# Phenotypic variation in dorsal fin morphology of coastal bottlenose dolphins (*Tursiops truncatus*) off Mexico

Eduardo Morteo [Corresp., 1] , Axayácatl Rocha-Olivares [2] , Rodrigo Morteo [3] , David W Weller [4]

[1] Instituto de Ciencias Marinas y Pesquerías/Instituto de Investigaciones Biológicas, Universidad Veracruzana, Boca del Río/Xalapa, Veracruz, Mexico

[2] Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, Mexico

[3] Facultad de Ciencias Administrativas y Sociales, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico

[4] Southwest Fisheries Science Center, Marine Mammal and Turtle Division, National Oceanic and Atmospheric Administration, La Jolla, California, United States of America

Corresponding Author: Eduardo Morteo
Email address: emorteo@uv.mx

Geographic variation in external morphology is thought to reflect an interplay between genotype and the environment. Morphological variation has been well-described for a number of cetacean species, including the bottlenose dolphin (*Tursiops truncatus*). In this study we analyzed dorsal fin morphometric variation in coastal bottlenose dolphins to search for geographic patterns at different spatial scales. A total of 533 dorsal fin images from 19 available photo-identification catalogs across the three Mexican oceanic regions (Pacific Ocean n=6, Gulf of California n=6 and, Gulf of Mexico n=7) were used in the analysis. Eleven fin shape measurements were analyzed to evaluate fin polymorphism through multivariate tests. Principal Component Analysis on log-transformed standardized ratios explained 94% of the variance. Canonical Discriminant Function Analysis on factor scores showed separation among most study areas (p<0.05) with exception of the Gulf of Mexico where a strong morphometric cline was found. Possible explanations for the observed differences are related to environmental, biological and evolutionary processes. Shape distinction between dorsal fins from the Pacific and those from the Gulf of California were consistent with previously reported differences in skull morphometrics and genetics. Although the functional advantages of dorsal fin shape remains to be assessed, it is not unlikely that over a wide range of environments, fin shape may represent a trade-off among thermoregulatory capacity, hydrodynamic performance and the swimming/hunting behavior of the species.

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3

4 Eduardo Morteo[1,2], Axayáctal Rocha-Olivares[3], Rodrigo Morteo[4], David W. Weller[5]

5 [1] Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Boca del Río, Veracruz,

6 Mexico

7

8 [2] Instituto de Investigaciones Biológicas, Universidad Veracruzana, Xalapa, Veracruz, Mexico

9

10 [3] Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja

11 California, Mexico

12

13 [4] Facultad de Ciencias Administrativas y Sociales, Universidad Autónoma de Baja California,

14 Ensenada, Baja California, Mexico

15

16 [5] NOAA Fisheries, Southwest Fisheries Science Center, Marine Mammal and Turtle Division, La

17 Jolla, California, USA

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19 **Corresponding Author:**

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21 Eduardo Morteo[1]

22 Email address: eduardo.morteo@gmail.com

24  **Abstract**

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26  and the environment. Morphological variation has been well-described for a number of cetacean

27  species, including the bottlenose dolphin (*Tursiops truncatus*). In this study we analyzed dorsal

28  fin morphometric variation in coastal bottlenose dolphins to search for geographic patterns at

29  different spatial scales. A total of 533 dorsal fin images from 19 available photo-identification

30  catalogs across the three Mexican oceanic regions (Pacific Ocean n=6, Gulf of California n=6

31  and, Gulf of Mexico n=7) were used in the analysis. Eleven fin shape measurements were

32  analyzed to evaluate fin polymorphism through multivariate tests. Principal Component Analysis

33  on log-transformed standardized ratios explained 94% of the variance. Canonical Discriminant

34  Function Analysis on factor scores showed separation among most study areas (p<0.05) with

35  exception of the Gulf of Mexico where a strong morphometric cline was found. Possible

36  explanations for the observed differences are related to environmental, biological and

37  evolutionary processes. Shape distinction between dorsal fins from the Pacific and those from the

38  Gulf of California were consistent with previously reported differences in skull morphometrics

39  and genetics. Although the functional advantages of dorsal fin shape remains to be assessed, it is

40  not unlikely that over a wide range of environments, fin shape may represent a trade-off among

41  thermoregulatory capacity, hydrodynamic performance and the swimming/hunting behavior of

42  the species.

43

44

**1. Introduction**

Fin shape in aquatic organisms has been suggested to reflect unique anatomical and physiological adaptations to different environmental conditions (Aleyev, 1977; Pauly and Palomares, 1989; Fish, 1998; Weller, 1998; Wright, 2000), and this is also widely accepted in cetaceans (Fish and Hui, 1991; Berta and Sumich, 1999; Fish and Rohr, 1999; Reynolds *et al*., 2000; Morteo, 2003). Morphological variation of the dorsal fin, to some extent, has been used for population and/or species identification (Lang and Pryor, 1966; Aleyev, 1977; Fish, 1998; Weller, 1998; Morteo *et al*., 2005; Felix et al., 2017).


The dorsal fin of delphinids is important at two functional levels: thermoregulatory and hydrodynamic. Little empirical evidence exists, however, regarding the integrated performance of dorsal fins for most cetacean species (Lang, 1966; Weller, 1998; Fish and Rohr, 1999; Meagher *et al*., 2002; Pavlov Westgate *et al*., 2007; Barbieri *et al*., 2010; and Rashad, 2012; van der Hoop *et al*., 2014). Estimating integrated performance is challenging since plasticity may be in part regulated by the energetic cost of different swimming behaviors related to locating, chasing, handling, and ingesting prey, thus maneuvering abilities may be important in feeding success, and the dorsal fin may play an important role for swimming stabilization (Weller, 1998; Fish and Rohr, 1999). Also, the dorsal fin is the only appendage that is constantly exposed to ambient air, and thus is subject to different thermoregulatory conditions from the rest of the body (Meagher *et al*., 2002; Westgate *et al*., 2007; Barbieri *et al*., 2010).


Bottlenose dolphins (*Tursiops truncatus*) have a worldwide distribution, occupying a variety of ecological conditions, and show substantial intraspecific phenotypic variation (Walker, 1981;

68    Vidal, 1993; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Hoelzel *et al.*, 1998; Turner and Worthy,

69    1998; Weller, 1998). Polyphenisms in traits whose functions arose as adaptations to new life

70    conditions (e.g. aquatic for terrestrial ancestors) may be directly linked to the environment, and

71    morphometric variations should be studied as a function of ecological differences (Stearns, 1989;

72    Gotthard and Nylin, 1995). Here we analyze phenotypic variation of bottlenose dolphin dorsal

73    fins in relation to respective habitats, ecology and behavior over different spatial scales. We

74    evaluated the degree of fin polymorphisms of 19 putative populations from Mexico, contrasting

75    them by location and region, in the context of relevant biological, ecological and geological

76    features. The goal of the study was to determine if observed morphometric variations follow the

77    stepping stone model, where the degree of differentiation among neighboring populations is

78    correlated with the migration distance travelled by individuals (Wright, 1943; Kimura, 1953).

