Variation in Dorsal Fin Morphology in Common Bottlenose Dolphin *Tursiops truncatus* (Cetacea: Delphinidae) Populations from the Southeast Pacific Ocean[1]

Fernando Félix,[2,3,9] *Koen Van Waerebeek,*[4,5] *Gian Paolo Sanino,*[5,6] *Cristina Castro,*[7] *Marie-Françoise Van Bressem,*[4] *and Luis Santillán*[4,8]

Abstract: Variation in dorsal fin morphology was assessed in five common bottlenose dolphin populations from the Southeast Pacific. We hypothesized that habitat specialization between coastal and offshore ecotypes would lead to differences in dorsal fin morphology. Photographs and direct measurements of dorsal fins were used to calculate three indexes: height/length base (h/b), width at half height/length base (a/b), and overhang of the dorsal fin tip/length base (falcateness) (s/b). The sample included 163 individuals (129 coastal and 34 offshore) from Ecuador, 60 individuals (nine coastal and 51 offshore) from Peru, and 25 individuals of an inshore community occurring in north-central Chile (Pod-R). Ontogenetic variation was found in coastal dolphins from Ecuador, where sex and age classes were best represented. A statistically significant difference was found in the a/b index between coastal specimens from Ecuador and Peru and among the three offshore groups. When offshore and Pod-R data were pooled and compared with data from coastal specimens from Ecuador and Peru, a significant difference was found in the s/b index. Overall, dorsal fins of offshore dolphins are relatively higher than fins of coastal individuals. However, the most consistent difference between ecotypes was the strong falcateness (high s/b) in offshore forms versus a more triangular shape (low s/b) in coastal forms. We propose that dorsal fin falcateness is a reliable criterion to visually distinguish between bottlenose dolphin ecotypes in this region. Proper identification in the field greatly facilitates research and helps focus management needs of the different bottlenose dolphin populations.

Keywords: coastal ecotype, offshore ecotype, management, ecology, falcateness, South America, Pacific Ocean, habitat, morphometrics, intraspecific variation

Bottlenose dolphins are widely distributed in tropical and temperate waters around the world. Several subspecies and local morphotypes have been described (e.g., Perrin 1984, Vermeulen and Cammareri 2009, Viloria-Gómora and Medrano-

González 2015), but currently only two species are widely recognized, the common bottlenose dolphin *Tursiops truncatus* and the Indo-Pacific bottlenose dolphin *Tursiops aduncus* (Hammond et al. 2012). For the former, two ecotypes usually referred to as coastal (or inshore) and offshore (or pelagic) forms have been described along much of its distribution range (e.g., Duffield et al. 1983, Perrin 1984, Van Waerebeek et al. 1990, 2016, 2017, Mead and Potter 1993, Hoelzel et al. 1998). If not parapatric, both ecotypes may live in sympatry in some places (Vermeulen and Cammareri 2009), yet substantial genetic differences have been found (Natoli et al. 2004, Tezanos-Pinto et al. 2009). Morphological and socio-ecological differences between bottlenose dolphin ecotypes are expected to be associated with habitat specialization but may also be due to evolutionary constraints and spandrels. The coastal ecotype is found in small groups usually of a dozen animals or less, is generally resident or semiresident, and shows fine-scale population structure and lower mtDNA diversity (Hoelzel et al. 1998, Parsons et al. 2002, Natoli et al. 2004, Sanino et al. 2005, Rosel et al. 2009, Tezanos-Pinto et al. 2009, Richards et al. 2013). In the offshore ecotype, groups are substantially larger and more variable in size and are distributed along extended areas (Scott and Chivers 1990, Sanino et al. 2005, Van Waerebeek et al. 2017).

Major morphological differences between coastal and offshore forms have been recognized in body and cranial traits as well as coloration (e.g., Perrin 1984, Van Waerebeek et al. 1990, Mead and Potter 1993, Viloria-Gómora and Medrano-González 2015, Ott et al. 2016). Most of these characteristics are difficult if not impossible to assess in free-ranging animals. Morphology of dorsal fins (DF) has been used to differentiate between offshore and inshore ecotypes in southern Brazil (Simões-Lopes 1997, Simões-Lopes and Daura-Jorge 2008), between morphotypes in Argentina, and among coastal populations in the Pacific and Atlantic coasts of Mexico (Morteo 2004, Morteo et al. 2017). Sexual dimorphism in DF size has been reported in Atlantic coastal bottlenose dolphins, with adult males having significantly taller fins than adult females (Hearst et al. 1990). Ontogenetic variation and sexual dimorphism in DF are also present in several other cetacean species, such as killer whales (*Orcinus orca*) (Bigg et al. 1987), spinner dolphins (*Stenella longirostris*) (Perrin 1975), dusky dolphins (*Lagenorhynchus obscurus*) (Van Waerebeek 1993), and Dall's porpoises (*Phocoenoides dalli*) (Jefferson 1989).

