CENTRO DE INVESTIGACIÓN CIENTÍFICA Y DE EDUCACIÓN
SUPERIOR DE ENSENADA

CICESE
MR

PROGRAMA DE POSGRADO EN CIENCIAS EN ECOLOGÍA MARINA

DORSAL FIN MORPHOLOGICAL DIFFERENTIATION IN BOTTLENOSE DOLPHINS (*Tursiops truncatus*) ALONG MEXICAN COASTS: AN ADAPTIVE APPROACH

TESIS

que para cubrir parcialmente los requisitos necesarios para obtener el grado de
MAESTRO EN CIENCIAS

Presenta:

EDUARDO MORTEO ORTIZ

Ensenada, Baja California, agosto del 2004

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RESUMEN de la tesis que presenta **Eduardo Morteo Ortiz**, como requisito parcial para la obtención del grado de MAESTRO EN CIENCIAS en ECOLOGÍA MARINA. Ensenada, Baja California. Agosto del 2004.

DIFERENCIACIÓN MORFOLÓGICA DE LA ALETA DORSAL DEL TURSIÓN (*Tursiops truncatus*) EN COSTAS MEXICANAS: UN ENFOQUE ADAPTATIVO

Resumen aprobado por:

Dr. Axayácatl Rocha Olivares
Director de Tesis

RESUMEN

El conocimiento sobre las variaciones geográficas en las especies es necesario para determinar sus límites biológicos y ecológicos, así como para entender procesos evolutivos básicos. La forma de las aletas en los animales acuáticos puede relacionarse con las condiciones ambientales y biológicas, tales como el hábitat y la conducta. Se estudió la variación fenotípica de la aleta dorsal de tursiones costeros (*Tursiops truncatus*) en escalas espaciales diferentes y se relacionó con la dispersión de las poblaciones.

Usando criterios estrictos, se obtuvieron 327 imágenes de la aleta dorsal provenientes de 12 catálogos de foto-identificación disponibles en las costas mexicanas (Océano Pacífico=3, Golfo de California=6 y, Golfo de México=3). Se desarrolló un programa de computadora (Fin Shape v1.3) para medir digitalmente 11 parámetros de la forma de aleta. Los errores por la calidad de las imágenes y el funcionamiento del programa fueron insignificantes (<0.1%), mostrando la confiabilidad del sistema.

Se usaron las mediciones computarizadas para calcular proporciones estandarizadas transformadas por medio de logaritmos. Los polimorfismos de la aleta se evaluaron a través de pruebas multivariadas. Mediante un Análisis de Componentes Principales (PCA) se explicó el 90% de la variación en tres Factores. Los resultados del PCA se incluyeron en un Análisis Canónico de Funciones Discriminantes (CDFA), el cual mostró separación entre en la mayoría de los sitios de estudio ($p<0.05$); sin embargo, a nivel regional sólo se encontraron diferencias significativas entre las localidades del Golfo de California. La estructura geográfica en el Golfo de California fue hasta cierto punto consistente con lo encontrado en otro estudio basado en morfometría craneal. Dicha estructura no coincidió con el modelo de Aislamiento/Diferenciación por Distancia ($p>0.05$), y la evidencia molecular sólo apoya parcialmente las tendencias geográficas; por consiguiente, los resultados de este estudio podrían reflejar los primeros pasos de divergencia micro-evolutiva dentro del Golfo de California.

La variación geográfica en una escala mayor se determinó mediante otro CDFA que agrupó los datos en regiones (Océano Pacífico, Golfo de California, y Golfo de México), y se encontraron diferencias significativas ($p <0.05$) entre ellas. La validación estadística

($p<0.05$) mostró que las localidades a prueba se agruparon dentro de su región de origen; sin embargo, no hubo distinción clara entre el Pacífico y el Golfo de California. La diferenciación morfológica regional puede explicarse por vicariancia debida a eventos geológicos y sus consecuencias ecológicas.

La variabilidad fenotípica en la forma de la aleta dentro de las localidades fue muy baja (tamaño mínimo de muestra *a posteriori* = 20); de igual forma, los polimorfismos de la aleta en los tursiones de las costas mexicanas fueron menos variables comparados con otras localidades alrededor del mundo y otras especies. Los factores espacio-dependientes ambientales, biológicos y genéticos que pueden ser la causa de estas pequeñas diferencias son: 1) La cobertura espacial de este estudio pudo no ser lo bastante amplia como para considerar cambios ambientales mayores dentro de las regiones, por lo cual las presiones selectivas no fueron muy distintas; 2) alternativamente, la alta movilidad de los delfines pudo homogeneizar las frecuencias de los estados del carácter, disminuyendo la separación; 3) si las muestras locales representan poblaciones genéticamente distintas, puede no haber pasado el tiempo suficiente para que la diferenciación morfológica ocurra en regiones específicas; y 4) alternativamente, las diferencias morfológicas pueden ser el resultado de la plasticidad fenotípica.

Considerando las tendencias geográficas, se sugieren dos relaciones causales potenciales; éstas se basan en hidrodinámica y termoregulación. Aunque éstas aún no se demuestran, se sospecha sobre las ventajas funcionales de las diferentes formas de la aleta dorsal; de esta manera se formulan especulaciones como hipótesis futuras y se revisan los posibles métodos para evaluar dicha funcionalidad.

Los resultados de este trabajo sugieren que un intervalo ambiental más amplio, la forma de la aleta puede ser el resultado de un esquema de costo-beneficio entre la capacidad de termorregulación, el desempeño hidrodinámico y el comportamiento de los delfines. Se sugieren algunos de los posibles mecanismos que determinan la forma de la aleta dorsal; basados en teorías biológicas y genéticas, éstos incluyen: restricciones evolutivas y genéticas, heredabilidad, cambios alométricos y ontogénicos, dimorfismo sexual, asimilación genética, y exaptaciones.

Palabras clave: *Tursiops truncatus*, morfología de la aleta, adaptaciones.

ABSTRACT of the thesis presented by **Eduardo Morteo-Ortiz** as a partial requirement to obtain the MASTER OF SCIENCE degree in MARINE ECOLOGY. Ensenada, Baja California, Mexico. August 2004.

DORSAL FIN MORPHOLOGICAL DIFFERENTIATION IN BOTTLENOSE DOLPHINS (*Tursiops truncatus*) ALONG MEXICAN COASTS: AN ADAPTIVE APPROACH

Abstract approved by:

PhD. Axayácatl Rocha-Olivares
Thesis Director

SUMMARY

Knowledge on geographically structured variation is needed to determine biological and ecological boundaries and also to understand basic evolutionary processes in species. Fin shape in aquatic animals may be related to environmental and biological conditions such as habitat and behavior. Dorsal fin phenotypic variation in coastal bottlenose dolphins (*Tursiops truncatus*) was studied over different spatial scales, and related to population dispersal.

A total of 327 dorsal fin images from 12 available photo-identification catalogs in Mexican coasts (Pacific Ocean=3, Gulf of California=6 and, Gulf of Mexico=3) were selected using stringent criteria. A computer based system (Fin Shape v1.3) was developed to digitally measure 11 fin shape parameters. Errors for image quality and software operation were negligible (<0.1%), thus showing system reliability.

Fin polymorphisms were evaluated through multivariate tests. Principal component analysis on log-transformed standardized measurement ratios explained 90% of the variance. Canonical Discriminant Function Analysis (CDFA) on factor scores showed separation among most localities ($p<0.05$), but significant differences in dorsal fin shape on a regional basis were found only within the Gulf of California. Geographically structured variation within this region was, to some extent, consistent with that found on a separate study based on skull morphometrics. This pattern did not fit the Isolation/Differentiation by Distance model ($p>0.05$), and molecular evidence only partially supports geographic trends; therefore, observations reported here may be indicative of the early steps of microevolutionary divergence within the Gulf of California.

Assessment of variation on a greater scale was performed by a new CDFA grouping data on a regional basis. Significant differences ($p<0.05$) were found among all regions (Pacific Ocean, Gulf of California, and Gulf of Mexico). Statistical validation ($p<0.05$) showed that localities grouped within their original region; however, there was no clear distinction between the Pacific and the Gulf of California. Regional morphological differentiation may be attributed to vicariance as a result of plate tectonics and its ecological consequences.

Fin shape phenotypic variability within localities was very low (*a posteriori* estimated minimum sample size = 20); also, fin polymorphisms in bottlenose dolphins along Mexican coasts were less distinct compared to other locations around the world or other species. The environmental, biological and genetic space-dependent factors thought to be the cause of these slight differences are: 1) spatial coverage of this study may not be large enough to account for major environmental breaks within regions, thus making selective pressures not very distinct; 2) alternatively, the high mobility of these dolphins may homogenize frequencies of character states, thus fading separation; 3) if local samples represent genetically distinct populations, not enough time may have elapsed for morphological differentiation within specific regions; and 4) alternatively, morphological differences may be the result of phenotypic plasticity.

Two potential causal relationships are discussed regarding geographical trends; these were based on thermoregulation and hydrodynamics. Although functional advantages of different dorsal fin shapes are not yet demonstrated, they are strongly suspected; thus speculations are formulated as future hypotheses and possible methods are revised to assess fin functionality.

Results from this work suggest that over a wider range of environments, fin shape may be a trade-off among thermoregulatory capacity, hydrodynamic performance and behavioral characteristics. Several insights are suggested as possible mechanisms determining dorsal fin shape; based on biological and genetic theories, these include: evolutionary and genetic constraints, heritability, allometric and ontogenetic changes, sexual selection, genetic assimilation, and exaptations.

Key words: *Tursiops truncatus*, fin morphology, adaptations.

Dedication

To my family and friends...

To the memory of my teacher Armando Rodríguez Pinal…

To Akela and the dolphins...

To my princess...

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“When a variation is of the slightest use to a being, we cannot tell how much of it to attribute to the accumulative action of natural selection, and how much to the conditions of life”

Charles Darwin (1859)

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SYNOPSIS (Spanish)

La mayoría de las especies varían geográficamente en sus características (morfológicas, fisiológicas, conductuales, etc.). Los estudios con tursiones [*Tursiops truncatus* (Montagu, 1821)] (Figura 1) y otros delfines han mostrado estructura en la variación morfológica externa e interna, así como en sus patrones de coloración, y en sus características poblacionales, tales como el tamaño y estructura del grupo o en sus patrones de asociación y conducta.

Describir y elucidar las variaciones geográficamente estructuradas es importante para determinar los límites biológicos y ecológicos entre poblaciones; estos son de relevancia en el manejo de los recursos y también necesarios para entender los procesos evolutivos básicos. La mayoría de los estudios morfológicos que involucran variación geográfica se han enfocado en describir los patrones de distribución de los polimorfismos; sin embargo, en la mayoría de los casos no se discute la existencia de relaciones causales. Como las causas de tales patrones son generalmente difíciles entender, a menudo es necesaria información biológica y ecológica.

La forma de la aleta dorsal en los cetáceos es usada para la identificación de las especies y se ha propuesto que en los animales acuáticos refleja adaptaciones fisiológicas bajo condiciones ambientales diferentes; por ello, su importancia en la hidrodinámica y termorregulación de los cetáceos es ampliamente aceptada. Debido a ello se ha pensado que la forma de la aleta dorsal se relaciona con hábitats y conductas de alimentación específicas.

Las fotografías de la aleta dorsal en delfines y la foto-identificación son técnicas no invasivas con muchas ventajas y aplicaciones en el estudio de cetáceos, tales como la determinación del ámbito hogareño, patrones de movimiento, dinámica de la población, organización de los grupos y su estructura social. Recientemente, las técnicas fotográficas también se han usado para evaluar la variación geográfica en la morfología de los cetáceos en vida libre.

En los últimos años se ha realizado un gran esfuerzo económico y logístico en el desarrollo de estudios de poblaciones de tursiones; sin embargo, sólo algunos integran la información en escalas geográficas amplias. En el Primer Capítulo de este estudio, se incorporan los catálogos de foto-identificación disponibles a lo largo de las costas mexicanas para evaluar la variabilidad fenotípica de la aleta dorsal en diferentes escalas espaciales. En el Segundo Capítulo, se utiliza un enfoque evolutivo para interpretar esta variabilidad, haciendo énfasis en lo que se conoce sobre el origen, desarrollo y función de la aleta dorsal en esta especie.

La hipótesis de este trabajo es que debido a que existen factores biológicos y ecológicos que son espacialmente variables, y siendo la aleta dorsal una adaptación, su morfología presenta estructura geográfica en escalas espaciales diferentes. El objetivo de este estudio fue evaluar el grado de polimorfismos de la aleta dorsal y compararlo entre localidades y entre regiones.

I. Diferenciación morfológica de la aleta dorsal de los tursiones (*Tursiops truncatus*) en costas mexicanas

Se utilizaron criterios estrictos para seleccionar 327 imágenes de la aleta dorsal de los tursiones en 12 localidades a lo largo de las costas mexicanas (Tabla I, Figura 2). Los métodos y procedimientos matemáticos y estadísticos utilizados se muestran en la Figura 3. Del catálogo fotográfico de cada área de estudio se eligieron al azar aproximadamente 30 de las imágenes que cumplieron con los criterios de selección. Se desarrolló un programa de computadora (Fin Shape v1.3) para realizar 11 mediciones (Figura 4) que describen parámetros de la forma de la aleta dorsal (Figura 5). Los errores en las mediciones debido al uso del programa (0.01%) y la calidad de las imágenes (0.1%) fueron insignificantes.

Para evaluar la variabilidad fenotípica general, se construyeron contornos representativos de las aletas de cada sitio y se identificó la variabilidad en cada una de las mediciones realizadas (Figura 6). La variabilidad morfológica local se evaluó primero mediante el análisis de la contribución de cada aleta a la variabilidad total local; esto se logró mediante la adición progresiva de aletas seleccionadas al azar, a través de un análisis similar a una curva de "rarefacción" (Figura 7); mediante este proceso se determinó que el tamaño mínimo de muestra fue de 20 aletas por sitio (representan más del 90% de la variabilidad local). Se calcularon índices estandarizados dividiendo los valores de las mediciones, y se transformaron por medio de logaritmos para que la distribución de las variables fuera normal. Se encontró una correlación alta y significativa ($p<0.05$) entre la mayoría de estos índices, por lo cual se utilizó un Análisis de Componentes Principales (PCA) (Tabla II); mediante este procedimiento se agruparon 10 de los 11 índices en tres

Factores, los cuales representaron el 90% de la variabilidad observada (Tabla III). Para evaluar las diferencias entre localidades, los resultados del PCA fueron sometidos a un Análisis de Funciones Discriminantes (DFA) (Tabla IV). Se encontró que todas las localidades presentaron diferencias significativas (Tablas V, VI, VII, VIII y IX); las Distancias Cuadradas de Mahalanobis (SMD) obtenidas del DFA se usaron en un análisis de conglomerados (Figura 8) como medida de las diferencias morfológicas; mediante este análisis se encontraron dos grupos principales: el primero contuvo a todas las localidades del Golfo de México y una del Golfo de California (Bahía Santa María); el segundo agrupó indistintamente las localidades del Pacífico y del Golfo de California. Dichos datos fueron evaluados mediante un modelo de Aislamiento/Diferenciación por Distancia (Figura 9); sin embargo, no se encontró correlación ($p>0.05$) entre las distancias geográficas y las diferencias morfológicas para el Pacífico y el Golfo de California (Figura 10).

Para evaluar la variabilidad fenotípica regional, los datos del PCA se agruparon en: Pacífico, Golfo de California y Golfo de México. Se excluyó la información de tres localidades seleccionadas al azar (San Quintín, San Jorge y Tamiahua) y se aplicó un DFA; este análisis mostró diferencias significativas entre regiones (Tablas X, XI, XII, XIII, XIV y XV). Para validar estadísticamente las agrupaciones obtenidas, se incluyeron los datos de las tres localidades y se sometieron a otro DFA para verificar si se diferenciaban de su región de origen (Tabla XVI); en este caso, sólo el Golfo de México fue diferente, y no hubo un patrón claro entre el Pacífico y el Golfo de California (Tabla XVII, XVIII, XIX, XX y XXI, Figura 11).

Para hacer inferencias sobre la variación morfológica de las aletas de los tursiones entre localidades, se deben considerar los siguientes aspectos: 1) La cobertura espacial de este estudio pudo no ser lo bastante amplia como para considerar cambios ambientales mayores dentro de las regiones, por lo cual las presiones selectivas no fueron muy distintas; 2) alternativamente, la alta movilidad de los delfines pudo homogeneizar las frecuencias de los estados del carácter, disminuyendo la separación; 3) si las muestras locales representan poblaciones genéticamente distintas, puede no haber pasado el tiempo suficiente para que la diferenciación morfológica ocurra en regiones específicas; y 4) alternativamente, las diferencias morfológicas pueden ser el resultado de la plasticidad fenotípica.

En el caso del Golfo de México, cualquiera de las alternativas propuestas puede ser la causa de que no se encontraron diferencias morfológicas en las aletas dorsales; lo mismo ocurre en el caso del Pacífico, específicamente para Ensenada y San Quintín. Sin embargo, el Golfo de California presenta un patrón diferente; otros estudios con tursiones en el Golfo han reportado esta estructura utilizando datos morfométricos del cráneo. Esta estructura geográfica se ha encontrado en otros taxa como invertebrados y peces, e incluso en mamíferos como el lobo marino de California (*Zalophus californianus californianus*). La explicación más común es la oceanografía del Golfo, la cual conforma barreras ecológicas para la distribución de las especies (Figura 12). Se ha propuesto que la temperatura superficial del mar no es un factor importante para la distribución de los delfines a gran escala; sin embargo, los cambios bruscos en escalas pequeñas (como en el centro del Golfo de California) podrían influir en sus movimientos. Es posible que estas diferencias ecológicas influyan en la diversidad de los hábitos alimentarios de los delfines, por lo cual estos desarrollan diferentes estrategias para capturar a sus presas; como la maniobrabilidad es importante para la alimentación y el comportamiento social de los delfines, las características en las aletas dorsales podrían ser el resultado del la selección de individuos más aptos. Los datos moleculares de tursiones también han reportado estructura en el Golfo de California, por lo cual estas evidencias podrían reflejar los primeros pasos de divergencia micro-evolutiva.

La información bibliográfica sobre la biología y ecología de los tursiones en costas mexicanas muestra evidencias sobre la posible existencia de sub-poblaciones, las cuales se muestran en la Figura 13.

En lo que respecta a las diferencias regionales, estas podrían explicarse mediante eventos geológicos y sus consecuencias ecológicas; por ejemplo, la similitud entre el Pacífico y el Golfo de California puede deberse a un posible intercambio de individuos y de genes durante la formación de la península. Por otra parte, la diferenciación de estas dos regiones con el Golfo de México puede ser el resultado del aislamiento ocasionado por el cierre del estrecho de Panamá (vicariancia).

II. Causas relacionadas al ambiente, mecanismos genéticos de los polimorfismos y métodos para evaluar el desempeño de la aleta dorsal del tursión (*Tusiops truncatus*)

Los organismos generalmente presentan restricciones eco-fisiológicas manifestadas en la variación fenotípica asociada a su genotipo (norma de reacción). Algunas diferencias fenotípicas han sido suficientes para determinar cuantitativamente diferentes formas en las especies y posibles poblaciones genéticamente diferenciadas. Por ello, es posible que la variabilidad fenotípica sea adaptativa (selección de algunos fenotipos del genotipo). La determinación de la aptitud es normalmente muy compleja; sin embargo, es posible que los polimorfismos de la aleta dorsal sean resultado de restricciones funcionales derivadas de posibles ventajas hidrodinámicas y de termoregulación.

Desde el punto de vista anatómico (hidrodinámica), la forma de la aleta dorsal en los delfines es importante para el nado, ya que proporciona estabilidad y maniobrabilidad bajo el agua. Varios estudios sugieren que las aletas con cierto aspecto geométrico reflejan adaptaciones eficaces para nadar grandes distancias o a velocidades altas.

Desde la perspectiva fisiológica (termorregulación), los cetáceos usan adaptaciones vasculares (*rete mirabilia*) para aumentar la eficacia de intercambio de calor. Se ha reportado que las aletas (principalmente la dorsal) pueden funcionar como ventanas termales para disipar calor dependiendo de la demanda térmica.

Basado en estas consideraciones, la respuesta más eficaz para el nado, buceo y termoregulación puede ser regulada por presiones ambientales relacionadas principalmente con los hábitos alimentarios (velocidad requerida de nado, maniobrabilidad, profundidad de buceo, tiempo de inmersión y cambios de temperatura). Por consiguiente, ya sea conductual, anatómica o fisiológica, la respuesta tiene una fuerte base selectiva, y puede ser el resultado de selección natural.

Debido a lo anterior, si la forma de la aleta dorsal refleja una adaptación, la causa puede involucrar una demanda energética especial en diferentes escalas de tiempo. Con base en la teoría de forrajeo óptimo, los requerimientos metabólicos a corto plazo (minutos, horas) pueden relacionarse con el gasto de energía inmediato debido a los diferentes modos de nado o comportamientos. A mediano plazo (días, semanas, meses), el gasto de energía puede relacionarse con la abundancia y disponibilidad de alimento, y la reproducción. A largo plazo (años, décadas), los costos metabólicos pueden relacionarse con el arrastre hidrodinámico del cuerpo (cambios ontogénicos o alométricos) y la temperatura de agua. Por otra parte, la respuesta fisiológica a la pérdida de calor en el corto plazo (minutos, horas) involucra la restricción del flujo de sangre hacia las aletas. A mediano plazo (días, semanas, meses) la respuesta puede ser conductual, aumentando el tiempo en la superficie. A largo plazo (generaciones) la respuesta podría ser adaptativa, al aumentar la longitud total del cuerpo de animal (regla de Bergman), y/o disminuyendo la longitud de los apéndices (regla de Allen) y con esto, la superficie de intercambio térmico en las aletas.

Con base en las consideraciones anteriores, la variación morfológica de la aleta dorsal en esta especie puede relacionarse directamente con el desempeño hidrodinámico y termoregulatorio. Por ejemplo, en este estudio, la punta de la aleta dorsal fue una de las dimensiones más variables; de modo que ésta puede ser una señal importante para entender cómo el ambiente influye en este caracter.

La capacidad de termorregulación se relaciona directamente con el tamaño de la aleta dorsal, pero la relación con su forma no es tan evidente. Se ha observado que el calor se transmite más eficazmente en la parte distal de la aleta dorsal de los tursiones. Aunque por razones estructurales se piensa que las aletas más altas y falcadas podrían involucrar un flujo de calor más directo y eficaz, este patrón podría deberse más a la distribución vascular subyacente que a la forma misma de la aleta dorsal.

Con respecto al desempeño hidrodinámico, se ha observado que las quillas delgadas y falcadas mejoran la maniobrabilidad y permiten cambios rápidos de dirección en los vehículos acuáticos; las quillas con bases anchas proporcionan mayor estabilidad y trayectorias rectas al avanzar. Este argumento es consistente al encontrar aletas más falcadas en el Pacífico y el Golfo de California (dónde el oleaje y las corrientes de marea son de gran magnitud) y menos falcadas en el Golfo de México (corrientes de marea y oleaje de menor magnitud). Este patrón puede indicar que un mar más dinámico requiere mayor maniobrabilidad (Figura 14), especialmente al buscar alimento; por lo tanto, las aletas dorsales falcadas pueden ser ventajosas en estas condiciones, ya que teóricamente se desempeñan mejor en altas velocidades y en ambientes muy dinámicos.

Los argumentos anteriores sugieren que en un rango amplio de ambientes, la forma de la aleta dorsal podría reflejar un esquema de "costo-beneficio" entre las capacidades de termorregulación y el desempeño hidrodinámico, además de otros factores.

III. Posibles mecanismos que determinan la forma de la aleta dorsal

Aunque los mecanismos de adaptación y el concepto mismo continúan en un intenso debate, es un hecho que la presencia y/o modificación de ciertos rasgos (en este caso la aleta dorsal) confiere una aptitud diferencial a los individuos; sin embargo, no debe ignorarse que la aptitud puede ser el resultado de la función directa del carácter o simplemente un sub-producto. A menos que puedan demostrarse los mecanismos genéticos específicos, no debe suponerse que la plasticidad fenotípica observada es adaptativa. Por lo tanto, para elucidar los posibles mecanismos que determinan la forma de la aleta dorsal en los tursiones, a continuación se incorpora la información biológica y ecológica de esta especie en el enfoque de teorías evolutivas y genéticas.

a) Restricciones evolutivas

Al menos para los tursiones de este estudio, la alta correlación entre muchas de las mediciones de la aleta dorsal sugiere que su forma es altamente dependiente de unos cuantos parámetros. Por lo tanto, su similitud con la aleta dorsal de otros delfines (*Delphinus* spp. y *Stenella* spp) (Figura 15) puede representar restricciones evolutivas derivadas del plesiomorfismo en los antepasados del delfín. Sin embargo, se ha señalado que las restricciones evolutivas tienen un papel menor al explicar las diferencias poblacionales en un rasgo que varía de una manera cuantitativa; adicionalmente, como la variación de este carácter en los tursiones parece aumentar con la escala geográfica y las aletas dorsales en la familia Delphinidae son muy variables (Figura 16), es posible que, además de las restricciones evolutivas (si existen), la forma de la aleta pueda variar en respuesta al ambiente y las restricciones genéticas.

b) Restricciones genéticas

Teóricamente, la plasticidad fenotípica limitada o las normas de reacción restringidas en las especies o poblaciones pueden causar diseños similares (Figura 17). Debido a que se han encontrado fenotipos no convencionales de la aleta dorsal en algunas poblaciones de tursiones, esto sugiere que la plasticidad fenotípica es alta; por este motivo, las restricciones genéticas no parecen ser el caso.

c) Heredabilidad en la forma de la aleta dorsal

El desarrollo de aletas polimórficas debe tener un fuerte componente genético; estos polimorfismos pueden programarse antes del nacimiento (heredabilidad), o a lo largo del desarrollo (ontogenia). Observaciones de tursiones silvestres y en cautiverio, han mostrado que la aleta dorsal de las crías es muy similar a la de sus madres (Figura 18). Otras observaciones sobre distribución vascular en la aleta dorsal del delfín manchado (*Stenella attenuata*), han mostrado patrones muy similares en parejas madre-cría. Lo anterior sugiere una fuerte herencia de este rasgo, lo cual podría explicar la baja variabilidad morfológica encontrada en las localidades de este estudio.

