soft-tissue samples from 131 specimens for genetic analysis. Powder from teeth and bone was collected by low speed drilling using the sterile technique described in Morin *et al*. (2006). The powder was stored at room temperature. When soft tissues were available, skin or muscle was collected and stored in a 20% salt-saturated solution of dimethyl sulfoxide (DMSO) and frozen at −20°C. DNA extraction and sequencing followed the protocols in Lowther (2006).

We were successful in extracting and sequencing mtDNA for 98 of the 131 samples; the sequence data were analyzed together with those from the 171 previously analyzed (Lowther 2006) or newly collected biopsy samples, for a total of 269. For the remaining 41 osteological specimens, all from strandings or captures on the mainland, either no tissue sample was collected or DNA extraction or sequencing failed. Coastal biopsy samples were from <1 km from shore and offshore samples from beyond that limit.

Morphometrics

Cranial and postcranial measurements and tooth counts were taken with dial calipers and anthropometers by WFP and WAW as in Perrin (1975) with addition of three measurements: minimum palatal width anterior to the pterygoid hamuli (PALW), length of the left pterygoid hamulus (PTLN), and maximum dimension of the left mandibular condyle (MWMC). WFP and WAW measured a series of the same skulls to intercalibrate their methods. Measurements were made to the nearest millimeter except TOOW (diameter of tooth at mid-row), which was measured to the nearest tenth mm. Counts of teeth or alveoli were made for both left and right upper and lower rows, and the highest upper (HIUP) and highest lower (HILO) counts were included in the analyses. When a count was available for only one side, it was used as an estimate of the highest count. Finally, we added a variable (MXTH) that was the maximum of HIUP and HILO; this variable was used only in the classification analyses.

Genetic Analyses

The 269 mtDNA control-region sequences were represented by 56 haplotypes. Of these, five haplotypes were from biopsied coastal dolphins and 34 were from offshore dolphins either biopsied, live-captured, bycaught in an offshore fishery, or stranded in the Channel Islands (Lowther 2006). We recovered 128 sequences, represented by 27 haplotypes, from stranded dolphins of unidentified ecotype. Of this set, 80 sequences and eight haplotypes corresponded to those from dolphins of only one known ecotype and were thus identified to the respective ecotype. The stranded

dolphins having "new" haplotypes not retrieved from the known coastal or offshore dolphins or obtained from both ecotypes (only one haplotype) remained unidentified and were assigned to ecotype based on morphology with randomForest, as described further.

Statistical Analyses

Our first goal in the analyses was to characterize and compare the two series in terms of the individual measurements (recognizing that the variables are likely inter-correlated; see later). Because of larger size of the coastal series, we first examined sexual dimorphism in that series with permutation *t*-tests for each measurement separately. In each test, the observed difference in means between sexes for a measurement ($\Delta\mu$) was compared to a distribution of differences generated under the null hypothesis of no dimorphism by randomly permuting each sample's assignment to sex in 1,000 iterations. Statistical significance was assessed as the proportion of iterations in which $\Delta\mu$ was greater or less than the observed $\Delta\mu$, depending on whether the observed value was greater or less than zero, respectively. Differences between ecotypes were examined with a second permutation test. For those measurements that showed significant sexual dimorphism in the coastal series in the first test, we conducted separate ecotype analyses for each sex. All analyses were conducted using R v.2.10.1 (R Development Core Team 2009).

We further compared the cranial measurements for the two series with a Bayesian approach. We only analyzed measurements for which we had more than three samples within each ecotype. We constructed uniform priors based on ranges reported for the cranial measurements and meristics in *T. truncatus* by True (1889), Ogawa (1938), Tomilin (1957), Hersh *et al*. (1990), Gao *et al.* (1995), Robineau and Vely (1997), Wang *et al.* (2000), and Kemper (2004). For all measurements, the mean (μ), and precision ($\tau = 1/\sigma^2$) of a normal distribution were estimated. Each parameter was indexed by ecotype (*e*) and sex (*s*), producing the following likelihood function for the *i*th sample:

$$x_i \sim N(\mu_{e_i s_i}, \tau_{e_i s_i}).$$

Priors for precision (τ) were set to Gamma(10^{-4}, 10^{-4}). MCMC runs for each measurement consisted of 100,000 burn-in iterations, followed by 10,000 sampling iterations, with samples collected from the posterior every 10th iteration. Eight independent MCMC chains were run for each measurement. Posteriors for the mean value of an ecotype were calculated as the weighted mean between the posteriors for each sex ($\mu_{es=m}$ and $\mu_{es=f}$) with $\tau_{es=m}$ and $\tau_{es=f}$ as the respective weights. Posteriors for sexual dimorphism within an ecotype were the differences between the posteriors $\mu_{es=m}$ and $\mu_{es=f}$. Similarly, posteriors for differences among ecotypes were the difference between $\mu_{e=offshore}$ and $\mu_{e=coastal}$, with the geometric mean of $\tau_{es=m}$ and $\tau_{es=f}$ as the respective weights for each ecotype. The Bayesian analyses were conducted with the *BRugs* v.0.5–3 package in R (Lunn *et al.* 2009).

To assign specimens of unknown ecotype, we created a Random Forest (RF) (Breiman 2001) classifier using the randomForest v.4.5–34 package in R (Liaw and Wiener 2002). For the classifier, those adult specimens that had either been collected offshore, alive coastally, or were classified based on mtDNA haplotypes unique to one of the two ecotypes were used as the training data set. In the RF, we only used

measurements which were missing in three or fewer of the unknowns, as we wanted to ensure that the classifier would work on most specimens. Thus, we ended up using all of the skull measurements and meristics except for TOOW. The "known" adult specimens used to create the classifier were restricted to those with no more than two skull measurements missing, for which there were 32 coastal and nine offshore skulls. Because of the disparity in sample size, we assigned priors (randomForest parameter *classwt*) to each sample as the inverse of their respective ecotype's sample size. We also conducted a conventional Linear Discriminant Analysis (LDA) but obtained higher accuracy of classification with RF (LDA data not shown). A second Random Forest classifier was constructed for juveniles and adult specimens that could not be classified in the first due to missing data. Only HILO and MXTH were used in this RF as these two variables were present for all samples but one. Using HIUP would have excluded eight more samples, and the remaining variables would have excluded the rest of the samples. Both adult and juvenile specimens of known ecotype were used in the training data. For the RF runs, the following parameter values were used: the number of variables sampled at each split (*mtry*) = 13, the number of trees in the Random Forest (*ntree*) = 20,000, with all other parameters set to their defaults. The randomForest R objects used for classification are available from the authors upon request.

Because the cranial measurements are intercorrelated to varying degree (*e.g.,* rostrum length is contained within overall skull length, and any suites of features involved in particular functions can be expected to be correlated), we also examined the data with principal component analysis (PCA) on all known and RF-classified adult specimens to determine positions of the specimens along major multivariate axes and to identify the variables most influential in separating any apparent clusters corresponding to the two ecotypes. PCA is a multivariate analysis without *a priori* identification of groups or clusters. All skull variables were used, and missing data were as imputed using the *rfImpute* function in the randomForest package with *mtry* = 13, *ntree* = 10,000, and *classwt* set to the inverse of the population frequency as in the classification RF.