Offshore bottlenose dolphins are distributed more or less continuously off the west coast of South America, south to at least Aisén Region (Chilean Patagonia). Range of coastal-form bottlenose dolphins seems to be restricted to Colombia to south-central Peru, with very limited and discontinuous presence farther south. Preliminary evidence suggests that most nearshore observed animals in Chile may compose opportunistic incursions by the offshore population [see Van Waerebeek et al. (2017) and references therein]. As elsewhere, coastal and offshore ecotypes have been described off Peru based on habitat, morphological traits, parasite loads, and feeding habits (Van Waerebeek et al. 1990, Santillán et al. 2008). Molecular studies have confirmed population structure of this species in the Southeast Pacific (Sanino et al. 2005, Bayas 2015). Coastal bottlenose dolphins inhabiting the inner estuary of the Gulf of Guayaquil in Ecuador are genetically divergent from other coastal and offshore populations in the Southeast Pacific (Bayas 2015). A small and discrete population, referred to as Pod-R, genetically more related to the offshore ecotype than to the Peruvian coastal stock, has been identified near coastal islands off north-central Chile (González et al. 1989, Sanino and Yáñez 2000, 2001, Sanino et al. 2005). Based on control region mtDNA, Sanino et al. (2005) reported a high net interpopulational distance (2.9%) between the Peruvian coastal and offshore ecotypes, and an even higher distance (3.3%) with the Chilean offshore stock. However, a single, wide-ranging "Peru-Chile offshore stock" is supported (Sanino et al. 2005). Some specimens that stranded in Ecuador, presumably from the offshore ecotype, grouped with a haplotype from the Gulf of California (Bayas 2015).

Understanding population structure is crucial because the species is regularly recorded as bycatch in small-scale fisheries in Ecuador and Peru (where direct catches are also reported), as well as victims of vessel collisions, especially with propellers (e.g., Van Waerebeek et al. 1994, 1997, 2007, Mangel et al. 2010, Félix et al. 2012, Félix et al. 2017). In Ecuador, the bottlenose dolphin is considered a vulnerable species due to population decrease of the coastal ecotype inhabiting the inner Gulf of Guayaquil (Jiménez and Álava 2014, Félix et al. 2017). In Peru, the species is under legal protection (Ley No. 26385); marine protected areas exist but these safeguard coastal habitat only in a limited way. In Chile, two small marine reserves were created, with a goal, among others, of shielding Pod-R from direct capture events (Sanino and Yáñez 2000) and promoting its sustainable use through tourism activities that still have not been successfully regulated (Sanino and Yáñez 2000, 2001).

During field observations, we learned empirically to visually distinguish between dolphins of coastal and offshore populations based on DF shape. We hypothesized that phylogenetic differences and habitat specialization between both ecotypes inhabiting the Southeast Pacific are reflected not only in cranial features (Van Waerebeek et al. 1990, Santillán et al. 2008), but also in external morphological differences, such as the shape of the DF. We applied a small set of measurements, to both DF photographs and specimens from Ecuador, Peru, and Chile to quantify morphological variation. Photogrammetry allowed us to confirm differences between ecotypes as well as ontogenetic changes in the coastal ecotype.

MATERIALS AND METHODS

The Study Area

The study area extends over ca. 3,200 km from southwestern Ecuador (01° S) to central Chile (30° S). A small sample from the Galápagos Islands was also included (01° N, 90° W) (Figure 1). The zone is characterized by high primary productivity due both to the cold Humboldt Current flowing north to ca. 5° S, and to the continental runoff from the Gulf of Guayaquil, the largest estuary on the west coast of South America. The Gulf of Guayaquil is fringed with mangrove forests combined with small islands, creating an extensive network of channels that penetrate about 100 km into the mainland (Stevenson 1981). The northern gulf has extensive beaches and low cliffs. Peru's coastline consists of sandy beaches interrupted by rocky cliffs except for a small mangrove area in the north (Tumbes). Strong, year-round upwelling characterizes most of the Peruvian coast as well as northern and central Chile (Chávez et al. 1989, Thiel et al. 2007). The climate in the study area varies from tropical in the north (Ecuador, Tumbes) to subtropical in northern and central Peru and temperate in southern Peru and in most of Chile.