Entre las posibles explicaciones de este fenómeno se encuentra que el mismo gen (o genes) controlan varios rasgos (pleiotropía), o que los genes que codifican estos rasgos se encuentran estrechamente ligados (hitch hiking). Sin embargo, tales interpretaciones deben tomarse con reserva, ya que la heredabilidad puede variar con el ambiente en que se mide.

d) Cambios alométricos y ontogénicos

No se cuenta con información sobre los cambios alométricos y ontogénicos en el tursión; comparativamente, se han encontrado alteraciones mayores en este carácter durante el desarrollo del delfín tornillo (*Stenella longirostris*) (Figuras 19 y 20). A diferencia de los delfines tornillo machos (dónde la forma de la aleta dorsal puede reflejar la madurez sexual y testículos de mayor tamaño), la aleta dorsal en el tursión podría tener una contribución pequeña a la aptitud global comparada con otros rasgos morfo-fisiológicos. Adicionalmente, aún cuando la forma de la aleta podría ser importante en la reproducción (debido a los vasos sanguíneos que van desde las aletas a los testículos y ayudan en el enfriamiento del semen para la viabilidad reproductiva), actualmente no hay evidencias disponibles para correlacionar la forma (o el tamaño) de la aleta con el potencial reproductor de la especie; y esto sólo debe ser significativo cuando los delfines machos son sexualmente maduros. Por consiguiente, basado en la mejor evidencia disponible, un sistema ontogénico para regular la forma de la aleta dorsal no parece económico en esta especie.

Comparativamente, los efectos a largo plazo de una aleta dorsal sub-óptima en la maniobrabilidad y la capacidad de conducción térmica, pueden potencialmente causar efectos negativos en las habilidades de alimentación y el potencial reproductivo. Esto disminuiría la aptitud individual, permitiendo que fenotipos mejores adaptados tengan más éxito en la reproducción (selección Darwiniana).

e) Dimorfismo sexual de aleta dorsal

El dimorfismo sexual puede ser importante al determinar la variabilidad de fenotípica de aleta dorsal. Se ha sugerido que los cambios en la forma de la aleta dorsal de los delfines tornillo pueden tener una connotación sexual, al indicar la madurez (Figura 20). Esto puede relacionarse con restricciones estructurales e hidrodinámicas asociadas a un mejor desempeño durante el combate para el acceso a las hembras; adicionalmente, pueden representar una señal visual durante los despliegues sexuales.

Existen pocos estudios sobre el dimorfismo sexual en el tursión y los resultados son controversiales. Estas diferencias sexuales en la forma de la aleta dorsal podrían indicar diferencias biológicas; por ejemplo, algunos estudios han reportado que las aletas de los delfines machos adultos son de mayor tamaño y se encuentran más dañadas (debido a las interacciones sociales más activas y la competencia reproductiva).

Debido a los criterios para la selección de imágenes en este estudio, es posible que las pruebas estén sesgadas en favor de las hembras y/o animales jóvenes físicamente maduros. Esto pudo tener algún efecto en la discriminación entre localidades; por ejemplo, los tursiones jóvenes y las hembras de algunas áreas poseen ámbitos hogareños más restringidos o no se mueven tanto como los machos; esto se ha atribuido principalmente a factores sociales y ecológicos dirigidos hacia una mayor permanencia en áreas aprovisionadas y protegidas. En los animales jóvenes esto es posiblemente debido al cuidado de los padres y/o defensa contra depredadores; además, las hembras también podrían necesitar protección contra el acoso de los machos y tener requisitos enérgicos más altos para la producción de crías. Debido a lo anterior, el uso de un número mayor de hembras y animales jóvenes en los análisis de este estudio podría incrementar artificialmente la separación entre localidades.

Como las fotografías de la aleta dorsal no son útiles para establecer el sexo en los tursiones, existe la posibilidad de que la variabilidad dentro de las poblaciones pudiera haberse subestimado, incrementando la separación entre las muestras locales. Sin embargo, debido a la posible inclusión de machos adultos y a que se pudo diferenciar eficazmente entre algunas localidades a pesar del posible sesgo de sexo-edad, o el dimorfismo sexual, los resultados se hacen robustos.

f) Asimilación genética

Conocido también como el efecto Baldwin, este concepto sugiere que las demandas ambientales actúan sobre los genes de la especie. El mecanismo sugerido involucra un estímulo ambiental inicial, el cual promueve cierta conducta o caracter. Si es útil, este rasgo prevalece dentro de la población, y aquellos individuos con predisposición genética ganan ventaja selectiva sobre los otros; así el carácter es asimilado genéticamente. Por consiguiente, un carácter que normalmente se expresa en ciertas situaciones ambientales se fija en la población, y no requiere factores ambientales para expresarse.

Basado en la frecuencia de los estados del carácter entre las poblaciones putativas, y la baja variabilidad dentro de las localidades, este mecanismo puede explicar las distintas formas de aletas en los diferentes ambientes. Sin embargo, aunque existen evidencias, los supuestos de este mecanismo aún no se demuestran (la aleta dorsal como un rasgo plástico que es heredable y que su misma forma es una adaptación). Asimismo, la separación genética entre las poblaciones puede ser un requisito previo para que ocurra la asimilación genética, ya que el flujo genético desvanecería la separación.

g) No adaptación o selección del caracter (exaptaciones)

Para describir los cambios evolutivos es necesario tener algún conocimiento sobre el estado inicial del carácter; sin embargo, no existe registro fósil para determinar la condición ancestral de la aleta dorsal en este género o cómo ha cambiado. Se ha propuesto que la variación fenotípica de los caracteres puede deberse a que el organismo no es capaz de ajustarse a los cambios ambientales; por lo tanto, esta variación podría no tener bases genéticas. De igual forma, los alelos pueden fijarse por deriva en una población pequeña a pesar de la selección natural, y esta fijación de alelos no aptos puede ser común si los coeficientes de selección son pequeños y si muchos genes están involucrados. A pesar de lo anterior y aunque no se ha demostrado una relación causa-efecto, las evidencias sugieren que la forma de la aleta dorsal del tursión puede ser resultado de la selección Darwiniana. De esta forma, las presiones selectivas en el largo plazo podrían regir la evolución de las poblaciones de esta especie para satisfacer condiciones ambientales específicas (variables o estables), cambiando el fenotipo prevaleciente; de esta manera se podría generar un patrón geográfico de variación morfológica completamente diferente.

IV. Métodos para la evaluación del desempeño de la aleta dorsal

Aunque se ha estudiado la anatomía de la aleta dorsal de algunos cetáceos, su funcionalidad aún no se entiende totalmente. No se ha encontrado una relación clara entre la morfología de la aleta dorsal de los delfines (familia Delphinidae), con los rasgos biológicos y ecológicos de las especies; por consiguiente, se ha concluido que la aleta dorsal pudo adquirir funciones diferentes a través de la divergencia evolutiva. Por este motivo, la comparación entre varias poblaciones de la misma especie puede ser un mejor método para entender estas relaciones. Actualmente existen análisis cuantitativos de la forma de la aleta dorsal para 19 localidades diferentes dentro de la distribución del tursión y éstas deberían usarse para valorar su funcionalidad. El desempeño hidrodinámico y termoregulatorio de la aleta dorsal puede ser evaluado mediante los métodos propuestos a continuación.

a) Desempeño hidrodinámico

El desempeño hidrodinámico puede evaluarse midiendo el arrastre y la formación de vórtices causados por las aletas dorsales. Se pueden obtener moldes de fibra de vidrio de las aletas dorsales de los tursiones varados, y éstas pueden personalizarse para construir aletas representativas de otras localidades. Como los análisis preliminares de cortes transversales en la aleta dorsal de tursiones (Figura 21) han mostrado algunas tendencias lineales (Figura 22), se pueden diseñar representaciones confiables en 3-D únicamente basadas en los contornos de la aleta o en imágenes como las utilizadas en este trabajo (Figura 23).

Para evaluar la formación de vórtices se propone el experimento mostrado en las figuras 24 y 25. Con este método se obtendrían imágenes de la dinámica de flujo para ser analizadas a través de software como PIV Sleuth; estas imágenes se generarían para varios tipos de aletas con el fin de identificar las áreas de variación a diferentes velocidades de flujo y ángulos de ataque. Los resultados podrían relacionarse con las condiciones ambientales en cada sitio de estudio para hacer inferencias sobre la eficacia del diseño de la aleta dorsal de cada localidad.

Por otro lado, la evaluación del arrastre puede lograrse mediante experimentos de remolque (Figura 26). Otro método para medir el arrastre son los experimentos de caída libre (Figura 27). La eficacia de los diseños de la aleta será medida evaluando su resistencia en un rango de condiciones de flujos diferentes y ángulos de ataque.

b) Desempeño térmico

El desempeño térmico puede evaluarse por medio de los patrones de distribución de calor en diferentes formas de la aleta, mediciones directas del flujo de calor, descripción de la anatomía vascular y modelado matemático. La mayoría de estos métodos involucra experimentos o deben validarse con animales vivos; por consiguiente, los delfines en cautiverio son fuentes invaluables de datos bajo condiciones semi-controladas.

Las imágenes infrarrojas proporcionan datos directos de la distribución espacial de calor en las aletas (Figura 28). Tales patrones deben analizarse para diferentes individuos bajo las mismas condiciones experimentales y deben correlacionarse con la vasculatura subyacente. Por otra parte, las mediciones directas de los flujos de calor se basan en transductores sobre la aleta. Se deben colocar dos transductores al menos en tres áreas diferentes y se recomiendan mediciones en ambos lados de la aleta (Figura 29). Se debe monitorear la temperatura del aire, agua y la del interior del cuerpo del delfín, así como los cambios en la respiración y frecuencia cardiaca. Para correlacionar las mediciones de flujo de calor con la vasculatura subyacente se deben realizar varias sesiones con individuos diferentes bajo las mismas condiciones experimentales.

La anatomía vascular de la aleta dorsal ha sido poco estudiada y en algunos casos con un número limitado de especimenes; sin embargo, ésta parece variar individualmente y puede relacionarse estrechamente con los patrones de distribución térmica en los apéndices. La mejor manera de describir la distribución de venas y vasos es mediante el examen directo de secciones transversales de los apéndices; sin embargo, los varamientos de delfines muertos pueden ser poco frecuentes y sus aletas pueden haberse dañado o degradado a través de la descomposición. Por consiguiente, se proponen técnicas indirectas y menos exactas que pueden ser usadas en delfines muertos y vivos; cabe destacar que a pesar de ser menos precisos, éstos métodos son más rápidos y fáciles de aplicar.

La radiografía se ha usado para este propósito al menos en el tursión y el delfín manchado (*Stenella attenuata*). A pesar de su baja resolución, la vasculatura mayor puede observarse fácilmente (Figura 30). Se puede obtener una mejor resolución con los nuevos equipos radiográficos digitales y se pueden ajustar para examinar las capas como en una tomografía. Por otro lado, los equipos de ultra-sonido son dispositivos menos costos y portátiles; además son muy comunes entre el personal veterinario de los parques de fauna silvestre en cautiverio. No se han realizado experimentos u observaciones para validar este método; por consiguiente, deben hacerse varios experimentos con animales vivos y muertos para evaluar su confiabilidad.

Una vez descrita la anatomía vascular, se pueden usar métodos matemáticos para evaluar el desempeño en la termoregulación. Algunas de las dimensiones de la aleta (normalmente la altura y ancho) pueden obtenerse fácilmente de los datos morfométricos estándar; así pueden calcularse las medidas restantes de la forma de la aleta por medio de trigonometría y los resultados de esta investigación. Para comparar los resultados se recomienda escalar las mediciones de las aletas a los valores reales.

FOREWORD

The flexible behavior of bottlenose dolphins [*Tursiops truncatus* (Montagu, 1821)] allows them to use different habitat types (Leatherwood and Reeves, 1990; Scott *et al.*, 1996; Wells and Scott, 1999). This may cause differentiation in population characteristics, such as group size and structure, or in their association patterns and behavior (Wells *et al.*, 1980, Duffield *et al.*, 1983; Perrin, 1984; Kenney, 1990; Mead and Potter, 1990; Ross and Cockroft, 1990; Wells *et al.*, 1990; Ballance, 1992; Curry and Smith, 1997; Rossbach and Herzing, 1999).

In addition, associated to their wide distribution, bottlenose dolphins present great phenotypic variability and their morphology can change abruptly in regions of close proximity. Some of the main polymorphisms are: total length, appendage size of pectoral, dorsal and caudal fins, skull morphometrics, teeth number on maxillae, and dorsal fin shape (Walker, 1981; Ross and Cockroft, 1990; Weller, 1998; Vidal, 1993; Turner and Worthy, 1998; Wang *et al.*, 2000; Reeves *et al.*, 2002). Other polymorphisms found in the species are: pigmentation patterns, hemoglobin types, association patterns among individuals, whistle types, and genetics; other traits have also been used to differentiate these dolphins such as: prey items, parasitic load, and stable isotope signatures (Walker, 1981; Duffield *et al.*, 1983; Hersh and Duffield, 1990; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Bazúa, 1997; Hoelzel *et al.*, 1998; Rossbach and Herzing, 1999; Walker *et al.*, 1999; Wang *et al.*, 1999; Caldwell *et al.*, 2001; Möller and Beheregaray, 2001; Díaz *et al.*, 2003).

Most organisms vary geographically in morphological, physiological, behavioral, and other characteristics (Pianka, 1994). Earlier studies of geographic variation in delphinids have shown structured variation in external and internal morphometrics, as well as color patterns (Perrin, 1972, 1984; 1997; Perrin *et al.*, 1976; Perrin *et al.*, 1991; Perrin *et al.*, 1994; Walker, 1981; Duffield *et al.*, 1983; Schnell *et al.*, 1986; Hersh and Duffield, 1990; Ross and Cockroft, 1990; Vidal, 1993; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Hoelzel *et al.*, 1998; Turner and Worthy, 1998; Weller, 1998; Rossbach and Herzing, 1999; Walker *et al.*, 1999; Wang *et al.*, 1999, 2000; Caldwell *et al.*, 2001; Möller and Beheregaray, 2001; Reeves *et al.*, 2002; Díaz *et al.*, 2003).

Detecting and elucidating geographic variation may be valuable to determine biological and ecological boundaries among populations, which are very important in resource management and also necessary to understand basic evolutionary processes (Schnell *et al.*, 1986; Perrin *et al.*, 1994). Most studies examining morphologic variation on geographical scales have focused on describing the pattern and distribution of polymorphisms, and the probable existence of causal relationships, in most cases, is not discussed (Schnell *et al.*, 1986; Gotthard and Nylin, 1995). Since causal relationships of such patterns are generally difficult to understand, biological and ecological information is often needed.

Fin shape in cetaceans is used to some extent for species identification. Fin shape in aquatic animals has been suggested to reflect physiological adaptations to different environmental conditions (Aleyev, 1977; Pauly and Palomares, 1989; Fish, 1998; Weller, 1998; Wright, 2000), and its importance in thermoregulation and hydrodynamics of cetaceans is widely accepted (Fish and Hui, 1991; Berta and Sumich, 1999; Fish and Rohr, 1999; Reynolds *et al.*, 2000). For this reason, fin shape has been related to specific habitats and feeding behaviors (Lang and Pryor, 1966; Aleyev, 1977; Fish, 1998; Weller, 1998).

Dorsal fin photographs of free-ranging dolphins and photo-identification are non-invasive techniques with many advantages and applications to cetacean studies (Defran *et al.*, 1990; Hammond *et al.*, 1990) such as determination of home-range, movement patterns, population dynamics, group organization, and social structure (Caldwell, 1955; Würsig and Würsig, 1977; Würsig, 1978; Shane, 1980; Ballance, 1992; Heckel, 1992; Schramm, 1993; Scott *et al.*, 1996; Defran *et al.*, 1999; Guzón, 2002; Morteo *et al.*, 2004). Recently, photographic techniques have also been used to assess geographical variation in free ranging cetaceans (Perrin *et al.*, 1991; Weller, 1998; Díaz *et al.*, 2003; Ortega *et al.*, 2004).

There has been great economical and logistic effort devoted to studies of bottlenose dolphin populations; however, only a few integrate information over wide geographic scales. In Chapter One of this study I incorporate the available photo-identification catalogs of bottlenose dolphins along Mexican coasts to assess the phenotypic variability of the dorsal fin at different spatial scales. In Chapter Two, an evolutionary approach is used to interpret this variability, based on what is known about the origin, development and function of the dorsal fin in this dolphin species.

CHAPTER ONE

DORSAL FIN MORPHOLOGICAL DIFFERENTIATION OF BOTTLENOSE DOLPHINS (*Tursiops truncatus*) ALONG MEXICAN COASTS

1. INTRODUCTION

Most dolphin taxonomical research has been based on beached dead animals or bycatches, and in some cases on few specimens. Taxonomy has relied on skeletal measurements, parasitic load and stomach content, as well as on samples difficult to gather from free ranging animals (e.g. skin, blubber, muscle, or blood). Differentiation in all these characters among allopatric, parapatric, and sympatric dolphin populations are often thought to reflect genetic separation (Perrin, 1972; Walker, 1981; Duffield *et al.*, 1983; Perrin, 1984; Hersh and Duffield, 1990; Ross and Cockroft, 1990; Perrin *et al.*, 1991; Vidal, 1993; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Turner and Worthy, 1998; Weller, 1998; Wang *et al.*, 1999, 2000; Wells and Scott, 1999; Reeves *et al.*, 2002; Díaz *et al.*, 2003); however, due to the high variability, evidence is often contradictory. Based on morphological data, taxonomic and systematic research on the genus *Tursiops* has led to the description of up to 20 nominal species and subspecies (Wells and Scott, 1999). However, due to the uncertainty associated to the systematic value of much variation, only *Tursiops aduncus* and *T. truncatus* have been formally recognized in the recent literature (Perrin, 1984; Van Waerebeek, *et al.* 1990; Wiley *et al.*, 1994; Rice, 1998; Wells and Scott, 1999; Wang *et al.*, 1999, 2000; Perrin *et al.*, 2002; Reeves *et al.*, 2002).

Genetic differences have been found among different populations of bottlenose dolphins (Hoelzel *et al.*, 1998; Wang *et al.*, 1999; Caldwell *et al.*, 2001; Möller and Beheregaray, 2001; Parsons *et al.*, 2002; Krützen *et al.*, 2004; Segura, In progress); some authors suggest these differences may represent high potential for speciation in the genus (Natoli *et al.*, 2004); also, studies have revealed complex phylogeographic patterns highlighting the unresolved systematics of this genus (Wells and Scott, 1999; Reynolds *et al.*, 2000; Mead and Potter, 2004; Natoli *et al.*, 2004; Segura, In progress). Disagreement between molecular and morphological data in this genus is based on Mayr's (1969) biological species concept, in which the degree of morphological differentiation is not sufficient to define species boundaries; and theoretically, even when genetically distinct, species status can only be achieved by demonstrating reproductive isolation between genotypes.

Polyphenisms (phenotypic polymorphisms) (Stearns, 1989) in a species relate both to genetic (reaction norm) and environmental (natural selection) factors (Gotthard and Nylin, 1995). In traits whose functions arose as adaptations to new life conditions (e.g. aquatic for terrestrial ancestors) polymorphisms may be directly linked to the environment, and morphometric variations should be studied as function of ecological differences.

Due to the wide distribution of the genus *Tursiops*, great phenotypic variability is expected; in fact, some polymorphisms (physical characteristics, blood-tissue chemistry, and behavior) have already been related to environmental causes (food resources, parasites and diseases, or oceanographic characteristics) (Walker, 1981; Duffield *et al.*, 1983; Hersh and Duffield, 1990; Ross and Cockroft, 1990; Weller, 1991; Vidal, 1993; Perrin *et al.*, 1994; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Bazúa, 1997; Hoelzel *et al.*, 1998; Turner and Worthy, 1998; Weller, 1998; Rossbach and Herzing, 1999; Walker *et al.*, 1999; Caldwell *et al.*, 2001; Möller and Beheregaray, 2001; Reeves *et al.*, 2002; Díaz *et al.*, 2003).

Dorsal fin phenotypic differentiation has been found in geographically isolated bottlenose dolphin populations (Weller, 1998). This variation needs to be analyzed on smaller geographical scales in the context of biological and ecological data to provide insight into the mechanisms governing these geographically structured trends. In this chapter, dorsal fin phenotypic variability is investigated as a function of the environment from an evolutionary perspective; the hypothesis is that since biological and ecological factors are spatially variable, fin polymorphisms are thought to be geographically structured.

2. BACKGROUND

Detailed reviews on the biology of the bottlenose dolphin can be found elsewhere (Leatherwood and Reeves, 1990; Reynolds *et al.*, 2000; Perrin *et al.*, 2002); this section presents an overview on the evolution, distribution, adaptations, and morphology of the species. A review on the computational approaches for the assessment of polymorphisms is also presented.

2.1. Evolution and distribution of bottlenose dolphin

Fossil records of the genus *Tursiops* are relatively recent and there is only a moderate quantity of specimens (Barnes, 1990). Because most fossils have been found and described in Italy (*Tursiops osennae*, *T. capellinii*, *T. cortesii*, *T. brocchii*, *T. miocaenus*, and *T. astensis*), Pilleri (1985) proposed the Mediterranean as the center of origin of the genus; however, the oldest *Tursiops* fossil (approximately 5 Mya) was found in the Atlantic (North Carolina, USA), and fossil records from the Pliocene and Pleistocene suggest the genus was by then already as widely distributed as their Kentriodontid ancestor (Barnes, 1978, 1990).

Therefore, it is not clear where this genus emerged and how it dispersed to its current distribution; however, recent molecular data suggest coastal populations may have been founded by oceanic dolphins (Natoli *et al.*, 2004).

Modern bottlenose dolphins are found practically in all worlds' oceans between 40 degrees north and south (Leatherwood, 1979; Carwardine, 1995; Wells and Scott, 1999; Reeves *et al.*, 2002); however, there are reports of more northern sightings (Orr, 1963; Wolf *et al.*, 1987; SWFSC, 2000). Their distribution can be either continuous or discrete and includes tropical and temperate waters (Scott *et al.*, 1996). They use a great variety of pelagic and coastal habitats, such as open and closed seas, bays, lagoons, channels, and even rivers (Hoese, 1971; Leatherwood, 1975, 1979). The wide geographic distribution and the large depth range they inhabit reflect their great adaptability (Wells *et al.*, 1980, Duffield *et al.*, 1983; Perrin, 1984; Kenney, 1990; Mead and Potter, 1990; Ross and Cockroft, 1990; Wells *et al.*, 1990; Ballance, 1992; Curry and Smith, 1997).

2.2. Adaptations, morphology, and polymorphisms

Cetaceans share some physiological and anatomical synapomorphic characters with the rest of mammals. Although some features are reminiscent (e.g. facial hair, olfactory nerves, and pelvic bones), these have been clearly inherited from their terrestrial ancestors (Barnes, 1990; Berta and Sumich, 1999; Hoelzel, 2002). A counter-current blood system, the *rete mirabile*, is used in thermoregulation (Castellini, 2002). Except for the dorsal fin, most cetacean adaptations to the marine environment (fusiform body, short neck, subcutaneous blubber, pectoral and caudal fins) are convergent in other groups of marine mammals such as sirenians (e.g. manatee) and pinnipeds (e.g. seals) (Barnes, 1990).

Because of their terrestrial origin, the dorsal fin of cetaceans is considered a derived trait (although absent in some species, e.g. *Lissodelphis* spp.). Unfortunately, there are no fossil records of this structure, since its fibrous composition prevents fossil preservation.

Compared to other delphinids, the bottlenose dolphin is relatively more robust, has a wider skull and shorter rostrum, a marked angle between the melon and the rostrum, longer flippers and a moderately higher and more falcate dorsal fin (Reeves *et al.*, 2002); these traits tend to be highly variable. Total length of mature specimens ranges between 2.4 and 3.8 m (Reeves *et al.*, 2002) and seems to be inversely correlated to water temperature (Perrin, 1984; Hersh and Duffield, 1990; Ross and Cockroft, 1990; Barros, 1991; Wells and Scott, 1999). Coloration pattern is formed by gray shades, being darkest at the back and lighter over the ventral portion of the body with no clear dorso-ventral demarcation (Figure 1).

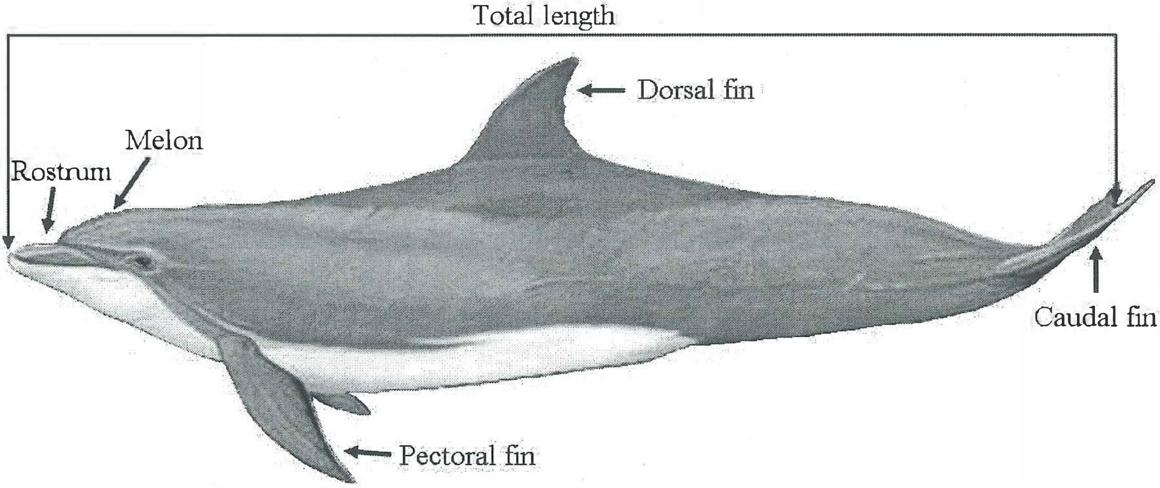

Figure 1. Schematic of a typical bottlenose dolphin (*Tursiops truncatus*) (modified from the Whale and Dolphin Conservation Society).

Figura 1. Esquema de un tursión típico (*Tursiops truncatus*) (modificada de Whale and Dolphin Conservation Society).

The existence of two ecotypes (coastal and oceanic) has been reported worldwide from phenotypic and genetic data (Walker, 1981; Perrin, 1984; Hersh and Duffield, 1990, Hoelzel *et al.*, 1998; Rossbach and Herzing, 1999; Natoli *et al.*, 2004). Oceanic animals generally grow larger and darker, and their pectoral fins are smaller than coastal dolphins; other differences have been found in cranial morphology, mainly in jaws and teeth which have been associated to their different feeding ecology (Mermoz, 1977; Walker, 1981; Hersh and Duffield, 1990; Hersh *et al.*, 1990a; Ross and Cockroft, 1990; Van Waerebeek *et al.*, 1990; Vidal, 1993; Gao *et al.*, 1995; Turner and Worthy, 1998). Although genetic data support limited gene flow between ecotypes in some regions, they are considered the same species (Hoelzel *et al.*, 1998; Caldwell *et al.*, 2001).

2.3. Computational approaches for assessment of polymorphisms

Polymorphisms have been important cues to suspect species subdivisions. Weller (1998) analyzed dorsal fin photographs of free ranging bottlenose dolphins to assess the degree of morphological variation among eight coastal localities on a global scale (California, Texas, Baja California, Costa Rica, Isla de Cocos, Brazil, Argentina, and New Zealand) finding significant statistical differences among Texas, Brazil, Argentina, and Costa Rica. This study highlights the degree of dorsal fin polymorphisms in the species and suggests adaptive explanations for these differences.