79

80    **2. Methods**

81    **2.1. Study area**

82    Sampling locations were selected considering the following: 1) Geographic coverage should

83    include most of the species distribution within Mexican coastal waters, 2) Locations should

84    represent most of the existing conditions of habitat variability for the species in Mexico, 3)

85    Distances among adjacent locations should allow for individual exchange considering the

86    dispersal capabilities of the species, and 4) Photo-identification catalogs of coastal bottlenose

87    dolphin populations must be available. Detailed descriptions on the ecology of the study areas

88    and the biology of dolphin populations in those areas are provided elsewhere (see Espinosa, 1986,

89    Ballance, 1987; Salinas and Bourillón, 1988; Acevedo, 1989; Ballance, 1990, 1992; Delgado,

90    1996, 2002; Caldwell, 1992; Heckel, 1992; Schramm, 1993; Silber *et al.*, 1994; Silber and Fertl,

91    1995; López, 1997, 2002; Defran *et al.*, 1999; Díaz, 2001; Orozco, 2001; Reza, 2001; Guzón,

92    2002; Morteo, 2002; Rodríguez *et al.*, 2003; Ladrón de Guevara and Heckel, 2004; Morteo *et al.*,

93    2004; Ramírez *et al*., 2005; Mellink-Bijtel and Orozco-Meyer, 2006; Pérez-Cortés, 2006;

94    Rodríguez-Vázquez, 2008; Morteo *et al*., 2012, 2014, 2015, In press; Ruiz-Hernández, 2014;

95    Zepeda-Borja, In prep.). Study areas were grouped by region into 1) Pacific Ocean, 2) Gulf of

96    California and 3) Gulf of Mexico (Fig. 1). For instance, 1) the Mexican Pacific (i.e. localities EN,

97    SQ, BM, MZ, BB and PE in Fig. 1) features an open habitat with a narrow continental shelf as a

98    result of active processes of plate tectonics, thus coastal bathimetry has a steeper slope (usually

99    depths >40 m are reached at <2 km from the shore), where swells are typically high (>1.5 m); the

100   average sea surface temperature (SST) turns warmer through a north-south gradient (15-30 °C)

101   and productivity is mostly dominated by coastal upwellings via ocean circulation and local

102   primary producers (i.e. kelp beds); also, except for the southern portion of the study area (i.e.

103   locality PE in Fig. 1), rainfall and coastal vegetation have little influence on the ecology of these

104   areas, even within the estuaries and lagoons. 2) Conversely, the Gulf of California is a

105   semiclosed habitat where ocean currents are complex due to the intrincate bathimetry and the

106   tidal regime; it has an exceptionally high primary productivity driven mostly by seasonal

107   upwellings, shallow thermoclines and a wind-mixed water column. The Gulf of California has

108   been divided into three oceanographic and biogeographically different regions from north to

109   south, such that: a) northern coastal waters (i.e. UG and SJ in Fig. 1) are shallow (<10 m),

110   usually warmer (>20 °C) with high salinity and strong tidal currents (up to 1 m s$^{-1}$); in contrast b)

111   the central coast (i.e. BL and BK in Fig. 1) is steeper due to the deep Canal de Ballenas and

112   Tiburon Island passages (>1000 m), with colder SST (<20 °C) due to frequent upwellings, and

113   features high swells (>2 m) formed by strong winds (> 5 m s$^{-1}$); and c) the southern area (i.e. LP

114    and SM in Fig. 1) has shallow bays (<20 m) bordered by a deeper coastal waters (>100 m)

115    situated at the entrance to the Gulf; wave height and SST are highly variable throughout the year

116    (except in location SM) and so is primary productivity due to the influence of the several water

117    masses coming in from the Pacific. Finally, the Gulf of Mexico (i.e. TA, NA, VR, AL, TB, TL

118    and HO in Fig. 1) is a very shallow area (usually depths around 20 m are reached over 4 km from

119    the shore) where tides are very low (<1 m) and most of the oceanic circulation is driven by the

120    loop current that carries warm waters (mean SST >26 °C) from the Caribbean into the Gulf.

121    Although the region is classified as an open habitat, many dolphin populations inhabit shallow

122    (depth <10 m) lagoons (i.e. TA, TB and TL) or semi-protected coastal waters surrounded by

123    reefs (i.e. VR) or islands (i.e. HO), thus swells are also very low (<1 m). Coastal productivity is

124    usually higher around continental water bodies due to nutrient runoffs, especially during the

125    rainy season; thus the ecology of most of these areas is strongly influenced by temporal changes

126    in wind and rain regimes.

127
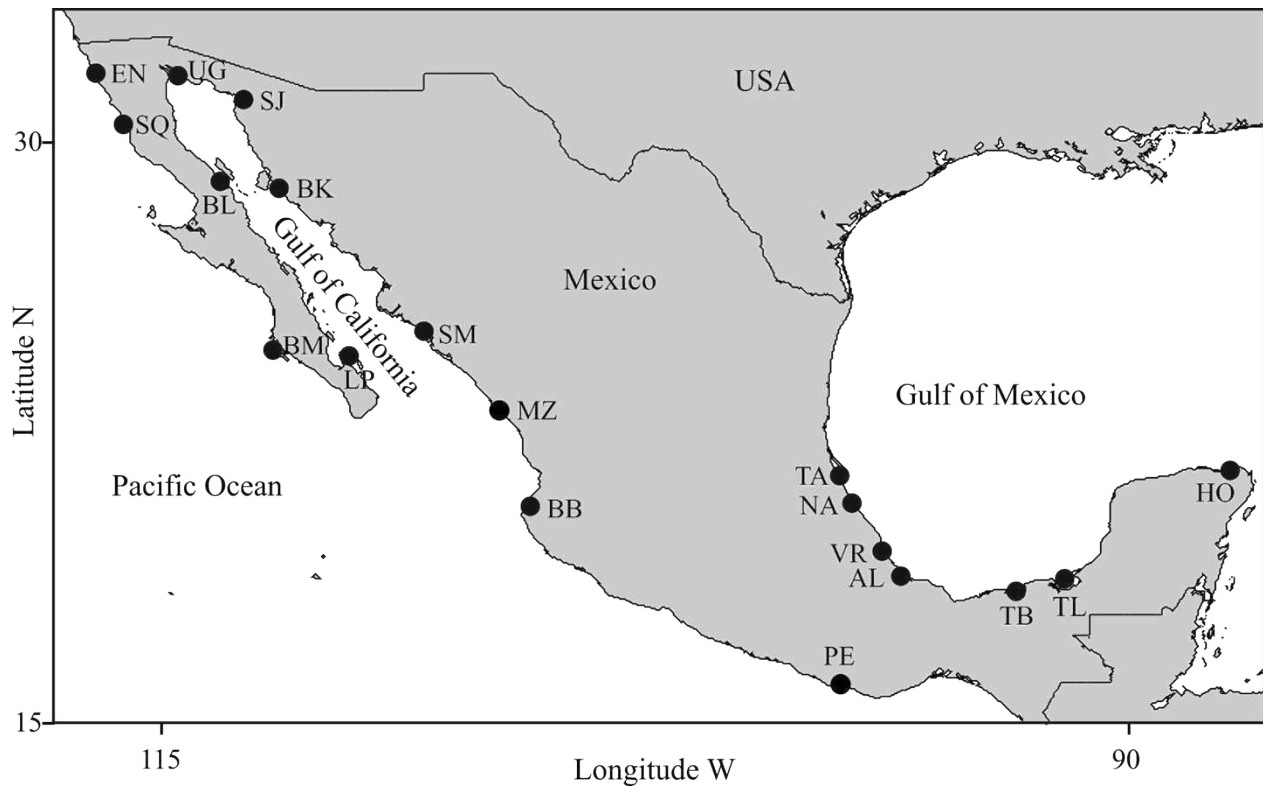
**Figure 1. Study areas.** 1) Pacific Ocean: EN=Ensenada, Baja California; SQ=San Quintin, Baja California; BM=Bahia Magdalena, Baja California; MZ=Mazatlán, Sinaloa; BB=Bahia Banderas, Jalisco; PE=Puerto Escondido, Oaxaca; 2) Gulf of California: UG=Upper Gulf of California, Sonora; SJ=Bahia San Jorge, Sonora; BL=Bahia de los Angeles, Baja California; BK=Bahia Kino, Sonora; SM=Bahia Santa Maria, Sinaloa; LP=La Paz, Baja California Sur; 3) Gulf of Mexico: TA=Tamiahua, Veracruz; NA=Nautla, Veracruz; VR=Veracruz Reef System, Veracruz; AL=Alvarado, Veracruz; TB=Tabasco, Tabasco; TL=Terminos Lagoon, Campeche; HO=Holbox, Quintana Roo.