Finally, we estimated the stranding frequency of offshore samples by conducting a bootstrap assignment procedure. In each of 1,000 iterations, stranded specimens with mtDNA haplotypes that were exclusive to an ecotype were automatically assigned to that ecotype. For those specimens with shared haplotypes or for which we did not have sequence data, ecotype assignment was based on each specimen's assignment probability from the RF analysis. The result of this procedure is a distribution of the fraction of assignments made to the offshore ecotype.

Results

Genetic Analyses

We encountered 56 haplotypes: four only in the known coastal series, 33 only in the known offshore series, and 1 shared by both (Table 1). We assigned seven mainland-stranded specimens to the offshore ecotype and 73 to the coastal ecotype based on possession of a haplotype occurring only in the known-ecotype series. Stranded specimens possessing "new" haplotypes (not observed in either known-ecotype series) or the single haplotype occurring in both series were considered to be of unknown ecotype for the morphological comparisons.

Table 1. Frequency of mtDNA haplotypes in coastal, offshore, and mainland-stranded common bottlenose dolphins from California waters.

Haplotype	GenBank Acc #	Coastal	Offshore	Stranded
CA_Ttru_01	HQ206659	26	1	28
CA_Ttru_02	HQ206660	16	0	31
CA_Ttru_03	HQ206661	17	0	24
CA_Ttru_04	HQ206662	6	0	15
CA_Ttru_05	HQ206663	0	9	1
CA_Ttru_06	HQ206664	4	0	3
CA_Ttru_07	HQ206665	0	4	1
CA_Ttru_08	HQ206666	0	3	2
CA_Ttru_09	HQ206667	0	4	0
CA_Ttru_10	HQ206668	0	4	0
CA_Ttru_11	HQ206669	0	4	0
CA_Ttru_12	HQ206670	0	2	2
CA_Ttru_13	HQ206671	0	3	0
CA_Ttru_14	HQ206672	0	3	0
CA_Ttru_15	HQ206673	0	1	1
CA_Ttru_16	HQ206674	0	2	0
CA_Ttru_17	HQ206675	0	2	0
CA_Ttru_18	HQ206676	0	2	0
CA_Ttru_19	HQ206677	0	2	0
CA_Ttru_20	HQ206678	0	2	0
CA_Ttru_21	HQ206679	0	0	2
CA_Ttru_22	HQ206680	0	2	0
CA_Ttru_23	HQ206681	0	2	0
CA_Ttru_24	HQ206682	0	2	0
CA_Ttru_25	HQ206683	0	0	1
CA_Ttru_26	HQ206684	0	0	1
CA_Ttru_27	HQ206685	0	1	0
CA_Ttru_28	HQ206686	0	1	0
CA_Ttru_29	HQ206687	0	1	0
CA_Ttru_30	HQ206688	0	0	1
CA_Ttru_31	HQ206689	0	1	0
CA_Ttru_32	HQ206690	0	0	1
CA_Ttru_33	HQ206691	0	0	1
CA_Ttru_34	HQ206692	0	0	1
CA_Ttru_35	HQ206693	0	0	1
CA_Ttru_36	HQ206694	0	1	0
CA_Ttru_37	HQ206695	0	0	1
CA_Ttru_38	HQ206696	0	1	0
CA_Ttru_39	HQ206697	0	1	0
CA_Ttru_40	HQ206698	0	0	1
CA_Ttru_41	HQ206699	0	1	0
CA_Ttru_42	HQ206700	0	0	1
CA_Ttru_43	HQ206701	0	0	1
CA_Ttru_44	HQ206702	0	1	0
CA_Ttru_45	HQ206703	0	1	0
CA_Ttru_46	HQ206704	0	0	1
CA_Ttru_47	HQ206705	0	0	1
CA_Ttru_48	HQ206706	0	1	0

Table 1.   (Continued)

Haplotype	GenBank Acc #	Coastal	Offshore	Stranded
CA_Ttru_49	HQ206707	0	0	1
CA_Ttru_50	HQ206708	0	1	0
CA_Ttru_51	HQ206709	0	1	0
CA_Ttru_52	HQ206710	0	1	0
CA_Ttru_53	HQ206711	0	1	0
CA_Ttru_54	HQ206712	0	1	0
CA_Ttru_55	HQ206713	0	0	1
CA_Ttru_56	HQ206714	0	1	0
Total		69	71	125

T-test Comparisons

In the coastal series, males were larger than females at $\alpha = 0.05$ in 17 of the 28 cranial measurements. Females had a greater minimum width of the palate. The two sexes did not differ in number of teeth. Details of the analysis of dimorphism are given in Supporting Information Table S1. Comparison of the coastal and offshore series (Table 2) showed difference at $\alpha = 0.05$ in 23 of the 28 measurements and both tooth counts. In both sexes, the coastal animals on average had a broader rostrum at the base, broader temporal fossa, shorter pterygoid hamulus, lesser minimum width of the palate, wider mandibular condyle, and about one tooth less in each row. Coastal females had a shorter overall skull length, shorter rostrum, shorter distance from rostrum tip to external nares and to internal nares, lesser parietal width, smaller antorbital process, shorter upper tooth row, longer lower tooth row, and shorter mandibular ramus. Coastal males had a broader rostrum at $^1/_2$ and $^3/_4$ length, broader external nares, greater zygomatic width, broader premaxillaries, deeper mandibular ramus, and larger teeth.

Bayesian Analysis

Posterior distributions of sexual dimorphism within each ecotype and example distributions of measurements showing the greatest differentiation between sexes are shown in Figure 2; the distributions for the other measurements and tooth counts are given in Supporting Information Figure S1. Males were larger than females with greater than 50% probability for 28 of 30 measurements in the coastal series and 11 in the offshore series. Offshore skulls were larger in 16 of 30 measurements. Considering those measurements with probabilities above about 80% and below about 20% in Figure 3, the offshore ecotype had a greater number of teeth (HIUP and HILO), longer rostrum (TIPP and ROST), greater palatal width (PALW), larger internal nares (INTN) and longer pterygoid hamuli (PTLN); and the coastal ecotype had larger mandibular condyles (MWMC), larger temporal fossa (FOSH), larger teeth (TOOW), greater postorbital width (POST), larger external nares (EXTN) and broader rostrum (ROSH and ROS3).

Random Forest Classification of Adults

The RF classifier for adult skulls (of known origin or with haplotype recorded from only either offshore or coastal) had an error rate of 3.6%, correctly classifying

Table 2. *T*-test comparison of cranial measurements (in cm) and tooth counts of coastal and offshore series of common bottlenose dolphins (*T. truncatus*) from California.