Different computer-assisted approaches have been used to quantitatively analyze the shape in traits of marine mammals, for example:

1) Geometric morphometrics have been tested on 3-D images of marine mammals (Hiby and Lovell, 1990; Higa *et al.*, 2002) with software like TpsDig v1.30 (Rohlf, 2000); however, working in difficult field conditions with free-ranging animals makes obtaining good pictures from all angles very difficult. Also, because most dorsal fin images used in photo-identification are two-dimensional (2-D), fixed landmarks to construct 3-D images are not easily identifiable.

2) Fourier analyses have also been used to describe shapes without using sets of homologous landmarks (James and McCulloch, 1990); this procedure captures fine details in shapes making image analysis more accurate. Nieda (1999) used a variant of this method (Fast Fourier Transforms) to analyze diffraction patterns of dorsal fin images in several dolphin species. This technique successfully differentiated among species. Intra-specific comparisons were made on a single population of bottlenose dolphins, using some individuals from Tamiahua lagoon (also used in this study). Results showed that 86% of these dolphins differed anywhere from 1 to 6%, leading to a maximum difference of 61% (one dolphin with half fin missing) (Nieda, 1999); however, no criteria were used to standardize data or image quality; also, images were not selected on a random basis and had to be substantially modified first. Thus this technique is very time consuming and prone to subjective biases.

3) Fin Scan software (Kreho *et al.*, 1999; Araabi *et al.*, 2000) uses curvature functions to construct low and high level string representations of the trailing edge of the dorsal fins; then the program calculates dissimilarities to compare among individuals. Interaction with user is minimum and it is has been found to be accurate. However, regardless of the

potential to assess morphological differences, Fin Scan was primarily designed to help in photo-identification tasks, such as sorting and matching individuals.

4) Finally, analyses of measurement ratios have already demonstrated dorsal fin differentiation in bottlenose dolphins (Weller, 1998). The program Fin Morphology (Weller, 1998) is a computer routine specifically developed to measure angles and distances in dorsal fins. Interaction with user is required, but accurate measurements can be gathered very fast.

3. HYPOTHESIS

- Variation of dorsal fin morphology in bottlenose dolphins is geographically structured at different spatial scales.

4. OBJECTIVE

- To assess the degree of dorsal fin polymorphisms along Mexican coasts and compare it among localities and among regions.

5. STUDY AREAS

Detailed descriptions of the studied locations in Mexico are presented elsewhere (Balance, 1987; Salinas and Bourillón, 1988; Acevedo, 1989; Heckel, 1992; Schramm, 1993; Silber *et al.*, 1994; Silber and Fertl, 1995; Reza, 2001; Delgado, 2002; Guzón, 2002; Morteo, 2002). In this section I summarize relevant biological and ecological aspects of the dolphins in each locality, such as: distribution, abundance, ranges and movements, habitat use, school size, and reproductive seasons. Feeding habits are detailed in Morteo *et al.* (In progress). Locations are grouped by region: Pacific Ocean, Gulf of California and Gulf of Mexico (Figure 2).

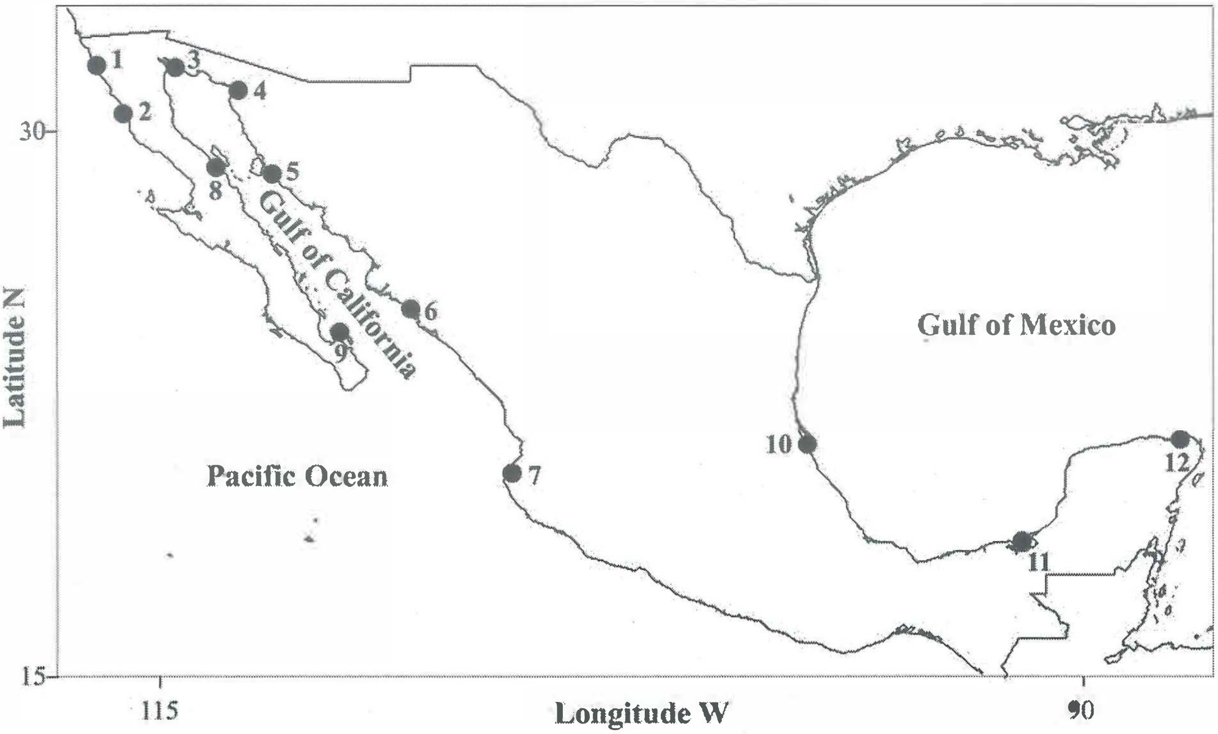

Figure 2. Study areas. 1) ENS = Ensenada, Baja California; 2) SQ = San Quintin, Baja California; 3) UGC = Upper Gulf of California, Sonora; 4) SJ = Bahia San Jorge, Sonora; 5) BK = Bahia Kino, Sonora; 6) SM = Bahia Santa Maria, Sinaloa; 7) BB = Bahia Banderas, Jalisco; 8) BLA = Bahia de los Angeles, Baja California; 9) LP = La Paz, Baja California Sur; 10) TA = Tamiahua, Veracruz; 11) TE = Terminos Lagoon, Campeche; 12) HO = Holbox, Quintana Roo.

Figura 2. Áreas de estudio. 1) ENS = Ensenada, Baja California; 2) SQ = San Quintín, Baja California; 3) UGC = Alto Golfo de California, Sonora; 4) SJ = Bahía San Jorge, Sonora; 5) BK = Bahía Kino, Sonora; 6) SM = Bahía Santa María, Sinaloa; 7) BB = Bahía Banderas, Jalisco; 8) BLA = Bahía del los Ángeles, Baja California; 9) LP = La Paz, Baja California Sur; 10) TA = Tamiahua, Veracruz; 11) TE = Laguna de Términos, Campeche; 12) HO = Holbox, Quintana Roo.

5.1. Eastern Pacific Ocean

5.1.1. Ensenada, Baja California

Bottlenose dolphins in this area have been studied at least since the early 80's (Hansen, 1983; Espinosa, 1986, Sandoval, 1987; Caldwell, 1992; Defran *et al.*, 1999; Guzón, 2002). Based on individual identification, these animals have been estimated to travel at least 470 km between Ensenada (northern Baja California, Mexico) and Santa Barbara (California, USA), suggesting they may belong to a single widespread population (Defran *et al.*, 1999). No strong site fidelity or seasonal movements are evident in Ensenada; however, there is a slight increase in relative abundance and nursing groups during summer (Guzón, 2002). The most reliable abundance estimate ranges between 205–306 dolphins for the California Coastal Stock which includes at least some dolphins from Ensenada (NOAA, 2000). Mean school size for this area has been estimated between 7.8 and 16.4 dolphins (Espinosa, 1986; Sandoval; 1987; Guzón, 2002). Dolphins preferred the northern and central portion of the coastline inside Bahia Todos Santos, and no dolphins were sighted on the southern shore. No detailed information exists on the feeding habits of bottlenose dolphins in Ensenada; however, Hanson and Defran (1993) documented possible prey preferences on bottlenose dolphins from San Diego; Guzón (2002) used this evidence to relate spatial and temporal distribution of dolphins in Ensenada to the abundance of Queenfish (*Seriphus politus*) and White Croacker (*Genyonemus lineatus*).

5.1.2. San Quintin, Baja California

Bottlenose dolphins in San Quintin have not been studied in detail, and the available information comes from a few studies carried out in 1990, 1999–2000 and 2001 (Caldwell, 1992; Morteo, 2002; Morteo *et al.*, 2002). Based on individual identification, Caldwell (1992) found that these dolphins may be considered a separate population from Ensenada. Dolphins identified in San Quintin are thought to be part of a larger population distributed southward along the coast. Although the photo-identification catalog analyzed by Morteo (2002) contained 220 different dolphins, there are no accurate abundance estimates, and the real distribution of this population remains unknown. Reports on movements and site fidelity documented slightly evident patterns through an increase in relative abundance during summer, and few individuals were resighted in the area several years later (Morteo, 2002; Morteo *et al.*, 2004). Most nursing groups were sighted during summer; however, no seasonal trend was evident (Morteo, 2002). Mean school size has been estimated between 6.3 and 14.3 dolphins (Caldwell, 1992; Morteo, 2002; Morteo *et al.* 2002); however, Morteo *et al.* (2004) discussed a bias in school size estimates caused by a bimodal trend due to larger aggregations in feeding zones. No detailed information is currently available on the feeding habits of these dolphins; however they have been seen foraging for a few hours close to the entrance (Morteo *et al.*, 2004) or inside San Quintin bay (Morteo *et al.* 2002).

5.1.3. Bahia Banderas, Jalisco

During 1982-1985 the bottlenose dolphin was found throughout the year, all around the bay, and was the second in occurrence among dolphin species (Salinas and Bourillón, 1988). No abundance estimations were reported; however, more than 200 different individuals have been identified through photographic methods (Rodríguez *et al.*, 2003). Their distribution area was estimated to be 55.7 km^2 with a marked preference for the northwestern portion of the bay, where all feeding activities and most calves occurred (Salinas and Bourillón, 1988). Shallow water (<50 m) was preferred by these dolphins, which may influence group size (Salinas and Bourillón, 1988). New data (1998-2004) obtained during tourist whale-watching surveys partially support time-space distribution trends, also suggesting residence patterns for some of these animals (Morteo *et al.*, In progress). Mean group size is 6.0 dolphins, where single dolphins are frequent during winter and the largest aggregations (up to 30 dolphins) occur during spring; also, nursing groups are generally larger (5.3 – 9.2 dolphins) than feeding aggregations (4.4 dolphins) (Salinas and Bourillón, 1988). Some slight seasonal movement patterns are apparent and, most births occur during fall-winter. Feeding records of these dolphins are scarce but commonly associated to spotted dolphins (*Stenella attenuata*), and include jacks (*Caranx hippos*) and mackerels (*Scomber japonicus*) (Salinas and Bourillón, 1988).

5.2. Gulf of California

5.2.1. Upper Gulf of California, Sonora

The bottlenose dolphin has been reported along the Upper Gulf of California; however, no formal population studies have been published for this area (Silber *et al.*, 1994; Silber and Fertl, 1995). Silber *et al.* (1994) reported 140 sightings of this species along the upper gulf during 1986–1989, from both marine and aerial surveys. Groups averaged 10.1 dolphins. No temporal trends were reported; however, a spatial pattern showed these dolphins were the first in occurrence in waters less than 10 km offshore and below 10 m depth, mostly over the eastern coast. Also, sea surface temperature and water clearness were lowest for bottlenose dolphin sighting locations. This species was the only marine mammal seen in the Upper Gulf of California. Silber and Fertl (1995) report that density of dolphins was higher inside the river than in most other areas of the upper gulf and it did not appear to diminish as far as 12 km inland from the river mouth. Although some mothers and their calves have been observed during opportunistic sightings while looking for vaquita (*Phocoena sinus*) (L. Rojas, Pers. Comm.[1]), no detailed information is currently available on calving season, and feeding habits of these dolphins; however, Silber and Fertl (1995) reported beach-feeding behavior to prey on mullet (*Mugil* sp.).

5.2.2. Bahia San Jorge, Sonora

Dolphins in this shallow location were studied by Orozco (2001) during 1999–2000. A seasonal spatial pattern was evident with dolphins entering the bay during summer and fall to feed and reproduce. Based on photo-identification data these dolphins are thought to be part of a larger population with no apparent residence patterns; however, seven dolphins (3% of the individuals) were found in the area throughout the study. Although Orozco (2001) identified 217 different individuals, no abundance estimate has been made. Mean group size ranged between 7.5–38.3 dolphins with no seasonal trends. Information on feeding habits comes from opportunistic fish samples and dolphin interaction with fishing gears.

5.2.3. Bahia de los Angeles, Baja California

No investigation has been carried out on the biology of the bottlenose dolphin (Tershy *et al.*, 1990; Tershy *et al.*, 1991, Tershy, 1992; Vidal *et al.*, 1993). Breese and

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[1] Lorenzo. Rojas, National Program for Marine Mammal Research, INE (Ensenada, Baja California, Mexico).

Tershy (1993) reported no seasonal trends in the 715 sightings of this species during 1985–1986, and reported it as the second most abundant dolphin in the area. Inshore groups (<5 km from shore) averaged 8.5 dolphins, while mean groups size was 110 for offshore dolphins. Current work in Canal de Ballenas (Ladrón de Guevara and Heckel, 2004) has recorded and photographed the species on several occasions; most of these sightings have occurred around the smaller islands or close to shore. According to interviews with local fishermen, bottlenose dolphins in Bahia de los Angeles are commonly seen in small groups (< 10 dolphins) mainly around the sand bar close to the mouth and inside the bay at the southwestern protected areas. No detailed information is currently available on calving season or feeding habits; however, there is an opportunistic record of night feeding on the western coast inside the bay; dolphins presumably preyed on mullet (*Mugil* sp.) (author's personal observation).

5.2.4. Bahia Santa Maria, Sinaloa

Surveys in this area were carried out during 1999–2000 (Reza, 2001) and there is another research in progress (E. Carrillo[2], Pers. Comm.). Bottlenose dolphins use this bay mainly for feeding and reproduction, and most were found in the central-south portion. Abundance estimates for these dolphins range between 691 and 1,115 animals, and show slight evidence of seasonality with higher abundance during the rainy season (May-October). Photo-identification data suggest that most dolphins in the area were transient and they may occur on a seasonal basis; however, 12 dolphins (16.7% of the individuals) were found throughout the study. Mean school size ranged between 7.8 to 10.58 animals

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[2] Edna Carrillo, MSc student in Marine Ecology at CICESE (Ensenada, Baja California, Mexico).

with no evident seasonal trends; however, most nursing groups were found during the rainy season and mostly during July. Information on feeding habits of these dolphins consists in anecdotic reports of fishermen and direct observation (Reza, 2001).

5.2.5. Bahia Kino, Sonora

Bottlenose dolphins in Bahia Kino were individually identified during 1983–1984. Ballance (1987) reported that most of these animals were not resident and only one was consistently sighted in the area. The majority of these dolphins (75%) were sighted inside the bay; although some were seen in the adjacent estuarine systems. No abundance estimations exist for this population; however, Ballance (1987, 1990, 1992) reports that most dolphins in the area (155 different individuals) were identified by the end of the study. No evident movement patterns were acknowledged from survey data and no information is available on calving season. Mean school size was estimated as 15 animals (Ballance, 1987, 1990, 1992) and information on the feeding habits of dolphins in the area comes from stomach contents of a single specimen (Ballance, 1987).

5.2.6. La Paz, Baja California Sur

A number of studies have been carried out on the ecology and biology of bottlenose dolphins in La Paz (Michel, 1986; Acevedo, 1989; Alba, 1997; Díaz, 2001; Rojo, 2002; Valadez, 2002). Acevedo (1989) first identified a possible resident population with a 87 km^2 home range; several feeding zones as well as transient routes for these animals have also been documented (Acevedo, 1989; Díaz, 2001; Valadez, 2002). During a six-year study, Valadez (2002) identified 114 individuals with three residence patterns: transient dolphins (18.4%) were observed only once during the study; indirect residents (57.9%)

were observed only during one year; and direct residents (23.7%) were sighted up to six years. Abundance estimates from several years with different models range between 26 and 180 dolphins; however, 40 to 85 dolphins is considered a more accurate estimate (Acevedo, 1989; Díaz, 2001; Valadez, 2002). Rojo (2002) found that calving was evenly distributed across the year, with a slight increase during summer. Mean group size ranged between 12–26 dolphins and larger aggregations were found on feeding grounds (Acevedo, 1989; Díaz, 2001). Interactions with boats were frequent, but not with fishing gears. Feeding habits of these dolphins are not detailed, and most studies suggest mullet (*Mugil* sp.) as common prey (Acevedo, 1989; Díaz, 2001; Valadez, 2002).

5.3. Southern Gulf of Mexico

5.3.1. Tamiahua Lagoon, Veracruz

Bottlenose dolphins in Tamiahua Lagoon were individually identified during 1990–1992. Many of these dolphins were found outside the lagoon, although they use it frequently to feed and reproduce (Schramm, 1993). Abundance estimates were between 21 and 58 dolphins and at least part of the population (32%) was present year-around (Heckel, 1992; Schramm, 1993). The studies also report a decrease in relative abundance during the northerly wind season (November-February) compared to the rainy season (July-October) (Heckel, 1992; Schramm, 1993). Reproductive peaks were observed during spring and fall, and school size varied seasonally with mean values between 2.0 and 5.3 dolphins (Heckel, 1992). There was no information on specific feeding habits of these dolphins; however, Heckel (1992) and Schramm (1993) summarized general data from other studies in the Gulf of Mexico, showing a wide range of prey species.

5.3.2. Terminos Lagoon, Campeche

Escatel (1997) first surveyed this area to photo-identify bottlenose dolphins; Delgado (2002) rearranged the data and completed the catalog during 1995-1998. In total, 1,987 dolphins were identified, and many new individuals were discovered on every survey. Recapture rates were relatively low, and transient animals were observed to travel at least 320 km in 1,404 days; however, one individual was consistently found in the lagoon for up to ten years. Bottlenose dolphins were found everywhere in the lagoon; common routes were described on both its entrances, and these were preferred on a seasonal basis. Several behaviors were recorded inside this lagoon, but feeding was the most common. Delgado (2002) reports higher relative abundances during the rainy season (June-September) and lower during the windy season (October-January). Mean school size was 12.35 animals with no seasonal trends, and dolphins frequently exchanged group membership; however, nursing groups were significantly larger. Most calves and neonates were observed during the dry season (February-May). Feeding habits of these animals were directly recorded during day and night and interactions with boats and fishing gear were common.

5.3.3. Yalahau Lagoon (Holbox Island), Quintana Roo

Lechuga (1996) carried out photo-identification surveys during 1993–1994, and Delgado (1996, 2002) sampled this location during 1994–1998. A total of 310 dolphins were identified by Lechuga (1996), and 344 by Delgado (2002), although no comparisons are available between both these catalogs. New individuals frequently appeared on every survey, and photo-identification data from Delgado (2002) showed that a few animals (1%) were resident during a three-year period, and some others (1%) revisited the area three years later. In both studies, most dolphins were commonly sighted in two areas close to the shore outside the lagoon (north of Holbox Island); also, one dolphin identified by Delgado (2002) was found to have moved 800 km west towards Campeche in 247 days; thus there appears to be a single widespread population in the southeastern Gulf of Mexico. Relative abundance was higher during the rainy season (June-September) and lower during the dry season (February-May), and most calves and neonates were observed early in the windy season (October-January) and only inside the lagoon. Delgado (2002) also reported no reproductive behavior during February-April. Group membership frequently changed and mean school size was between 7.6–9.3 animals (Lechuga, 1996; Delgado, 1996, 2002). School size was larger during the rainy months but there was no seasonal difference; however, nursing groups were significantly larger (Delgado, 1996). Dolphin activities in the area were variable, but feeding was by far the most common observed activity; interactions with boats and fishing gear were also frequent (Delgado, 2002).

6. METHODS

The following diagram (Figure 3) is presented to show an overview of the sequence of procedures to assess the morphological differentiation of the dorsal fin in the bottlenose dolphin.

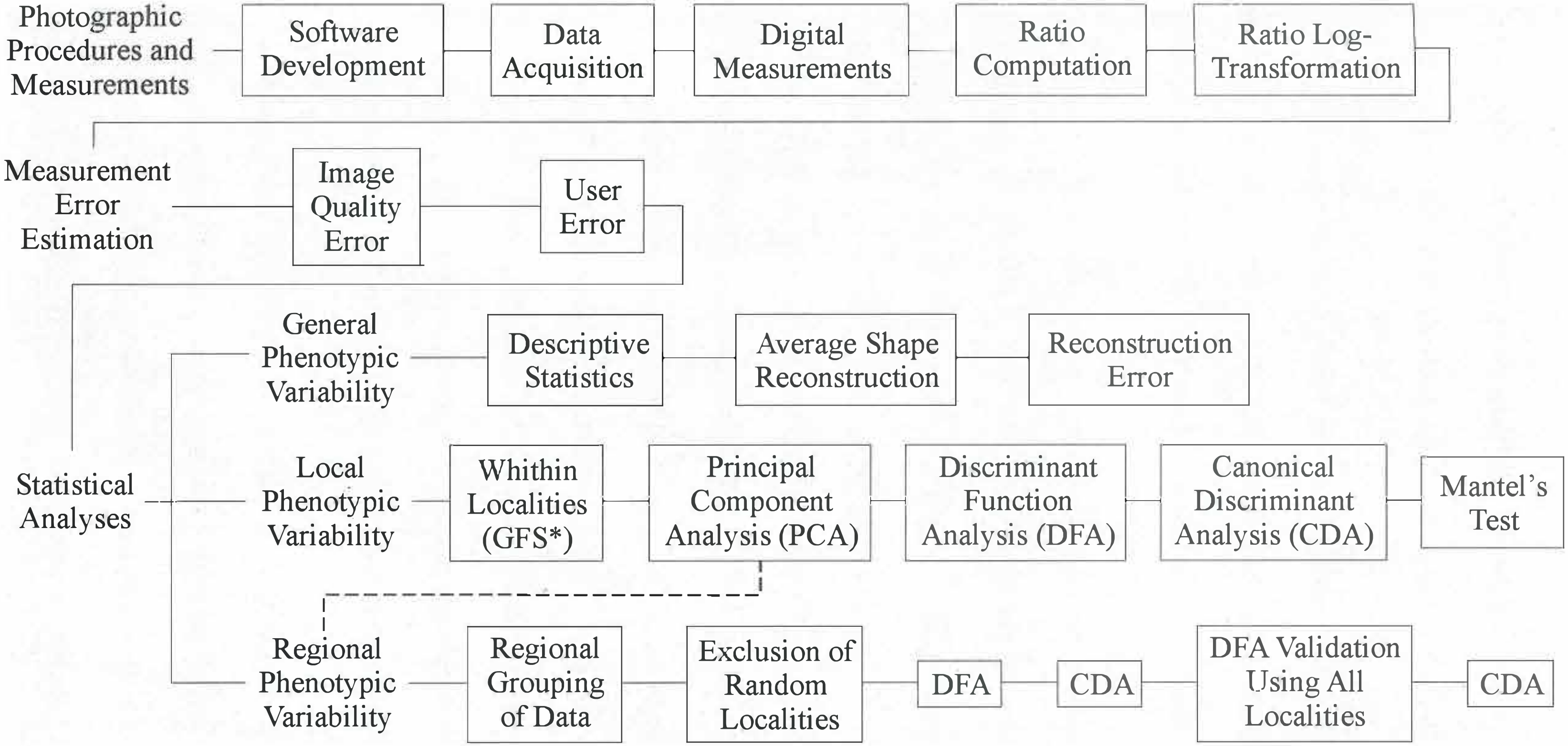

Figure 3. Diagram of mathematical and statistical procedures for the assessment of dorsal fin morphological differences in the bottlenose dolphin. Straight lines show sequential steps; dashed line shows data input required for subsequent analysis. *=General Fin Shape Index (see 6.4.2 Local phenotypic variability).

Figura 3. Diagrama de procedimientos matemáticos y estadísticos para la evaluación de diferencias morfológicas en la aleta dorsal de los tursiones. Las líneas continuas muestran pasos secuenciales; la línea punteada muestra datos requeridos para análisis subsecuentes. *= Índice General de la Forma de la Aleta (ver 6.4.2. Variabilidad fenotípica local.).

6.1. Data acquisition

Dorsal fin images were obtained from high quality photographs of 327 bottlenose dolphins from 12 locations along Mexican coasts (Figure 2).

Image quality was crucial for the analysis, thus the best picture (printed or digital), negative or slide from each individual was selected from larger photo-identification catalogs according to the following criteria (modified from Weller, 1998):

1. Images must come from animals judged as physically mature, since ontogenetic changes of the dorsal fin in bottlenose dolphins are unknown.
2. Dorsal fins must be entirely visible, including the front and rear insertions in the dorsum.
3. Dorsal fins must be orthogonal to the lens axis (non-parallaxed), to prevent photographically induced distortions.
4. Dorsal fins must be as complete as possible, to avoid biases caused by non-natural forms (truncated, sliced and missing fins).
5. Fins should be at least one ninth the size of the frame, to allow for good resolution.
6. Pictures should come from individuals sighted in different schools, to reduce the possibility of animals being genetically related (heritability of this trait is unknown).

Images not fulfilling at least the first four criteria were excluded from the analysis. Once candidate images were obtained, approximately 30 different individuals were randomly selected from each locality. These randomly chosen images were then compared in each locality to avoid potential duplicates in samples (which did not occur). Because most of these pictures were taken less than 1 km offshore, individuals were assumed to belong to the coastal form of the species (see appendix A for confounding factors).

6.2. Photographic procedures and measurements

Some negatives and slides were projected and traced by hand on a paper sheet with a 10 x 17 cm rectangle following Defran *et al.* (1990); these tracings were digitized with a standard scanner at 400 dpi resolution. Due to their small size, printed pictures were digitized with a standard scanner at 600 dpi; and negatives (or slides) were converted at 2000 dpi, with a CanoScan FS-4000-US digitizer.

All selected images were processed and measured by a single trained operator following Weller (1998). A semi-automated software (Fin Shape v1.3) was developed in C++ (Morteo *et al.*, In progress). This program was based on Elsberry's[3] (Weller, 1998) and was used to systematically measure dorsal fin silhouettes of dolphins. Eleven measurements were obtained from each of the 327 dorsal fins including fin's surface area (Figure 4). Measurements began from the tip and the base of the dorsal fin. Following Weller (1998), the tip (A, Figure 3) was the most distant point from the frontal insertion of the fin in the dolphin's back. The base of the fin (B, Figure 4) was defined in the region where the contour of the back is interrupted by the angular change of the dorsal fin.