Samples Used

ECUADOR: DF of coastal bottlenose dolphins photo-identified between 2005 and 2017 during a long-term study in the Gulf of Guayaquil were used (Félix et al. 2017). The population in the gulf is organized in partially discrete subunits referred to as communities [animals with a higher degree of association than with neighbor communities, sensu Wells et al. (1987)]. Animals from four coastal communities in the inner estuary (Posorja, Data de Posorja, Estero Salado, and Bajoalto) and a coastal community located at Salinas in the northern border of the Gulf of Guayaquil were included (Figure 1). In addition, photographs of offshore bottlenose dolphins taken opportunistically off Salinas and Puerto López during whale-watching trips in 2005–2010 and off San Cristóbal Island in the Galápagos archipelago in 2005 were also included in the analysis. Photographs were taken with digital cameras (8 to 24 megapixels) with 70–300 mm and 100–400 mm zoom lenses. The Ecuadorian sample (EC) included 163 individuals (129 coastal and 34 offshore).

PERU: The sample from Peru consisted mainly of freshly dead bottlenose dolphins,
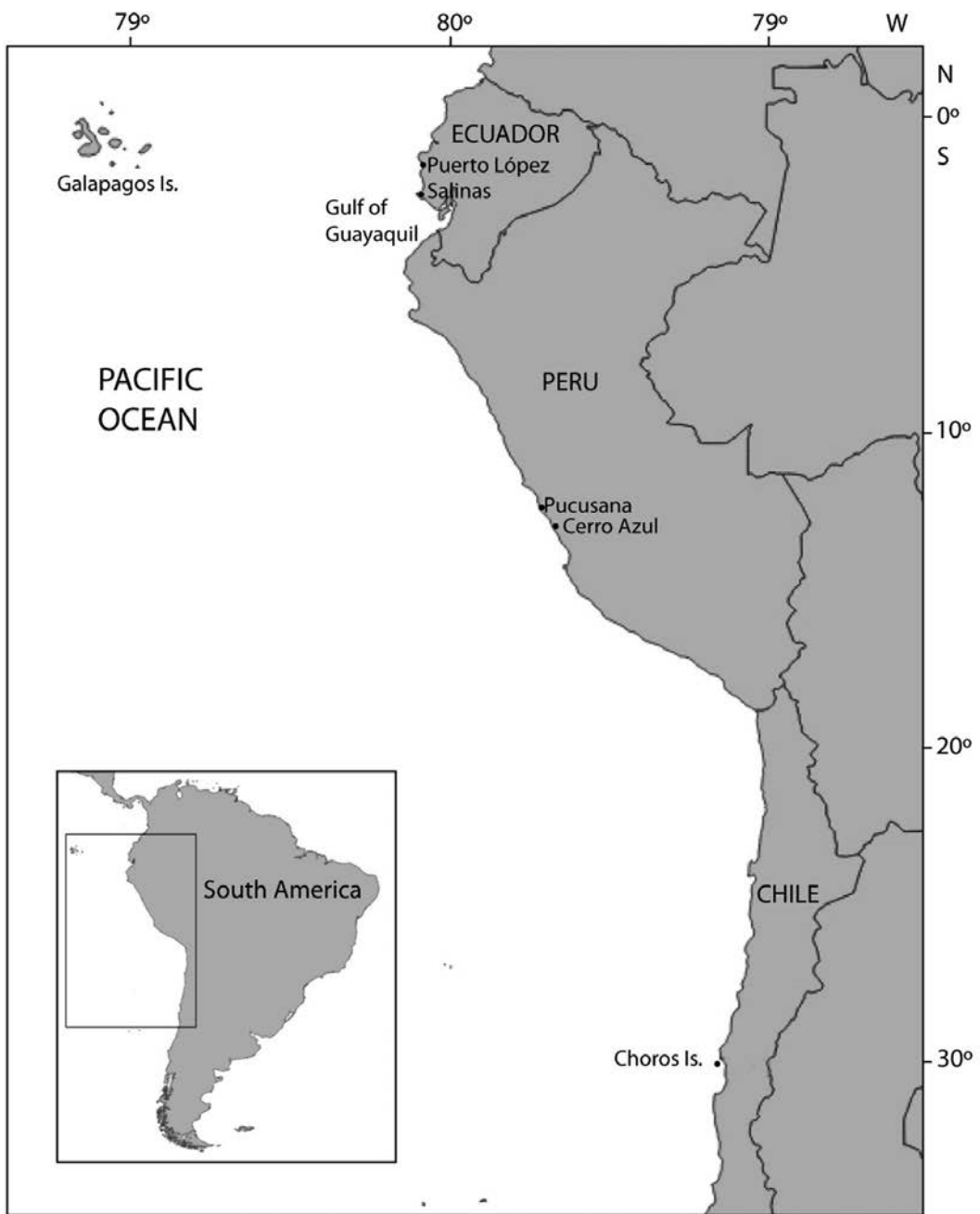
FIGURE 1. The study area, covering the coasts of three countries in the southeastern Pacific (Ecuador, Peru, and Chile).

both offshore and coastal specimens, landed at several Peruvian fishing ports, but mostly at Pucusana and Cerro Azul (Figure 1) in 1985–1994 (e.g., Van Waerebeek et al. 1990, 1997, Van Waerebeek and Reyes 1994). DF base length and height were measured on the carcasses in situ. Two other parameters (see below) were measured on scans (with Minolta Dimage Scan Dual III) of 35 mm color slides. A small additional sample consisted of photos of free-ranging dolphins off central Peru (Pucusana, Chilca, Cerro Azul, and Tambo de Mora). Both analog and digital cameras with 50 mm fixed and 70–300 mm zoom lenses were used. The Peruvian sample (PE) included 60 individuals (nine coastal and 51 offshore).