Measurement/Count	Acronym	Sex	Coastal				Offshore				P
			N	Mean	SD	Range	n	Mean	SD	Range	
Condylobasal length	CBLN	M	14	519.4	14.00	495–548	9	514.1	25.85	479–570	0.2640
		F	15	499.4	16.22	471–527	3	533.0	15.13	516–545	0.0057*
Length of rostrum	ROST	M	14	277.4	10.97	260–301	9	282.0	18.16	253–317	0.2228
		F	15	267.6	10.08	254–286	3	290.3	9.29	280–298	0.0057*
Rostrum width at base	ROSW	M	16	133.7	5.64	123–142	9	128.9	7.66	117–145	0.0452*
		F	14	127.9	7.15	115–138	3	136.0	6.93	128–140	0.0423*
Width of rostrum at $^1/_2$ length	ROSH	M	15	89.9	4.53	82–97	9	84.1	4.65	78–91	0.0053*
		F	14	83.6	5.02	75–93	3	82.0	7.94	73–88	0.3348
Width of rostrum at $^3/_4$ length	ROS3	M	15	68.7	6.96	59–83	9	61.0	4.61	55–67	0.0034*
		F	14	62.0	7.23	50–73	3	60.0	7.21	52–66	0.3533
Width of PMXs at $^1/_2$ length	PMXH	M,F	32	48.3	3.89	42–56	12	47.0	3.95	41–54	0.1840
Rostrum tip to external nares	TIPN	M	15	335.2	11.88	314–362	9	332.9	20.65	301–376	0.3700
		F	14	322.1	11.82	308–344	3	348.3	11.59	335–356	0.0056*
Preorbital width	PREO	M	16	237.2	8.12	226–251	9	236.2	16.78	215–272	0.4388
		F	14	225.5	8.04	213–236	3	241.7	11.02	229–247	0.0108*
Postorbital width.	POST	M	16	270.9	11.54	248–283	9	262.0	15.56	241–292	0.0554
		F	14	257.5	10.47	239–270	3	245.0	36.37	206–251	0.1543
Width of external nares	EXTN	M	16	61.8	2.93	57–68	9	57.2	4.35	52–66	0.0029*
		F	13	59.5	3.26	53–66	3	59.7	1.53	58–61	0.5326
Zygomatic width	ZYGO	M	16	275.7	9.99	255–290	9	265.7	18.93	243–304	0.0483*
		F	14	261.9	10.65	241–278	3	268.0	17.06	249–273	0.2316
Greatest width of premaxillaries	PMXM	M	16	100.8	4.19	90–108	9	95.3	4.77	89–106	0.0053*
		F	14	93.9	5.12	87–105	3	99.0	4.00	95–103	0.0932
Parietal width	PARI	M,F	34	187.5	8.37	172–208	12	186.8	10.43	168–202	0.4057

Continued

Table 2. (Continued)

Measurement/Count	Acronym	Sex	Coastal				Offshore				P
			N	Mean	SD	Range	n	Mean	SD	Range	
Height of braincase	BRNH	M,F	32	144.2	9.21	132–176	12	148.3	9.73	136–172	0.1121
Length of temporal fossa	FOSL	M,F	34	119.5	8.66	104–136	12	116.0	5.62	107–125	0.1039
Height of temporal fossa	FOSH	M,F	34	82.6	6.54	71–95	12	77.6	7.06	67–89	0.0164*
Length of orbit	ORBI	M,F	34	67.9	2.81	61–73	12	67.7	5.47	61–80	0.4379
Length of antorbital process	ANTO	M	16	55.9	4.04	50–65	9	56.9	6.25	50–71	0.3285
		F	14	52.1	3.38	45–58	3	59.7	8.39	50–65	0.0201*
Rostrum tip to internal nares	TIPP	M	15	333.1	13.18	307–367	9	339.0	21.17	310–383	0.2080
		F	13	320.2	12.59	303–347	3	359.7	13.05	345–370	0.0041*
Width of internal nares	INTN	M,F	34	78.4	6.90	56–90	12	82.0	4.73	77–94	0.0493*
Length of pterygoid hamulus	PTLN	M	16	68.0	6.10	54–80	9	73.8	8.20	62–86	0.0313*
		F	13	63.2	6.15	55–78	3	80.3	4.16	77–85	0.0033*
Minimum width of palate	PALW	M,F	32	43.2	5.97	29–65	12	50.5	8.14	38–66	0.0015*
Length of upper tooth row	UPRO	M	15	243.5	9.27	223–262	9	243.7	14.65	223–273	0.4830
		F	14	235.8	9.37	220–251	3	255.0	10.39	243–261	0.0062*
Length of lower tooth row	LORO	M	14	240.3	7.76	223–254	9	235.7	15.61	205–264	0.1962
		F	13	231.8	11.75	207–252	3	250.7	12.50	238–263	0.0144*
Length of ramus	RAML	M	14	443.1	12.16	423–468	9	435.8	26.72	392–494	0.1948
		F	13	422.9	16.29	395–453	3	455.3	15.04	438–465	0.0066*
Height of ramus	RAMH	M	15	100.1	4.18	92–106	9	95.2	7.23	86–110	0.0272*
		F	14	93.4	4.54	86–101	3	96.3	6.43	89–101	0.1996
Max. width of mandibular condyle	MWMC	M	15	49.2	4.91	39–56	9	39.3	3.00	35–45	0.0001*
		F	14	45.9	3.78	41–51	3	38.7	1.53	37–40	0.0002*
Diameter of tooth at mid-row	TOOW	M	14	9.71	1.009	8.5–11.6	5	7.22	0.42	6.6–7.6	0.0120*
		F	12	8.77	0.684	7.9–10.3	2	7.40	0.28	7.2–7.6	0.4584
Highest upper tooth count	HIUP	M,F	58	22.3	0.97	20–24	22	23.9	1.27	22–28	0.0001*
Highest lower tooth count	HILO	M,F	61	22.2	0.81	20–24	24	23.1	1.03	22–26	0.0001*