## 2.2. Photographic procedures

Dorsal fin shapes were obtained from high quality images; since our methods involved only non-invasive data collection (i.e. pictures were taken onboard a boat that was 15-50 m away from the animals), an institutional review board was unnecessary. Also, original photographs from wild dolphins were obtained through a federal permit (SGPA/DGVS/518) from Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT). The remaining images came from photo-identification catalogs in other published and unpublished scientific research; thus it was assumed that all these were approved by their institutional review boards (if applicable) and were

145    issued with the federal permits for their field work, such that these can be consulted in each case.

146    Most of the pictures were obtained during the late 90's and the following decade, comprising at

147    least 21 different years of information (see Table I). The oldest photographic material was

148    collected in the early 80's (e.g. Bahía Kino by Ballance, 1987) or 90's (e.g. Tamiaha Lagoon by

149    Heckel, 1992; Schramm, 1993), but some catalogs were updated over the following years (e.g.,

150    Ensenada by Espinosa, 1986; Guzón, 2002); however, the average duration of sampling effort for

151    each of these studies was 2.6 years (s.d.=2.1) (see Table I).

152

153    Image quality was crucial for the analysis, thus the best image from each individual was selected

154    from the photo-identification databases according to the following criteria (modified from Weller,

155    1998): 1) Images only of mature dolphins; 2) Dorsal fins entirely visible, as complete as possible,

156    and non-parallaxed; 3) Fins size at least one ninth of the entire picture; 4) Whenever possible,

157    pictures from individuals sighted in different schools were selected in order to minimize chances

158    of genetic relatedness (i.e. trait heredity). Images not fulfilling at least the first three criteria were

159    excluded. Due to the variety of sources and formats, 32% of the material came from film-based

160    images, and a similar proportion was from digital pictures, whereas 28% were fin contour traces

161    in paper and 8% came from printed pictures (see Table I).

162

163    Approximately 30 different individuals were randomly selected from each locality; these were

164    later compared to avoid potential inter-study area matches (which did not occur). All individuals

165    were assumed to belong to the coastal form of the species, as specified in the original catalogs.

166

167    **2.3. Digital measurements**

168    We developed a software routine (Fin Shape v1.3) in the computer language Borland Builder

169    C++ 5.0, to specifically measure angles and distances between landmarks of dorsal fins

170    following Weller (1998) and Morteo *et al.* (2005). Images were digitized at high resolution (3000

171    dpi), as needed, and measured consistently by a single trained operator (E. Morteo). Following

172    Weller (1998), the anterior insertion point of the dorsal fin on the body (B) was identified by an

173    abrupt change in the contour of the dolphin's back; also, the tip of the dorsal fin (A) was

174    identified as the landmark furthest from point B (Fig. 2). Once these two points were identified, a

175    connecting straight line was automatically drawn, and additional lines were projected departing

176    from B at 30°, 20°, 10° and 5° below segment AB. The operator then identified where these lines

177    intersected the edge of the fin, and their lengths were computed (in pixels).

178

179    Eleven measurements were obtained from each image along with the surface area (Fig. 2); these

180    describe four qualitative shape parameters according to Weller (1998): 1) Base length: Distance

181    from the leading edge to the trailing edge of the fin; 2) Depth: Distance from the fin tip to the

182    anterior insertion on the body; 3) Rake: Amount that the tip of the fin extends beyond the base of

183    the trailing edge; and 4) Foil: Curvature of the leading edge of the fin.

184

185    Since preliminary software trials by Morteo *et al.* (2005) showed that repeated measures of the

186    same image, and also of several different images from the same individual, yielded very little

187    variations (i.e. <0.1%), it was assumed that the operator was able to correctly identify the

188    features of the fin, and that image quality across all photographic formats was sufficient to

189    prevent measuring bias. Measurements were used to calculate 11 indexes for each individual

190      through the following standardized ratios (modified from Weller, 1998): $C_{30}B/AB$, $C_{20}B/AB$,

191      $C_{10}B/AB$, $C_{5}B/AB$, $C_{30}D/AB$, $C_{20}D/AB$, $C_{10}D/AB$, $C_{5}D/AB$, $AO/OB$, $DO/C_{30}O$, $AC_{30}^{2}/area$.



192
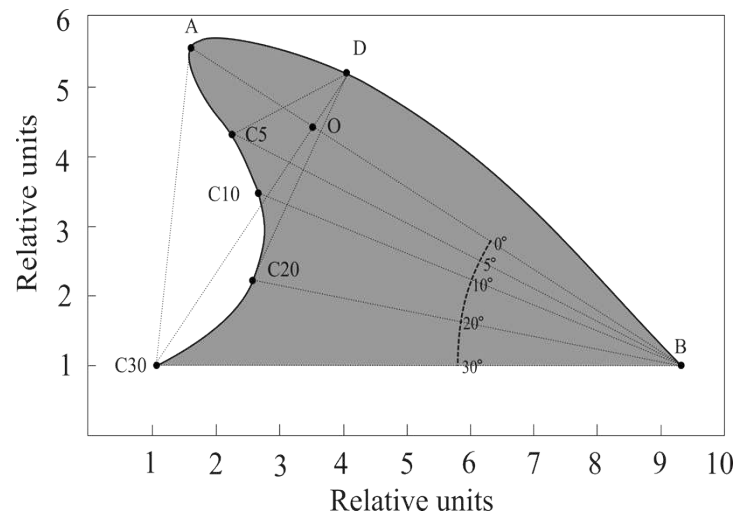
**Figure 2. Reference points and measurements computed by FinShape software to acquire morphological landmarks.** A=Tip; B=Base. Points $C_{5}$, $C_{10}$, $C_{20}$ and $C_{30}$ indicate angles (degrees) relative to line AB. Point D is the intersection of a line departing from $C_{30}$ with the fin's leading edge, this line is also perpendicular to line AB. Point O is the intersection of lines AB and $C_{30}D$. Surface area (shaded) was calculated considering line $C_{30}B$ as the limit.

