Morphological variation in dorsal fins among common bottlenose dolphin populations in the Southeast Pacific Ocean

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ABSTRACT

Variation in dorsal fin morphology was assessed in five bottlenose dolphin (Tursiops truncatus) populations from the Southeast Pacific. We hypothesized that habitat specialization between coastal and offshore ecotypes led 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 (9 coastal and 51 offshore) from Peru and 25 individuals of an inshore form from north-central Chile (Pod-R). Values were logarithmically transformed to allow one-way ANOVAs and t-tests. Ontogenetic variation was found in coastal dolphins from Ecuador, with indices significantly different among age/classes. All indices were higher in juveniles and calves, suggesting a stronger (allometric) growth of the dorsal fin base (b) than in the upper parts of the fin. Hence only adults and subadults were considered in further analysis.

Statistically significant differences were found in h/b and a/b indices between coastal specimens from Ecuador and Peru, and between offshore specimens from Ecuador and Peru, and Pod-R. Offshore and Pod-R data were pooled and compared with coastal specimens from Ecuador and Peru; significant differences were found in indices h/b and s/b. Offshore dorsal fins are relatively higher than coastal fins. However the most consistent and visible difference between ecotypes was the strong falcateness (high s/b) in the offshore forms vs. a more triangular shape (low s/b) in coastal forms. Except one outlier, all other cases could be correctly classified through ocular inspection by experienced observers. Chile's Pod-R represents a unique case of an inshore form with strong falcateness, a typical offshore trait.

Ecuadorian offshore form showed highest relative dorsal fin height (h/b), followed by Peruvian coastal form, Pod-R, Peruvian offshore and, lowest, Ecuadorian coastal. Relative fin width at mid-height (a/b) was widest in Peruvian coastal stock, followed by Ecuadorian offshore, Peruvian offshore, Ecuadorian coastal and narrowest in Chilean Pod-R. The latter had also the highest falcateness index of all groups, consistent with their extremely falcate dorsal fins. Extreme values for two of three indices agree with marked molecular differences between Pod-R dolphins and Peruvian dolphins and, to a lesser degree, Chilean offshore. Pod-R may represent a recent radiation into the coastal environment from offshore ancestors, a sort of 'transitional form'. High falcateness may be retained due to particularities of the local environment, e.g. fairly deep water.

Key Words: South America, Pacific Ocean, habitat, morphometrics, intraspecific variation.

INTRODUCTION

The bottlenose dolphin (Tursiops truncatus) is widely distributed in tropical and tempered 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 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 as to coastal (or inshore) and offshore forms have been described along much of its distribution range (e.g. Duffield et al., 1983; Perrin 1984; Van Waerebeek et al., 1990; Mead and Potter, 1993; Hoelzel et al., 1998; Van Waerebeek et al., 2016). 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; Sanino et al., 2005; Tezanos-Pinto et al., 2009). Morphological and socio-ecological differences between the two forms would be associated with habitat specialization. The coastal ecotype is found in small groups usually of a dozen animals or less, is generally resident and shows fine-scale population structure. In the offshore ecotype, groups are substantially larger and more variable in size and distribute along extended areas (Scott and Chivers, 1990; 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).

Major morphological differences between coastal and offshore forms have been recognized in body and cranial traits as well as colouration (Perrin, 1984; Van Waerebeek et al., 1990; Mead and Potter, 1990; 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, 1996; Simões-Lopes and Daurá-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 species such as killer whales (*Orcinus orca*) (Bigg et al., 1987), spinner dolphins (*Perrin*, 1975), dusky dolphins (*Lagenorhynchus obscurus*) (Van Waerebeek, 1993) and Dall’s porpoises (*Phocoenoides dalli*) (Jefferson, 1989).