Note: Males and females analyzed separately for measurements in which coastal series exhibited sexual dimorphism at $\alpha = 0.05$ (Supporting Information Table S1). *$P < 0.05$.
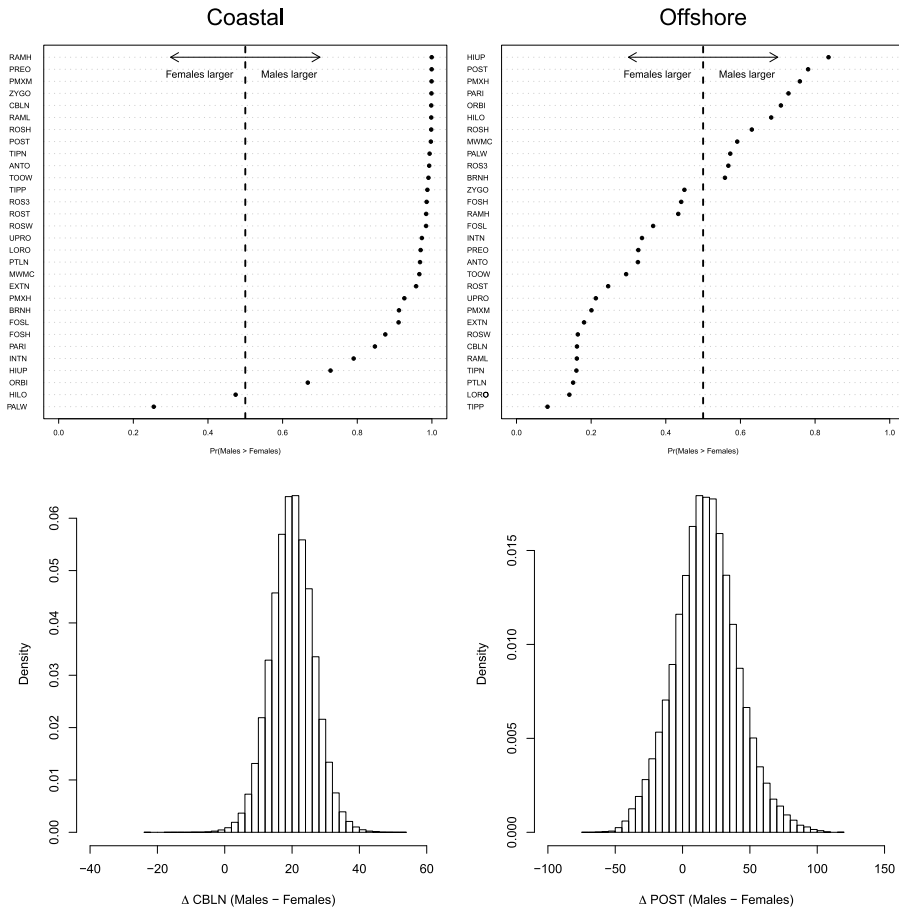
Figure 2. Posterior distributions of sexual dimorphism in coastal and offshore skulls. Upper panels shows probability of Males > Females from posterior distributions of all measurements. Bottom panels show posterior distributions of sexual dimorphism for two extreme measurements in the two ecotypes. See Supporting Information Figure S1 for results for all variables.

all 21 coastal skulls and six of seven offshore skulls. The overall error rate for the secondary RF designed to classify juveniles and adults unclassifiable in the first was much larger at 38.8%. However, the error rate for offshore specimens was far lower than for the first RF; it correctly classified 23 out of 24 skulls, *vs.* 29 out of 61 coastal skulls.

Figure 4 shows the distribution of assignment probabilities for skulls from mainland strandings after sequential use of the RF classifying algorithms. Under a rule in which assignments are accepted at probability >0.5, three of the 23 unknown adult skulls classifiable in the first RF would be classified as offshore and the remaining 20 as coastal (as shown in Fig. 4). If the assignment probability requirement were increased to >0.75, only two of these specimens would be assigned to offshore and
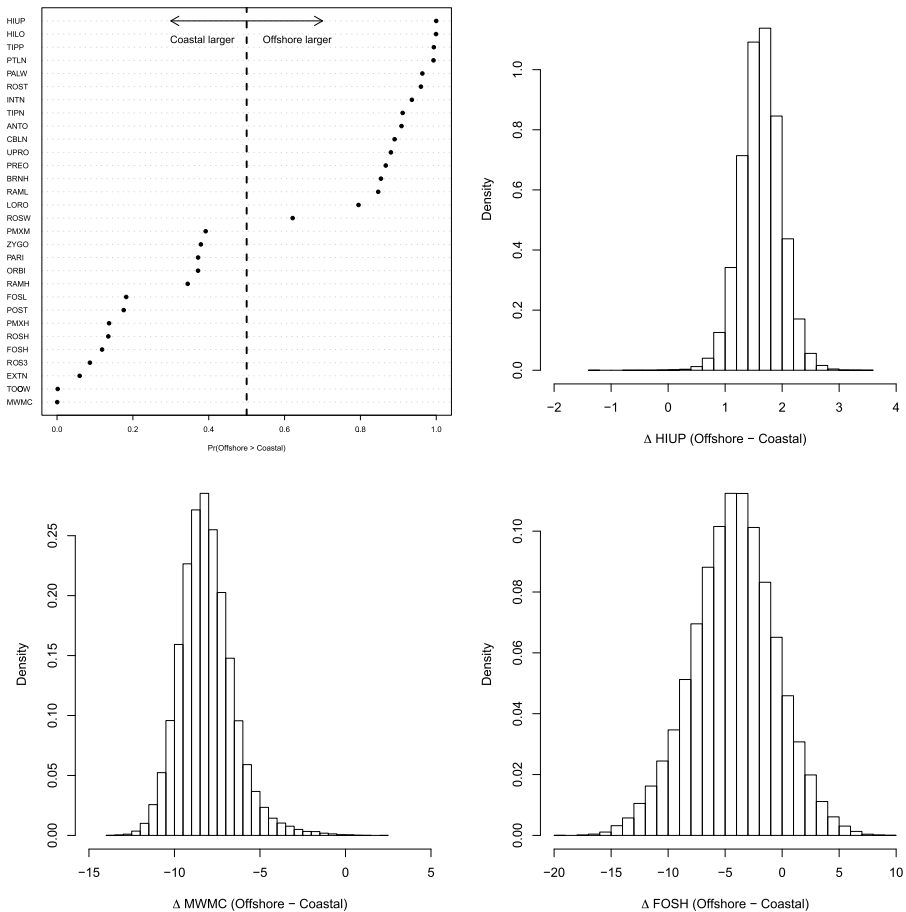
Figure 3. Posterior distributions for difference in means between ecotypes. Upper left panel shows probability of Offshore > Coastal from posterior distributions of all measurements. Remaining three panels show posterior distributions of differences for extreme measurements where Offshore is larger (HIUP), or Coastal is larger (MWMC and FOSH). See Supporting Information Figure S1 for results for all variables.

19 to coastal. In total, assignment probabilities were generated for 48 of 49 stranded specimens that were not assignable based on unambiguous mtDNA haplotypes.