CHILE: All individuals sampled belonged to the so-called Pod-R, considered the only remnant of a bottlenose dolphin population residing nearshore for extended periods in north-central Chile near Chañaral (29.039° S) and later Choros, Damas, Gaviota Island, and, occasionally, Pájaros Islets (Sanino and Yáñez 2000, 2001, Sanino et al. 2005). Despite its inshore behavioral ecology, Pod-R presented a high genetic divergence (mtDNA, control region) from the Peruvian nearshore ecotype and had a relatively closer affinity with the Chilean offshore stock (Sanino et al. 2005). The Chilean sample (CL) included 25 individuals belonging to Pod-R, probably an ancient adaptive radiation presenting intermediate morphological characters between the (occasionally) sympatric offshore ecotype dolphins and the Peruvian nearshore ecotype. Pod-R is currently managed as an evolutionary significant unit differentiated from all other bottlenose dolphin communities in Chile.

Age and Sex Classes

Because of limited samples, ontogenetic variation was studied only in the Ecuadorian coastal ecotype, where we distinguished four classes: females (adults regularly seen accompanied by a calf), adults of unknown sex, immatures (smaller than adults and not evidently associated with a potential mother), and calves (small, one-third to one-half of adult size, evi-

dently associated with an adult, presumably the mother). For the specimen samples from Peru, calves and juveniles (SL < 200 cm) were not considered, but several larger subadults were included, some of which were not yet sexually mature.

Treatment of Photographs and Measurements

Photographs of DF available from catalogs in Ecuador, Peru, and Chile were evaluated and selected according to the following criteria: (1) Angle: only photographs taken perpendicular to the body axis; (2) Surface: photographs showing the entire fin surface from the base to the tip, as well as some photographs with up to 10% of the base covered by water that could be digitally completed following the evident inclination of the dorsal fin edge; (3) Sharpness: only photographs showing the leading and trailing edges of the DF with good focus.

Suitable photographs were imported into Adobe Illustrator 5 and, if necessary, rotated to a horizontal position. With the "rectangle tool," three rectangles were created to measure the following distances: base length of DF (b), height of DF (h), width of DF at half height (a), and the overhang of the fin tip relative to the trailing edge at midfin (s) (Figure 2). The width and height were calculated automatically by the rectangle tool in millimeters with 0.1 mm accuracy. To find the midpoint of the DF, two diagonal lines were crossed connecting the opposite angles of the rectangle used to measure the base and height of the fin. Because the photographs have different sizes, the on-screen measurements in millimeters were used to calculate three indexes with the base length as covariate: h/b (height/base), a/b (width midfin/base), and s/b (overhang/base) or "falcateness." Measurements were made over the photograph's full size (100%) or reduced to a standard A4 size if photographs were larger. For Chilean individuals, measurements were made on reconstructed DF profiles, after correction of lens distortion, perspective, and horizon before cropping the image (Adobe Photoshop) (see Sanino and Yáñez 2001). All measurements were taken by a single researcher (F.F.)
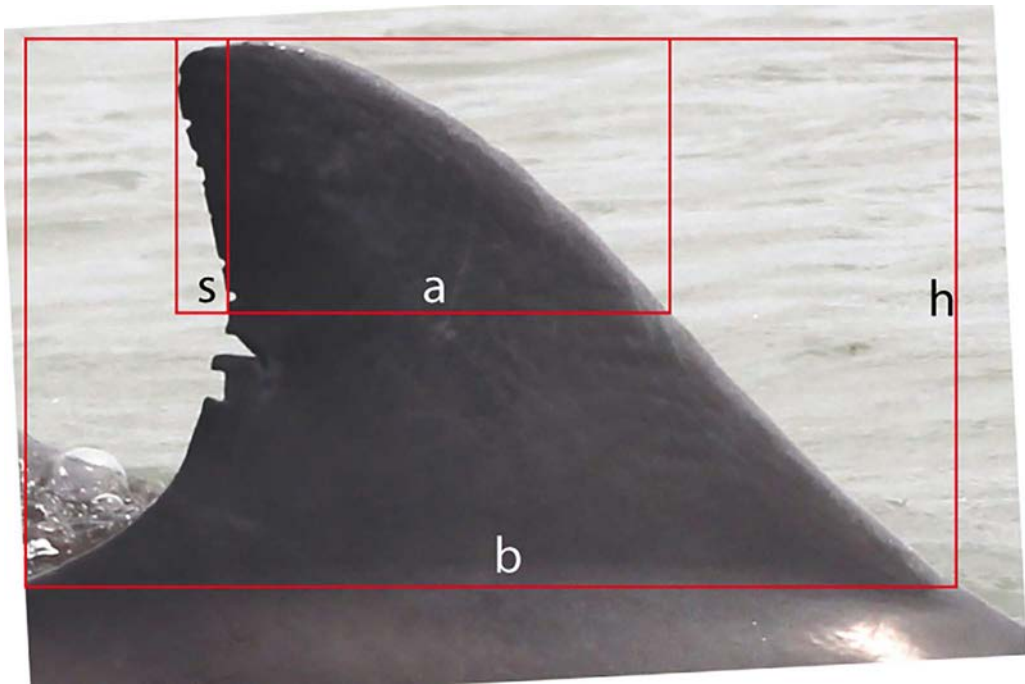
Figure 2. Four measurements taken on a (coastal) bottlenose dolphin dorsal fin photograph. This photograph was rotated 3 degrees counterclockwise to horizontality, then rectangles were superimposed and measurements calculated: b, base length; h, fin height; a, fin width at half-height; and s, overhang.