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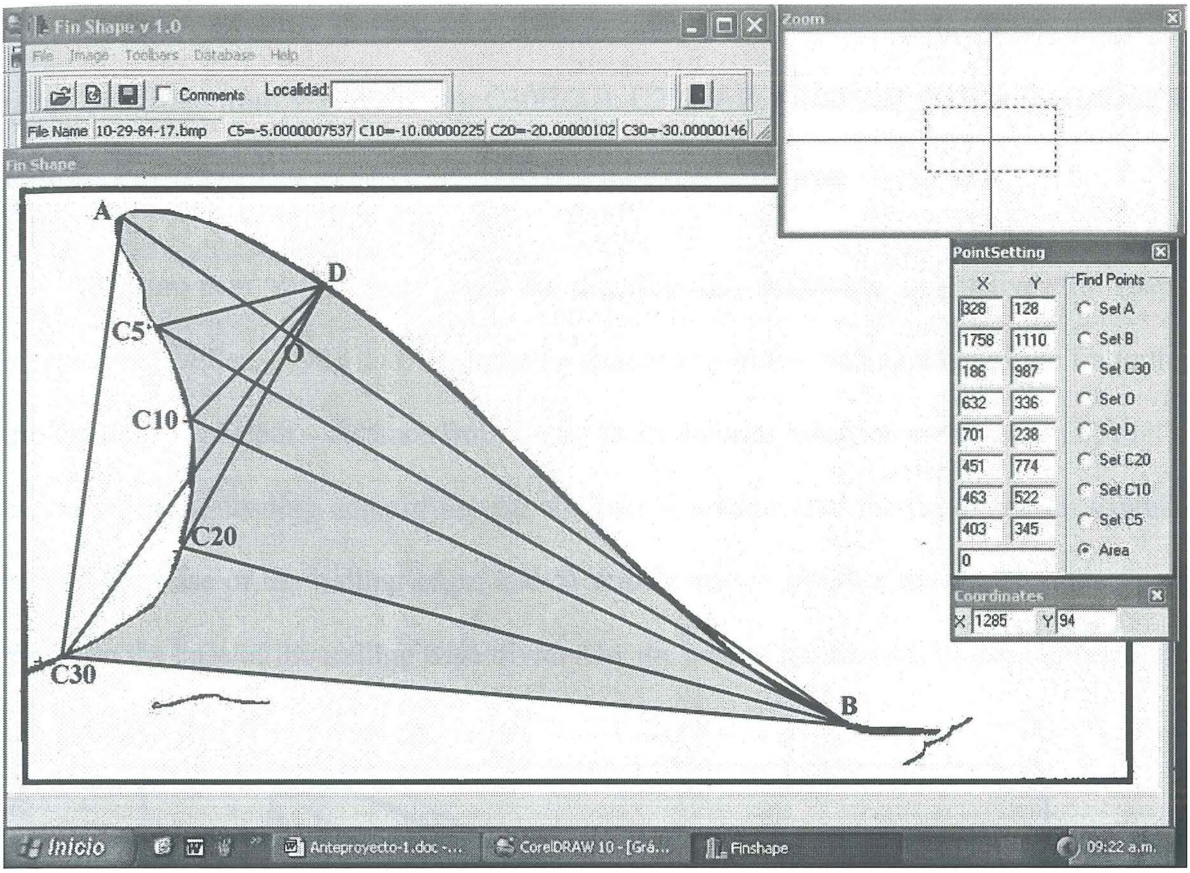
[3] Wesley Elsberry, Information Project Director at the National Center for Science Education (Oakland, CA, USA).



☐ Comments Localidad

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186	987	○ Set C30
632	336	○ Set O
701	238	○ Set D
451	774	○ Set C20
463	522	○ Set C10
403	345	○ Set C5
0		● Area

Coordinates

X 1285 Y 94

Figure 4. Software to acquire morphological landmarks and measurements of fin shape. A=Tip; B=Base. Points C5, C10, C20 and C30 indicate angles respect to line AB. Point D is the intersection of a line departing from C30 with the fin's leading edge, this line is also perpendicular to line AB. Point O is the intersection of lines AB and C30D. Fin's surface area (shaded) was calculated considering line C30B as the limit.

Figura 4. Programa para obtener las mediciones morfológicas de la forma de la aleta. A=Punta; B=Base. Los puntos C5, C10, C20 y C30 indican ángulos con respecto a la línea AB. El punto D es la intersección de una línea que parte de C30 con el borde anterior de la aleta, esta línea también es perpendicular a la línea AB. El punto O es la intersección de líneas AB y C30D. El área de la superficie de aleta (sombreado) fue calculada considerado como límite la línea C30B.

The computer program automatically drew several additional lines and the user defined their length by marking the intersections on the trailing edge of the fin (Figure 4). In order to maximize precision, the unit of measurement was the pixel.

Measurements in Figure 4 were used to calculate 11 indexes through the following ratios (modified from Weller, 1998): C30B/AB, C20B/AB, C10B/AB, C5B/AB, C30D/AB, C20D/AB, C10D/AB, C5D/AB, AO/OB, DO/C30O, AC30^2/area.

Measurement ratios were used to describe the following qualitative fin shape parameters (Weller, 1998): 1) Base length – distance from the leading edge of the fin to the trailing edge; 2) Depth – distance from fin tip to the anterior insertion on the body; 3) Foil – curvature of the leading edge of the fin; 4) Rake – amount that the tip of the fin extends beyond the base of the trailing edge; and 5) Aspect ratio – square distance from the tip of the fin to the base of the trailing edge divided by the area of the fin (AC30^2/area)(Figure 5).

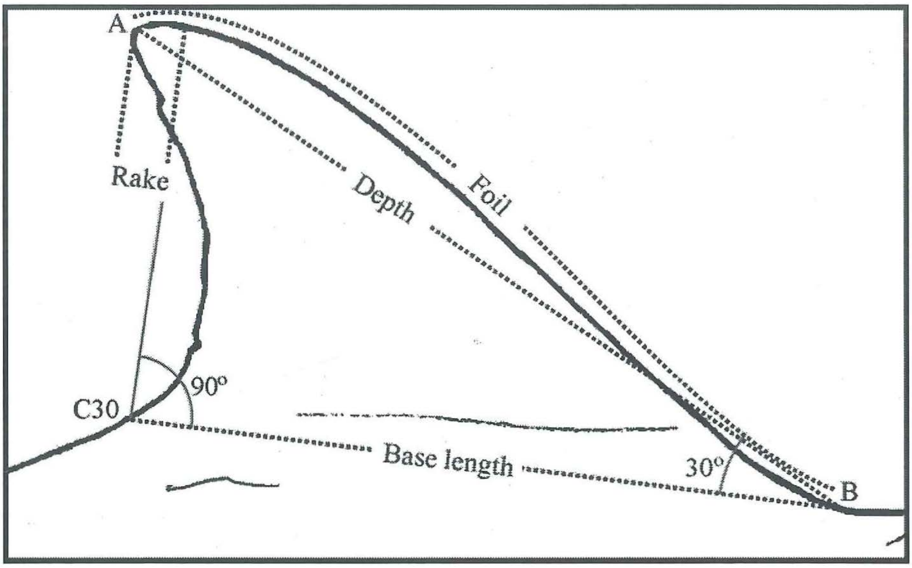

Figure 5. Qualitative fin shape parameters. A = Tip; B = Base. Dotted lines show shape parameters and light solid lines are guidelines.

Figura 5. Parámetros cualitativos de la forma de la aleta. A = Punta; B = Base. Las líneas punteadas muestran los parámetros y las líneas sólidas son las guías.

6.3. Measurement error estimates

The accuracy of measurements is highly dependent on fin size in the original photograph and the image resolution. Thus all scanned images were cropped to maximize fin size and measurement errors (in pixels) were calculated as a percentage of resultant image size (in pixels). This procedure allowed for error standardization according to graphic quality.

Although computerized, the measurement method was prone to human error; this was assumed to be caused by either user's visual accuracy, precision while acquiring coordinates with the "mouse", and/or fatigue. The first two errors were estimated by repeatedly measuring the same image and comparing measurements; variations were considered errors and these were averaged for each individual fin (Morteo *et al.*, In progress). To prevent fatigue, measurement sessions were accomplished in 1 hour periods followed by a 30 minute pause and no more than 4 sessions per day.

There was also a chance that errors occurred while tracing fins from photographs to tracings on paper. Therefore, several tracings from the same fin were measured for different random individuals, and average errors were calculated. These errors were not assessed when original images (digital pictures, negatives or slides) were unavailable.

6.4. Statistical analyses

6.4.1. General phenotypic variability

Variability in dorsal fin morphology was first assessed through descriptive statistical analysis of measurement ratios. Median ratio values were used to construct representative fin contours for each locality. Contours were standardized by fixing the length of measurement AB to 10 relative units, thus all contours were equally scaled. The remaining representative measurement values were obtained by mathematically solving related ratios (Morteo *et al.*, In progress). All of these measurements were used to calculate point coordinates using trigonometry (Morteo *et al.*, In progress). Error for design construction was estimated by comparing measurements obtained via ratios and trigonometrically; these differences were expressed as percentages of segment AB. Data dispersion was calculated as quartiles represented by bars and ellipses around median values of each point.

6.4.2. Local phenotypic variability

Local phenotypic variability was first assessed through a rarefaction-like analysis of the contribution of each dorsal fin to the total variance in each locality. Coefficients of variation (COV) from each log-transformed ratio were computed for every fin to standardize variability. These eleven COVs were later averaged for each individual to obtain an index of variability for the general fin shape (GFS). The proportional contribution of each individual GFS to the overall local variability was calculated by cumulative inclusion of randomly selected fins. This procedure also allowed the estimation of minimum sample size, indicated by the asymptotic inflection of the curve.

Quantitative analyses of geographic variation were performed on log-transformed ratios; the correlation matrices were examined among all variables to verify that covariances inside the groups were equivalent (Sei and Puri tests). Since some measurement ratios were highly correlated, a Principal Component Analysis (PCA) was performed to reduce the number of variables. Factors were tested (Kolmogorov-Smirnof) for multivariate normality; variances and covariances from these factors were verified to be homogeneous and correlation between means and variances was also verified across groups.

Individual scores from the PCA were later used to perform a Discriminant Function Analysis (DFA) to identify the descriptors that better discriminate among different localities (tolerance = 0.01) (Kachigan, 1991; Manly, 1994; Grimm and Yarnold, 1995). To determine separation among samples a non-stepwise Canonical Discriminant Analysis (CDA) was performed using a default tolerance of 0.01. All data were analyzed using Statistica v6.0 (Stat Soft™). Also, p values in multiple comparisons were later tested for significant differences by using the sequential Bonferroni correction (Rice, 1989).

Square Mahalanobis distances (SMD) from DFA were used to construct a Single Linkage Cluster Analysis dendrogram; this graphic represents dorsal fin morphometric dissimilarities among dolphins from different localities. Dissimilarities were calculated as percentages (100*linkage SMD/Max SMD). SMD were also used to test the Isolation/Differentiation by Distance (IDD) model. Mantel's one-tailed tests (α=0.05, Monte Carlo method and 10,000 permutations) with Pearson's correlation were performed to verify if morphometric variations were correlated with geographic distances (Perrin *et al.*, 1994). Because of the larger sample, this assessment was made only for the Pacific and Gulf of California using Excell's (Microsoft Office XP™) add-in XLStat-Pro v7.0 (Addinsoft™). Due to the coastal nature of these dolphins, geographic distances among localities were calculated following the coast line.

6.4.3. Regional phenotypic variability

Data were regrouped according to region and a new non-stepwise DFA (tolerance = 0.01) was performed using individual scores from the regrouped locations. Separation among regions was determined using a non-stepwise CDA (tolerance = 0.01). The model was validated by excluding data from three randomly selected localities (Tamiahua Lagoon, Bahia San Jorge, and San Quintin), and examining if they clustered in the correct region.

7. RESULTS

7.1. Data overview

Data obtained from the 12 available photo-id catalogs along Mexican coasts are summarized in Table I. Most catalogues contained data from three years or less; except for Bahia de los Angeles and the Upper Gulf of California, the fins used in this study account for less than half the individuals in each catalogue. It is also important to mention that for any particular location not all fins came from different schools.

Table I. Summary of data sources and sample size. Abbreviations for study areas follow those in Figure 2. Image format is classified by reliability from digital pictures (D), digitized negatives or slides (N), scanned pictures (P) and scanned traces (T). N.A.= not available.

Tabla I. Fuente de datos y tamaños de muestra. Las abreviaciones para las áreas del estudio siguen aquéllas en la Figura 2. El formato de la Imagen es clasificado con base en la confiabilidad en el siguiente orden: fotos digitales (D), negativos o diapositivas digitalizadas (N), fotos (P) y trazos (T) digitalizados. N.A. = no disponible.

Source(s)	Study area	Duration of photo-id effort (years)	Number of individuals in catalog	Sample size (%)	Image format	Number of pods
Espinosa (1986), Defran *et al.* (1999), Guzón (2002)	ENS	3	144	27 (19%)	N, T	20
Caldwell (1992), Morteo (2002), Morteo *et al.* (2004)	SQ	2	220	29 (13%)	N, T	16
Guzón (unpublished)+	UGC	< 1	28	23 (82%)	D	3
Orozco (2001)	SJ	1	217	24 (11%)	N, T	N.A.
Balance (1987, 1990, 1992)	BK	2	155	30 (19%)	N, T	17
Reza (2001)	SM	1	637	25 (4%)	N	N.A.
Rodríguez *et al.* (2003)	BB	6	60	28 (46%)	D	12
Ladrón de Guevara and Heckel (2004)	BLA	1	26	19 (73%)	D, N, P, T	4
Díaz (2001)	LP	1	66	29 (44%)	P	N.A.
Heckel (1992), Schramm (1993)	TA	3	51	20 (39%)	N	N.A.
Delgado (1991, 2002)	TE	5	1987	37 (2%)	D, T	N.A.
Delgado (1996, 2002)	HO	3	344	36 (10%)	T	N.A.
	Total	11 *	3,928	327 (32.5%**)	–	72

+Oscar Guzón, MSc student in Marine Ecology at CICESE (Ensenada, Baja California, Mexico).

* Total number of different years.

** Weighted average.

7.2. Error assessment

Repeated measurements of a single tracing (operator error) yielded a maximum standardized error (balanced by image size and resolution) of 0.01%, thus it was negligible. Measurements of different images of the same individual (image quality error) resulted in a maximum standardized error of 0.1%; thus it is assumed that image quality was not a considerable source of variability. For comparison purposes, the minimum standardized difference calculated for any measurement among local samples was 2%, the median was 10.5% and the maximum difference was 32%.

7.3. General phenotypic variability

7.3.1. Descriptive statistics

Total sample size (n) was 327 fins; descriptive statistics of log-transformed ratios were computed from fin measurements and three out of 11 log-transformed ratios were not normally distributed (K-S, $p<0.05$); these were mostly "base length-foil" related ratios (C30B/AB, C5B/AB, C5D/AB). There were also significant correlations ($p<0.05$) among most variables.

7.3.2. Construction of average fin shapes

Given that some variables were not normally distributed, the central tendency of samples was represented with the median; upper (75%) and lower (25%) quartiles were used as indicators of data dispersion (Figure 6). Error in contour construction was estimated to be as high as 2% of fin's total length based on paired comparisons of related ratios (Morteo *et al.*, In progress).

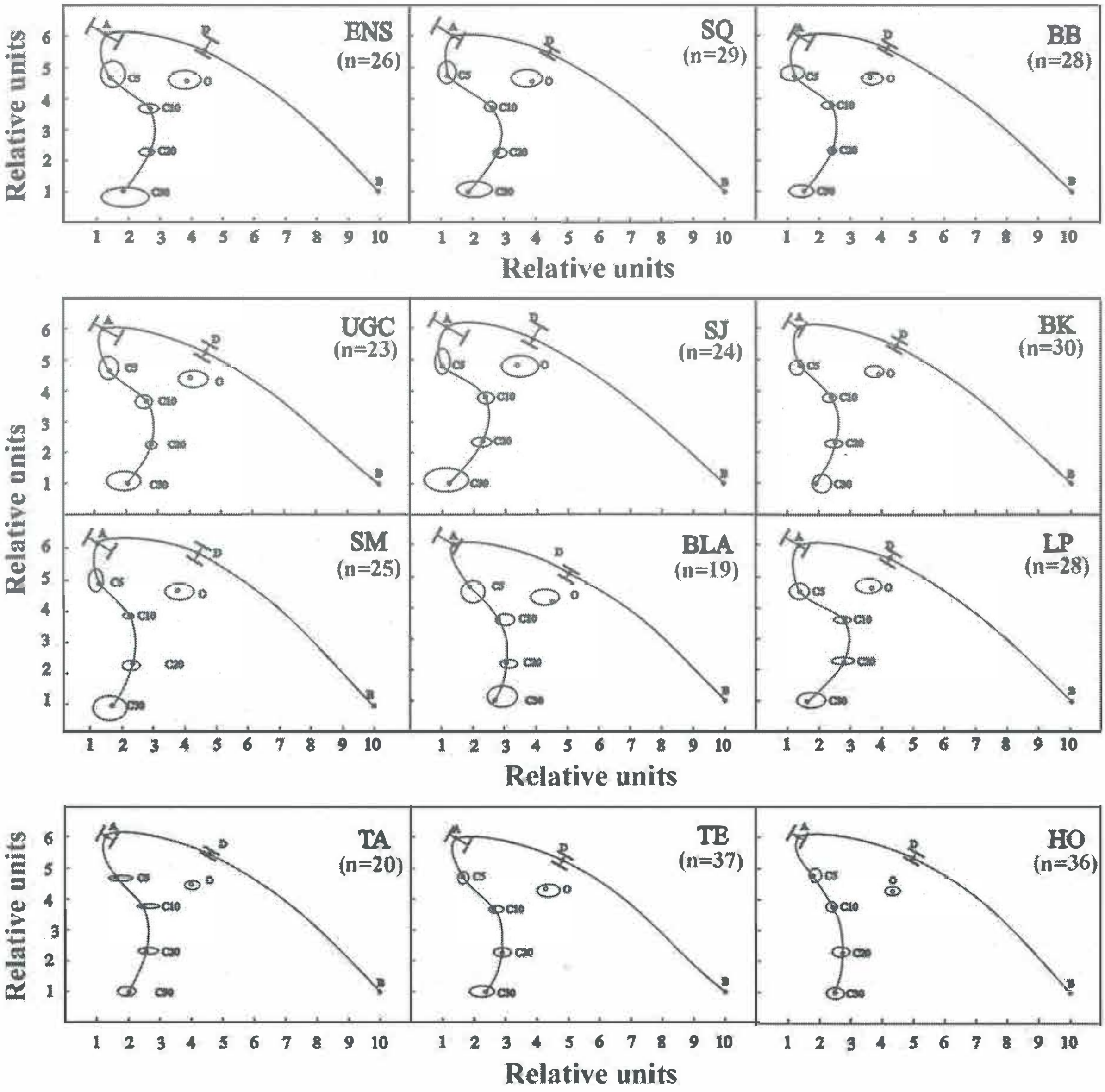

Figure 6. Average fin contours by locality (n=327). Contours are fin median values, thus they do not represent any particular fin. Error in design construction was estimated as high as 2% of fin's total length. Inner circles show median value; error bars and ellipses show variability expressed as quartiles (50% of data). Measurement AB is the same for all fins (10 relative units); also note that all points are referred to B, which is fixed at X=10, Y=1. ENS=Ensenada, SQ=San Quintin, UGC=Upper Gulf of California, SJ=Bahia San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas, BLA=Bahia de los Angeles, LP=La Paz, TA=Tamiahua, TE=Terminos Lagoon, HO=Holbox.

Figura 6. Contornos promedio de la aleta dorsal por localidad (n=327). Los contornos reflejan valores promedio, por lo cual no representan ninguna aleta en particular. El error en la construcción del diseño se estimó en un 2% de la longitud total de la aleta. Los círculos internos muestran el valor de la mediana; las barras de error y las elipses muestran la variabilidad expresada en cuartiles (50% de datos). La medida AB es la misma para todas las aletas (10 unidades relativas); cabe destacar que todos los puntos están referenciados con respecto a B, el cual está fijo en las coordenadas x=10, y=1. ENS=Ensenada, SQ=San Quintín, UGC= Alto Golfo de California, SJ=Bahía San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas, BLA=Bahía del los Ángeles, LP=La Paz, TA=Tamiahua, Laguna de TE=Términos, HO=Holbox.

Average fin contour reconstructions differed in each locality (Figure 6). Points A and C30 were the most variable, followed by points O and C5. Variability in points D, C10 and C20 was lower in at least 50% of measured fins from any particular locality; note the smaller ellipses near the median value.

Fin contours for the Gulf of Mexico (Holbox, Terminos, and Tamiahua) and Santa Maria were among the least falcate, in contrast to contours from the Pacific Ocean and the Gulf of California. Wide rounded tips were observed in San Jorge, Ensenada, San Quintin, and La Paz, while pointed tips were found in Holbox, Tamiahua, Terminos, and Bahia de los Angeles. Fins from Ensenada, San Jorge, Holbox, and Santa Maria were more foiled; and rake was larger for dolphins in the Gulf of Mexico, and Bahia de los Angeles. No differences in depth were assessed because of scaling procedures (depth = 10 relative units). Note that in spite of the differences in data source or sample size (Table I), measurements for dolphins within the Gulf of Mexico (lower row on Figure 6) were the least variable.

7.4. Local phenotypic variability

7.4.1. Variability and sample size effect within localities

The effect of sample size on variability was assessed through the cumulative GFS (General Fin Shape index = averaged COV) plotted against the number of individual fins within localities (Figure 7). Variability within populations increased as more fins were included; however, for each additional fin the increments became considerably smaller. Most localities stabilized their variability curves over the 19th sample; therefore minimum sample size was interpreted to be 20 individuals.

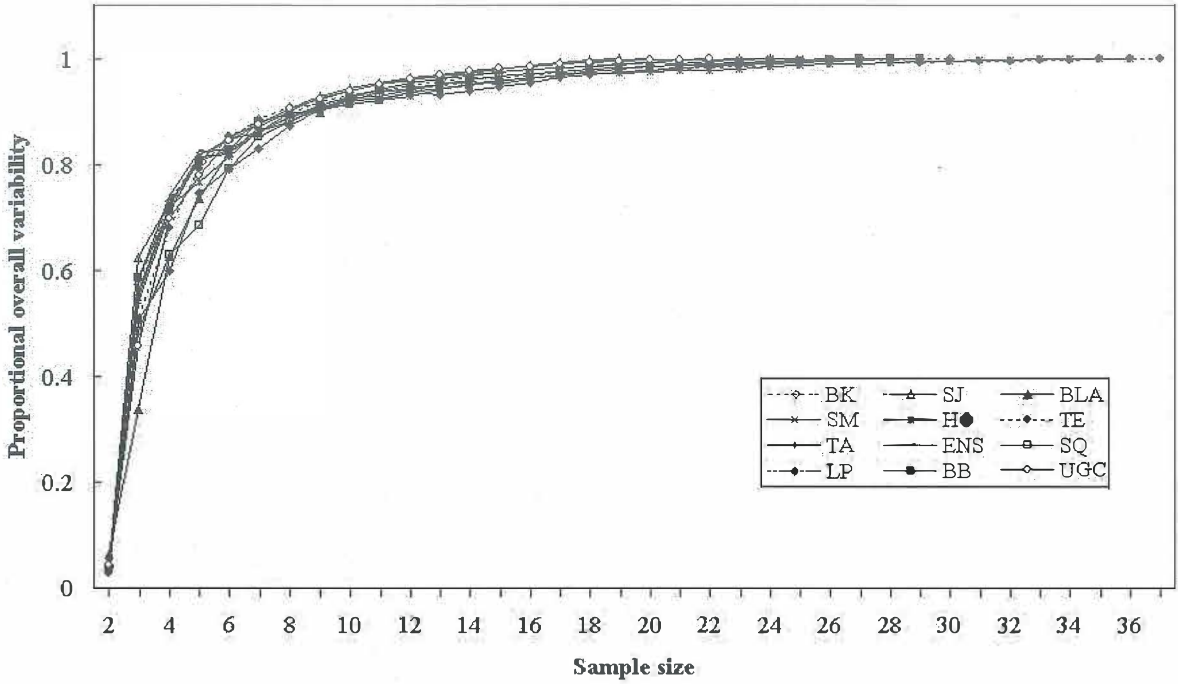

Figure 7. Dorsal fin morphological variability and sample size effect by location (n=327). Most localities reached an asymptote at the 19th sample; thus minimum sample size was 20 individuals. ENS=Ensenada (n=26), SQ=San Quintin (n=29), UGC=Upper Gulf of California (n=23), SJ=Bahia San Jorge (n=24), BK=Bahia Kino (n=30), SM=Bahia Santa Maria (n=25), BB=Bahia Banderas (n=28), BLA=Bahia de los Angeles (n=19), LP=La Paz (n=28), TA=Tamiahua (n=20), TE=Terminos Lagoon (n=37), HO=Holbox (n=36).

Figura 7. Variabilidad morfológica de la aleta dorsal y efecto del tamaño de muestra por localidad (n=327). La mayoría de las localidades alcanzó una asíntota en la muestra 19; por lo tanto el tamaño mínimo de muestra fue de 20 individuos. ENS=Ensenada (n=26), SQ=San Quintín (n=29), UGC=Alto Golfo de California (n=23), SJ=Bahía San Jorge (n=24), BK=Bahía Kino (n=30), SM=Bahía Santa María (n=25), BB=Bahía Banderas (n=28), BLA=Bahía del los Ángeles (n=19), LP=La Paz (n=28), TA=Tamiahua (n=20), Laguna de TE=Términos (n=37), HO=Holbox (n=36).

7.4.2. Factor analysis

Due to the high correlation between some log-transformed ratios, variables were reduced through Factor Analysis. The test (Table II) showed that 90% of the variance was explained by the first three factors and the remaining seven factors accounted for less than 2% each. Both Scree and Kaiser (discard factors with Eigenvalues <1.0) criteria were consistent in eliminating the remaining seven factors.

Table II. Factor Analysis of log-transformed ratios using all locations (n=327). Note the cumulative variance accounted for the first three Factors (*).

Tabla II. Análisis Factorial de mediciones transformadas para todas las localidades (n=327). Note la variación acumulativa explicada por los primeros tres Factores (*).

Factor	Eigenvalue	% Total Variance	Cumulative Eigenvalue	Cumulative Variance(%)
1	4.938049	44.89135	4.938049	44.89135
2	2.692965	24.48150	7.631014	69.37285
3	2.275938	20.69034	9.906952	90.06320*

The structure of factor loadings on the original variables (Table III) was not influenced by rotation techniques (Varimax, Equamax, Quartimax, and Biquartimax). Factor 1 accounts for most of the general triangle shape of the dorsal fin (C30B/AB); however, it is heavily weighted to "foil-base length" ratios (DO/C30O, C10D/AB, C5D/AB and AO-OB). Factor 2 groups all "depth-rake" ratios (C20B/AB, C10B/AB, C5B/AB), defining solely the trailing edge. Factor 3 combines "depth-foil" ratios, grouping the most (C30D/AB) and least (C20D/AB) variable ratios (Table III).