Principal Components Analysis

The first three components accounted for 67% of the variance. Loading coefficients for these components are given in Table 3. The coastal and offshore series overlapped almost completely for component 1 (Fig. 5) but showed strong separation for components 2 and 3 combined (Fig. 6). Measurements loading highest positively (defining offshore cluster) for both components 2 and 3 were the tooth counts (HIUP and HILO), palatal width (PALW) and length of the pterygoid hamuli (PTLN). Loading
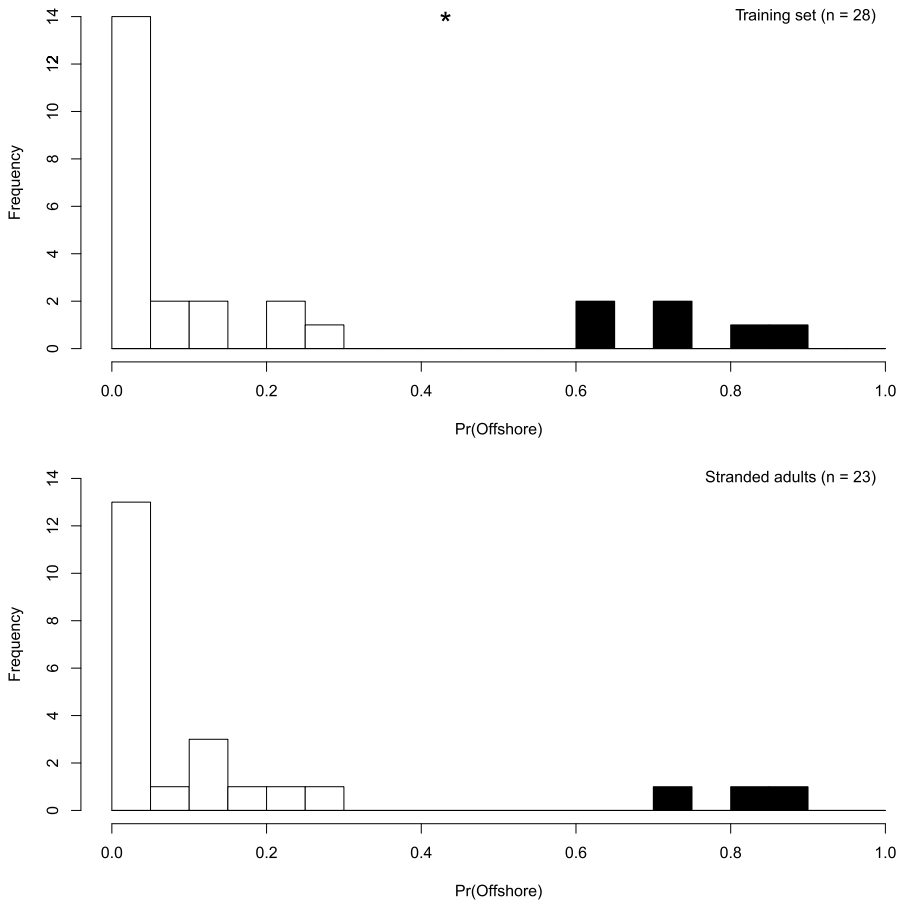
Figure 4. Distribution of assignment probabilities of adult skulls from the Random Forest analysis. Dark columns = known offshore (in upper panel) and assigned offshore with 50% criterion (in lower panel). Asterisk indicates known offshore specimen misclassified as coastal in training data.

highest negatively (defining coastal cluster) were size of mandibular condyles (MWMC), tooth size (TOOW), and size of the external nares (EXTN). Females and males did not show substantial separation on any of the first four components (Supporting Information Fig. S2).

Ecotype Composition of Mainland Strandings

The RF assignment probabilities of the mainland-stranded skulls including juveniles and skulls not included in RF analysis because of missing data values provided estimates of offshore-ecotype membership ranging from near certainty (of coastal membership) to 0 (Fig. 7). From the bootstrap assignment analysis, the median probability of a stranded specimen being from the offshore ecotype is approximately

Table 3. Variable loadings for first three Principal Components.

Measurement/count	PC1 (41%)	PC2 (19%)	PC3 (7%)
CBLN	−0.237	0.166	−0.163
ROST	−0.194	0.259	−0.189
ROSW	−0.229	−0.100	0.095
ROSH	−0.204	−0.187	0.162
ROS3	−0.182	−0.229	0.099
TIPN	−0.220	0.198	−0.219
PREO	−0.242	−0.016	0.123
POST	−0.192	−0.153	−0.039
ZYGO	−0.245	−0.099	−0.004
PMXM	−0.212	−0.117	−0.053
PARI	−0.139	−0.115	0.132
FOSL	−0.182	−0.179	−0.020
FOSH	−0.148	−0.232	0.045
ORBI	−0.084	0.008	−0.080
ANTO	−0.197	0.085	0.076
INTN	−0.192	0.019	0.201
UPRO	−0.195	0.224	−0.255
HIUP	−0.070	0.292	0.314
RAMH	−0.226	−0.141	−0.008
MWMC	−0.103	−0.234	−0.211
MXTH	−0.068	0.287	0.325
PMXH	−0.167	−0.189	0.207
EXTN	−0.127	−0.175	−0.142
TIPP	−0.203	0.243	−0.123
LORO	−0.213	0.161	−0.217
RAML	−0.240	0.157	−0.186
BRNH	−0.162	−0.141	0.235
PALW	−0.101	0.110	0.347
HILO	−0.053	0.234	0.210
PTLN	−0.174	0.169	0.169
TOOW	−0.069	−0.174	−0.174

Note: Percent of variance accounted for by each component in parentheses.

14% (95% CI = 0.11–0.17), indicating that a majority of strandings were of the coastal ecotype (Fig. 8).