to ensure consistency. The measurement error was estimated in coastal Ecuadorian specimens (six offshore, 13 coastal) at 0.90% (SD = 1.33) by measuring b, h, a, and s five times each, for a total of 380 measurements.

Statistical Treatment

A Pearson correlation test was used to assess relationship among the three ratios obtained. Because the ratios h/b and a/b were correlated ($P = .013$), statistical comparisons were conducted only on a/b and s/b ratios. However, the h/b ratio was still used for morphological comparisons. Ratios obtained were transformed logarithmically to normalize distributions and allow two parametric statistical tests, one-way analysis of variance (ANOVA) and Student's t test. Then a discriminant function analysis (DFA) was conducted to determinie whether the set of variables was effective in predicting category member-

ship. All analyses were implemented in the XLSTAT software for Excel.

RESULTS

Coastal-Ecuador Ecotype

The three DF indexes were calculated independently for four sex and age classes of Ecuadorian coastal specimens: adults of unknown sex, adult females, immatures, and calves (Table 1). The DF of calves and immatures have a proportionally higher, wider at midheight, and more falcate fin than those of adults. Significant differences were found in both a/b and s/b indexes (one-way ANOVA, $F = 10.5$; df = 3,120; $P < .001$ and $F = 2.75$; df = 3,108; $P = .045$, respectively). This was confirmed post hoc by obtaining $P < .001$ and $P = .003$ for pairwise t tests of adults (adult females and unknown-sex adults) versus immatures (calves and immatures), for a/b and

TABLE 1

Comparison of Mean Values of Three Dorsal Fin Indexes among Age and Sex Classes in Ecuadorian Coastal Ecotype (All Samples from the Gulf of Guayaquil, 2005–2017)

Class	h/b			a/b			s/b		
	Value	SD	n	Value	SD	n	Value	SD	n
Adults, unknown sex	0.612	0.07	82	0.468	0.035	77	0.047	0.029	68
Adult females	0.586	0.066	15	0.461	0.04	15	0.032	0.028	13
Calves	0.693	0.078	13	0.513	0.022	13	0.061	0.031	12
Immatures	0.664	0.075	19	0.505	0.043	19	0.059	0.03	19

TABLE 2

Confusion Matrix of Cross-Validation for Four Age Classes of Ecuadorian Coastal Individuals, Showing How DFA Classified Observations (Rows Represent Actual Groups and Columns the Predicted Groups)

From/to	Adults, Unknown Sex	Adult Females	Immatures	Calves	Total	% Correct
Adults, unknown sex	64	0	6	1	71	90
Adult females	13	0	1	0	14	0.07
Immatures	12	0	2	5	19	26
Calves	8	0	2	3	13	15
Total	97	0	11	9	117	61

TABLE 3

Comparison of Mean Values for Three Dorsal Fin Indexes between Coastal Ecuadorian and Coastal Peruvian Bottlenose Dolphins

Site	h/b			a/b			s/b		
	Value	SD	n	Value	SD	n	Value	SD	n
Coastal EC	0.609	0.067	97	0.466	0.035	92	0.044	0.028	86
Coastal PE	0.676	0.078	9	0.516	0.037	7	0.07	0.027	7

s/b indexes, respectively. The age/class DFA shows that overall 61% of the observations were correctly assigned (Table 2). Adults of unknown sex had the highest rate of individuals correctly classified (90%) and adult females the lowest. In the case of calves and immatures, only 26% and 15%, respectively, were correctly classified, and several calves were assigned as immatures and vice versa. These results suggest that there is a stronger (allometric) length growth of the DF base and width at midheight (b and a) than in the upper parts of the fin. In view of the ontogenetic variation, data for calves and immatures were not further used.