## 2.4. Morphological variation

200      Average dorsal fin contours were constructed by locality based on median adimensional ratio

201      values. In order to scale these contours, segment AB was fixed to 10 relative units, thus all fin

202      representations would have the same depth. The remaining segments were calculated through

203      mathematical and trigonometrical equations that solved the related ratios using their

204      correspondent median values (Morteo *et al.*, 2005) (see appendix A); since the latter were not

205      normally distributed, point Cartesian coordinates were computed from each median

206      measurement, and data dispersion was represented as quartiles (upper=75% and lower=25%)

207      indicated by bars and ellipses around the calculated median points. This procedure follows a

208      Procrustean approach (Peres-Neto and Jackson, 2001), where distortion, scale and rotation are

209      controlled to provide variation specificity for each reference point measure within the fin.

210

211 **2.5. Statistical analyses**

212 Phenotypic variability was assessed on log-transformed ratios (Zar, 1996) at three geographic

213 scales: 1) within localities, 2) among localities (Isolation-Differentiation by distance), and 3)

214 among oceanic regions.

215

216 Variation within localities was designed as a test for sample representativity through a

217 rarefaction analysis. Local coefficients of variation (COV) were computed for each log-

218 transformed ratio; which were later averaged to obtain a general index for the local variability of

219 the fin (GIV). Variation among localities and regions was assessed through multivariate analyses

220 of log-transformed ratios; since most of these ratios were highly correlated, a Principal

221 Component Analysis (PCA) was performed. Individual scores from the PCA were used to

222 perform a Discriminant Function Analysis (DFA) (tolerance = 0.01) (Kachigan, 1991; Manly,

223 1994; Grimm and Yarnold, 1995). Assumptions for multivariate tests were verified, and a non-

224 stepwise Canonical Discriminant Analysis (CDA) was performed to determine separation among

225 samples (tolerance=0.01). Also, *p* values in multiple comparisons were later tested for significant

226 differences by using the sequential Bonferroni correction (Rice, 1989). All data were analyzed

227 using Statistica v6.0 (Stat Soft™).

228

229 Finally, Squared Mahalanobis Distances (SMD) from the DFA were used to construct a

230 dendrogram (Single Linkage Cluster Analysis) and dissimilarities were expressed as percentages

231 (100*linkage SMD/Max SMD). SMDs were also used to perform an analysis of differentiation

232 by distance, in which we correlated the matrix of phenotypic differentiation among localities

233 (SMDs) with a matrix of geographic distances using a Mantel one-tailed test ($\alpha=0.05$, Monte

234 Carlo and 10,000 permutations) as implemented in the Excel (Microsoft Office XP™) add-in

235 XLStat-Pro v7.0 (Addinsoft™). Due to the coastal nature of these dolphins, geographic distances

236 among localities (km) were calculated roughly following the coastline, thus these represent

237 minimum separations among localities. Finally, we performed partial Mantel tests for each

238 region in order to determine the contribution of each dataset to the general model.

239

240 **3. Results**

241 **3.1. Data overview**

242 A total of 5,653 dorsal fins were analyzed from the photo-id catalogs available at the 19

243 locations (Table I). From all the images that fulfilled the quality criteria, a total of 533

244 individuals were randomly selected (representing 32.3% of fins or individuals from all the

245 catalogs). Except for Bahia de los Angeles, the Upper Gulf of California, and Puerto Escondido,

246 the fins used in this study accounted for less than half the number of identified individuals; also,

247 when sighting data were available, for any particular location most fins came from different pods,

248 such that the average proportion of individuals from different pods at each study area was 61.2%

249 (s.d.=12.8%).

250

251 **Table I. Summary of data sources and sample size.** Abbreviations for study areas follow those in
252 Figure 1.

| Source(s) | Area | Duration (y) | $N_{Cat}$ | Sample (%) | Format | Pods |
|---|---|---|---|---|---|---|
| Espinosa (1986), Defran *et al.* (1999), Guzón (2002) | EN | 3 | 144 | 27 (19%) | S, T | 20 |
| Caldwell (1992), Morteo (2002), Morteo *et al.* (2004) | SQ | 2 | 220 | 29 (13%) | S, T | 16 |
| Pérez-Cortés (2006) | BM | 5 | 211 | 30 (14%) | S | 27 |
| Zepeda-Borja (In prep.) | MZ | 3 | 210 | 30 (14%) | D | 26 |
| Rodríguez *et al.* (2003), Rodríguez (2008) | BB | 6 | 60 | 28 (46%) | D | 12 |
| This work | PE | < 1 | 24 | 21 (87%) | D | 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| This work | UG | < 1 | 28 | 23 (82%) | D | 3 |
| Orozco (2001), Mellink & Orozco (2006) | SJ | 1 | 217 | 24 (11%) | S, T | N.A. |
| Ladrón de Guevara and Heckel (2004) | BL | 1 | 26 | 19 (73%) | D, S, P, T | 4 |
| Balance (1987, 1990, 1992) | BK | 2 | 155 | 30 (19%) | S, T | 17 |
| Reza (2001) | SM | 1 | 637 | 25 (4%) | S | N.A. |
| Díaz (2001) | LP | 1 | 66 | 29 (44%) | P | N.A. |
| Heckel (1992), Schramm (1993) | TA | 3 | 51 | 20 (39%) | S | N.A. |
| Ramírez *et al.* (2005) | NA | 1 | 148 | 30 (20%) | S | 17 |
| Ruiz-Hernández (2014), Morteo *et al.* (2015) | VR | 2 | 93 | 30 (32%) | D | 30 |
| Morteo *et al.* (2012, 2014, 2017) | AL | 8 | 282 | 30 (11%) | S, D | 30 |
| López (1997, 2002) | TB | 2 | 750 | 35 (4%) | S | 28 |
| Delgado (2002) | TL | 5 | 1987 | 37 (2%) | D, T | N.A. |
| Delgado (1996, 2002) | HO | 3 | 344 | 36 (10%) | T | N.A. |
| Total | | 21 * | 5653 | 533 (32.3%**) | − | 234 |

$N_{Cat}$=Number of individuals in the catalog. Image format is classified by reliability from digital pictures (D), digitized negatives or slides (S), scanned pictures (P) and scanned traces (T). N.A.= not available.* Total number of different years. ** Weighted average.

### 3.2. General phenotypic variability

The Cartesian position of each landmark in the standardized fins varied in decreasing order as follows A→$C_{30}$→O→D→$C_5$; also, landmarks $C_{10}$ and $C_{20}$ were the least variable in all cases (represented by smaller ellipses) (Fig. 3). Fins within the Gulf of Mexico (Fig. 3C) showed the least variability overall; these were also the least falcate, contrasting with all the fin contours from the Pacific (Fig. 3A) and most from the Gulf of California (Fig. 3B). Average fin contours featured a larger base length for the fins from the Pacific and the Gulf of California (except Bahia de los Angeles). Wide rounded tips were also found for most Pacific dolphins (except for Puerto Escondido), and pointed tips prevailed in dolphins from the northern Gulf of California (Fig. 3B) (except San Joge, Santa María and La Paz) and the Gulf of Mexico (Fig. 3C). Also, fins from the Pacific and the Gulf of California had more foil, and most of their tips did not extend further from the posterior basal landmark (i.e. less rake) as in fins from the Gulf of Mexico (except for Bahia de los Angeles and Bahia Kino in the northern Gulf of California).

270 Finally, fins from the Gulf of Mexico and the northern Gulf of California were slightly taller

271 ($AC_{30}$), thus the surface area was also larger.