DISCUSSION

Sexual Dimorphism

The extent of sexual dimorphism in skull measurements and meristics documented here is comparable to that previously reported for the species for some regions and greater than reported for others. In multivariate analysis of stranded adults and juveniles from the Gulf of Mexico, adult bottlenose dolphins from Texas exhibited sexual dimorphism, but those from Florida did not (Turner and Worthy 2003); the Texas males and females differed in all but 6 of 35 measurements, similar to the *t*-test results for California coastal dolphins. In analyzing 32 cranial characters in
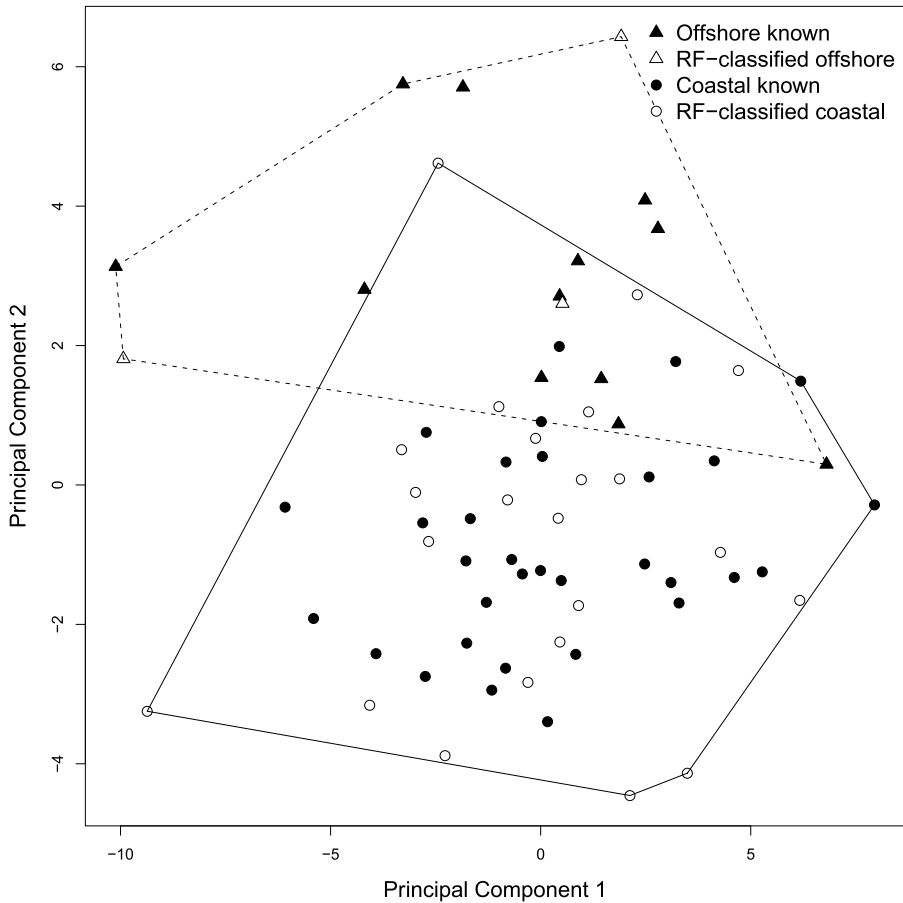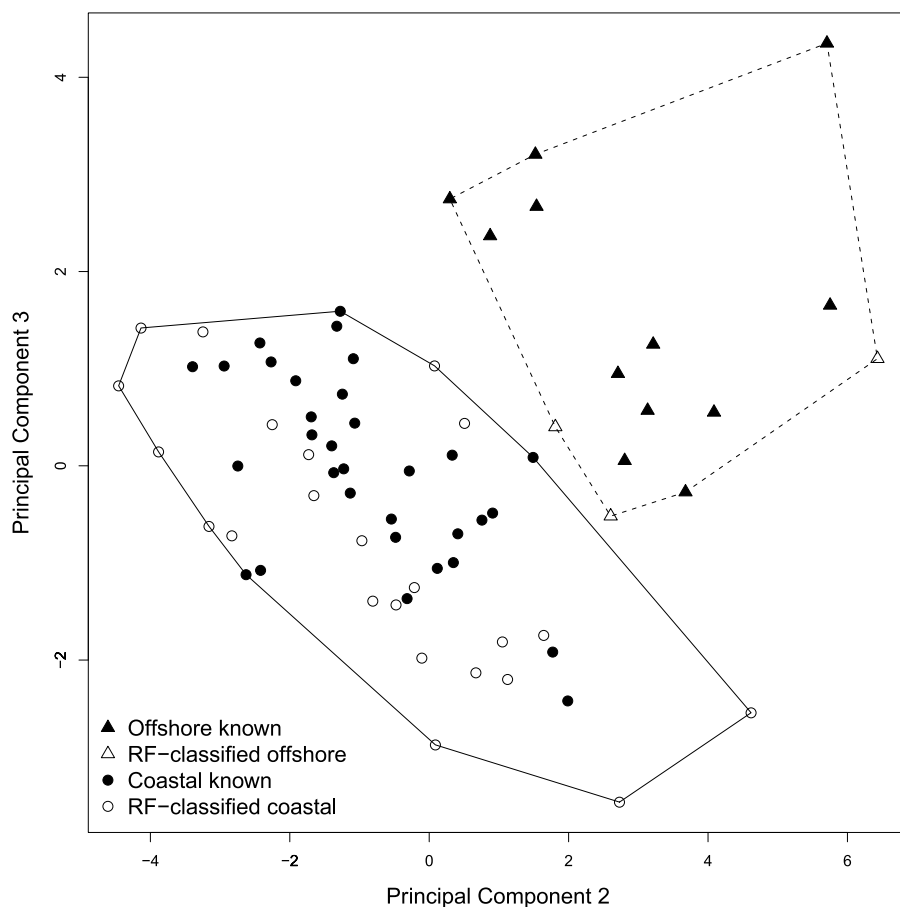
Figure 5. Distribution of adult skulls on first and second Principal Components. Skulls are identified to ecotype. RF-classified offshore/coastal = skulls assigned to offshore or coastal ecotype in the RF analysis based on morphology.

66 skulls, Hersh *et al.* (1990) found male common bottlenose dolphins from the coast of Florida to have on average about one more tooth in each row and parietal width a few millimeters greater than females. Their series did not differ in other features. Kemper (2004) found no significant differences between sexes in a mixed sample of 65 common bottlenose dolphins and Indo-Pacific bottlenose dolphins (*T. aduncus*) from South Australia, and Wang *et al.* (2000) found none in 17 males and 14 females from China. The collective results suggest that cranial sexual dimorphism is a geographically variable feature in the species. This variation may be related to variation in breeding system, as has been suggested for external dimorphism correlated with testis size in two forms of the spinner dolphin (*Stenella longirostris*) in the eastern tropical Pacific (Perrin and Mesnick 2003). Geographic variation in dimorphism occurs widely in mammals, reported recently for, among others, the spinner dolphin, *S. longirostris* (Perrin and Mesnick 2003), short-beaked common

Figure 6. Distribution of adult skulls on second and third Principal Components. Skulls are identified to ecotype. RF-classified offshore/coastal = skulls assigned to offshore or coastal ecotype in the RF analysis based on morphology.

dolphin, *Delphinus delphis* (Murphy *et al.* 2006), the polar bear, *Ursus maritimus* (Bechshoft *et al.* 2008), the black bear, *Ursus americanus* (Mahoney *et al.* 2001) and the common bushtail possum, *Trichosurus vulpecula* (Isaac and Johnson 2003) and correlated with variation in breeding system in the last.