Table III. Factor loadings (Rotation Varimax normalized) showing structure of variables for all locations (n=327). * = Loadings >0.70.

Tabla III. Cargas de los Factores (Rotación Varimax normalizada) mostrando estructura de variables para todas las localidades (n=327). * = Cargas >0.70.

Log-transformed ratio	Factor 1	Factor 2	Factor 3
C30D/AB	-0.330963	-0.017706	0.931169*
C30B/AB	-0.707288*	0.232801	0.654120
DO/C30O	0.833429*	-0.474988	0.161033
C20B/AB	-0.292384	0.794920*	0.474047
C10B/AB	0.004365	0.984711*	0.093781
C5B/AB	0.101617	0.958494*	-0.133356
C20D/AB	0.381345	0.042413	0.905396*
C10D/ AB	0.954939*	0.137952	0.118987
C5D/AB	0.859684*	0.241574	-0.420214
AO/OB	0.706947*	-0.241366	-0.654029
S^2/A	0.041071	-0.025318	-0.509889
Expl. Var.	3.698079	2.938474	3.270399
Prp. Totl.	0.336189	0.267134	0.297309

7.4.3. Discriminant analysis

Scores from Factor Analysis were computed for samples in all locations, thus resulting in values for three new variables (Factors 1, 2 and 3). These three variables were normally distributed (K-S, p>0.2) and were used in a Discriminant Function Analysis. Variances and covariances were homogeneous across groups, and no correlation was found between means and variances across groups from these variables; thus it is assumed that the statistical significance of the test is reliable.

The twelve location Discriminant Function Analysis was highly significant (Wilks' Lambda: 0.44442, $F_{(33,922)}=8.8617$, $p<0.00001$, n=327). All three Factors significantly ($p<0.00001$) contributed to the model (Table IV).

Table IV. Local Discriminant Function Analysis summary. Discrimination was highly significant among the twelve locations (Wilks' Lambda: 0.44442, $F_{(33,922)}=8.8617$, $p<0.00001$, n=327).

Tabla IV. Resumen del Análisis Local de Funciones Discriminantes. La discriminación fue altamente significativa entre las doce localidades (Wilks' Lambda: 0.44442, $F(_{33,922})=8.8617$, $p<0.00001$, n=327).

Factor	Wilks' Lambda	Partial Lambda	F-remove (11,313)	p-level	Toler.	1-Toler (R-Square)
1	0.699858	0.606265	18.89880	0.000001	0.974416	0.025584
2	0.522872	0.811478	6.76050	0.000001	0.970560	0.029440
3	0.506895	0.837056	5.66471	0.000001	0.995966	0.004034

Squared Mahalanobis Distances (SMD) (Table V) indicated that all sites were significantly different ($p<0.05$) from a minimum of four and maximum nine other locations. The most distinctive samples were from Holbox (nine significant differences) followed by Tamiahua, San Jorge, La Paz, and Ensenada (eight significant differences); Bahia de los Angeles, Terminos, Bahia Banderas, Santa Maria, and Bahia Kino were different to other seven localities; finally, San Quintin and the Upper Gulf of California were the less distinctive sites, being different to other four and six localities, respectively.

Table V. Local Squared Mahalanobis and geographic Distances (n=327). Values over the principal diagonal are geographic distances along the coastline (km); values under the principal diagonal are Squared Mahalanobis distances. ENS=Ensenada, SQ=San Quintin, UGC=Upper Gulf of California, SJ=Bahia San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas, BLA=Bahia de los Angeles, LP=La Paz, TA=Tamiahua, TE=Terminos Lagoon, HO=Holbox.

Tabla V. Distancias Cuadradas de Mahalanobis y distancias geográficas locales (n=327). Los valores sobre la diagonal principal son distancias geográficas a lo largo de la costa (km); los valores bajo la diagonal principal son las distancias Cuadradas de Mahalanobis. ENS=Ensenada, SQ=San Quintín, UGC=Alto Golfo de California, SJ=Bahía San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas, BLA=Bahía de los Ángeles, LP=La Paz, TA=Tamiahua, TE= Laguna de Términos, HO=Holbox.

Study area	ENS	SQ	UGC	SJ	BK	SM	BB	BLA	LP	TA	TE	HO
ENS	0	220	2870	**3040***	**3340***	**3730***	**4540***	**2520***	1820	N.A.	N.A.	N.A.
SQ	0.522	0	2650	2820	3120	**3510***	4320	2300	1600	N.A.	N.A.	N.A.
UGC	0.551	0.481	0	**170***	450	**1110***	**1720***	350	1050	N.A.	N.A.	N.A.
SJ	**3.205***	1.197	**2.783***	0	**300***	980	1580	**480***	**1180***	N.A.	N.A.	N.A.
BK	**1.068***	0.244	0.716	**1.119***	0	**690***	1380	750	**1450***	N.A.	N.A.	N.A.
SM	**4.666***	**2.155***	**2.927***	0.857	**1.920***	0	600	**1420***	**2120***	N.A.	N.A.	N.A.
BB	**2.170***	0.591	**1.678***	0.185	0.737	0.753	0	**2020***	**2720***	N.A.	N.A.	N.A.
BLA	**1.665***	1.306	0.363	**3.569***	1.080	**2.910***	**2.455***	0	**700***	N.A.	N.A.	N.A.
LP	0.633	1.009	1.148	**3.412***	**2.203***	**4.548***	**2.172***	**2.750***	0	N.A.	N.A.	N.A.
TA	**4.442***	**2.248***	**2.284***	**1.781***	**1.672***	0.421	**1.437***	**1.662***	**4.994***	0	786	1428
TE	**4.361***	**2.488***	**1.982***	**2.718***	**1.997***	0.938	**2.049***	1.187	**4.863***	0.161	0	642
HO	**6.223***	**3.923***	**3.251***	**3.754***	**3.333***	**1.255***	**3.080***	**2.133***	**6.527***	0.408	0.178	0

* = significant distances (table wide, $\alpha<0.05$) after Bonferroni correction.
N.A.= Not applicable.

The cluster analysis of dissimilarities as percentages in Figure 8 shows two principal clusters. Dissimilarities among locations are consistent to some extent with major geographic divisions of the study area. The first cluster (lower area in figure 8) is composed by localities from the Gulf of Mexico and Santa Maria (Gulf of California); the second branch is represented by localities from the Pacific and Gulf of California.

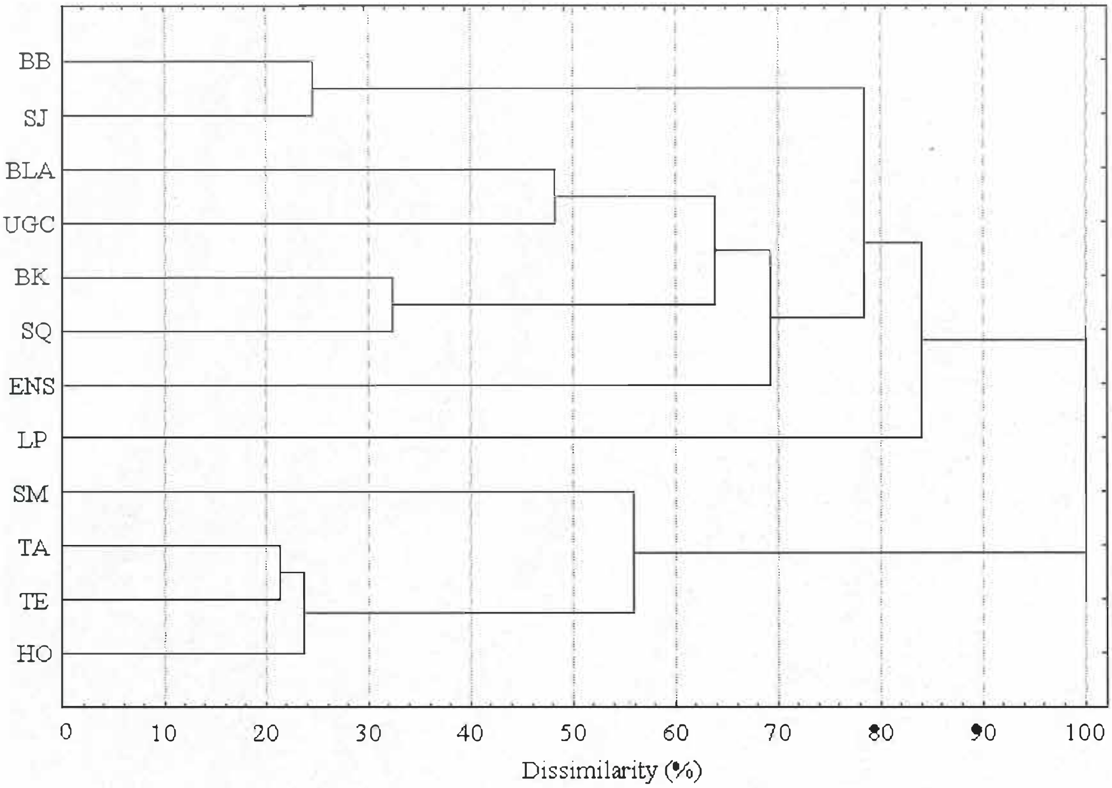

Figure 8. **Dendrogram of morphometric dissimilarities for all locations** (n=327). Dissimilarities are percentages based on the maximum Squared Mahalanobis distance (Table VI). Two major branches are observed; these are almost consistent with major geographical divisions of the study area. ENS=Ensenada, SQ=San Quintin, UGC=Upper Gulf of California, SJ=Bahia San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas, BLA=Bahia de los Angeles, LP=La Paz, TA=Tamiahua, TE=Terminos Lagoon, HO=Holbox.

Figura 8. Dendrograma de disimilitud morfométrica para todas las localidades (n=327). La disimilitud es un porcentaje de la máxima Distancia Cuadrada de Mahalanobis (Tabla VI). Se observan dos ramas principales; éstas son casi consistentes con la división geográfica del área del estudio. ENS=Ensenada, SQ=San Quintín, UGC=Alto Golfo de California, SJ=Bahía San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas, BLA=Bahía de los Ángeles, LP=La Paz, TA=Tamiahua, TE= Laguna de Términos, HO=Holbox.

The overall correct classification mean score was roughly 27% (ranging from 0 to 61.1%). It was higher compared to the 11.3% expected by chance. Holbox, La Paz, Bahia Kino, Terminos and Bahia Banderas had the best correct classification (above 28%), while the worst (below 5%) were for Tamiahua Lagoon, San Quintin, and the Upper Gulf of California (Table VI).

Table VI. Local Classification matrix (n=327). Rows are observed classifications; columns are predicted classifications. Values in bold show percentages of correct classification greater than expected by chance (11.3%). p is the *a priori* classification probability. Location type is divided in either mainland (M) or peninsular (P). The last row is the number of individual fins classified by the model in each location. ENS=Ensenada, SQ=San Quintin, UGC=Upper Gulf of California, SJ=Bahia San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas, BLA=Bahia de los Angeles, LP=La Paz, TA=Tamiahua, TE=Terminos Lagoon, HO=Holbox.

Tabla VI. Matriz de Clasificación local (n=327). Las Filas representan la clasificación observada; las columnas son la clasificación predicha. Los valores en negrita muestran los porcentajes de clasificación correcta mayores que los esperados al azar (11.3%). p es la probabilidad de clasificación *a priori*. Las localidades están divididas por tipo en continentales (M) o peninsulares (P). La última fila es el número de aletas individuales clasificadas por el modelo en cada localidad. ENS=Ensenada, SQ=San Quintín, UGC=Alto Golfo de California, SJ=Bahía San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas, BLA=Bahía de los Ángeles, LP=La Paz, TA=Tamiahua, TE= Laguna de Términos, HO=Holbox.

Study area	Location type		ENS	SQ	UGC	SJ	BK	SM	BB	BLA	LP	TA	TE	HO
		%	p=0.083	p=0.089	p=0.070	p=0.073	p=0.092	p=0.076	p=0.086	p=0.058	p=0.089	p=0.061	p=0.113	p=0.110
ENS	P	**22.2**	6*	2	2	0	5	0	0	0	9	0	2	1
SQ	P	3.4	3	1*	2	1	3	1	3	2	7	0	6	0
UGC	M	4.3	6	0	1*	1	3	0	0	1	5	0	3	3
SJ	M	**25.0**	2	0	0	6*	4	2	2	0	1	0	4	3
BK	M	**36.7**	4	1	1	2	11*	2	2	1	2	0	3	1
SM	M	**20.0**	0	0	0	4	3	5*	3	1	0	0	6	3
BB	M	**28.6**	1	2	0	2	3	2	8*	0	4	0	4	2
BLA	P	**15.8**	2	1	0	0	2	1	0	3*	3	0	6	1
LP	P	**48.3**	4	2	1	2	2	0	2	2	14*	0	0	0
TA	P	0.0	0	1	0	0	1	2	1	1	0	0*	10	4
TE	M	**32.4**	1	0	0	2	4	2	0	1	1	0	12*	14
HO	M	**61.1**	0	0	0	0	1	3	1	2	1	0	6	22*
Total		27.2$^+$	29	10	7	20	42	20	22	14	47	0	62	54

* Number of cases correctly classified.

$^+$ Average

It is worth mentioning that in the Gulf of California 14% of 130 “mainland” individuals where incorrectly classified as “peninsular” dolphins; and 23% of 48 “peninsular” dolphins were incorrectly classified as “mainland” individuals (Table VI).

The nature of the discrimination function was examined by a Canonical Analysis; table VII shows that three roots significantly contributed to the discrimination of localities ($p<0.005$).

Table VII. Local Chi-Square tests with successive roots removed (n=327). Values in bold show significant contribution to the model ($p<0.05$).

Tabla VII. Pruebas locales de Chi-cuadrada con raíces sucesivas removidas (n=327). Los valores en negrita muestran contribuciones significativas al modelo ($p <0.05$).

Root	Eigenvalue	Canonical R	Wilks' Lambda	Chi-Square.	df	p-level
1	0.670901	0.633656	0.444422	258.2970	33	**0.000001**
2	0.249610	0.446934	0.742586	94.7909	20	**0.000001**
3	0.077653	0.268435	0.927943	23.8192	9	**0.004597**

The standardized coefficients for these three roots (Table VIII) indicated that the first root was weighted more heavily by Factor 1. The second root was marked by Factor 3 and the third root was characterized by Factor 2. Eigenvalues derived from Canonical Discriminant Analysis showed that 100% of the discrimination among groups could be accounted for these roots. Root 1 was the most useful for group discrimination, accounting for 67.2% of the variance. Discriminatory power for roots 2 and 3 was 25% and 7.3% respectively (Table VIII).

Table VIII. Local Standardized Coefficients of Canonical Variables for all locations (n=327).

Tabla VIII. Coeficientes Estandarizados de Variables Canónicas para todas las localidades (n=327).

Factor	Root 1	Root 2	Root 3
1	**-0.932611***	-0.275591	-0.279367
2	-0.524464	0.466187	**0.732597***
3	-0.098713	**0.854803***	-0.514678
Eigenval	0.670901	0.249610	0.077653
Cum.Prop	0.672135	0.922204	1.000000

* Highest contribution by Factor.

Examination of means for canonical variables (Table IX) showed that higher contributions of Root 1 discriminated mostly Holbox, La Paz, Ensenada, Terminos, and Tamiahua, in that order. Root 2 separated San Jorge and Bahia de los Angeles, and Root 3 differentiated Bahia Kino, albeit at lower magnitude.

Table IX. Local Means of Canonical Variables (n=327). ENS=Ensenada, SQ=San Quintin, UGC=Upper Gulf of California, SJ=Bahia San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas, BLA=Bahia de los Angeles, LP=La Paz, TA=Tamiahua, TE=Terminos Lagoon, HO=Holbox.

Tabla IX. Medias locales de Variables Canónicas (n=327). ENS=Ensenada, SQ=San Quintín, UGC=Alto Golfo de California, SJ=Bahía San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas, BLA=Bahía de los Ángeles, LP=La Paz, TA=Tamiahua, TE= Laguna de Términos, HO=Holbox.

Study area	Root 1	Root 2	Root 3
ENS	**1.18158***	-0.308915	0.129450
SQ	0.61497	0.117685	0.114757
UGC	0.50014	-0.547748	0.030336
SJ	0.02969	**1.017880***	0.122922
BK	0.34085	0.107962	**0.514274***
SM	-0.70645	0.596525	-0.202431
BB	0.13414	0.664481	-0.083593
BLA	0.03534	-0.831317	0.260149
LP	**1.20643***	-0.136753	**-0.631612***
TA	-0.85491	0.052201	0.093246
TE	-0.86229	-0.324196	-0.023626
HO	**-1.24798***	-0.359679	-0.169851

* Major discriminatory contributions

7.4.4. Isolation/Differentiation by Distance Model

Local Square Mahalanobis distances between the Pacific and Gulf of California were tested for correlation with geographic distance (Table V). They showed no significant correlation (Mantel's test, r=0.079, p=0.325), even with Log-transformed geographic distances (Mantel's test, r=0.086, p=0.287) (Figure 9). Another interpretation of these results was made for the Gulf of California (Figure 10); the comparison of theoretical and observed variation showed a slight possibility of individual exchange between mainland and peninsula or the intrusion of oceanic dolphins which may fade separation.

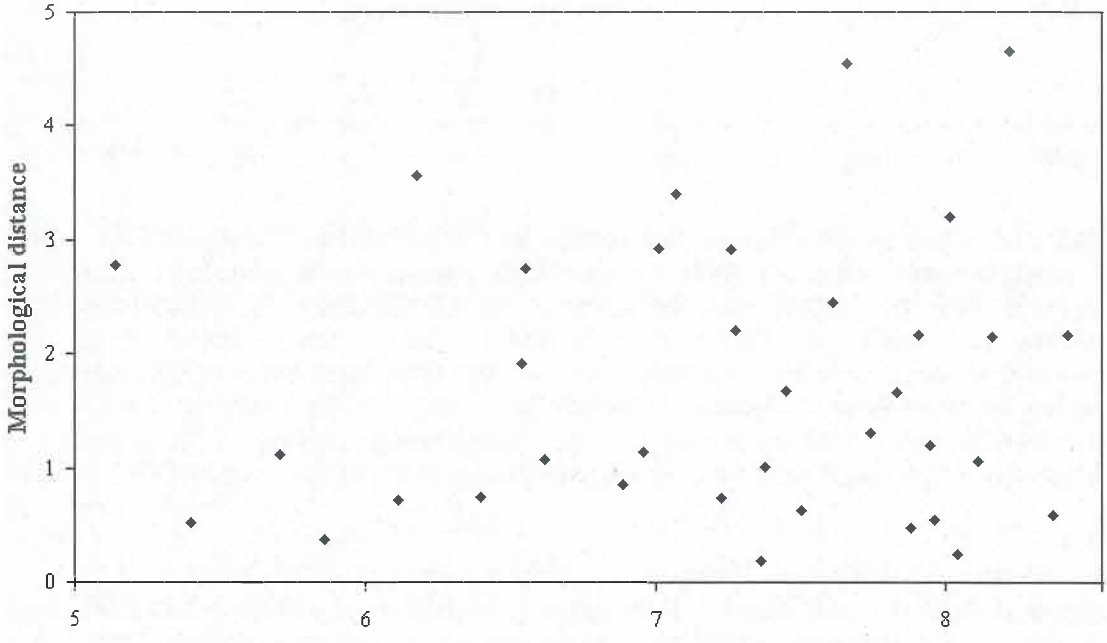

Figure 9. Scatter plot of geographic and morphologic distances for the Pacific and the Gulf of California (n=234). Values over the vertical axis are Squared Mahalanobis distances from the Discriminant Function analysis (Table VI). No significant correlation (Mantel's test, r=0.086, p=0.287) was found.

Figura 9. Correlación entre distancias geográficas y morfológicas en el Pacífico y el Golfo de California (n=234). Los valores en el eje vertical son las Distancias Cuadradas de Mahalanobis provenientes del Análisis de Funciones Discriminantes (Tabla VI). No se encontró correlación significativa alguna (prueba de Mantel, r=0.086, p=0.287).

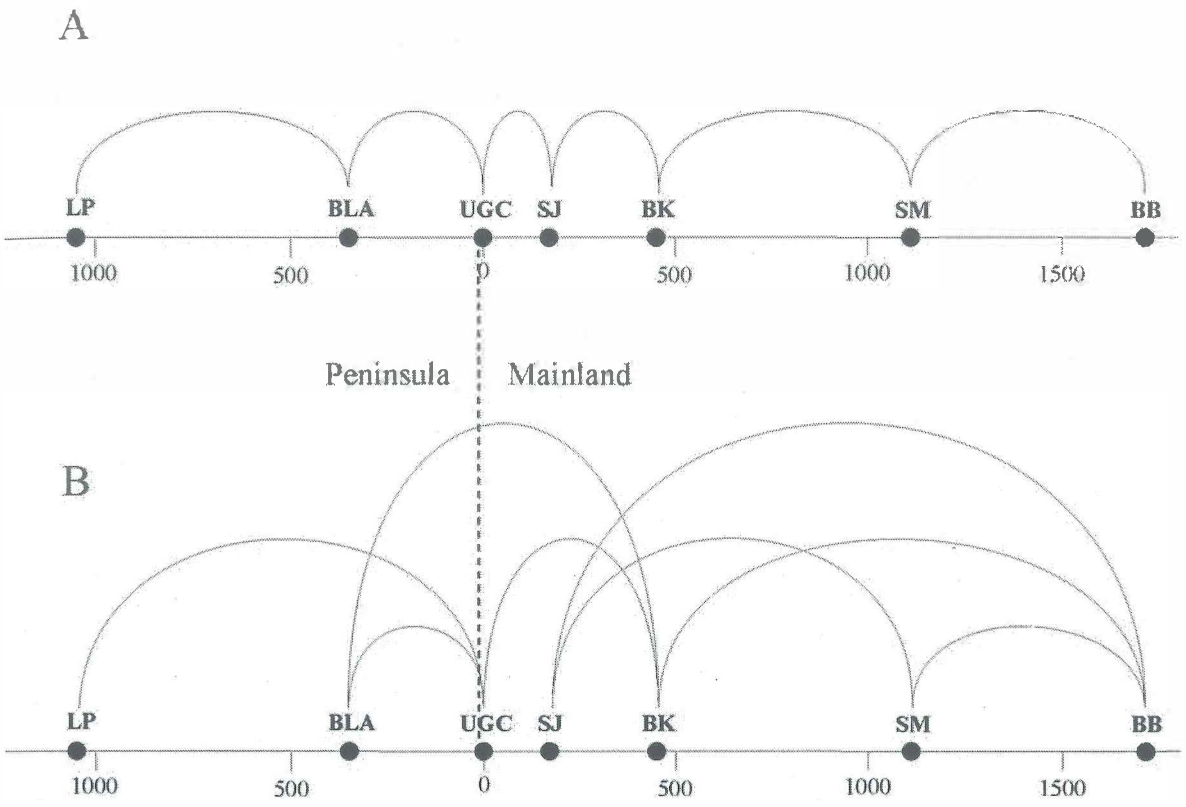

Figure 10. Comparison of theoretical and observed variation in dorsal fins within the Gulf of California. Horizontal axis represents distance (km) along the coast with the Upper Gulf of California as the origin. East and west are right and left sides, respectively. The curves link sites with no statistical morphological differences (Table VIII). A) Theoretical morphological similarities; B) Observed trend. Note that one connection (BLA-BK) trespasses the 0 km boundary (dashed line), showing a slight possibility of individual exchange between mainland and peninsula or the intrusion of oceanic dolphins which may fade separation. LP=La Paz, BLA=Bahia de los Angeles, UGC=Upper Gulf of California, SJ=San Jorge, BK=Bahia Kino, SM=Bahia Santa Maria, BB=Bahia Banderas.

Figura 10. Comparación de la variación teórica y observada en las aletas dorsales de tursiones en el Golfo de California. El eje horizontal representa la distancia (km) a lo largo de la costa desde el Alto Golfo de California. Las curvas unen los sitios sin diferencias morfológicas (Tabla VIII). A) similitudes morfológica teóricas; B) tendencia observada. Note que una conexión (BLA-BK) traspasa el límite de 0 km (línea punteada), mostrando una ligera posibilidad de intercambio individual entre continente y península o la intrusión de delfines oceánicos que pueden diluir la separación. LP=La Paz, BLA=Bahía de los Ángeles, el UGC=Alto Golfo de California, SJ=San Jorge, BK=Bahía Kino, SM=Bahía Santa María, BB=Bahía Banderas.

7.5. Regional phenotypic variability

In order to assess variation at a higher geographic scale, data were regrouped according to oceanic region (Pacific Ocean, Gulf of California, and Gulf of Mexico). Bahia Banderas was pooled with samples from the Gulf of California because this locality is often considered part of the mouth of the Gulf, and also because it was grouped within the same cluster in the assessment of local morphological variation (Figure 8).

7.5.1. Discriminant analysis

Scores from local PCA were used as data for the regional analysis (Factors 1, 2, and 3). The three regions Discriminant Function Analysis was highly significant (Wilks' Lambda: 0.6639157, $F_{(6,498)} = 18.86421$, $p<0.00001$, n=254). Only the first two factors significantly contributed to the model ($p<0.05$, Table X). Squared Mahalanobis Distances (Table XI) also indicated significant differences among the three regions ($p<0.05$).

Table X. Regional Discriminant Function Analysis summary. Discrimination was highly significant among the three regions (Wilks' Lambda: 0.6639157, $F_{(6,498)} = 18.86421$, $p<0.00001$, n=254). Significant contributions ($p<0.05$) by factor are in bold.

Tabla X. Resumen del Análisis Regional de Funciones Discriminantes. La discriminación fue altamente significativa entre las tres regiones (Wilks' Lambda: 0.6639157, $F_{(6,498)} = 18.86421$, $p <0.00001$, n=254). Las contribuciones significativas ($p <0.05$) por factor se encuentran en negritas.

Factor	Wilks' Lambda	Partial Lambda	F-remove (2,249)	p-level	Tolerance	1-Toler (R-Square)
1	0.954011	0.695921	54.39971	**0.000001**	0.992338	0.007662
2	0.687292	0.965988	4.38356	**0.013458**	0.994330	0.005670
3	0.675987	0.982143	2.26368	0.106103	0.997718	0.002282

Table XI. Regional Squared Mahalanobis Distances (n=254). GC=Gulf of California, PO=Pacific Ocean, GM= Gulf of Mexico.

Tabla XI. Distancias Cuadradas de Mahalanobis regionales (n=254). GC=Golfo de California, PO=Océano Pacífico, GM =Golfo de México.

Study area	PO	GC	GM
PO (n=27)	0		
GC (n=154)	**0.790030***	0	
GM (n=73)	**4.457803***	**1.777081***	0

* Significant distances (table wide, $\alpha<0.05$) after Bonferroni correction.