Bottlenose dolphin distributes more or less continuously off the west coast of South America. 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 are genetically divergent from other coastal and offshore populations in the Southeast Pacific (Bayas, 2015). A small and discrete population more related with the offshore ecotype, referred as to Pod-R, has been identified near coastal islands off central-north Chile (González et al., 1989; Sanino and Yáñez 2000, 2001; Sanino et al., 2005). Based on control region mt-DNA, 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. On the other hand, the offshore ecotype off Peru and Chile are considered a single, wide-ranging 'Peru-Chile offshore stock' (Sanino et al., 2005). Some specimens 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 reported as bycatch in small-scale fisheries in Ecuador and Peru -where also direct catches are reported- as well as victims of vessel collision (Van Waerebeek et al., 1994, 1997, 2007; Mangel et al., 2010; Félix et al., in press). 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 N° 26385), marine reserves exists but only protects coastal areas in a limited scale. In Chile two small Marine Reserves were created, among others, to protect Pod-R from direct capture events (Sanino and Yáñez 2000) and promote its sustainable use through tourism activities that still have not been successfully regulated (Sanino and Yáñez, 2000, 2001).

Based on field observations, the authors learned empirically to distinguish between coastal and offshore dolphins based on DF shape. We hypothesized that phylogenetic differences and habitat specialization between both ecotypes inhabiting the Southeast Pacific are also reflected in major morphological differences, such as the form of the dorsal fin. For this purpose, we applied a small set of measurements to dorsal fin photographs of specimens from Ecuador, Peru and Chile looking for such morphological differences. The method allowed us to confirm the presence of differences between both ecotypes as well as of ontogenetic changes in the coastal ecotype.

### METHODS

**The study area**

The study area extends over ca. 3,200 km from SW Ecuador (01°S) to central Chile (30°S). A small sample from the Galapagos Islands was also included (01°S, 90°W) (Figure 1). The zone is characterized by high primary
productivity due to the cold Humboldt Current flowing north to ca. 5°S, plus the continental runoff from the Gulf of Guayaquil. The Gulf of Guayaquil is fringed with mangrove forests combined with small islands creating an extensive network of channels that penetrate around 100km into the mainland (Stevenson, 1981). The northern gulf shows 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 with high productivity characterizes most of the Peruvian coast as well as northern and central Chile.

The climate in the area varies from tropical in the north (Ecuador, Tumbes) to subtropical in Peru and temperate in most of Chile. It is highly influenced by the SE Pacific anticyclone that regulates the strength of the Humboldt Current and the seasonal presence of the inter-tropical convergence zone in the south-central part of Ecuador and northern Peru (Wyrtki, 1966). A well-defined rainy season occurs between January and March, however along Peru and northern Chile a desert climate prevails with little local rainfall, although mud-laden runoff from summer rains in the Andes reaches the sea in Peru through seasonal rivers. Thus, the marine environment presents different conditions in terms of sea water temperature, productivity, salinity and rainfall regime.

![Figure 1. The study area covering the coasts of three countries in the Southeast Pacific (Ecuador, Peru and Chile).](image)

**Source of data**

**Ecuador**

Mainly dorsal fins 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). Animals were included from four coastal communities in the inner estuary (Posorja, Data de Posorja, Estero Salado and Bajoalto) and a community located at Salinas (Figure 1). Additionally, photographs of offshore bottlenose dolphins taken opportunistically off Salinas and Puerto López during whalewatching trips in 2005-2010, and off San Cristobal Island in the Galapagos Archipelago in 2005 were also included in the analysis. All photographs were taken with digital cameras (8 to 24 megapixels) with zoom lenses 70-300mm and 100-400mm. The Ecuadorian sample (EC) included 163 individuals (129 coastal and 34 offshore).
Peru

The sample from Peru consisted mainly of freshly dead bottlenose dolphins, 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, 1994, 1997). Dorsal fin base length and height were measured directly on the carcasses. Two other parameters (see below) were measured on scans (Minolta Dimage Scan Dual III) of 35mm colour slides. A small additional sample consisted of photos of free-ranging dolphins off central Peru (Pucusana, Chilca, Cerro Azul, Tambo de Mora). A variety of both analog and digital cameras with 50 mm fixed and 70-300 mm zoom lenses were used. The Peruvian sample (PE) included 60 individuals (9 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 central-north Chile near Chañaral (29.039°S) and later Choros, Damas, Gaviota and, occasionally, Pájaros Islands (Sanino and Yañez 2000, 2001; Sanino et al., 2005). Despite its inshore behavioural 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 presently managed as an evolutionary significant unit differentiated from all other bottlenose dolphin communities in Chile.