Morphological Differentiation and Functional/Ecological Implications

Most differences between the coastal and offshore skulls are in features associated with feeding. The larger temporal fossa (origin of a larger temporal muscle yielding a stronger bite), stouter rostrum, more robust mandibular joint, and larger teeth of the coastal ecotype suggest that it may be more adapted to feeding on larger, tougher prey than the offshore ecotype. Perrin (1975) suggested a similar adaptation in tooth size and other features of the skull in the coastal subspecies of the pantropical
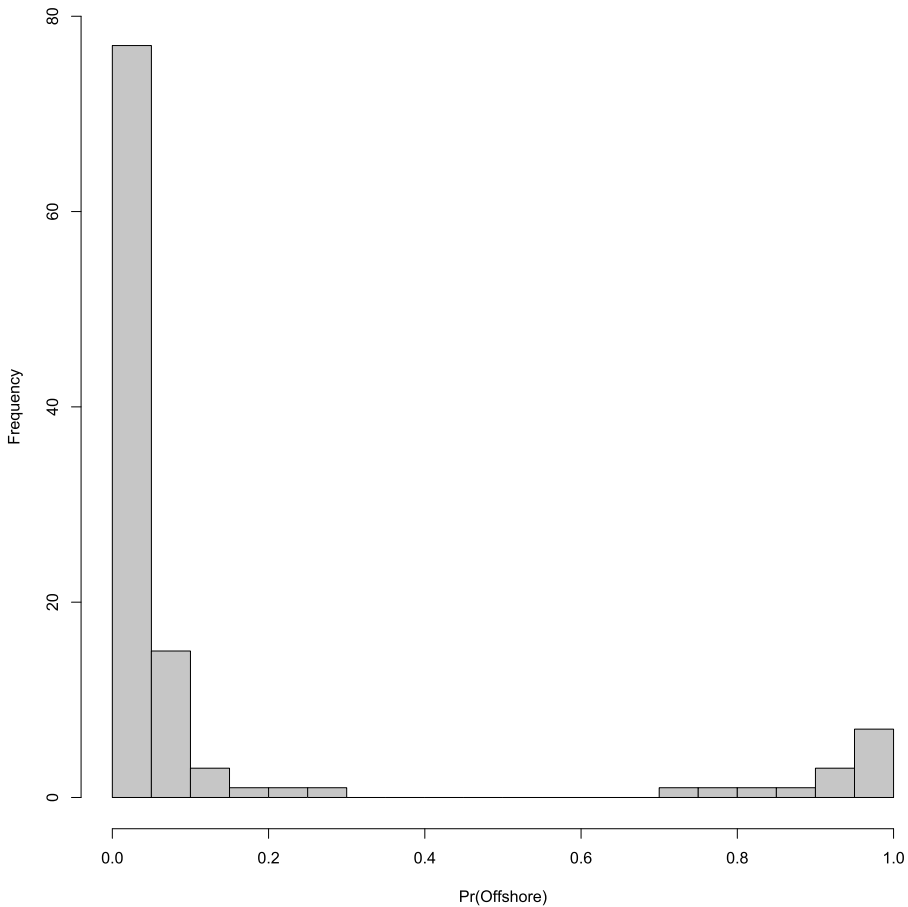
Figure 7. Distribution of assignment probabilities for all skulls from strandings. As-signment probabilities include those based on mtDNA sequence, and adult and juvenile assignments from the Random Forest analyses.

spotted dolphin, *Stenella attenuata graffmani*, of the eastern Pacific coast of tropical America; however, comparison of the diets of coastal and offshore spotted dolphins has not been carried out to confirm the hypothesis. A direct comparison of the diets of California coastal and offshore bottlenose dolphins is also lacking, but Walker (1981) reported that stomach contents of 17 pelagic bottlenose dolphins in the eastern tropical Pacific contained primarily small epipelagic and mesopelagic fishes (*e.g.*, myctophids, melamphaeids, exocoetids, and small scombrids) and squids of various sizes, whereas nine stranded presumed coastal bottlenose dolphins from California (which may in fact have included some offshore dolphins; see earlier) included larger shallow-water and benthic fishes, such as sciaenids, batrachoidids, serranids, pomacentrids, and embiotocids, as well as smaller prey. A similar difference in stomach contents between coastal and offshore bottlenose dolphins was reported by Mead and Potter (1990) and by Van Waerebeek *et al.* (1990) for the western
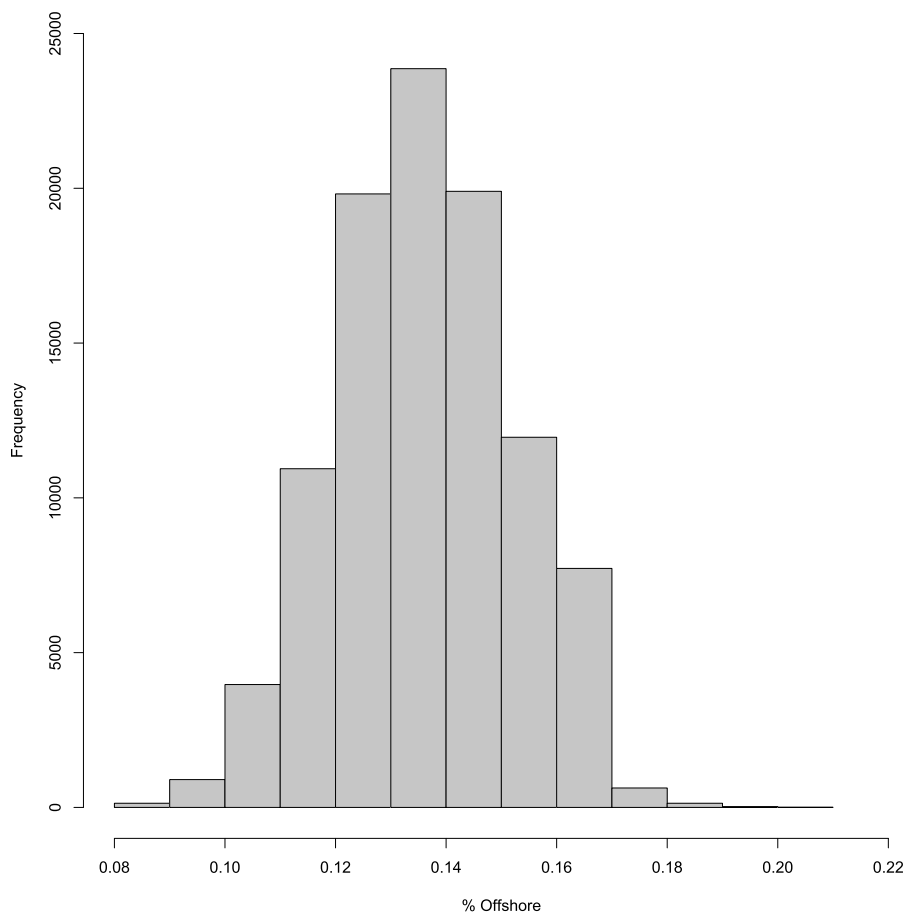
Figure 8. Distribution of Pr(Offshore) from bootstrap analysis of assignment probabilities. Median = 0.14, 95% CI − 0.11–0.17.

Atlantic and Peru. The diet of the offshore ecotype in California waters may parallel that of the tropical eastern Pacific and eastern Atlantic and Peruvian pelagic animals in size and consistency of prey. Van Waerebeek *et al.* (1990) found coastal dolphins to have larger teeth than those from offshore in 19 bottlenose dolphins from Peru, a result similar to ours.

Rostral length (unlike rostral width) is not different between the two ecotypes, accounting for the lesser number of teeth in the coastal form (about two fewer in each row); larger teeth in the same linear space necessarily means fewer teeth.

The larger internal nares in the offshore ecotype (also reported by Mead and Potter [1995] for offshore *vs.* inshore bottlenose dolphins from the eastern Atlantic) may relate to efficiency of air exchange in deeper diving; deep diving by offshore bottlenose dolphins in the western Atlantic is suggested by hemoglobin profiles (Hersh and Duffield 1990) and telemetry data (Klatsky *et al.* 2007). The narrower width of the bony palate at the anterior terminus of the pterygoid hamuli (also reported by

Mead and Potter 1990, for the offshore Atlantic dolphins) and the longer pterygoid hamuli may be involved in differential sound production used in tracking smaller and more elusive prey. The pterygoid hamulus in Delphinidae is excavated and inflated, containing an extension of the middle ear cavity, the pterygoid sinus (Fraser and Purves 1960). The elaborated pterygoid sinus is thought to insulate the ear from direct feedback through bony transmission of echolocation sounds produced in the dorsally located nasal sacs (Nummela 2009), and thus variation in extent of the pterygoid sinuses reflected in shape and size of the hamuli may indicate differentiation in echolocation or hearing.