272
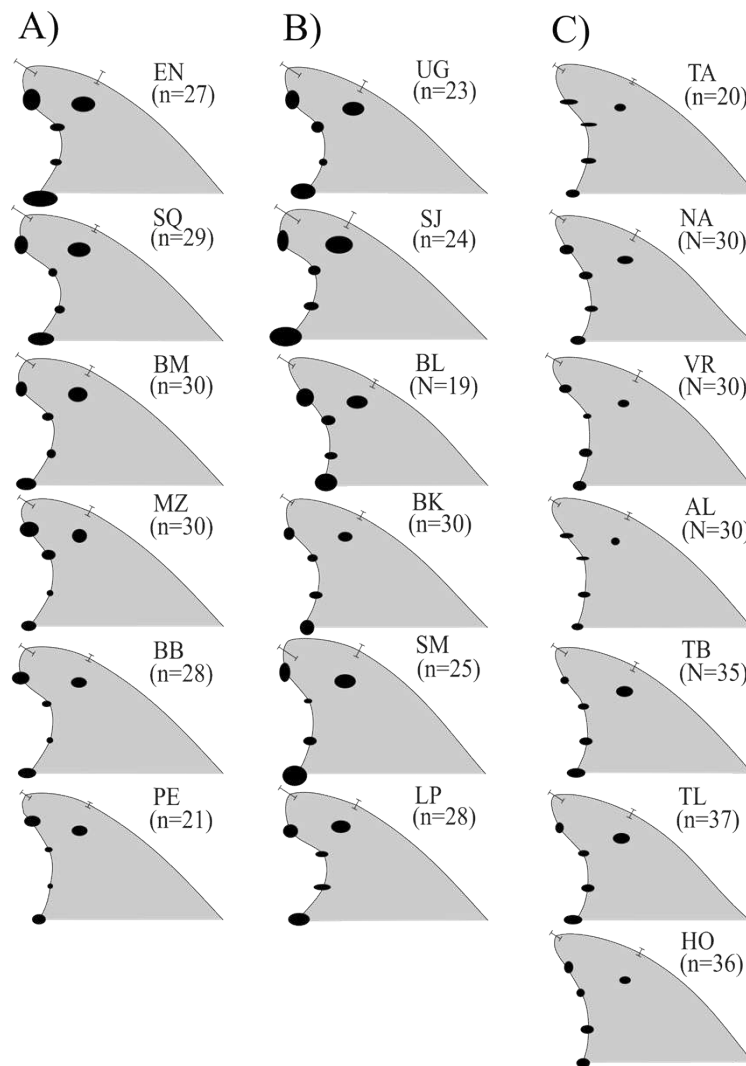
**Figure 3. Median dorsal fin contours by study areas** (N=533 dorsal fins). Regional divisions are grouped in columns: A) Pacific Ocean, B) Gulf of California and C) Gulf of Mexico. Contours reflect median values of shape and do not represent any particular dorsal fin. Study area codes follow those in Figure 1, and sample size is shown in parenthesis; error bars and ellipses show variability expressed as quartiles (50% of data). Measurement AB (i.e. from the tip to the anterior insertion into the body) is the same for all fins (10 relative units).

279

## 3.3. Variability within localities

281    As expected, variability within localities increased as more fins were included in rarefaction

282    curves; however, these reached an asymptote at the 19th sample (>95% of the local variability) in

283    most localities; therefore the minimum sample size was inferred as 20 individuals (Fig. 4).
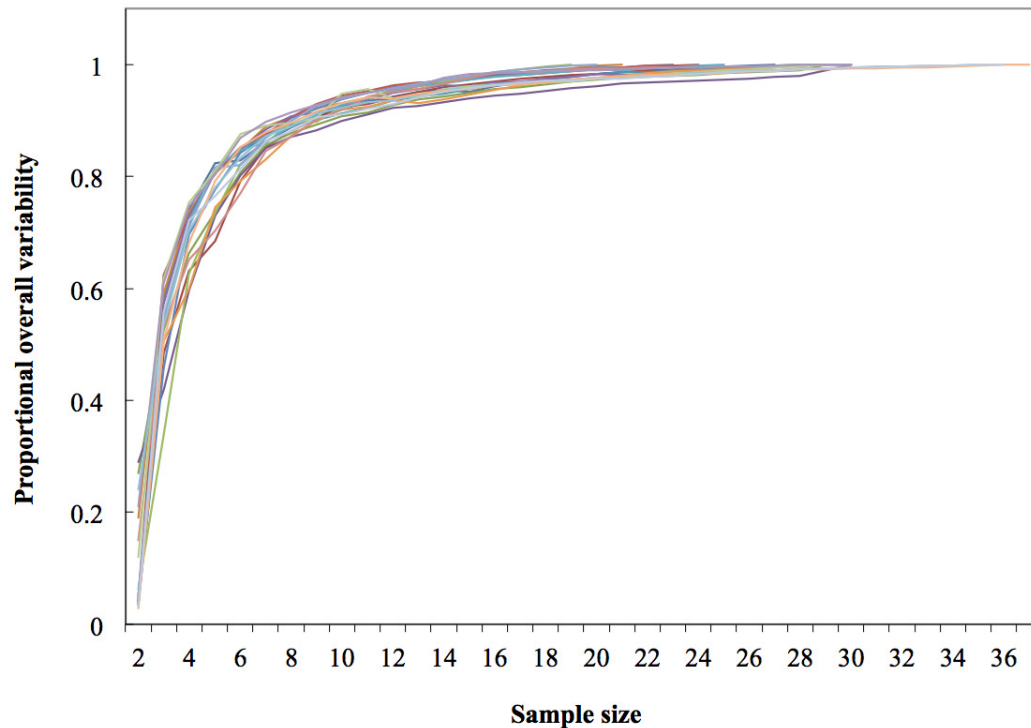


284

285    **Figure 4. Dorsal fin morphological variability and sample size effect within the 19 study areas**
286    (N=533 dorsal fins).
287

288    **3.4. Variability among localities**

289    The PCA performed on all eleven log-transformed ratios showed that 94.7% of the variance was

290    explained by the first three factors, and the remaining seven factors accounted for less than 2%

291    each, thus they were not useful in the following analyses (Table II).

292

293  Scores from PCA were normally distributed (p>0.2), and the DFA among the 19 locations was

294  highly significant (Wilks' Lambda: 0.44442, $F_{(33,922)}$=8.8617, p<0.00001, n=533). All three

295  factors contributed significantly (p<0.00001) to the model (Table II).