The overall correct classification score was 56.6% (ranging from 0 to 88.3%), and it was lower to the 60.6% expected by chance. The Gulf of Mexico had the best (88.3%) correct classification, while the Pacific and the Gulf of California were 0.0 and 58.9% (Table XII). The nature of the discrimination examined by Canonical Analysis (Table XIII) showed that only root 1 significantly contributed to the discrimination of regions ($p<0.05$).

Table XII. Regional Classification matrix (n=254). Rows are observed classifications; columns are predicted classifications. Values in bold show percentages of correct classification greater than expected by chance (41%). p value is the *a priori* classification probability. The last row is the number of individual fins classified by the model in each location. GC=Gulf of California, PO=Pacific Ocean, GM= Gulf of Mexico.

Tabla XII. Matriz de clasificación regional (n=254). Las filas son la clasificación observada; las columnas son la clasificación predicha. Los valores en negrita son los porcentajes de clasificación correcta mayores que lo esperado al azar (41%). El valor de p es la probabilidad de clasificación *a priori*. La última fila es el número de aletas individuales clasificadas por el modelo en cada localidad. GC=Golfo de California, PO=Océano Pacífico, GM =Golfo de México.

Study area	Percent	PO p=0.106	GC p=0.606	GM p=0.287
PO (n=27)	0.0	0*	25	2
GC (n=154)	**88.3**	1	136*	17
GM (n=73)	**58.90**	0	30	43*
Total	**56.6**$^{+}$	1	191	62

* Number of cases correctly classified.
$^{+}$ Average

Table XIII. Regional Chi-Square tests with successive roots removed (n=254). Value in bold shows significant contribution to the model ($p<0.05$).

Tabla XIII. Pruebas regionales de Chi-cuadrada con raíces sucesivas removidas (n=254). El valor en negritas muestra la contribución significativa al modelo ($p <0.05$).

Root	Eigenvalue	Canonical R	Wilks' Lambda	Chi-Square.	df	p-level
1	0.476947	0.568267	0.663916	102.4000	6	**0.000001**
2	0.019817	0.139398	0.980568	4.9057	2	0.086046

The standardized coefficients for these two roots (Table XIV) indicated that the first root was weighted more heavily by Factor 1. The second root was marked by Factor 3. Eigenvalues derived from Canonical Discriminant Analysis showed that 100% of the discrimination among groups could be accounted by two roots. Root 1 was the most useful for group discrimination, accounting for 96% of the variance, discriminatory power for root 2 was roughly 4%. Examination of means for canonical variables (Table XV) showed that Root 1 discriminated mostly the Pacific and the Gulf of Mexico, while the second root barely contributed to discrimination.

Table XIV. Regional Standardized Coefficients of Canonical Variables (n=254).

Tabla XIV. Coeficientes Estandarizados de las Variables Canónicas regionales (n=254).

Factor	Root 1	Root 2
1	**0.973898***	-0.084251
2	0.314570	0.340327
3	-0.044065	**0.942773***
Eigenval	0.476947	0.019817
Cum.Prop	0.960108	1.000000

* Highest contribution by Factor.

Table XV. Regional Means of Canonical Variables (n=254). PO=Pacific Ocean, GC =Gulf of California, GM= Gulf of Mexico.

Tabla XV. Medias de las Variables Canónicas regionales (n=254). PO=Océano Pacífico, GC=Golfo de California, GM=Golfo de México.

Study area	Root 1	Root 2
PO (n=27)	**-1.06341***	-0.343008
GC (n=154)	-0.29618	0.095243
GM (n=73)	**1.01814***	-0.074057

* Major discriminatory contributions.

7.5.2. Statistical validation

Scores from the excluded localities were included in the analysis to validate the regional assessment. The Discriminant Function Analysis was highly significant (Wilks' Lambda: 0.6308591, $F_{(15,881)}$ = 10.66671, $p<0.00001$, n=327). All factors significantly contributed ($p<0.01$) to the model (Table XVI).

Table XVI. Summary of Discriminant Function Analysis for statistical validation. Discrimination was highly significant among the study areas (Wilks' Lambda: 0.6308591, $F_{(15,881)}$ = 10.66671, $p<0.00001$, n=327). Values in bold show significant contribution by factor ($p<0.05$).

Tabla XVI. Resumen del Análisis de Funciones Discriminantes para la validación estadística. La discriminación fue altamente significativa entre las áreas de estudio (Wilks' Lambda: 0.6308591, $F_{(15,881)}$ = 10.66671, $p<0.00001$, n=327). Los valores en negrita muestran la contribución significativa por factor ($p<0.05$).

Factor	Wilks' Lambda	Partial Lambda	F-remove (2,249)	p-level	Toler.	1-Toler (R-Square)
1	0.892275	0.707023	26.43747	**0.000001**	0.991700	0.008300
2	0.674343	0.935517	4.39760	**0.000692**	0.990865	0.009136
3	0.667822	0.944652	3.73812	**0.002651**	0.998140	0.001860

Squared Mahalanobis Distances (SMD) (Table XVII) indicated significant differences among all these areas ($p<0.05$). Cluster analysis shows that locations roughly grouped with their area of origin (Figure 11).

Table XVII. Regional Squared Mahalanobis Distances for statistical validation (n=327). GC=Gulf of California, PO=Pacific Ocean, GM=Gulf of Mexico, SQ= San Quintin, TA=Tamiahua, SJ=San Jorge.

Tabla XVII. Distancias Cuadradas de Mahalanobis para la validación estadística regional (n=327). GC=Golfo de California, PO=Océano Pacífico, GM=Golfo de México, SQ = an Quintín, TA=Tamiahua, SJ=San Jorge.

Study area	PO	GC	GM	SQ	TA	SJ
PO (n=27)	0					
GC (n=154)	**0.823984***	0				
GM (n=73)	**4.516119***	**1.765620***	0			
SQ (n=29)	0.428911	0.131938	**2.802577***	0		
TA (n=20)	**3.733477***	**1.152475***	0.223753	**1.933139***	0	
SJ (n=24)	**2.645095***	**0.956110***	**2.950191***	**0.996774***	**1.638064***	0

* Significant distances (table wide, $\alpha<0.05$) after Bonferroni correction.

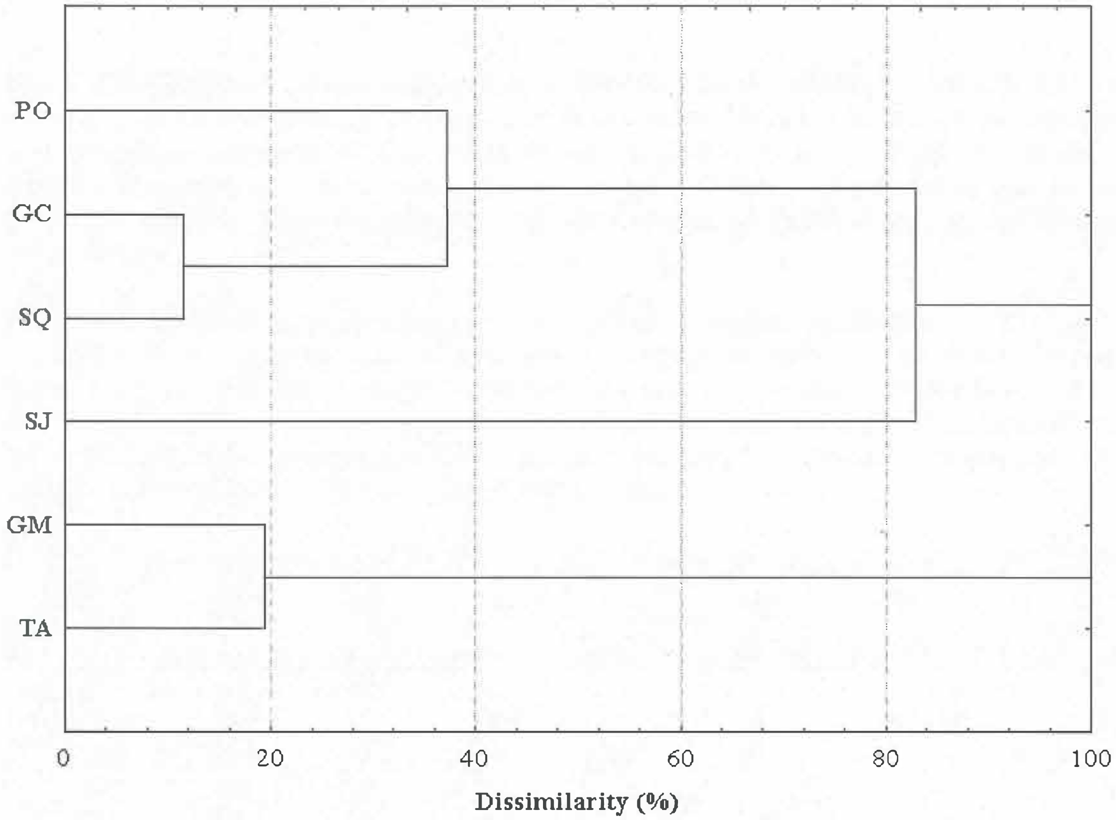

Figure 11. Dendrogram of morphometric dissimilarities for validation of regional assessment (n=327). Dissimilarities are percentages based on the maximum Squared Mahalanobis distance. Note that tested localities roughly grouped with their original region; however, the clusters formed by the localities in the Gulf of California and the Pacific were not consistent. PO=Pacific Ocean, GC=Gulf of California, GM=Gulf of Mexico, SQ=San Quintin, SJ=Bahia San Jorge, TA=Tamiahua.

Figura 11. Dendrograma de disimilitud morfométrica para la validación regional (n=327). La disimilitud es un porcentaje basado en la máxima Distancia de Cuadrada de Mahalanobis. Cabe destacar que en general, las localidades probadas se agruparon con su región original; sin embargo, los grupos formados en el Golfo de California y el Pacífico no fueron consistentes. GC=Golfo de California, PO=Océano Pacífico, GM=Golfo de México, SQ =San Quintín, TA=Tamiahua, SJ=San Jorge.

The overall correct classification score was 55.4% (range 0−87.7%). It was higher compared to the 47% expected by chance. The Gulf of California had the best (87.7%) correct classification, followed by the Gulf of Mexico (60.3%) and San Jorge (8.3%); the rest showed no correctly classified cases (Table XVIII).

Table XVIII. Regional Classification matrix for statistical validation (n=327). Rows are observed classifications; columns are predicted classifications. Values in bold show percentages of correct classification greater than expected by chance (47%). p is the *a priori* classification probability. The last row is the number of individual fins classified by the model in each location. GC=Gulf of California, PO=Pacific Ocean, GM= Gulf of Mexico, SQ=San Quintin, SJ=San Jorge, TA=Tamiahua.

Tabla XVIII. Matriz de Clasificación regional para la validación estadística (n=327). Las filas son la clasificación observada; las columnas son la clasificación predicha. Los valores en negrita muestran los porcentajes de clasificación correcta mayores a lo esperado al azar (47%). p es la probabilidad de clasificación *a priori*. La última fila es el número de aletas individuales clasificadas por el modelo en cada área de estudio. GC=Golfo de California, PO= Océano Pacífico, GM =Golfo de México, SQ=San Quintín, SJ=San Jorge, TA=Tamiahua.

Study area	%	PO	GC	GM	SQ	TA	SJ
		p=0.083	p=0.471	p=0.223	p=0.0887	p=0.061	p=0.073
PO	0.0	0*	25	2	0	0	0
GC	**87.7**	2	135*	17	0	0	0
GM	**60.3**	0	29	44*	0	0	0
SQ	0.0	0	29	0	0*	0	0
TA	0.0	0	16	4	0	0*	0
SJ	8.3	0	18	4	0	0	2*
Total	**55.4**$^{+}$	2	252	71	0	0	2

* Number of cases correctly classified
$^{+}$ Average

The nature of the discrimination examined by Canonical Analysis (Table XIX) showed that the first two roots significantly contributed to discrimination ($p<0.05$).

Table XIX. Regional Chi-Square tests with successive roots removed for statistical validation (n=357). Values in bold show significant contribution to the model ($p<0.05$).

Tabla XIX. Pruebas regionales de Chi-cuadrada con raíces sucesivas removidas para la validación estadística (n=357). Los valores en negrita muestran la contribución significativa al modelo ($p <0.05$).

Root	Eigenvalue	Canonical R	Wilks' Lambda	Chi-Square.	df	p-level
1	0.445910	0.555332	0.630859	148.1063	15	**0.000001**
2	0.092727	0.291305	0.912165	29.5568	8	**0.000253**
3	0.003263	0.057030	0.996748	1.0474	3	0.789794

The standardized coefficients for these two roots (Table XX) indicated that the first root weighted more heavily by Factor 1. The second root was marked by Factor 3. Eigenvalues derived from Canonical Discriminant Analysis showed that 100% of the discrimination among groups could be accounted for three roots. Root 1 was the most useful for group discrimination, accounting for 82.3% of the variance, discriminatory power for root 2 was roughly 17.1%, while root 3 accounted for only 0.6%.

Table XX. Regional Standardized Coefficients of Canonical variables for statistical validation (n=327).

Tabla XX. Coeficientes Estandarizados de variables Canónicas para la validación estadística regional (n=327).

Factor	Root 1	Root 2	Root 3
1	**-0.976340***	0.125041	-0.198730
2	-0.317694	-0.616315	**0.726943***
3	0.043008	**-0.795398***	-0.606099
Eigenval	0.445910	0.092727	0.003263
Cum.Prop	0.822864	0.993979	1.000000

* Highest contribution by Factor

Examination of means for canonical variables (Table XXI) showed that Root 1 discriminated mostly the Pacific and the Gulf of Mexico, while Root 2 discriminated San Jorge.

Table XXI. Regional Means of Canonical Variables for statistical validation (n=327). PO=Pacific Ocean, GC =Gulf of California, GM=Gulf of Mexico, SQ=San Quintin, TA=Tamiahua, SJ=San Jorge.

Tabla XXI. Medias de Variables Canónicas para la validación estadística regional (n=327). GC=Golfo de California, PO= Océano Pacífico, GM =Golfo de México, SQ=San Quintín, SJ=San Jorge, TA=Tamiahua.

Study area	Root 1	Root 2	Root 3
PO (n=27)	**1.02912***	0.472663	0.090748
GC (n=154)	0.26169	0.024503	-0.047347
GM (n=73)	**-1.04858***	0.144235	-0.001740
SQ (n=29)	0.60110	-0.014384	0.065829
TA (n=20)	-0.76206	-0.201852	**0.131599***
SJ (n=24)	0.26121	**-0.942100***	0.017798

* Major discriminatory contribution by root

8. DISCUSSION

8.1 Measurement method and error estimates

The software developed in this research (Fin Shape v1.3) is not the only computer-assisted system for dorsal fin image analysis, but the other programs were either unavailable or not specifically developed to analyze dorsal fin shape. Quantitative analysis of shape can be accomplished by at least four different computer-assisted approaches: Geometric morphometrics (Hiby and Lovell, 1990; Higa *et al.*, 2002), Fourier analyses (Nieda, 1999), Fin Scan software (Kreho *et al.*, 1999; Araabi *et al.*, 2000), and Measurement Ratios (Weller, 1998).

The software developed here (Fin Shape v1.3) has the same functionality as Fin Morphology; but it also incorporates measurements of fin surface area (Morteo *et al.*, In progress). Note that measurement accuracy affects the degree of morphometric change that can be estimated; however, in spite of the variety of techniques available to quantitatively compare dorsal fin images, except for the software used here, no standardized error estimations are currently available to compare all these methods. Given the variety of computer-based tools to quantitatively assess morphological variation, performance comparisons among methodologies and the incorporation of all these techniques in a single integrated software are strongly recommended.

The measurements and methods for digital conversion of photographic materials used in this research proved to be very accurate; for instance, compared to the smallest level of variation among measurements of local samples (2%), both software operator and image quality errors (0.01% and 0.1%, respectively) were extremely low; thus it is assumed that image conversion and measurement methods did not represent considerable sources of error. It is assumed that standardized protocols for digital conversion of photographic materials may significantly improve image quality (Markowitz *et al.*, 2003a,b; Mizroch, 2003; Santos *et al.*, 2003; Mazzoil *et al.*, 2004).

Error for reconstruction of fin contours was not bigger than 2%; however, contours were reconstructed only to obtain graphic representations of overall differences, thus they were not quantitatively evaluated. Contours were based on median values, and the median value of the differences was five times higher (10.5%) than the error; therefore it is assumed that in spite of the relatively high construction error, there is still a safe margin to judge visually differences among localities.

8.2 General phenotypic variability

Average fin shape reconstructions for bottlenose dolphins in Mexican waters showed a certain degree of phenotypic variability; fins ranged from almost triangular to falcate and from rounded to pointed tips (Figure 6). However, most of the variability was observed over the trailing edge, primarily in base length and rake measurements, and followed by foil dimensions (Figure 6). Since dorsal fins are to some extent elastic, some degree of deformation is expected while the dolphin curves its back, especially before submergence; this may explain some amount of variation primarily in base length. However, only 23 images (7% of total sample) captured dolphins in this position, most other similar pictures were discarded because the front insertion of the dorsal fin was already below the water surface. Thus it is unlikely that fin deformation accounts for most of this variability.

It is also noteworthy that although aspect ratio values fell within those reported for the species (Fish and Rohr, 1999), these had the highest variability. Therefore, contrary to former predictions (Weller, 1998), although this index may in fact reflect hydrodynamic performance (Lang, 1966; Aleyev, 1977; Fish and Rohr, 1999; Wright, 2000), it was not effective in discriminating among the studied putative populations.

The trailing edge was highly variable among dolphins from different localities (Figure 6); this is consistent with Weller's (1998) results over a wider geographic scale. However, the central portion of trailing edge was the least variable region within putative populations (Figure 6); although most naturally induced marks useful for identification occur in this region (Weller, 1998; Delgado, 2002), this may be explained at least in part by the measurement method (Weller, 1998). Also, dorsal fin rake and foil measurements differed in dolphins from some localities; possible explanations for these observations are discussed later based on functional principles of thermoregulation and hydrodynamics.

8.3. Local phenotypic variability

Dorsal fin shapes were different enough to discriminate among local samples; other authors have obtained similar results by comparing only fin size, although such evidence is contradictory. In Chinese waters, Gao *et al.* (1995) analyzed height and width of the dorsal fin related to total body size and found differences between a southern and a northern form. Hersh and Duffield (1990) also found differences in total body length of oceanic and coastal bottlenose dolphins from the Atlantic and the Gulf of Mexico (Florida, USA), but no differences in dorsal fin height were found. Other studies have also found phenotypic variability in several other traits (Walker, 1981; Ross and Cockcroft, 1990; Vidal, 1993; Turner and Worthy, 1998; Díaz *et al.*, 2003).

Some sites in this study showed similarities in dorsal fin shapes of some neighboring localities. Since the argument of clinal morphometric variation was not supported (Figure 10), especially within the Gulf of California, fin shape similarities among proximate locations may reflect individual exchange. These findings were not consistent with the Isolation/Differentiation by Distance (IDD) model; for it was hypothesized that as distance between sites increases, the prevailing phenotype should become more distinct. Assumptions of this model are: 1) individuals have restricted home ranges; 2) genetic interchange among localities is low or negligible; and 3) there is no evolutionary convergence. Additionally, differentiation rate may increase if selective forces are geographically structured.

A priori usefulness of this model may be ruled out by the biology of the species, as well as environmental and genetic scale-dependent factors. Since bottlenose dolphins can reproduce year-round, and they can be highly mobile (Leatherwood and Reeves, 1990; Defran *et al.*, 1999; Reynolds *et al.*, 2000; Delgado, 2002; Wells and Scott, 2002), model assumptions are unlikely to be met. However, there is evidence on socially and environmentally produced boundaries delimiting populations in proximate locations (Caldwell, 1992; Gorgone *et al.*, 2003). In addition, environmental features are known to determine dolphin abundance and reproductive peaks, and in some cases these can fluctuate considerably along a coastline (Heckel, 1992; Schramm, 1993; Delgado, 2002; Guzón, 2002; Morteo, 2002); also, social behavior may potentially restrict reproductive attempts within a population. Therefore, the IDD model may work better in larger geographical scales; this may explain that local differences showed a *quasi* geographic pattern on a regional basis (Figure 9).

Since the IDD model was not supported (Figures 9 and 10), environmental, biological and genetic features thought to govern dolphin's dorsal fin polymorphisms will now be discussed on a regional basis; however, details on causal relationships and their mechanisms for fin shape regulation will be discussed later in Chapter Two.

8.3.1. Pacific Ocean

Caldwell (1992) conducted a photo-identification study and recognized two separate populations in the northeastern Pacific; however, dolphins from Ensenada and San Quintin have shown no significant differences in their dorsal fin shapes (Weller, 1998; this study). No research has been conducted in the 200 km coastal corridor between these two sites; therefore, Weller (1998) hypothesized that a single breeding population might be occurring along the west coast of North America but that it is ecologically or socially subdivided. This could be sustained by theoretical resource partitioning (e.g., food, space, females); for instance, an oceanic front occurring off the coast of Ensenada has been proposed to represent a possible ecological boundary due to the physico-chemical properties of water and increased primary productivity; however, the front varies seasonally and inter-annually in distribution and magnitude (Santamaría *et al.*, 2002). No strong evidence of overlap has been found in the distribution of both putative bottlenose dolphin populations, and individual exchange is very low (R.H. Defran[4], personal observation); therefore, the argument of a single population is thought to be poorly supported. Nevertheless, one may consider that the exchange of one dolphin per generation may be enough to prevent genetic differentiation between these areas. Molecular data would possibly serve to better address this question; in the mean time, an alternative solution is proposed.

Ensenada and San Quintin are separated by a relatively small distance and both areas are located within the same eco-region (Sullivan and Bustamante, 1999). Environmentally

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[4] Richard H. Defran, researcher at Psychology Department in San Diego State University (San Diego, CA, USA).

important phenomena in spatio-temporal small (upwellings, red and yellow tides, river discharges), medium (epidemic diseases, sea surface temperature, wave regime) and large scales (ocean currents, storms, ENSO[5], PDO[6]) frequently occur synchronically. Coastal physiography and bathymetry provide refuge for dolphin pods in both locations (Espinosa, 1986; Sandoval, 1987; Guzón, 2002; Morteo, 2002; Morteo *et al.*, 2002; Morteo *et al.*, 2004); no evidence of predation on bottlenose dolphins has been reported in either coast (Bravo, 2003; author's personal observation). These ecological features may explain similarities in relative abundance, calf numbers and seasonal trends in both areas (Guzón, 2002; Morteo, 2002; Morteo *et al.*, 2004). In addition, although San Quintin has been found to be more productive (Lara, 1975), fish diversity and prey availability may be considered analogous for the dolphin's diet (Rosales, 1997; Rosales and González, 2003); this analogy is supported by similar dolphin school sizes and larger aggregations in feeding zones (Espinosa, 1986; Sandoval; 1987; Caldwell, 1992; Guzón, 2002; Morteo, 2002; Morteo *et al.* 2002; Morteo *et al.*, 2004).

Since at least these important selective factors are similar in frequency, scale and magnitude, even if genetically distinct, there is no apparent reason to expect phenotypic variation among dolphins in both areas. In fact, detailed body morphometrics provided by Walker (1981) already support phenotypic similarity along the west coast of Baja California.

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[5] El Niño Southern Oscillation.

[6] Pacific Decadal Oscillation.

8.3.2. Gulf of California

In this region 62% of the comparisons among sites showed significant differences, even when geographic separation among localities was smaller compared to regions like the Gulf of Mexico. Vidal (1993) had already suggested geographically structured morphometric trends in the Gulf of California based on quantitative analyses of skulls from dead stranded bottlenose dolphins; although in her study separation was not robust, the division was roughly established with dolphins from the upper, mid and lower gulf; and subsequently divided in mainland and peninsular dolphins. The pattern has been reported in several taxa including invertebrates (Correa and Carvacho, 1992; De la Rosa *et al.*, 2000), fish (Riginos and Natchman, 2001), and marine mammals like the California sea lion (*Zalophus californianus californianus*) (Schramm, 2002; Aurioles *et al.*, 2004; Pedernera *et al.*, 2004; Porras *et al.*, 2004). These results are consistent with the quantitative analysis performed here (Table VI, Figure 8), and the most common explanation is the oceanography of this region causing habitat and resource partitioning.

The Gulf of California is a highly productive region; it is more than 2000 m deep from its mouth (~23°N) up to the midriff islands (~ 29°N); in contrast, 75% of the area in the upper portion is less than 200 m deep. Small tides and weak tidal currents occur in the lower gulf; in contrast, up to the Upper Gulf of California, the tidal cycle ranges several meters and the shallow coast presents strong tidal currents (Lavín and Organista 1988). Sea surface temperature (SST) is generally highly variable with a seasonal pattern (Castro *et al.*, 1994; Lavín *et al.*, 2003) (Figure 12). Based on temperature profiles and primary productivity, Hidalgo and Álvarez (2001) divided the gulf latitudinally in two regions during the cool season (November to the end of June) and in four regions the rest of the year; this division consistently occurs in the mid gulf around the islands, which has been proposed as a major ecological brake. In this region, lower temperatures generally occur in Canal de Ballenas, where water mixing and internal waves increase primary productivity (Gaxiola *et al.*, 2002). Also, a general tendency was found by Santamaría *et al.* (2000), where SST increases from the peninsula towards the eastern coast.