Difference in Stranding Rates

Roughly 86% of bottlenose dolphins stranded on the mainland are estimated to be of the coastal ecotype. The ratio of offshore to coastal population size is approximately 7.4:1 (3,495/450–500; Carretta *et al*. 2009). If mortality rates were similar for the two ecotypes, this would imply that the probability of a carcass stranding on the mainland is roughly 50 times as great for the coastal ecotype as for the offshore ecotype. Although distance from shore and the effects of wind and currents could be expected to affect the probability of stranding, this difference seems inordinately great. If mortality rates were higher in the coastal ecotype (*e.g.*, due to anthropogenic factors such as pollution: O'Shea *et al*. (1980) and Hansen (1990) reported that California coastal bottlenose dolphins had the highest levels of DDT contamination reported for any marine mammal), that would inflate the stranding ratio. Other factors that likely influence chances of strandings are scavenging of carcasses by sharks and simple decomposition leading to sinking; carcasses of offshore dolphins would be exposed to these factors longer than those of coastal dolphins.

Caveats and Needed Research

We have assumed that the bottlenose dolphins live-collected in the vicinity of the Channel Islands belong to an overall offshore population. This is consistent with the pattern of distribution of mtDNA haplotypes. However, it is possible that an island-associated population exists, separated to some extent from a larger offshore population in more pelagic waters. This possibility should be investigated with further biopsy sampling and analysis of mtDNA sequences and microsatellites.

In this study, bottlenose dolphins biopsied within one km of the shore were considered to be of the coastal ecotype and those biopsied farther offshore to be of the offshore ecotype. However, a longitudinal study of individually identified dolphins in central California (Santa Monica Bay and nearby areas) found that 31 of 406 dolphins that spent most of their time foraging <1 km from shore (most often between 10 and 100 m from shore, in waters <10 m deep) also occasionally ranged farther offshore for short periods, from 3 to 5 km from the coast (Bearzi *et al.* 2009). This suggests that the ranges of the two ecotypes overlap at least partially and at some times and that future genetic study and assignment of samples to ecotype should be combined with studies of individually identified dolphins. For the present study, the possible occasional spatial overlap in southern California could be expected to potentially lead to underestimation of differences because of possible misclassification of some biopsied dolphins sampled more than 1 km from shore.

The ecological significance of the cranial differences between the coastal and offshore ecotypes can be further investigated by direct comparison of stomach contents of stranded animals classified to ecotype by genetic or morphological criteria.

We have assumed that mtDNA haplotypes unique to an ecotype are diagnostic of that ecotype. However, this assumption is entirely based on our set of samples, and further sampling may indicate that more of these haplotypes are shared among the ecotypes. This is especially true for the relatively lightly sampled offshore ecotype; it may not yet be adequately characterized. Development of assignment methods for haplotypes that incorporate such uncertainty is needed.

Conservation and Management

As noted by Bearzi *et al.* (2009), coastal dolphins are particularly susceptible to anthropogenic threats, including pollution by DDTs and other contaminants. The cranial differences between the coastal and offshore bottlenose dolphins described here suggest that the two ecotypes have adapted evolutionarily to different habitats. If the small coastal population were to be extirpated, it could not necessarily be expected that its habitat would be recolonized by the larger offshore population. This emphasizes the importance of protecting the coastal population and the quality of its habitat.

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APPENDIX 1

Osteological specimens examined (Additional information on the specimens in Table S1):

CAS 22280, 23152, 23911, 25426, 26901, 26910, 27863; LACM 27094, 27401, 31426, 54638, 54639, 72294, 72295, 72493, 72549, 72552, 84028, 84029, 84031, 84032, 84033, 84034, 84036, 84055, 84056, 84058, 84059, 84065. 84097, 84119, 84120, 84164, 84194, 84242, 84248, 84250, 84267, 84269, 84270, 84271, 84276, 84285, 84292, 84293, 84294, 84957, 86022, 86024, 86091, 88905, 88918, 88925, 88942, 88983, 88984, 91309, 91320, 91781, 91862, 91886, 91913, 91936, 91958, 91994, 92014, 92043, 92069, 92072, 95350, 95366, 95387, 95391, 95459, 95471, 95483, 95509, 95510, 95518, 95527, 95662, 95664, 95685, 95828, 95953, 95956, 95967; MCZ 49082, 49083; SBMNH 2970, 2971, 2972, 2973, 3090, 3334, 3532, 3536, 3537, 3538, 3539, 3540, 3541, 3543, 3544, 3546, 3547, 3553, 3555, 3618, 3662, 3669, 4066, 4944; SDNHM 11102, 20143, 20144, 20145, 21212, 21213, 23334; SWFSC 58, 95; USNM 298239, 395924, 500851, 504353, 504844,

550011, 550012, 550021, 550023, 550097, 550125, 550193, 550194, 550919, A13022[1]; Walker 159.

Museum and collection acronyms: CAS = California Academy of Sciences, San Francisco, CA; LACM = Los Angeles County Museum, Los Angeles, CA; MCZ = Museum of Comparative Anatomy, Cambridge, MA; SBMNH = Santa Barbara Museum of Natural History, Santa Barbara, CA; SDNMH = San Diego Natural History Museum, San Diego, CA; SWFSC = Southwest Fisheries Science Center, La Jolla, CA; USNM = U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC; Walker = private collection of W. A. Walker.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1. Posterior distributions of means from Bayesian analyses. Variable abbreviation is given in title with total sample size in parentheses. Posteriors of dimorphism ("coastal.dimorph" and "offshore.dimorph") are defined as male–female means. Posterior of difference between ecotypes ("ecotype.diff") is defined as offshore–coastal mean as described in the Methods section.

Figure S2. Distributions of male (solid) and female (dashed) scores for first four Principal Components.

Table S1. Osteological specimens included, with collector's field number, SWFSC laboratory identification number for samples for which tissue (skin, tooth or bone) available for DNA extraction, haplotype from successful extractions (see Table 1), known ecotype stratum upon entry into RF (see text), and origin (stranding, live capture, fishery bycatch, or "taken"). Stratum in brackets for specimens assigned to ecotype solely on basis of haplotype.

Table S2. *T*-test comparison of cranial measurements (in cm) and tooth counts of female and male series of coastal common bottlenose dolphins (*Tursiops truncatus*) from California. $P < 0.05$ in bold.

[1]Holotype specimen of *Tursiops gillii* Dall, 1873; mandible only from dolphin taken by Scammon near Monterey (Scammon 1874).