We suggest that nearshore occurring bottlenose dolphins in Chilean Patagonia (Sanino and Van Waerebeek, 2008) are true offshore form individuals that opportunistically exploit nearshore habitat. This hypothesis would explain their evident offshore morphotype, including of dorsal fins, and their non-residency. These dolphins were however not represented in our sample.

Age and sex classes

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 to a potential mother) and calves (small 1/3-1/2 of adult size, evidently associated to an adult, presumably the mother). For the specimen samples from Peru, calves and juveniles (SL<200 cm) were not considered, however several larger subadults were included, some of which were not yet sexually mature.

Treatment of photographs and measurements

Photographs of dorsal fins available from catalogues 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 dorsal fin 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 dorsal fin (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 mid-fin (s) (Figure 2). The rectangles' width and height were calculated automatically by the tool with 0.1 mm accuracy. To find the midpoint of the dorsal fin, two diagonal lines were crossed connecting the opposite angles of the rectangle used to measure the base and height of the fin. As the photographs have different sizes, the measurements in mm were used to calculate three indexes with the base length as covariate: h/b (height/base); a/b (width mid-fin/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. In the case of Chilean individuals, measurements were made on reconstructed dorsal fin profiles, after correction of lens distortion, perspective and horizon before cropping the image (Adobe Photoshop) (Sanino and Yañez 2001). To avoid observer bias, all measurements were taken by a single researcher (FF).

The values (ratios) obtained were transformed logarithmically to normalize distributions and allow two types of parametric statistical tests, one-way ANOVA and Student’s t-test, implemented in the Excel ® data analysis package.
RESULTS

Coastal-Ecuador ecotype
The three indexes were calculated independently for the four sex and age classes of Ecuadorian coastal specimens (Table 1). All comparisons (ANOVA) tested statistically significant. The comparison for the h/b index showed that calves and immatures have a relatively higher DF than adults (One-way ANOVA, $F_{3,125}=4.6$, $p=0.004$), a relatively wider fin at mid-height (one-way ANOVA, $F_{3,120}=10.5$, $p=3.38E^{-6}$) and a relatively more falcate fin than adults (one-way ANOVA, $F_{3,108}=2.75$, $p=0.045$). The fact that all results concord suggest that there is a stronger (allometric) length growth of the dorsal fin base (b) than in the upper parts of the fin. Adult females had the smaller values in all three indexes and it was more evident in the s/b index, which suggests that ontogenetic changes would be more pronounced in this class. Potential sexual dimorphism, however, requires further analysis. In view of the ontogenetic variation, data for calves and immatures were not further used.

Table 1. Comparison of the mean values of three dorsal fin indexes among age and sex classes in Ecuadorian coastal ecotype. All samples are from the Gulf of Guayaquil, period 2005-2017.

<table>
<thead>
<tr>
<th>Class</th>
<th>h/b Value</th>
<th>SD</th>
<th>n</th>
<th>a/b Value</th>
<th>SD</th>
<th>n</th>
<th>s/b Value</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>0.586</td>
<td>0.066</td>
<td>15</td>
<td>0.461</td>
<td>0.040</td>
<td>15</td>
<td>0.032</td>
<td>0.028</td>
<td>13</td>
</tr>
<tr>
<td>Adults</td>
<td>0.612</td>
<td>0.070</td>
<td>82</td>
<td>0.468</td>
<td>0.035</td>
<td>77</td>
<td>0.047</td>
<td>0.029</td>
<td>68</td>
</tr>
<tr>
<td>Calves</td>
<td>0.693</td>
<td>0.078</td>
<td>13</td>
<td>0.513</td>
<td>0.022</td>
<td>13</td>
<td>0.061</td>
<td>0.031</td>
<td>12</td>
</tr>
<tr>
<td>Immatures</td>
<td>0.664</td>
<td>0.075</td>
<td>19</td>
<td>0.505</td>
<td>0.043</td>
<td>19</td>
<td>0.059</td>
<td>0.030</td>
<td>19</td>
</tr>
</tbody>
</table>