296

297  **Table II. Factor Analysis of log-transformed ratios using all locations** (N=533). Abbreviations for
298  study areas follow those in Figure 1. Note the cumulative variance accounted for the first three Factors (**\***).
299  Discrimination was highly significant among the twelve locations (Wilks' Lambda: 0.44442,
300  $F_{(33,922)}$=8.8617, p<0.00001, N=533).
301

| Factor | Eigenvalue | Cumulative Variance(%) | Wilks' Lambda | Partial Lambda | F-remove (11,313) | p-level |
|--------|-----------|----------------------|---------------|----------------|-------------------|---------|
| 1 | 5.69 | 44.89 | 0.70 | 0.61 | 18.90 | <0.001 |
| 2 | 2.98 | 72.79 | 0.52 | 0.81 | 6.76 | <0.001 |
| 3 | 2.43 | 94.74* | 0.51 | 0.84 | 5.66 | <0.001 |

302

303  SMDs (Table III) revealed widespread differentiation among locations. All sites were

304  significantly different (p<0.01) to at least twelve other study areas (i.e. Bahia Magdalena,

305  Mazatlan and Tamiahua). The most distinctive samples were from La Paz and Puerto Escondido

306  (18 significant differences), followed by San Jorge, Bahia de los Angeles (16 each), and Santa

307  Maria (15); all other locations were significantly different to 13 other sites.

308

309  **Table III. Matrix of squared Mahalanobis and geographic distances** (N=533). Values over the
310  diagonal are geographic distances along the coastline (km) and under the diagonal are Squared
311  Mahalanobis distances. Location codes follow those in Figure 1. Comparisons within regions are shaded.
312

| Study area | EN | SQ | BM | MZ | BB | PE | UG | SJ | BL | BK | SM | LP | TA | NA | VR | AL | TB | TL | HO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EN | 0 | 220 | 1352 | 4140 | 4540 | 5748 | 2870 | 3040 | 2520 | 3340 | 3730 | 1820 | - | - | - | - | - | - | - |
| SQ | 0.51 | 0 | 1132 | 3920 | 4320 | 5528 | 2650 | 2820 | 2300 | 3120 | 3510 | 1600 | - | - | - | - | - | - | - |
| BM | 0.59 | 0.47 | 0 | 2788 | 3188 | 4396 | 1607 | 1737 | 1257 | 2007 | 2677 | 557 | - | - | - | - | - | - | - |
| MZ | 0.41 | 0.34 | 0.60 | 0 | 400 | 1608 | 1439 | 1269 | 1789 | 969 | 279 | 2489 | - | - | - | - | - | - | - |
| BB | 2.22* | 0.59 | 0.58 | 0.62 | 0 | 1208 | 1720 | 1580 | 2020 | 1380 | 600 | 2720 | - | - | - | - | - | - | - |
| PE | 3.80* | 4.01* | 3.74* | 1.831* | 2.28* | 0 | 3047 | 2877 | 3397 | 2577 | 1887 | 3978 | - | - | - | - | - | - | - |
| UG | 0.55 | 0.48 | 1.413* | 0.87 | 1.67* | 4.21* | 0 | 170 | 350 | 450 | 1110 | 1050 | - | - | - | - | - | - | - |
| SJ | 3.10* | 1.18* | 0.944 | 1.17* | 0.18 | 5.03* | 2.69* | 0 | 480 | 300 | 980 | 1180 | - | - | - | - | - | - | - |
| BL | 1.56* | 1.30* | 1.928* | 0.96 | 2.40* | 3.12* | 0.35 | 3.55* | 0 | 750 | 1420 | 700 | - | - | - | - | - | - | - |
| BK | 1.06* | 0.23 | 0.481 | 0.91 | 0.73 | 3.73* | 0.71 | 1.10* | 1.07 | 0 | 690 | 1450 | - | - | - | - | - | - | - |
| SM | 4.60* | 2.14* | 1.817* | 2.16* | 0.75 | 4.68* | 2.87* | 0.85 | 2.88* | 1.87* | 0 | 2120 | - | - | - | - | - | - | - |
| LP | 0.620 | 1.00* | 0.898 | 1.92* | 2.16* | 5.32* | 1.14 | 3.40* | 2.72* | 2.19* | 4.536* | 0 | - | - | - | - | - | - | - |
| TA | 4.44* | 2.24* | 2.146* | 1.71* | 1.42* | 1.57* | 2.23* | 1.77* | 1.64* | 1.66* | 0.42 | 4.98* | 0 | 137 | 284 | 348 | 695 | 786 | 1428 |
| NA | 5.02* | 4.65* | 4.867* | 3.19* | 1.80* | 1.31* | 3.74* | 2.18* | 1.29* | 2.18* | 3.74* | 2.68* | 0.25 | 0 | 147 | 211 | 558 | 748 | 1326 |
| VR | 4.34* | 5.08* | 5.321* | 4.20* | 2.12* | 1.40* | 2.91* | 2.33* | 1.19* | 1.83* | 4.19* | 2.43* | 0.34 | 0.29 | 0 | 64 | 411 | 601 | 1179 |
| AL | 4.12* | 3.77* | 4.432* | 4.07* | 2.38* | 1.32* | 3.98* | 2.48* | 1.18* | 1.39* | 4.29* | 2.60* | 0.18 | 0.21 | 0.17 | 0 | 347 | 537 | 1115 |
| TB | 4.29* | 4.31* | 4.876* | 3.65* | 2.46* | 1.06* | 3.65* | 2.56* | 1.32* | 1.41* | 3.59* | 2.83* | 0.47 | 0.40 | 0.37 | 0.28 | 0 | 126 | 768 |
| TL | 4.34* | 2.47* | 4.145* | 2.86* | 2.04* | 1.25* | 1.89* | 2.70* | 1.17 | 1.98* | 0.92 | 4.85* | 0.15 | 0.52 | 0.35 | 0.47 | 0.21 | 0 | 642 |
| HO | 6.14* | 3.85* | 3.143* | 3.96* | 3.07* | 1.00 | 3.22* | 3.75* | 2.12* | 3.32* | 1.24* | 6.52* | 0.40 | 0.86 | 0.74 | 0.63 | 0.36 | 0.16 | 0 |

313
314 * = significant distances (α <0.01).
315 - = Not applicable.
316

317 Cluster analysis revealed two geographic groups, one corresponding to the localities from the

318 Gulf of Mexico, including Santa Maria (Gulf of California) as a geographic outlier, and the

319 second including localities from the Pacific and the Gulf of California exclusively (Fig. 5).

320 Puerto Escondido was the most distinct locality and was not nested in any of the geographic

321 groups.

322
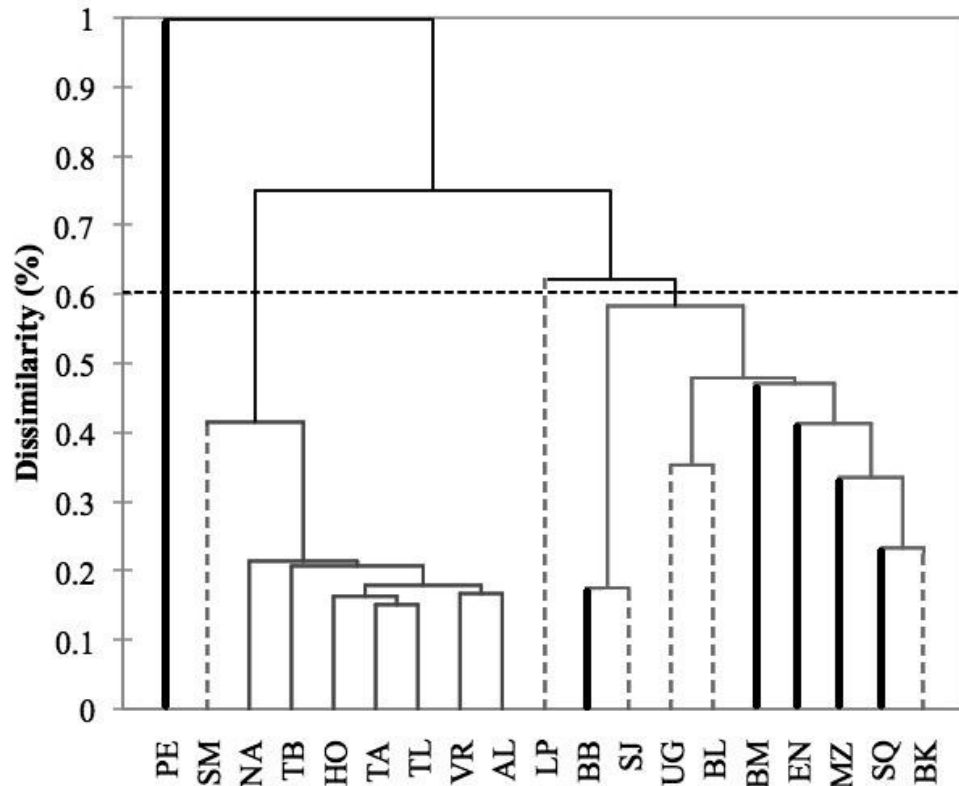
**Figure 5**. **Dendrogram based on morphometric distances among study areas** (N=533 dorsal fins).
Study area codes follow those in Figure 1. Values are proportions based on the maximum Squared
Mahalanobis distance (Table III). Major branches are somewhat consistent with the regional division of
the study areas: 1) Pacific Ocean (bold lines), 2) Gulf of California (dashed lines), 3) Gulf of Mexico (thin
lines).