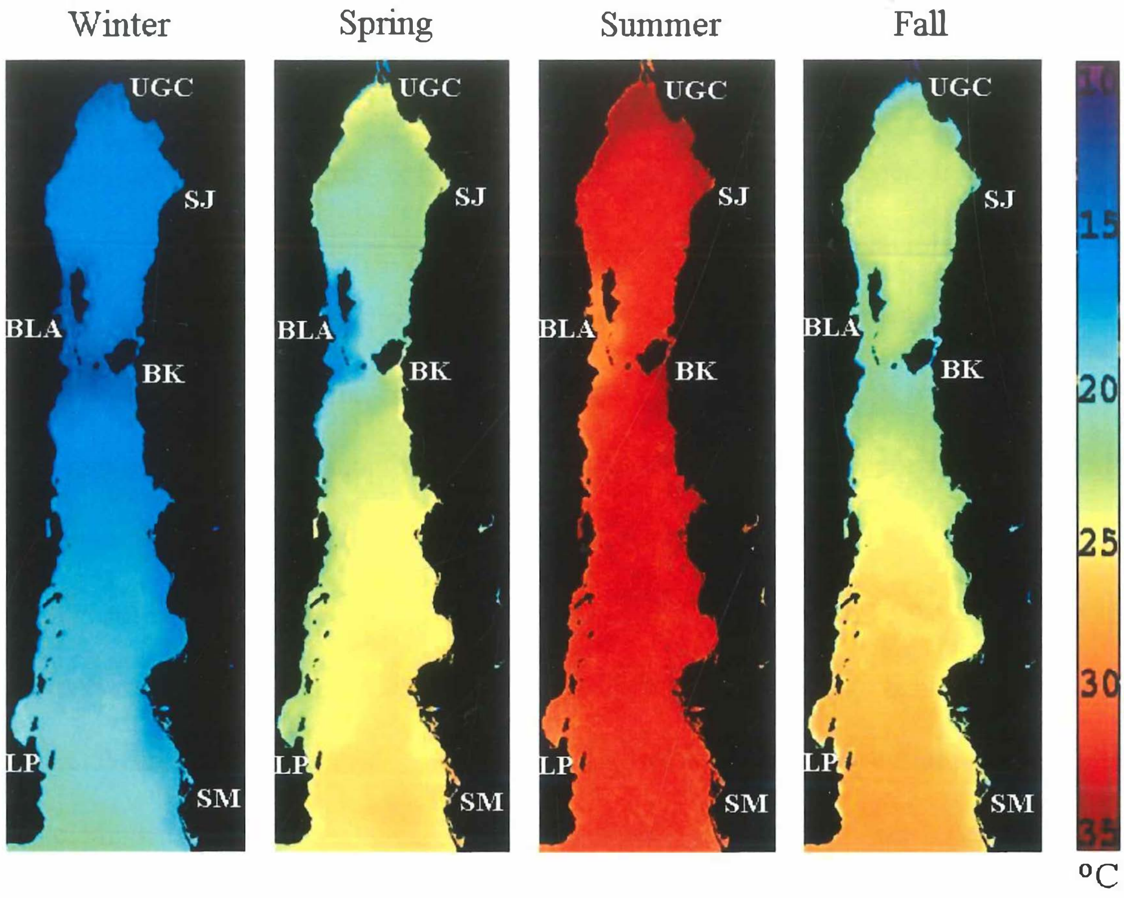

Figure 12. Average seasonal sea surface temperature for the Gulf of California during 1996-2001. UGC=Upper Gulf of California, Sonora; SJ=Bahia San Jorge, Sonora; BK=Bahia Kino, Sonora; SM=Bahia Santa Maria, Sinaloa; BLA=Bahia de los Angeles, Baja California; LP=La Paz, Baja California Sur. Modified from the Laboratory of Physical Oceanography at the Institute of Marine Sciences and Limnology (Universidad Nacional Autónoma de México) (Seaspace, 2003).

Figura 12. Temperatura superficial estacional del mar en el Golfo de California durante 1996-2001. UGC=Alto Golfo de California, Sonora; SJ=Bahía San Jorge, Sonora; BK=Bahía Kino, Sonora; SM=Bahía Santa María, Sinaloa; BLA=Bahía de los Ángeles, Baja California; LP=La Paz, Baja California Sur. Modificado del Laboratorio de Oceanografía Física del Instituto de Ciencias Marinas y Limnología (Universidad Nacional Autónoma de México) (Seaspace, 2003).

Since phenotypic geographic structure in bottlenose dolphin skulls and dorsal fin shape is to some extent consistent with the former oceanographical and ecological division, two issues are to be addressed: feeding ecology and thermoregulation.

It has been suggested that differences in skull morphometrics can be correlated to differences in feeding ecology (Walker, 1981, Vidal, 1993; Gao *et al.*, 1995). Based on this assumption, predators like the bottlenose dolphin may have developed a wide range of feeding techniques in response to a variety of prey and prey behaviors. For instance, beaching dolphins have been reported from the upper Gulf (Silber and Fertl, 1995); dolphins in some locations may or may not feed on fish discards from trawlers (Ballance, 1987; Acevedo, 1989; Orozco, 2001; Carrillo and Mellink, 2004); cooperative feeding is also very common (Reza, 2001); and nocturnal feeding bouts may be very important (Day, 1998), or more frequent in some cases (Delgado, 2002). Plasticity in feeding behavior may be in part regulated by the energetic cost of different swimming behaviors related to locating, chasing, handling, and ingesting prey (Johnson, 1999); thus maneuvering abilities may be important in feeding success, and the dorsal fin may play an important role for swimming stabilization.

Alternatively, sea surface temperature (SST) regime plays an important role in species distribution (Pianka, 1994; Valiela, 1995); thus it may somehow influence animals’ home ranges. For instance, structured populations of the California sea lion have been detected in the Gulf of California, based on morphometrics, genetics, prey preference, and epidemic bacterial analyses (Schramm, 2002; Aurioles *et al.*, 2004; Pedernera *et al.*, 2004; Porras *et al.*, 2004).

Given the wide distribution of the bottlenose dolphin, SST may not be an important issue at small scales; however, in the Gulf of California major temperature shifts occur within a few kilometers, especially in the central portion (Lavín *et al.*, 2003) (Figure 12). Movements of satellite tagged bottlenose dolphins in the Atlantic have shown avoidance of cold oceanic fronts (Wells *et al.*, 1999); thus quick temperature changes may trigger behavioral and physiological responses possibly influencing home ranges, but also food habits and consumption rates.

The former argument accounts mainly for latitudinal morphological differentiation across the gulf. It is noteworthy that 16.3% of the 178 individuals from the Gulf of California were misclassified as either "peninsular" or "mainland" dolphins (Table VI). However, in some cases there were significant differences ($p<0.05$) between both these shores (Table V) and this pattern was also found by Vidal (1993) based on skull morphology. Some possible explanations are differences in physiography, oceanography and ecology between the two coastlines (Wells *et al.*, 1981; Lavín *et al.*, 2003). Also, given the coastal nature of the putative populations in this study, and the pronounced depth between mainland and peninsula (up to 1,200 m in Canal de Ballenas) (Tershy and Breese, 1993), individual exchange across opposite shorelines may be low, especially in the mid and lower gulf (Figure 10). However, the intrusion of oceanic dolphins into both mainland

and peninsular populations may artificially increase variability and thus fade separation. Since no clear pattern was found, in addition to selective pressures, dorsal fin morphology may, in some way, be caused by possible genetic flow between the eastern and western shores.

Analyses of mtDNA (Segura, In progress) have shown that individuals from the upper Gulf of California are genetically differentiated from the rest; and no clear phylogeograpic pattern has been found within the rest of the gulf. In this study, morphological similarities in dorsal fin shape of the Upper Gulf of California may be due to the fact that all individuals analyzed came from 3 schools spotted the same day; thus there is a chance that these dolphins may not represent the prevailing phenotype in the area. The unresolved phylogeography within the gulf should be revised using more variable neutral genetic markers; however, if the rest of the gulf is in fact genetically homogeneous, morphological divergence would reflect a single norm of reaction, and the morphological observed differentiation in dorsal fins may be associated to different selective environments. Therefore, based on molecular analyses (Segura, In progress) in addition to skull (Vidal, 1993), and dorsal fin morphometrics (this study), we may at least be observing the early steps of microevolution.

There is a slight chance that morphological similarities between isolated localities (Santa María–Gulf of Mexico, and Bahia Kino–San Quintín) may be an artifact, resulted from the statistical classification functions (Table VI); however, similar environmental features, as well as genetic exchange may be possible explanations (details of the mechanisms for fin shape regulation are discussed in Chapter Two). For instance, unlike the rest of the study areas in the Gulf of California, Bahia Santa Maria is an enclosed estuarine system with two entrances, and the vegetal coverage along the shore is dense and abundant (Reza, 2001). Also, mean year-round SST values for Santa Maria range between 20–30°C (Reza, 2001). These environmental features are consistent with the study areas in the Gulf of Mexico (Heckel, 1992; Schramm, 1993; Lechuga, 1996; Delgado, 1996, 2002), which may cause that in spite of the differences in species diversity, both areas may have similar ecological roles. This may explain the small group size and similar feeding behavior of bottlenose dolphins in both areas (Heckel, 1992; Schramm, 1993; Lechuga, 1996; Delgado, 1996, 2002; Reza, 2001). Therefore, similar dorsal fin shapes in Santa Maria and the Gulf of Mexico may imply similar selective pressures and thus convergent evolution.

On the other hand, similarities between Bahia Kino and San Quintin may be based on geological events and the possibility of gene flow (details in 8.4.1 Phenotypic considerations of regional variability).

8.3.3. Gulf of Mexico

The fact that no statistical discrimination was found in the morphology of dorsal fins among localities in the Gulf of Mexico may be related to the behavior of the species in this region. For instance, Delgado (2002) states that there is a fairly large number of dolphins in Terminos Lagoon (at least 1,987 identified), and many of them might be transient. One of these individuals moved at least 800 km from Holbox Island to the western coast of the gulf (state of Campeche) in less than a year; and four other individuals moved between 240–320 km in 274–1,404 days. Lechuga (1996) and Delgado (2002) also reported that group membership is unstable; however, on average, dolphins from Holbox Island were closely associated with between 5 and 22 other dolphins (Lechuga, 1996; Delgado, 2002), while animals from Terminos Lagoon averaged 32 other individuals (Delgado, 2002). This implies that dolphins moving from place to place (especially males) traveling in large groups, may potentially reproduce with dolphins from other locations. Also, if transient aggregations are larger than local groups, numeric advantage may favor social and sexual interactions, especially between transient males and local females, thus increasing chances of gene flow.

There are no other photographic comparisons available among dolphins from Tamiahua, Holbox, and Terminos; however, according to Heckel (1992) and Schramm (1993), at least 68% of the dolphins from Tamiahua may be transient. Also, given the large movements reported for bottlenose dolphins in the Atlantic (Wells *et al.*, 1999; Delgado, 2002; Estrada and Hohn, 2004), genetic exchange may occur over a larger scale; thus it would not be surprising if no evident genetic structure is found, and there are no differences in dorsal fin morphology. Alternatively, not enough time may have elapsed for genetic and morphological differentiation among localities to develop (Hoelzel *et al.*, 1998; Möller and Beheregaray, 2001; Segura, In progress).

On the other hand, if these putative populations are in fact genetically distinct, morphological similarities in the trait may be based on the homogeneity and stability of the environment. For instance, compared to the Gulf of California, wave regimes and SST variations in the Gulf of Mexico are much lower in magnitude and frequency due to the influence of the Gulf Stream (Davis *et al.*, 1998); and because of its influence over a large area (Avise, 1992), selective pressures may be similar in spite of the larger distance among sites. This situation may explain not only similarities in shape, but also less overall variability in dorsal fins (Figure 6).

8.3.4. Discriminatory power and individual dispersal

While statistical discrimination of dorsal fin shapes in this study may be largely due to the low phenotypic variability within putative populations (based on the finding that only 20 individuals were sufficient to account for most local variability) (Figure 7), another possible explanation may be the image selection criteria. Consider first, that the use of mature animals introduces an age-based bias; then consider that dorsal fins had to be as complete as possible to avoid non-natural forms. Since some studies have reported higher rates of fin damage on mature or male dolphins, due to more active social interactions and reproductive competition (Weller, 1998; Perrin and Mesnick, 2003), the criteria used may have potentially biased sampling in favor of females and/or physically mature but young animals.

Young animals and females in some areas have more restricted home ranges or do not move as far as male bottlenose dolphins; this has been attributed to social and ecological factors primarily directed towards increasing time in provisioned and protected areas. In young animals this is possibly due to parental care and defense against predators; females may also need to avoid harassment from males and have higher energetic requirements for calf production (Scott *et al.*, 1996; Watson *et al.*, 2003; Krützen *et al.*, 2004).

Dorsal fin pictures are not useful to establish the gender of individual bottlenose dolphins; therefore, there is a slight chance that variability within populations could be underestimated and thus artificially enhance separation among local samples. In the worst case scenario, if all analyzed dolphins are females, the results would show some degree of site fidelity, reflected in geographically structured trends at least within the Gulf of California. However, if at least some physically mature young animals and males were included in the analysis (which seems to be the case in all localities), the results become robust, because they effectively discriminate among some locations in spite of the possible sex-age bias or even if sexual dimorphism actually exists.

8.4. Regional phenotypic variability

8.4.1. Phenotypic considerations

It has been commonly assumed that wide geographic coverage may be useful to distinguish, to some extent, causal relationships in morphological patterns from trends maintained primarily as a result of isolation by distance (Schnell *et al.*, 1986); accordingly, large sample sizes with good representation from several localities are thought to be needed to determine clinal morphological trends among dolphin forms (Gao *et al.*, 1995). Weller (1998) reported differences in dorsal fin shapes among coastal bottlenose dolphin populations from the Indian and Pacific oceans, and the Gulf of Mexico; however no discussion regarding separation is made on a regional basis.

In this study, major differences in dorsal fin shape were also found between the Gulf of Mexico and the Gulf of California; however, statistical validation of regional assessment showed no differences between the Pacific and the Gulf of California. A possible explanation is based on geological events; for instance, the Baja California peninsula began to separate from the mainland about 5.5 Mya (nearly the age of the genus *Tursiops*) (Riddle *et al.*, 2000); thus colonization and dispersal of bottlenose dolphins may have been on going since that time. Riddle *et al.* (2000) also suggested that during this separation (5.5−1 Mya), the peninsula was fragmented on several occasions by trans-peninsular seaways, connecting the Pacific and the Gulf; this transgression may partially explain similarities in dorsal fin shapes between the Pacific (Ensenada and San Quintin) and the upper Gulf of California (mostly the Upper Gulf of California and Bahia Kino) due to the possibility of gene flow.

Comparatively, divergence between Gulf of Mexico and Pacific populations ensued after the emergence of the Isthmus of Panama which closed the inter-oceanic canal (approx. 2.5 Mya) (Gore, 2003); therefore, morphological differences in the Gulf of Mexico may be attributed to vicariance.

8.5. Management implications

Knowledge on geographically structured variation is necessary to determine biological and ecological boundaries, which are very important in the development of management strategies. Based on the biology and ecology of cetaceans, evolutionary significant units (ESU) should be used instead of stocks or populations to define management policies (Dizon *et al.*, 1992; Rojas, 1992; Moritz, 1994; Vogler and Desalle, 1994).

The lack of biological and ecological information is an important problem when assesing risk status in wild populations; also, stock assessments require great amounts of field effort and large quantities of biological and genetic data. Photo-identification studies represent a relatively low cost alternative and, if properly conducted, basic information on free ranging animals can be acquired relatively fast (Hammond *et al.*, 1990). In addition, photographic techniques have also been useful to identify morphological variations in dolphin species (Perrin 1972, 1991; Weller, 1998; Díaz *et al.*, 2003; this study). Based on all evidence at hand, proposed geographic population subdivisions are shown in Figure 13. It is important to note not only the need of molecular and morphological data, but also the comparison of photographic catalogs among proximate locations.

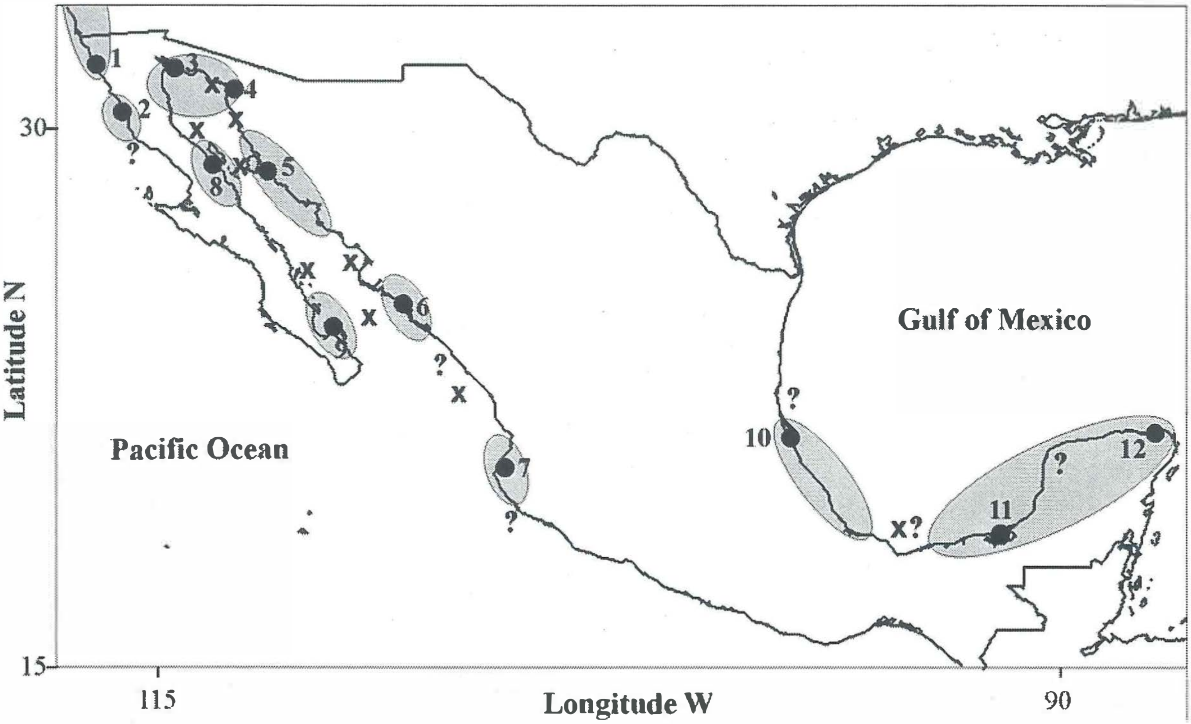

Figure 13. Geographic population subdivision based on literature. This subdivision was generated using all evidence at hand (photo-identification, molecular and morphological) including results from this research. **x** = no comparisons among photo-identified individuals; **?** = no available molecular or morphometric data. 1) Ensenada, Baja California; 2) San

Quintin, Baja California; 3) Upper Gulf of California, Sonora; 4) Bahia San Jorge, Sonora; 5) Bahia Kino, Sonora; 6) Bahia Santa Maria, Sinaloa; 7) Bahia Banderas, Jalisco; 8) Bahia de los Angeles, Baja California; 9) La Paz, Baja California Sur; 10) Tamiahua, Veracruz; 11) Terminos Lagoon, Campeche; 12) Holbox, Quintana Roo.

Figura 13. Subdivisión geográfica poblacional basada en literatura. Esta subdivisión se generó utilizando toda la evidencia disponible (foto-identificación, molecular y morfológica), incluyendo los resultados de esta investigación. x = sin comparación entre individuos foto-identificados; ? = datos moleculares o morfométricos no disponibles. 1) Ensenada, Baja California; 2) San Quintín, Baja California; 3) Alto Golfo de California, Sonora; 4) Bahía San Jorge, Sonora; 5) Bahía Kino, Sonora; 6) Bahía Santa María, Sinaloa; 7) Bahía Banderas, Jalisco; 8) Bahía de los Ángeles, Baja California; 9) La Paz, Baja California Sur; 10) Tamiahua, Veracruz; 11) Laguna de Términos, Campeche; 12) Holbox, Quintana Roo.

Therefore, although results from this research should be revised with further photo-identification, and correlated to morphological and genetic studies, they give a first approach in defining possible population divisions. Concordance among all these techniques would indicate that dorsal fin morphological variation may potentially serve as a practical and powerful tool for rapid population identification in free ranging bottlenose dolphins.

CHAPTER TWO

CAUSAL ENVIRONMENTAL RELATIONSHIPS, GENETIC MECHANISMS FOR POLYMORPHISMS AND METHODS TO EVALUATE PERFORMANCE OF THE DORSAL FIN IN THE BOTTLENOSE DOLPHIN (*Tursiops truncatus*)

1. POSSIBLE CAUSAL RELATIONSHIPS

A first step for interpreting adaptation is to determine the functionality of different character states (Lauder, 1996). Due to the interaction among traits (phenotypic and genetic) in a single organism, which can compensate one another, determination of individual fitness is usually very complex (Gould and Lewontin, 1979). Organisms generally present eco-physiological restrictions that are manifested in the quantity of phenotypic variation associated to their genotype (reaction norm). Some of these phenotypic differences have been sufficient to determine quantitatively the existence of different forms in the species and the possibility of genetically differentiated populations (Perrin, 1972, 1984; Walker, 1981; Duffield *et al.*, 1983; Hersh and Duffield, 1990; Ross and Cockroft, 1990; Van Waerebeek, *et al.*, 1990; Perrin *et al.,* 1991; Vidal, 1993; Ford *et al.*, 1994; Wiley *et al.*, 1994; Gao *et al.*, 1995; Goodwin *et al.*, 1996; Turner and Worthy, 1998; Weller, 1998; Wells and Scott, 1999; Reeves *et al.*, 2002; Díaz *et al.*, 2003; Ortega *et al.*, 2004; this study). If this is the case, it is possible that phenotypic variability could be adaptive (selection of phenotypes from the genotype). Thus in this section, fin polymorphisms will be discussed in terms of their functional constraints inferred from the possible advantages in hydrodynamics and thermoregulation.

1.1. Anatomical considerations

Swimming is a primary component of a dolphin's time and energy budget (Fish and Hui, 1991); thus it has played a major role in the evolution of the taxonomic group (Hui, 1987). It has been assumed that cetaceans have evolved behavioral adaptations to minimize swimming energy expenditure (Fish and Hui, 1991); factors such as sexual, social and foraging behavior (e.g. solitary *vs.* cooperative feeding), prey size, abundance and behavior, habitat type (e.g. pack ice, open ocean, or shallow waters), maneuverability, and characteristic swimming speed are thought to influence body morphology (Lang and Pryor, 1966; Aleyev, 1977; Fish, 1998; Weller, 1998; Perrin and Mesnick, 2003).

Dorsal fin shape in dolphins is particularly important for swimming performance (Lang, 1966; Fish and Hui, 1991; Marshall, 2002), for it provides stability and maneuverability underwater (turning rates as high as 450 deg s^{-1} with a turn radius as low as 11−17% of body length) (Fish and Rohr, 1999). The percentage of appendage surface area in cetaceans ranges from 14 to 42% for the flippers, 0 to 18% for the dorsal fin, 16 to 48% for the peduncle, and 22 to 37% for the flukes (Fish, 1997 cited in Fish and Rohr, 1999). Drag added by the appendages has been estimated as high as 28% of total body drag; therefore, it has been assumed that dolphins have a propulsive efficiency as high as 90% (Lang and Pryor, 1966).

Several studies suggest that due to morphological similarities and hydrodynamic principles, fins with certain geometric aspects reflect effective adaptations for swimming great distances or at high speeds (Pauly and Palomares, 1989; Fish, 1998; Fish and Rohr, 1999; Wright, 2000). Lang (1966) determined that dorsal fins in two dolphin species (*Lagenorhynchus obliquidens* and *Delphinus bairdi*) and a porpoise (*Phocoenoides dalli*) have an ideal design for underwater operation, and by analyzing their structure it is possible to predict the maximum speed achieved by each species. This is important for dolphins, since drag forces caused near the water surface are 4 to 5 times higher than those caused by an animal swimming submerged at the same speed; this is due to energy loss involved in wave formation and breaking the superficial tension (Williams *et al.*, 1993; Reynolds *et al.*; 2000; Williams, 2002). However, no inferences are available to account for intraspecific variability.

1.2. Physiological considerations

Cetaceans rely on blubber and vascular adaptations (*rete mirabilia*) to regulate heat transfer. Since blubber (up to 93% lipid) has about a third of the water's thermal conductance, it acts as a relatively good insulator (Castellini, 2002). Blubber thickness in cetaceans may vary seasonally; however, it can be bypassed through the blood circulation system (Whittow, 1987; Hokkanen, 1990).

Since skin temperature approximately equals that of the water at all times (Whittow, 1987; Hokkanen, 1990), and some marine mammals may experience a decrease in environmental temperature as great as 23°C while diving (Whittow, 1987), produced heat must equal losses to the environment to maintain constant body temperature (Castellini, 2002).

Heat loss through body surface occurs in the form of radiation, evaporation, conduction, and convection towards water and air; the last two being the most important (Hokkanen, 1990; Castellini, 2002). On the other hand, body surface gains heat when the heart sends hot blood through vascularization, by heat conduction through muscular tissues or by absorption of solar radiation (Whittow, 1987; Reynolds, *et al.*, 2000; Meagher *et al.*, 2002).

Some authors have reported that fin temperatures (primarily dorsal fin) are consistently above sea surface temperature (Cuyler *et al.*, 1992; Noren *et al.*, 1999a,b); thus fins in marine mammals may function as thermal windows to dissipate heat depending on the thermal demand (Meagher *et al.*, 2002). This occurs through a blood counter-current system (*rete mirabilia*) that increases efficiency of heat exchange (Reynolds *et al.*, 2000; Meagher *et al.*, 2001; Pabst *et al.*, 2001).

Several studies on swimming bottlenose dolphins have found a relationship among heart beat rate, swimming speed, diving, and thermoregulation (Williams *et al.*, 1993 ; Noren *et al.*, 1999a,b; Meagher *et al.*, 2002). As expected, body temperature increases with exercise, so does heart beat rate and thus blood flux. Overheating due to surface swimming may be normally compensated by the thermoregulatory system; however, diving shows a different pattern. Diving requires oxygen conservation, so dolphins experiment bradycardia (decrease in heart beat rate) and blood flux is restricted to endure immersion time (Castellini, 2002). This may increase core temperature; however, diving dolphins may also switch between different diving modes (due to changes in buoyancy), thus changing energy expenditure (Williams, 2002). In spite of individual variability in heat dissipation strategies and patterns (Cuyler *et al.*, 1992; Meagher, 2001; Meagher *et al.*, 2002), a trend in the responses of diving dolphins has been suggested; therefore, heat transfer from fins is attenuated while diving and increased during surface recovery (Williams *et al.*, 1993; Noren *et al.*, 1999b).

1.3. Energetic considerations

Based on these considerations, responses for swimming, diving, and thermoregulation may be shaped by environmental pressures such as: required swimming speed and maneuverability, dive depth, submergence time and temperature shifts; all these may be primarily related to food habits. Therefore, behavioral, anatomical, or physiological responses are thought to have a strong selective basis (discussed later), and may be the result of natural selection.

Biological design as a result of natural selection, assumes that animals have already performed the "cost-benefit" analysis (Fish and Rohr, 1999). Therefore, if dorsal fin shapes reflect adaptations, the causes may involve special energetic demands in different time scales.

Based on the theory of optimal foraging, metabolic requirements in the short term (minutes to hours) may be related to immediate energy expenditure due to different swimming modes or behaviors (Schoener, 1971; Johnson, 1999). In the mid term (days to weeks or months), energy expenditure may be related to food abundance and availability and also to reproduction (Hui, 1987), by moving between highly productive regions or by migratory events (Schoener, 1971). In the long term (years, decades), metabolic costs may be related to body's hydrodynamic drag (ontogenetic or allometric changes) and water temperature. For instance, since drag increases with speed, and heat loss is dominated by convection (Hokkanen, 1990; Castellini, 2002), for a swimming animal, heat transfer across the skin/water boundary (chill factor) will increase with velocity (Hind and Gurney, 1997). This argument links anatomical and physiological responses, which also depend on the time scale. In short periods (minutes, hours) physiological response to heat loss (Noren *et al.*, 1999b; Rommel *et al.*, 1999) occurs by restricting blood flux towards the fins in order to prevent heat loss through blubber insulation; if core temperature is high, the mechanism can be reversed by increasing blood flux towards the fins to rapidly dissipate heat. At mid term (days, weeks, months) the response to heat loss can be behavioral (Whittow, 1987; Reynolds *et al.*, 2000), by increasing surfacing time (since air conducts heat up to 25 times slower than water), or moving to warmer locations. In the long term (generations) response to heat loss could be adaptive, by increasing total length of animal's body (Bergman's rule), since the area-volume ratio diminishes, and/or by diminishing the length of appendages (Allen's rule) and with it the surface of thermal exchange in fins (Pianka, 1994).