Coastal Ecuador vs. coastal Peru
Statistically significant differences were found in h/b and a/b indexes between coastal specimens from Ecuador and Peru ($t$ test, $t=-2.08$, $p=0.039$ and $t=-3.46$, $p=7.8E^{-4}$, respectively). Peruvian coastal bottlenose dolphins showed dorsal fins relatively taller and relatively wider at mid-height than coastal Ecuadorian specimens (Table 2). However, the falcateness of the fin tip was not statistically different ($t=-1.25$, $p=0.21$). We acknowledge that the Peruvian sample was too small compared to the Ecuadorian sample requiring much caution in interpretation. Moreover several subadult animals in the coastal Peru sample could have skewed results.

Table 2. Comparison of the mean values for three dorsal fin indexes between coastal Ecuadorian and coastal Peruvian bottlenose dolphins.

<table>
<thead>
<tr>
<th>Site</th>
<th>h/b Value</th>
<th>SD</th>
<th>n</th>
<th>a/b Value</th>
<th>SD</th>
<th>n</th>
<th>s/b Value</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal EC</td>
<td>0.609</td>
<td>0.067</td>
<td>97</td>
<td>0.466</td>
<td>0.035</td>
<td>92</td>
<td>0.044</td>
<td>0.028</td>
<td>86</td>
</tr>
<tr>
<td>Coastal PE</td>
<td>0.676</td>
<td>0.078</td>
<td>9</td>
<td>0.516</td>
<td>0.037</td>
<td>7</td>
<td>0.070</td>
<td>0.027</td>
<td>7</td>
</tr>
</tbody>
</table>

Offshore ecotype
The three indexes were compared between the datasets of offshore animals from Ecuador and Peru and the
Chilean Pod-R (Table 3). Pod-R was included in this comparison because genetics and all three calculated indexes suggest this population is more related to the offshore ecotype. Statistically significant differences were found in indexes h/b and a/b but not in index s/b (One-way ANOVA, $F_{2,107} = 3.45$, $p = 0.035$; $F_{2,70} = 13.9$, $p = 7.9 \times 10^{-6}$; and $F_{2,69} = 2.23$, $p = 0.11$, respectively). Ecuadorian offshore specimens show dorsal fins relatively taller and wider (at mid-height) than all other groups examined. Chilean Pod-R dorsal fins were relatively narrower at mid-height than all other groups. The high DF falcateness was a common characteristic among all three populations, and reached the highest value of any group in Pod-R.

Table 3. Comparison of mean values of three dorsal fin indexes among offshore specimens of Ecuador and Peru and Pod-R from central-north Chile.

<table>
<thead>
<tr>
<th>Country</th>
<th>h/b Value</th>
<th>SD</th>
<th>n</th>
<th>a/b Value</th>
<th>SD</th>
<th>n</th>
<th>s/b Value</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecuador</td>
<td>0.686</td>
<td>0.074</td>
<td>34</td>
<td>0.492</td>
<td>0.042</td>
<td>34</td>
<td>0.177</td>
<td>0.058</td>
<td>33</td>
</tr>
<tr>
<td>Peru</td>
<td>0.639</td>
<td>0.082</td>
<td>51</td>
<td>0.474</td>
<td>0.043</td>
<td>14</td>
<td>0.159</td>
<td>0.058</td>
<td>14</td>
</tr>
<tr>
<td>Chile</td>
<td>0.649</td>
<td>0.097</td>
<td>25</td>
<td>0.435</td>
<td>0.040</td>
<td>25</td>
<td>0.193</td>
<td>0.048</td>
<td>25</td>
</tr>
</tbody>
</table>

Coastal vs. offshore
Offshore ecotype data and Pod-R were pooled as well as coastal ecotype data from Ecuador and Peru, and compared (Table 4). Significant differences were found in indexes h/b and s/b but not in a/b ($t$ test $t = 3.36$, $p = 9.2 \times 10^{-5}$; $t = 10.7$, $p = 2.2 \times 10^{-18}$; $t = 0.27$, $p = 0.78$, respectively). Index h/b show that dorsal fins of offshore animals were relatively taller and the s/b index shows that dorsal fins of offshore specimens were significantly more falcate than in coastal animals. In the case of the h/b index there is a wide overlapping range between both ecotypes being the offshore ecotype more variable than the coastal form (Figure 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 which the s/b index was zero or negative, which means in these animals the dorsal fin did not show curvature at all. This confirms our empirical understanding that offshore bottlenose dolphins have more falcate dorsal fins.