Coastal Ecuador Ecotype versus Coastal Peru Ecotype

Peruvian coastal bottlenose dolphins showed DF relatively taller, relatively wider at midheight, and slightly more falcate than those of coastal Ecuadorian specimens (Table 3). However, a significant difference was found

TABLE 4

Confusion Matrix of Cross-Validation for Coastal Ecuadorian versus Coastal Peruvian Samples, Showing How DFA Classified Observations (Rows Represent Actual Groups and Columns the Predicted Groups)

From/to	Coastal EC	Coastal PE	Total	% Correct
Coastal EC	85	1	86	99
Coastal PE	7	0	7	0
Total	92	1	93	91

TABLE 6

Confusion Matrix of Cross-Validation for Offshore Populations (Ecuador, Peru, and Pod-R), Showing How DFA Classified Observations (Rows Represent Actual Groups and Columns the Predicted Groups)

From/to	Ecuador	Peru	Pod-R	Total	% Correct
Ecuador	29	0	4	33	88
Peru	11	0	3	14	0
Pod-R	7	0	18	25	72
Total	47	0	25	72	65

TABLE 5

Comparison of Mean Values of Three Dorsal Fin Indexes among Offshore Specimens of Ecuador, Peru, and Pod-R from North-Central Chile

Country	h/b			a/b			s/b		
	Value	SD	n	Value	SD	n	Value	SD	n
Ecuador	0.686	0.074	34	0.492	0.042	34	0.177	0.058	33
Peru	0.639	0.082	51	0.474	0.043	14	0.159	0.058	14
Pod-R	0.649	0.097	25	0.435	0.04	25	0.193	0.048	25

only in the index a/b (t test, $t = 3.46$, $P < .001$). The DFA correctly assigned 99% of observations corresponding to coastal Ecuadorian individuals but failed to recognize any Peruvian individuals (Table 4). We acknowledge that the Peruvian sample was small compared to the Ecuadorian sample, requiring much caution in interpretation. Moreover, several sub-adult animals in the coastal Peru sample could have skewed the results somewhat.

Offshore Ecotype

The two independent indexes (a/b, s/b) were compared between the data sets of offshore animals from Ecuador, Peru, and the Chilean Pod-R (Table 5). Pod-R was included in this comparison because mtDNA genetics (see Sanino et al. 2005) and DF indexes calculated suggest that this population has clear affinity to the offshore ecotype. Ecuadorian offshore specimens showed DF relatively taller and wider (at midheight) than those of the other groups. Chilean Pod-R DF were relatively narrower at midheight than those of Ecuador

and Peru animals. The high DF falcateness was a common characteristic among all three populations, but reached the highest value in Pod-R. Significant difference was found in the a/b index among offshore groups but not in the s/b index (one-way ANOVA, $F = 13.9$; df = 2,70; $P < .001$ and $F = 2.23$; df = 2,69; $P = .11$, respectively). Overall the DFA correctly assigned 65% of the observations, with Ecuadorian specimens being better differentiated (88%) than Pod-R (72%) and Peruvian individuals (0%) (Table 6). Peruvian offshore individuals were more similar to Ecuadorian offshore animals than to those in Pod-R, but there is an important overlap among the three groups.

Coastal Ecotype versus Offshore Ecotype

Data for the offshore ecotype and Pod-R were pooled, as well as coastal ecotype data from Ecuador and Peru, and compared (Table 7). DF of offshore animals were relatively taller and more falcate than those of coastal animals. A significant difference was found in

TABLE 7

Comparison of Mean Values for Three Dorsal Fin Indexes between Coastal and Offshore Specimens from the
Southeast Pacific (Data Sets from the Three Countries Were Pooled in One of the Two Categories Accordingly)

Ecotype	h/b			a/b			s/b		
	Value	SD	*n*	Value	SD	*n*	Value	SD	*n*
Coastal	0.609	0.067	97	0.466	0.035	92	0.044	0.028	86
Offshore	0.656	0.085	110	0.469	0.048	73	0.179	0.055	72

index s/b but not in index a/b (*t* test, $t = 10.7$, $P < .001$ and $t = -0.27$, $P = .78$, respectively). In the case of the a/b index there is a wide overlapping range between both ecotypes,
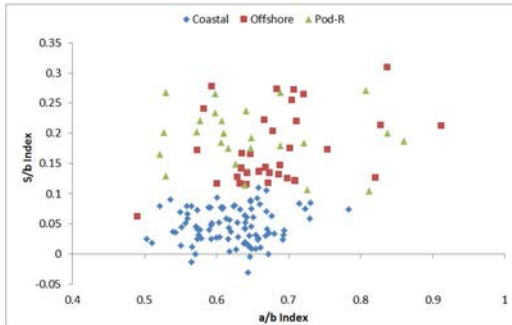