329    A significant correlation was found between the Squared Mahalanobis and geographic distances

330    (Mantel test, r=0.35, *p*<0.001); thus supporting the hypothesis of differentiation by distance and

331    a stepping-stone dispersal model. Most of the contribution to the model came from samples

332    within the Gulf of Mexico (partial Mantel test, r=0.60, *p*<0.001), followed by the Gulf of

333    California (partial Mantel test, r=0.50, *p*=0.054) and the Pacific (partial Mantel test, r=0.44,

334    *p*=0.093). This correlation broke down when samples from the Pacific and the Gulf of California

335    were analyzed together (Mantel test, r=0.20, *p*>0.11).

336

337    **4. Discussion**

### 4.1. Heredity and individual dispersal as mechanisms for phenotypic variability

338

339    Morphological variations in dorsal fin characteristics of bottlenose dolphins inhabiting Mexican

340    coastal waters were observed, even among study areas in near proximity (Figs. 1 and 5); this

341    variation was evident in the averaged fin contour reconstructions (Fig. 3), which showed

342    significant differences among most localities (Table III, Fig. 5). Such statistical discrimination

343    may be largely due to the low phenotypic variability within putative populations, such that a

344    small number of individuals (~20) were needed to obtain at least 95% of the expected variability

345    within any given locality (Fig. 4). Therefore, it is reasonable to assume that dorsal fin shape may

346    be under strong selection acting over individuals with particular dorsal fin phenotypes. However,

347    methodological and biological contexts must be considered in order to prevent misleading

348    interpretations. For instance, the use of photographs may introduce some level of unaccounted

349    bias in age/sex representation in the sample (Hersh and Diffield, 1990; Gao *et al*., 1995; Weller,

350    1998; Perrin and Mesnick, 2003).

351

352    A similar line of reasoning can be applied to the regional clusters found in this study. For

353    instance, the high migratory rates documented for bottlenose dolphins in the northern Mexican

354    Pacific (Defran *et al*., 2015) may explain the inter-study area dorsal fin similarities (Fig. 3) and

355    low dissimilarity values (Table III) despite the large distances among sites (Figs. 1 and 5).

356    Detailed body morphometrics provided by Walker (1981) already support phenotypic similarity

357    of bottlenose dolphins along the west coast of Baja California.

358

359    Results from the Gulf of California stand in sharp contrast to those from the Pacific in that even

360    when geographic separation among localities was relatively low, 73% of the comparisons within

361   this region showed significant differences (Table III, Fig. 5). There is currently no information

362   on migration rates for dolphins among all these areas; however, based on morphometric analyses

363   of skulls from dead stranded bottlenose dolphins, Vidal (1993) suggested a geographic

364   regionalization akin to the differentiation found in this study. This pattern has been reported in

365   several other taxa including invertebrates (Correa and Carvacho, 1992; De la Rosa *et al*., 2000),

366   fish (Riginos and Natchman, 2001), and other marine mammals like the California sea lion

367   (*Zalophus californianus californianus*) (Schramm, 2002; Aurioles *et al*., 2004; Pedernera *et al*.,

368   2004; Porras *et al*., 2004). Contrasting oceanographic patterns (Lavín *et al*., 2003) may

369   contribute to this separation, causing habitat and resource partitioning. Moreover, Segura *et al.*

370   (2006) also found genetic structure in bottlenose dolphins within the Gulf of California, which

371   supports our findings. Overall, molecular and phenotyoic co-variation (i.e., skull and dorsal fin

372   morphometrics) point to the possibility of the early steps of microevolutionary divergence in *T.*

373   *truncatus* from the Gulf of California.

374

375   Conversely, no significant morphological differences were found within the Gulf of Mexico, but

376   fin shapes were significantly correlated with distance among locations (Table III, Fig. 5). Similar

377   to the highly migratory movements of dolphins along the Pacific coast, bottlenose dolphins in the

378   Gulf of Mexico also appear to have large home ranges. For instance, Delgado (2002)

379   documented one individual that moved at least 800 km from Holbox Island to the western coast

380   of the Gulf in less than a year; he also found four other individuals that moved 240−320 km in

381   274−1,404 days. Martinez-Serrano *et al.* (2011) and Morteo *et al.* (2017) also found large home

382   ranges (>100 km) and individual movements (100-300 km) for dolphins in the northwestern Gulf

383   of Mexico. Since dolphins may potentially reproduce with individuals from other locations,

384   genetic exchange occurs over a large scale (Islas, 2005); however, evidence also suggests a

385   certain degree of genetic structure and restricted gene flow that is consistent with sex-specific

386   dispersal patterns (Islas, 2005; Caballero *et al.*, 2011), which may enhance homogeneity in

387   character states by male dispersion, but also promote differentiation through female restricted

388   home ranges (e.g. Morteo *et al.*, 2014), potentially resulting in the observed clinal morphological

389   trends.

390

391   Male dispersal patterns seem to be a dominant feature in the western Gulf of Mexico (Morteo *et*

392   *al.*, 2014), thus our morphological results seem concordant with genetic data; however,

393   morphological similarities in this trait may be also be attributed to the homogeneity and stability

394   of the environment (a possible mechanism is further discussed in section 4.3). For instance,

395   compared to the Gulf of California, tides, wave regimes and SST variations in the Gulf of

396   Mexico are much lower in magnitude and frequency due to the influence of the Loop Current

397   (Davis *et al.*, 1998); and because of its influence over a large area (Avise, 1992), selective

398   pressures may be similar in spite of the larger distance among sites. This situation may explain

399   not only the similarities in shape among neighboring locations, but also the smaller overall

400   variability observed in these dorsal fins (Fig. 3).

401

402   **4.2. Dorsal fin phenotypic variability as a function of geographic/geological scales.**

403   Similar studies have also pointed out the potential utility of using geographic variation in dorsal

404   fin shape for bottlenose dolphin population discrimination over wide geographic ranges (i.e.