Table 4. Comparison of mean values for three dorsal fin indexes between coastal and offshore specimens from the Southeast Pacific. All datasets from the three countries were pooled in one of the two categories accordingly.

<table>
<thead>
<tr>
<th>Ecotype</th>
<th>h/b Value</th>
<th>SD</th>
<th>n</th>
<th>a/b Value</th>
<th>SD</th>
<th>n</th>
<th>s/b Value</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal</td>
<td>0.609</td>
<td>0.067</td>
<td>97</td>
<td>0.466</td>
<td>0.035</td>
<td>92</td>
<td>0.044</td>
<td>0.028</td>
<td>86</td>
</tr>
<tr>
<td>Offshore</td>
<td>0.656</td>
<td>0.085</td>
<td>110</td>
<td>0.469</td>
<td>0.048</td>
<td>73</td>
<td>0.179</td>
<td>0.055</td>
<td>72</td>
</tr>
</tbody>
</table>

Figure 3. Index s/b vs index h/b in coastal, offshore and Pod-R. Falcateness (s/b) optimally differentiates coastal and offshore ecotypes in Ecuador and Peru. Pod-R dolphins show falcateness similar to the offshore ecotype. The unique offshore outlier (with lowest s/b) had been visually recognised as atypical (MFB-185).
Figure 4. Photographs of bottlenose dolphins used, showing the typical form of the dorsal fin in coastal (above) and offshore (below) ecotypes in the Southeast Pacific. Falcateness is significantly more pronounced in the offshore ecotype, while coastal animals have more triangular fins.

DISCUSSION

Morphological differences in dorsal fins between coastal and offshore bottlenose dolphins in the Southeast Pacific have been confirmed in this study by comparing three simple proportions. These findings are consistent with previous studies in the region based on cranial characteristics, genetics, habitat use, parasites and ecology (Van Waerebeek et al., 1990; Santillán et al., 2008; Sanino et al., 2005; 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. analogue versus digital photography; and processed raster images from Chile); 2) varying deviations from perpendicularity; 3) the different time scales of the information; 4) whether the photos were from live or dead animals, e.g., most $h$ and $b$ values from Peru were highly accurate being actual body measurements on fresh carcasses. Therefore, these results should be considered promising but preliminary.

The most consistent difference between the coastal and offshore ecotypes was the strong falcateness (high $s/b$) in the offshore form and in Pod-R (Figure 4). This characteristic constitutes a diagnostic feature to differentiate between both ecotypes in the field. Till date, only a single Peruvian offshore specimen (MFB-185), with a $s/b$ of 0.0625, did not fit this pattern. While useful for this region and others, e.g. southern Brazil (Simoes-Lopes and Daura-Jorge, 2008), it does not necessarily apply to other regions. In the eastern North Pacific dorsal fins of inshore bottlenose dolphins are noticeably more falcate 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 SE Pacific offshore phenotype (falcate DF, dark colouration, short beaks) live nearshore and sympatriically with others that show a typical coastal phenotype (Vermeulen and Cammareri, 2009). Using up to 11 measures and angles estimated from photographs on the dorsal fin surface, Morteo (2004) found that the most useful features for differences among coastal populations of bottlenose dolphins in Mexico were the foil vs. base length (curvature of the anterior border vs. base length), deep rake (amount that tip of the fin extends beyond the base of the trailing edge) and depth vs. foil (length from the anterior insertion of the dorsal fin-curve of the anterior border). We do not rule out that such measurements might provide additional information to differentiate between offshore and coastal populations in the SE Pacific as well, but for the purpose of having an easily assessed feature in the field, the falcateness of the dorsal fin tip is highly discriminatory and sufficient.