FIGURE 3. Index s/b versus index a/b in coastal, offshore, and Pod-R bottlenose dolphins. DF falcateness (s/b) optimally differentiates coastal and offshore ecotypes in Ecuador and Peru. Pod-R dolphins show falcateness similar to that of the offshore ecotype. The unique offshore outlier (with lowest s/b) had been visually recognized as atypical (MFB-185).

with the offshore ecotype being more variable than the coastal form (Figures 3 and 4). In the case of the s/b index, the overlap range between coastal and offshore ecotypes is minimal. There were a few coastal individuals for whom the s/b index was zero or negative, which means in those animals the DF did not show curvature at all. The DFA correctly classified 98% of coastal animals and 96% of offshore animals (Table 8). Statistics confirmed our empirical understanding that

TABLE 8

Confusion Matrix of Cross-Validation of Coastal versus
Offshore Groups, Showing How DFA Classified
Observations (Rows Represent Actual Groups and
Columns the Predicted Group)

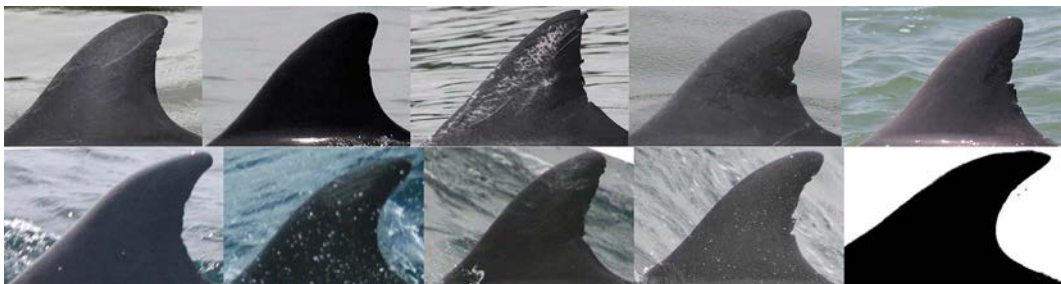| From/to	Coastal	Offshore	Total	% Correct
Coastal	90	2	92	98
Offshore	3	69	72	96
Total	93	71	164	97

FIGURE 4. Dorsal fins of some of the bottlenose dolphins used in this study, showing the typical shape in coastal (*above*) and offshore (*below*) ecotypes in the Southeast Pacific. Falcateness is significantly more pronounced in the offshore ecotype, whereas coastal animals have more triangular fins.

offshore bottlenose dolphins have more fal-cate DF compared to more triangular fins in coastal animals.

<div align="center">DISCUSSION</div>

This study confirmed differences in the shape of DF between coastal and offshore bottle-nose dolphins in the Southeast Pacific by comparing three simple proportions. These findings are consistent with previous studies in the region based on cranial characteristics, molecular genetics, habitat use, parasites, and feeding ecology (Van Waerebeek et al. 1990, 2017, Sanino et al. 2005, Santillán et al. 2008, Bayas 2015). Although the trends appear to be well-defined, we recognize that different sources of bias may have been introduced during the sampling and measuring process, including (1) differences in the quality and size of photographs (e.g., analog versus digital photography, and processed raster images from Chile); (2) slight deviations from per-pendicularity; (3) photos were used from both live and dead animals (e.g., most h and b values from Peru were highly accurate, being actual body measurements on fresh carcasses). Future more homogeneous and larger sam-ples (particularly from coastal Peru) should improve robustness of the analyses.

The most consistent difference between the coastal and offshore ecotypes was the strong DF falcateness (high s/b) in the off-shore form and in Pod-R (Figure 4). This characteristic constitutes a useful diagnostic feature to visually differentiate between eco-types in the field. Only a single Peruvian offshore specimen (MFB-185), with a s/b of 0.0625, did not fit this pattern. Although this characteristic is useful for this region, in-cluding also Chilean Patagonia (Sanino and Van Waerebeek 2008, Van Waerebeek et al. 2017), southern Brazil, and perhaps Argen-tina (Simões-Lopes and Daura-Jorge 2008), it does not necessarily apply to other regions. In the eastern North Pacific DF of inshore bottlenose dolphins are noticeably more fal-cate than in Ecuador and Peru (see Viloria-Gómora and Medrano-González 2015). In coastal Río Negro, central Argentina, three animals (and a calf) showing a Southeast Pa-