405   Indian and Pacific oceans *vs.* the Gulf of Mexico), thus intrinsic differences are somewhat

406   implied (Weller, 1998); however, due to the wide geographic scale of such comparisons, random

407    fin phenotypes may occur due to vicariance. Therefore, there was no other study to provide

408    further insight in the dorsal fin morphology of bottlenose dolphins by using a larger sample at a

409    smaller scale.

410

411    Moreover, the major differences in dorsal fin shapes found between the Pacific, the Gulf of

412    Mexico and the Gulf of California were consistent with the stepping stone dispersal model

413    (Table III); however, there was no clear difference between the Pacific and the Gulf of California.

414

415

416    The geological history of the region may shed light on the matter; for instance, the divergence

417    between the Gulf of Mexico and Pacific populations ensued after the emergence of the Isthmus

418    of Panama, which closed the inter-oceanic canal (approx. 2.5 Mya) (Gore, 2003); therefore,

419    morphological differences with the Gulf of Mexico may also be attributed to vicariance.

420    Conversely, the Baja California peninsula began to separate from the mainland about 5.5 Mya;

421    during this separation (5.5−1 Mya) the peninsula was fragmented on several occasions by trans-

422    peninsular seaways, connecting the Pacific and the Gulf (Riddle *et al.*, 2000). It is unclear how

423    these hypothetical connections between the proto-Gulf of California and the Pacific may have

424    affected coastal populations of bottlenose dolphins; however, this intermittent isolation may

425    account for the lack of differentiation in dorsal fin shape between the Pacific (Ensenada and San

426    Quintin) and the northern Gulf of California.

427

428    **4.3. Could dorsal fin phenotypic variability be an adaptive trait?**

429    Local phenotypic variability in dorsal fins may be the result of individual heredity and dispersal,

430    but natural selection may also be at play. While empirical data on the possible functional

431    advantages of dorsal fin characteristics are sparse, it has been argued that some features are

432    adaptive (Fish and Hui, 1991; Weller, 1998; Berta and Sumich, 1999; Fish and Rohr, 1999;

433    Reynolds *et al*., 2000). As a whole, dorsal fin shape may be a trade-off between

434    thermoregulatory capacities and hydrodynamic performance. For instance, regardless of the

435    study location, the central portion of the trailing edge (represented by points C10 and C20, Fig. 2)

436    was the least variable section of the dorsal fin overall (Fig. 3). This finding may reflect a

437    hydrodynamic constraint, since computer simulations for hypothetical dorsal fins have found that

438    this region produces the least turbulence (Pavlov and Rashad, 2012). On the other hand, studies

439    on thermoregulation efficiency in dorsal fins point out the importance of surface area and

440    vascularization in temperature regulation (Meagher *et al*., 2002; Morteo, 2004; Westgate *et al*.,

441    2007; Barbieri *et al*., 2010). For instance, veins and vessels in the dorsal fins of male dolphins

442    are directly connected to the testicles (which are inside the body), helping in heat dissipation

443    (Rommel *et al*., 1994; Rommel *et al*., 1999).

444

445    The functional significance of other morphometric characters (i.e. foil, rake, depth, base lenght)

446    are less clear. Weller (1998) explained how the shape of surfboard fins and water craft keels

447    confer different levels of maneuverability, speed and performance; he further suggested how

448    variation in these parameters in the dorsal fins may relate to site specific hydrodynamic

449    performance required for prey chase and capture by dolphins.  For instance, contrasting fin

450    shapes have been described for the two ecotypes of this species in the southeast Pacific which

451    have different feeding habits, such that offshore individuals generally have wider and more

452    falcate fins than their coastal counterparts (Felix et al., 2017)

453

454    Alternatively, dorsal fin shape characteristics may be influenced by habitat variables unrelated to

455    prey capture. For instance, falcate and wider fins (which theoretically perform better at high

456    speeds or in highly dynamic environments) were found mainly in the Pacific (Fig. 3), where the

457    habitat of coastal bottlenose dolphins features swells as high as 5 m (Lizárraga *et al*., 2003); and

458    also in the Gulf of California, where tidal currents may exceed 3 m s$^{-1}$ (Álvarez, 2001).

459    Comparatively, less falcate fins were found in the Gulf of Mexico, where tidal currents and wave

460    heights are of lesser magnitude (Delgado, 2002).

461

462    Additionally, dorsal fins that were less falcate and with less foil were found in the western Gulf

463    of Mexico, whereas taller and wider (i.e. larger depth and base length) dorsal fins were found in

464    the northern Gulf of California; both of these features resulted in larger fin surface areas. These

465    coastal locations are very shallow (<20 m) and have a high potential for rising sea surface

466    temperatures (SST) due to high residency times resulting from reduced water circulation,

467    especially during low tides (Bianchi *et al*., 1999; Lavín and Marinone, 2003). SST plays an

468    important role in species distributions (Pianka, 1994; Valiela, 1995), and although it is not

469    supposed to influence dolphins movements overall (due to their high thermoregulatory

470    capacities), tagged bottlenose dolphins in the Atlantic have shown avoidance of oceanic fronts

471    (Wells *et al*., 1999). Consequently, rapid changes in temperature may trigger behavioral and

472    physiological responses possibly influencing home ranges, but also food habits and consumption

473   rates. Thus a possible cause for the apparent relationship with proportional dorsal fin area may be

474   that warmer habitats are more suitable for individuals that are better at handling heat excess.

475

476   In light of the above, there is a chance that unexpected morphological similarities between

477   geographically isolated localities (e.g. Santa Maria in the Gulf of California *vs.* Gulf of Mexico

478   sites, Fig. 5) are not an artifact of the classification functions (Table II), and may have a

479   biological/adaptive explanation. For instance, unlike the other study areas in the Gulf of

480   California, Bahia Santa Maria is an enclosed estuarine system with two entrances, and the

481   vegetal coverage along the shore is dense (Reza, 2001). Also, mean year-round SSTs are more

482   similar to those in the Gulf of Mexico than to the open Pacific coast (Heckel, 1992; Schramm,

483   1993; Delgado, 1996, 2002). Therefore, we speculate that similar dorsal fin shapes in the Gulf of

484   California and the Gulf of Mexico may reflect adaptive convergence influenced by similar

485   selective pressures.

486

487   We acknowledge that the relations described above may be coincidental and the former

488   arguments are exploratory. Therefore, independent evidence is needed to understand if these

489   polymorphisms reflect adaptive advantages and genetic mechanisms within and among

490   populations, or are just the result of different norms of reaction. Although the patterns of

491   morphological variation are somewhat consistent with biological and ecological features,

492   suggesting adaptive explanations for such differences, hydrodynamic and thermoregulatory

493   functions must be empirically assessed to determine if the character states found in this study are

494   different enough to influence individual fitness, and thus subject to selection.

495

496 **5. Conclusions**

497 Dorsal fins of bottlenose dolphins show a high degree of polymorphism and restricted local

498 variability. Dorsal fin polymorphisms were geographically structured at different spatial scales,

499 supporting the model of isolation/differentiation by distance overall. Genetic analyses may help

500 elucidate if the population structure is consistent with the morphological clinal variation

501 described here. Our findings also suggest that this trait may be influenced by natural selection,

502 but this hypothesis remains to be tested.

503

504 **6. Acknowledgements**

514

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