While a pronounced falcateness ($s/b$) is shared by offshore bottlenose dolphins in Ecuador, Peru and by Chilean Pod-R, the other two characteristics in these three populations showed some statistically significant differences. In terms of relative dorsal fin height ($h/b$), Ecuadorian offshore form showed the highest values, followed by Peruvian coastal form, Pod-R, then Peruvian offshore form and the lowest values shown by Ecuadorian coastal animals. With respect to relative fin width at mid-height ($a/b$), Peruvian coastal stock had the widest fins, followed by Ecuadorian offshore, Peruvian offshore, then Ecuadorian coastal and finally Pod-R. Thus, Chilean Pod-R individuals showed dorsal fins both the narrowest at mid-height and with the highest falcateness index of all groups examined, reflected in an extremely falcate aspect, noticeable by the naked eye (see figure 4). Such differences are consistent with a molecular study of these Pod-R dolphins which showed marked genetic differences with Peruvian offshore and, to a lesser degree, with Chilean offshore [not included in our analysis]. We consider Pod-R a case of a more recent radiation into the coastal environment from offshore, a sort of 'transitional form' that preserved the offshore high DF falcateness character due to particularities of the local environment, e.g. fairly deep water (Sanino et al., 2005). In this and other transitional forms, we suggest to use more characters to assess the belonging ecotype. Between the pure offshore and nearshore ecotypes, a gradient of cases molded by the environment may be expected.
Since Peruvian and Chilean offshore bottlenose dolphins are more closely related, a single, wide-ranging Peru-Chile offshore stock has been proposed (Sanino et al., 2005). Differences between Peruvian and Ecuadorian offshore specimens, geographically closer, could be attributed to either ecological factors (e.g. sea surface temperature, salinity, etc.) or a sampling bias as most measurements from Peru used to calculate the h/b index were actual body morphometrics and were not based on photographs. On the other hand, the sample used to calculate the a/b and s/b indexes in Peruvian specimens was small (n= 9) and likely did not capture all variability within the Peruvian ecotype. Considering that Ecuadorian offshore specimens have the tallest and second widest dorsal fins of all groups, it is unclear whether they form part of the Peru-Chile offshore stock or are more closely related to Central American (nominally represented by Tursiops muanau Andrews 1911) and Northeast Pacific populations (Bayas 2015).

In the case of the coastal dolphins, the large database from the Gulf of Guayaquil revealed significant allometric ontogenetic variation, mainly expressed in the relatively shorter DF base length in immatures, thus 'inflating' the three indexes in a similar way, as all have b as denominator. Dorsal fins of calves and immatures seem relatively higher (large h/b) and more falcate (large s/b) than in adults because their fin base is so short. When the body grows axially due to major (allometric) length growth of the vertebral column, the base length of the dorsal fin must also grow allometrically. As far as we know, this would be the first time that such ontogenetic variation is recorded in this species. 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 unavailable and instead arbitrary (relative) units were used, we were unable to establish sexual dimorphism in DF height, as found in Florida coastal bottlenose dolphins (Hearst et al., 1990). We suggest that ontogenetic variation from allometric growth is likely present also in the offshore ecotype but was not captured in our data. Some bias may have occurred amongst the Peruvian sample, as several specimens were sexual subadults (but >2.0m). Albeit differences with fully adults may be small, they could have some impact. Larger, more homogeneous samples will be welcome to confirm some of our findings.

Since 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 the shape of its dorsal fin is obvious. A reliable criterion to allocate individuals living in sympathy or parapatry to a specific ecotype, be it from sightings, strandings or bycatches, in the field or from photographs, facilitates research of distribution patterns, general biology and habitat use. However, as in the case of Pod-R, some prior evidence-guided interpretation may be necessary, as the criterion is not blindly applicable.

Generally, more studies are needed to elucidate the population structure of bottlenose dolphins of the Southeast Pacific, as well as their relationship with other populations in contiguous regions. With this aim, a new study has been initiated analyzing samples from Chile, including Patagonia, and Peru, to contribute to international efforts as well as to further evaluate the reproductive isolation of Pod-R.

REFERENCES


Hoelzel, A., Potter, C., and Best, P. 1998 Genetic differentiation between parapatric “nearshore” and “offshore”