cific offshore phenotype (falcate DF, dark coloration, short beaks) lived near shore and sympatrically with others that showed a typi-cal coastal phenotype (Vermeulen and Cam-mareri 2009). Using up to 11 measures and angles estimated from photographs on the DF surface, Morteo (2004) found that the most useful features to distinguish among coastal populations of bottlenose dolphins in Mexico were the foil (curvature of the ante-rior border versus base length), deep rake (amount that tip of the fin extends beyond the base of the trailing edge), and depth (length from the anterior insertion of the DF) versus foil. We do not rule out that such measurements might provide additional information to differentiate between offshore and coastal populations in the Southeast Pacific as well, but for the purpose of hav-ing an easily assessed feature in the field, the DF falcateness is highly discriminating and sufficient.

Although a pronounced falcateness (s/b) is shared by offshore bottlenose dolphins in Ecuador, Peru, and Chilean Pod-R, the other two DF indexes in these three populations showed some significant differences. In terms of relative DF height (h/b), Ecuadorian off-shore form showed the highest values, fol-lowed by Peruvian coastal form, Pod-R, then Peruvian offshore form, and the lowest values were shown by Ecuadorian coastal form. With respect to relative fin width at mid-height (a/b), Peruvian coastal stock had the widest fins, followed by Ecuadorian offshore, Peruvian offshore, Ecuadorian coastal, and finally Pod-R animals. Thus, Chilean Pod-R individuals showed DF both the narrowest at midheight and with the highest falcateness index of all groups examined, reflected in an extremely falcate aspect, noticeable by the naked eye (see Figure 4). These results are consistent with the marked differences in mtDNA (control region) found between Pod-R dolphins and Peruvian offshore and, to a lesser degree, Chilean offshore dolphins [not included in our analysis] (Sanino et al. 2005). We consider Pod-R a case of a recent radiation into the coastal environment from offshore stock, a sort of "transitional form" that preserved the offshore high DF falcate-

ness due to peculiarities of the Chilean coast [e.g., deep water near shore (Sanino et al. 2005)]. In this and other transitional forms, we suggest using more characters (e.g., Morteo et al. 2017) to assess ecotype. Between the pure offshore and nearshore ecotypes, a cline molded by local environmental factors may be expected. DF morphology, including size, would be shaped in response to particular skills developed by ecotypes for moving, thermoregulation, and chasing prey (Morteo et al. 2017). Performance of cetacean fins is a function of drag and lift, which is proportional to the square root of its aspect ratio (Fish and Battle 1995). Thus, taller and falcate fins would be more efficient for faster and long-distance traveler animals, whereas wider fins produce more lift by deflecting a greater mass of water and would be more relevant for maneuverability in shallow waters.

Because Peruvian and Chilean offshore bottlenose dolphins are closely related, a single, wide-ranging Peru-Chile offshore stock has been proposed (Sanino et al. 2005). Differences found between Peruvian and Ecuadorian offshore specimens, although parapatric, could be attributed to either ecological factors or a sampling bias because most measurements from Peru used to calculate the h/b index were actual body morphometrics taken from carcasses. However, the sample used to calculate a/b and s/b indexes in Peruvian specimens was too small (*n* = 9) to capture all variability. Considering that Ecuadorian offshore specimens have the tallest and second-widest DF of all groups, their affinity to the Peru-Chile offshore stock is unclear. Perhaps they are more closely related to the Eastern Tropical Pacific and Northeast Pacific populations (Bayas 2015).

The large database from the Gulf of Guayaquil revealed significant allometric ontogenetic variation in coastal dolphins, mainly expressed in the relatively shorter DF base length in immatures, affecting the three indexes similarly because all have b as denominator. DF of calves and immatures appear relatively higher (large h/b) and more falcate (large s/b) than in adults because their fin base is so short. With axial (length) growth of the vertebral column, the base length of the DF

must also grow allometrically. Adult females showed less-falcate fins with a wider base than a sample of adults of mixed sexes; however due to the indeterminate composition it was not possible to establish sexual dimorphism with any certainty. Besides, because absolute measurements were available for only a small Peruvian sample we were unable to establish sexual dimorphism in DF height, as found in Florida coastal bottlenose dolphins (Hearst et al. 1990). We suggest that allometric growth is likely present in the offshore ecotype also but was not captured in our data.

Because the DF is the most visible part of the animal when breathing, the advantage of being able to identify the ecotype quickly and reliably by DF shape is obvious. A reliable criterion to allocate individuals living in sympatry or parapatry to a specific ecotype, be it from sightings, strandings, or bycatches, in the field or from photographs, greatly facilitates research. However, as in the case of Pod-R, prior evidence-guided interpretation may be necessary in some areas, because the criterion is not blindly applicable.

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