1.4. Considerations on performance

The morphological variation found in the dorsal fin of this species may be related to thermoregulation and hydrodynamic performance. Information regarding these aspects will now be reviewed and discussed according to the results from this research. For instance, the tip and the base of the dorsal fin were the most variable measurements; thus these may be important cues to understand how the environment influences this trait.

Regarding thermal performance, the dorsal fin is highly irrigated by small veins and vessels which help in thermoregulation; infrared imaging suggests that temperature patterns across the fin may be influenced by the underlying vasculature (Meagher *et al.*, 2002). Direct measurements in bottlenose dolphins showed that the distal tip of the dorsal fin displayed the highest heat flux values during submergence (however, no clear pattern was observed with the fin in air) (Meagher, 2001). Meagher (2001) explained that considering a smaller cross sectional width on the distal tip of the fin, the arteries are closer to the skin surface, thus making heat transfer more direct. Also, although the average distance between the central arteries did not differ greatly across the fin, it was smaller at the distal section; this implies that heat may be transmitted more efficiently.

There is an evident relation between dorsal fin size (related to body mass) and thermoregulation (Allen´s rule) (Pianka, 1994); however, no direct relationship is evident with dorsal fin shape. Preliminary results by Morteo *et al.* (In progress) show that for structural reasons, the maximum width of the dorsal fin is directly related to its base length. If this is the case, taller or more falcate fins (like those found in the Pacific and the Gulf of California) would have, on average, a reduction in their overall maximum width, compared to shorter or triangular fins (like those in the Gulf of Mexico). Therefore, according to Meagher (2001), this may imply that in fins from the Pacific and the Gulf of California, veins may be close to the skin's surface over a larger portion of the fin's area, involving more direct and efficient heat flux. Since average sea surface temperature (SST) in either the Gulf of California or the Pacific is up to 10° C colder than the Gulf of Mexico, it would seem that greater thermal efficiency would be needed in the warmer locations, thus this argument is inverted; however, it is noteworthy that heat flux may strongly rely on the distribution pattern of the underlying vasculature more than on the actual shape of the dorsal fin.

Great variation has been found in vessel distribution in dorsal fins of bottlenose dolphins; for instance, Meagher (2001) found that superficial veins were more spaced on some fins; also, vein distribution was not bilaterally symmetric in at least one individual.

Therefore, dorsal fin vascular anatomy should be examined in several individuals from different populations of bottlenose dolphins; this would help to assess variation in vessel distribution and to elucidate the existence of possible patterns. These patterns may be important in thermoregulatory performance on a population basis. For instance, observations of vein-vessel distribution in dorsal fins of Pantropical spotted dolphins (*Stenella attenuata*) have shown to be very similar in mother-calf pairs (F. Townsend [7], personal observation).

Regarding hydrodynamic performance, keel design is very important in the maneuverability of many aquatic vehicles (Weller, 1998; Fish and Rohr, 1999). For instance, thin and falcate keels improve maneuverability and allow quick changes of direction; on the other hand, wide based keels provide higher stability and straight trajectories when advancing (Weller, 1998). Since no information is currently available on the hydrodynamic advantage of the different dorsal fin shapes, some apparent coincidences prove interesting. For instance, more falcate fins were found in the Pacific (Figure 6), where swells are as high as 5 m (Lizárraga *et al.*, 2003); and also in the Gulf of California, where tidal currents may exceed 3 m s^{-1} (Álvarez, 2001). Comparatively, less falcate fins were found in the Gulf of Mexico, where tidal currents and wave heights are of lower magnitude (Delgado, 2002).

This pattern may be explained considering that swimming in waves up to 4 m height must require a high degree of control (Figure 14); and this may be especially relevant while

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[7] Forrest Townsend, College of Veterinary Medicine, University of Florida (FL, USA).

looking for food inside kelp beds or through strong tidal currents. Although most of the navigation control relies on the flippers, falcate dorsal fins in the Pacific and the Gulf of California may help to complete this task, since falcate shapes theoretically perform better at high speeds or in highly dynamic environments.

It is also noteworthy that the central area of the trailing edge had the lowest variability within populations. This may imply that at least for dolphins in Mexican waters, some portions of the fin could be functionally more important and thus less variable. Therefore, although the functional thermoregulatory and hydrodynamic advantages are not yet demonstrated, they are strongly suspected (Weller, 1998); this suggests that in a wider range of environments, fin shape may be a trade-off between thermoregulatory capacities and hydrodynamic performance, among other factors.

Figure 14. Wave-riding bottlenose dolphins. Note that maneuverability may be influenced by dorsal fin hydrodynamic performance; this may be relevant in highly dynamic environments with large swells and strong tidal currents.

Figura 14. Tursiones montando una ola. Note que la aleta dorsal puede influenciar la maniobrabilidad y el desempeño hidrodinámico; esto puede ser importante en ambientes muy dinámicos con mareas amplias y fuertes corrientes de marea.

2. POSSIBLE MECHANISMS DETERMINING DORSAL FIN SHAPE

The study of adaptations is very difficult and prone to many interpretations; this is because within a species, a given trait may respond differently to particular evolutionary forces; furthermore, there might not be any selective basis available to identify why variations occur and how the differences originated (Gould and Lewontin, 1979).

Although mechanisms of adaptation and even the concept itself continues to be the subject of intense debate (Amundson, 1996), the presence and/or modification of certain traits (in this case the dorsal fin) provides differential fitness to individuals; however, it should not be ignored that fitness may be the result of direct function of traits or just a by-product (Gould and Lewontin, 1979).

Some species may represent variation that has accumulated rapidly; if this variation is adaptive, the outcome of positive Darwinian selection may be measured as the frequency of any particular character state in different populations or species. Accordingly, phenotypic variability and polymorphisms could be associated to different fitness levels among individuals in isolated or semi-isolated populations. This assumption is valid only in the absence of convergence, and if genetic drift and inbreeding within populations are not significant (Appendix A). Also, if these variations are predictable and either complex or numerous enough so it is unlikely that they have arisen by chance, they may be considered as adaptations (Gotthard and Nylin, 1995).

Environmental causes have been discussed earlier suggesting dorsal fin polymorphisms are indeed adaptations. However, Smith-Gill (1983) and Thompson (1991) argue that unless specific genetic mechanisms can be demonstrated, observed phenotypic plasticity should not be assumed to be adaptive. Therefore, in the following section, biological and ecological data are discussed in light of evolutionary and genetic theories to elucidate possible causal relationships governing dorsal fin shape in the bottlenose dolphin.

2.1. Evolutionary constraints

Dorsal fin shape in the bottlenose dolphin is common to other dolphins like *Delphinus* spp. and *Stenella* spp. (Figure 15). Similar fin shapes may represent evolutionary constraints which may be the result of a plesiomorphic fin shape present in the Kentridontidae or other dolphin ancestors. Although, variation seems to be larger as geographic coverage increases (Weller, 1998; this study), at least for the bottlenose dolphins in this study, the high correlation ($p<0.05$) among most measurement ratios suggest dorsal fin shape is strongly dependent on a few parameters. However, dorsal fins in the entire family Delphinidae are highly variable (Carwardine, 1995; Reeves *et al.*, 2002) (Figure 16), and at least in the bottlenose dolphins, killer whales (*Orcinus orca*) and spinner dolphins (*Stenella longirostris*) it has been found to be variable enough to discriminate among putative populations (Perrin, 1972; Perrin *et al.*, 1991; Ford *et al.*, 1994; Weller, 1998; Perrin and Mesnick, 2003; this study). Also, Gotthard and Nylin (1995) argue that evolutionary constraints probably have a minor role in explaining the difference between populations in a trait varying in a quantitative manner; therefore, it is assumed that in addition to evolutionary constraints, if present, fin shape may vary in response to environmental (hydrodynamic and thermal) and genetic constraints.

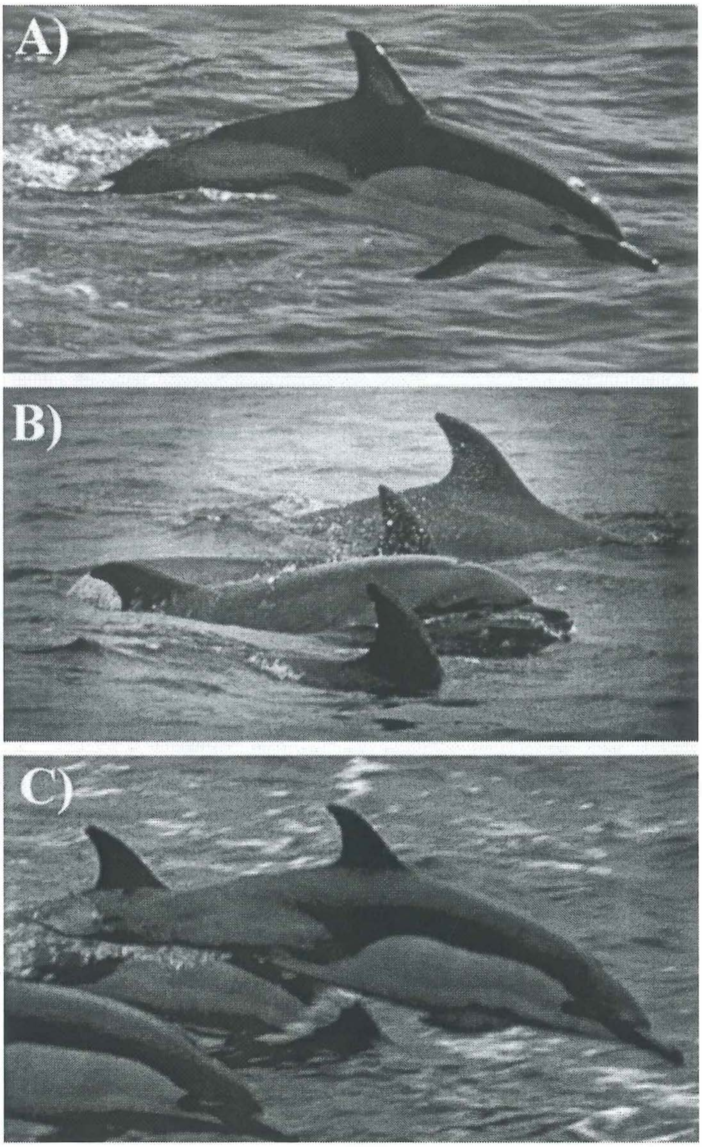

Figure 15. Fin shape similarities among delphinids. A) Clymene dolphin (*Stenella clymene*), B) Bottlenose dolphin (*Tursiops truncatus*) and C) Common dolphin (*Delphinus delphis*).

Figura 15. Similitudes en la forma de la aleta de los delfines. A) Delfín de Clymene (*Stenella clymene*), B) tursión (*Tursiops truncatus*) y C) delfín común (*Delphinus delphis*).

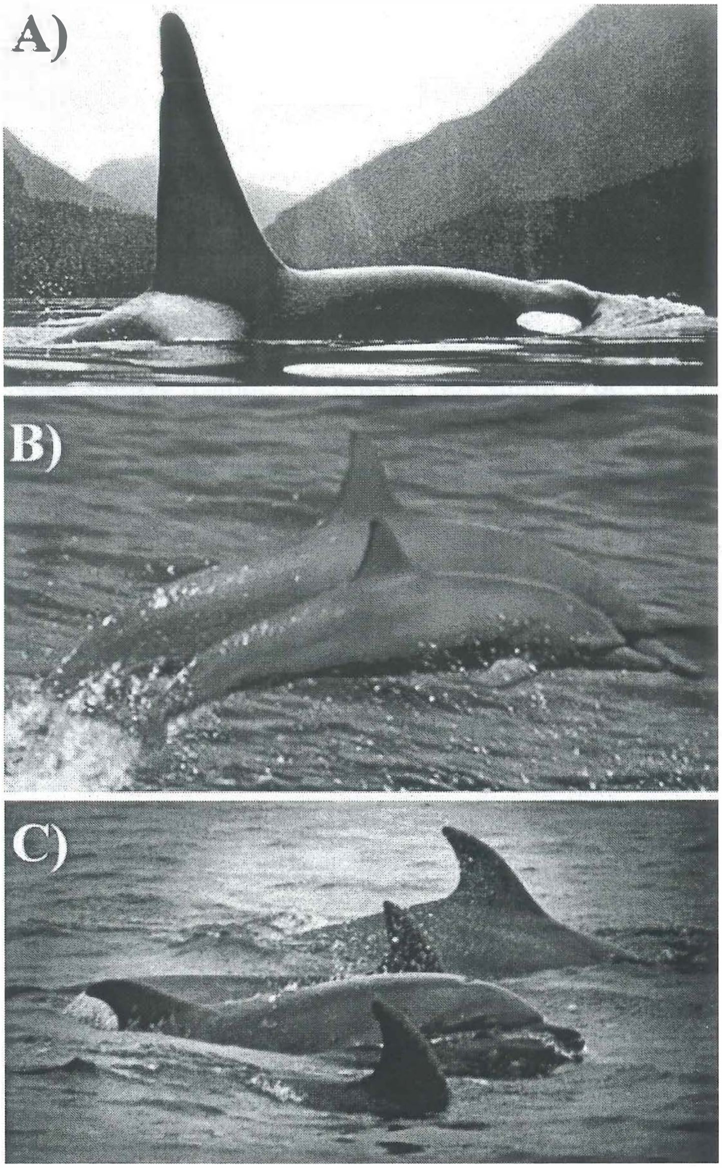

Figure 16. Fin shape differences among delphinids. A) Killer whales (*Orcinus orca*), B) Spinner dolphins (*Stenella longirostris*) and C) Bottlenose dolphins (*Tursiops truncatus*).

Figura 16. Diferencias en la forma de la aleta de los delfines. A) Orca (*Orcinus orca*), B) delfines tornillo (*Stenella longirostris*) y C) tursiones (*Tursiops truncatus*).

2.2 Genetic constraints

Phenotypic characters which are easily influenced by selection are considered evolutionarily plastic; while those resistant to change are genetically canalized (Smith-Gill, 1983; Stearns, 1989). Norms of reaction can change in evolution (Caswell, 1983) and in theory, limited phenotypic plasticity or restricted norms of reaction within species or populations may cause similar designs (Gotthard and Nylin, 1995) (Figure 17). The norm of reaction for dolphin phenotypes may be inflexible (Stearns, 1989), meaning that once a fin shape has been produced it cannot be reversed.

Conspicuously deviant fin phenotypes have been detected in some populations of bottlenose dolphins (Ballance, 1987; Díaz, 2001; Orozco, 2001; Delgado, 2002), spinner dolphins (Perrin, 1972; Perrin *et al.*, 1991; Perrin and Mesnick, 2003) and killer whales (Ford *et al.*, 1994), suggesting high phenotypic plasticity. Since significant differences have also been found in fin measurements of geographically, and ecologically separated bottlenose dolphin populations (Gao *et al.*, 1995; Weller, 1998; this study), limited phenotypic plasticity or restricted norms of reaction do not seem to be the case.

Because no genetic data are available to establish if these deviant morphotypes actually belong to a population, these might artificially inflate a populations norm of reaction; however, at least for bottlenose dolphins and killer whales, population membership of these conspicuous individuals has been based on residence or site fidelity patterns (Ballance, 1987; Ford *et al.*, 1994; Weller, 1998; Díaz, 2001; Orozco, 2001; Delgado, 2002). This indicates that genetic constraints are unlikely to cause similar fin shapes.

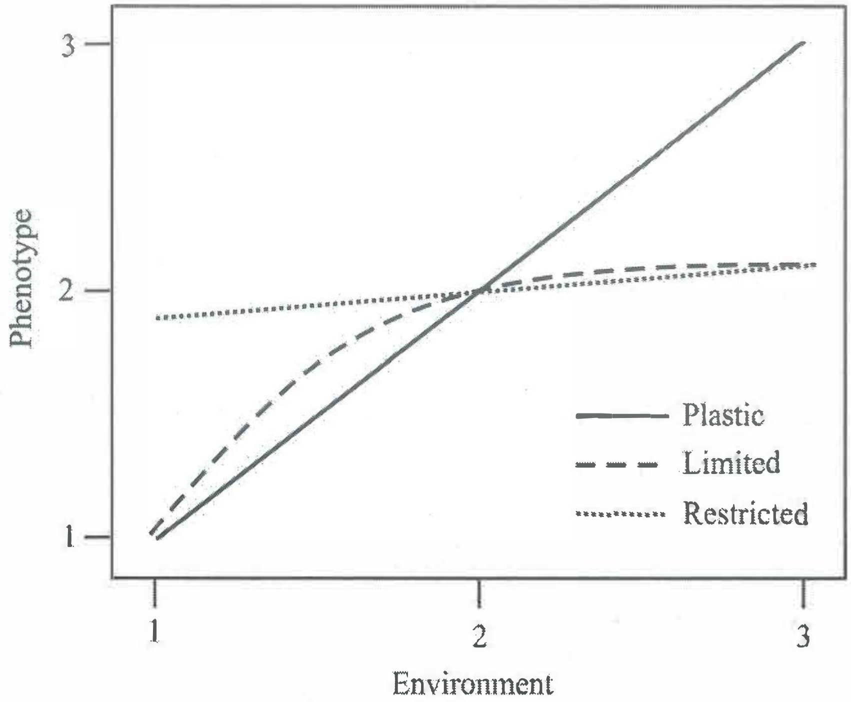

Figure 17. Norms of reaction for different theoretical populations or species. Solid line shows a plastic response to the environment; while dashed lines illustrate constrained responses. Restricted norms of reaction vary within a small range, and may have the same phenotype in spite of the environment; while limited norms of reaction, although broader, only achieve certain degree of response to environmental pressure. Note that all populations (or species) are convergent in phenotype 2, but just two of these develop phenotype 1 and only one is suitable for phenotype 3.

Figura 17. Normas de reacción en diferentes poblaciones teóricas o especies. La línea sólida muestra una respuesta plástica al ambiente; mientras las líneas punteadas ilustran respuestas confinadas. Las normas de reacción restringidas varían dentro de un rango pequeño, y pueden tener el mismo fenotipo a pesar del ambiente; las normas de reacción limitadas, aunque más amplias, sólo desarrollan cierto grado de respuesta a la presión ambiental. Note que todas las poblaciones (o especies) son convergentes en el fenotipo 2, pero sólo dos de ellas desarrollan el fenotipo 1, y sólo una desarrolla el fenotipo 3.

2.3. Heritability of dorsal fin shape

Development of polymorphic fins must have a strong genetic basis; either these can be programmed prior to birth (through heritability), or shaped throughout development (ontogeny). To my knowledge, no study has been published on the heritability of dorsal fin shape. However, experienced researchers on both captive and free ranging bottlenose dolphins have realized that conspicuous fin shapes in adults, mostly mothers, are also observed in their calves (A Delgado[8], D. Weller[9] and M.A. Rodríguez[10] pers. comms.) (Figure 18). Also, observations of vein-vessel distribution in dorsal fins of Pantropical spotted dolphins (*Stenella attenuata*) have shown very similar patterns in mother-calf pairs (F. Townsend, Pers. Comm. [7]), suggesting the strong heritability of this trait. The low variability found within populations in this study (Figure 6) supports this interpretation. A possible explanation may be that the same gene or genes influence various traits (pleiotropy) or that genes coding for these traits are closely linked (hitch hiking). However, such interpretation should be taken with care, because heritability may vary with the environment in which it is measured (Stearns, 1989).

It is noteworthy to consider that in this study, not all fins came from different schools for any particular location (Table I), this may imply that some individuals might be genetically related. Therefore, if fin shape is directly inherited from parents, samples might be pseudo-replicates.

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[8] Alberto Delgado, Via Delphi (Xcaret, Quintana Roo, Mexico).

[9] David Weller, Southwest Fisheries Science Center, NOAA (La Jolla, CA, USA).

[10] María Eugenia Rodríguez, Conexión con la Vida Silvestre, A.C. (Puerto Vallarta, Jalisco, Mexico).

This effect is not quantifiable in this study; however, because of the random selection of sample, the large number of individuals in most catalogues, the fact that most dolphins in the studies were transient animals, and that they frequently exchanged group membership (Lechuga, 1996; Delgado, 1996, 2002; Weller, 1998; Morteo *et al.*, 2004), direct genetic relatedness in samples (parents and siblings), if present, is assumed to be negligible.

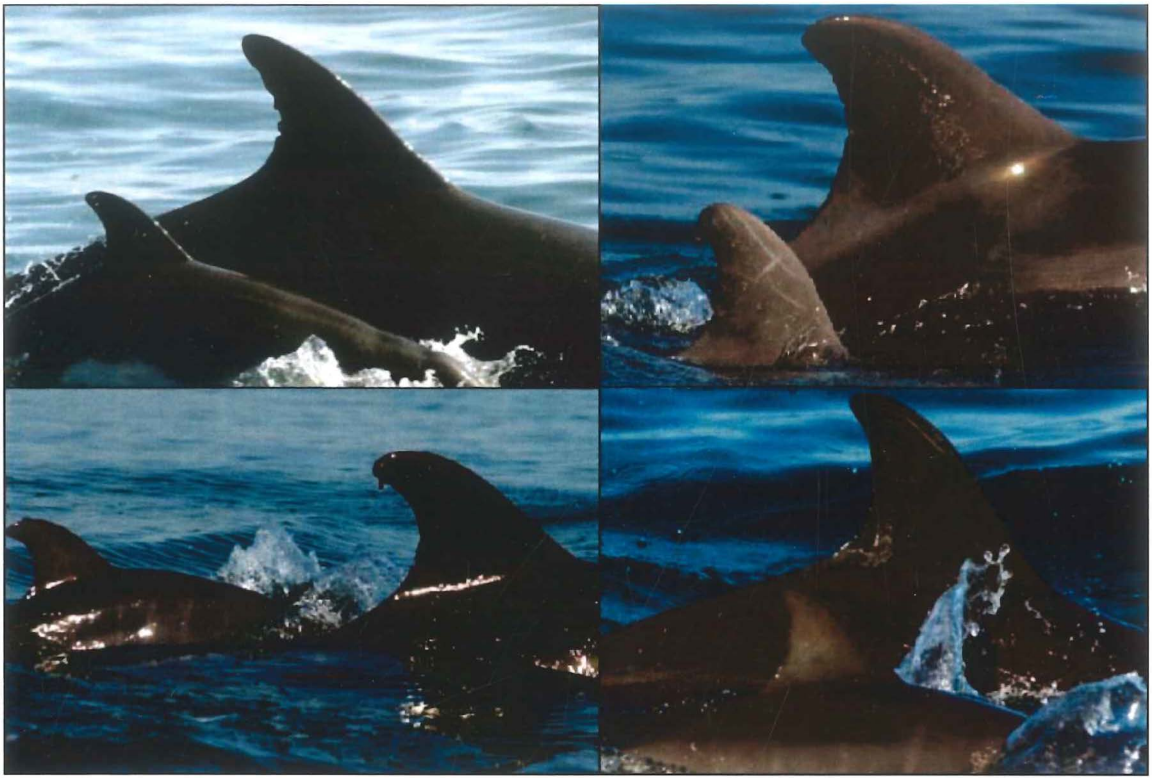

Figure 18. Fin shape of conspicuous mother-calf pairs in a bottlenose dolphin population. Bahia Banderas, Jalisco, Mexico (E. Lugo[11]).

Figura 18. Forma de la aleta en pares madre-cría de una población de tursiones. Bahía de Banderas, Jalisco, México (E. Lugo[11]).

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[11] Eduardo Lugo, Conexión con la Vida Silvestre, A.C. (Puerto Vallarta, Jalisco, Mexico).

2.4. Ontogenetic and allometric changes

To my knowledge, no study has been published on allometric and ontogenetic changes in the bottlenose dolphin, and no remarks about these aspects have been found in the literature. Comparatively, major alterations have been reported during the development of spinner dolphins (*Stenella longirostris*) (Perrin, 1972; Perrin *et al.*, 1991) (Figures 19 and 20).

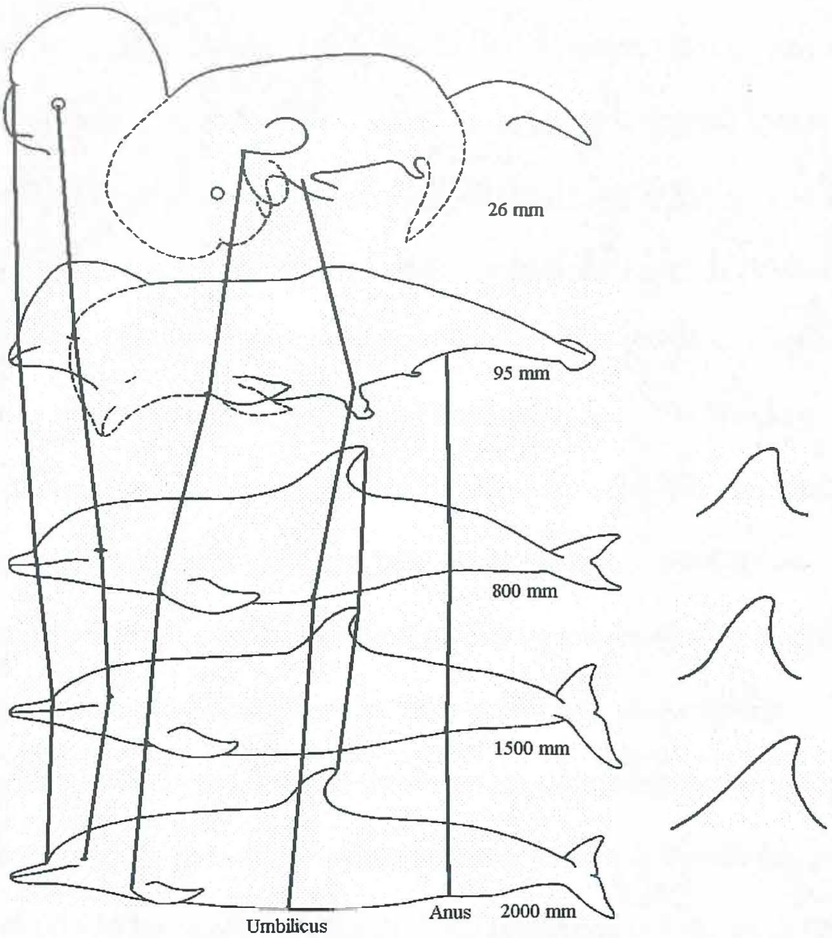

Figure 19. Allometric and ontogenetic changes in the spinne dolphins (*Stenella longirostris*). Fin shape through development is shown on the right (Adapted from Perrin, 1975).

Figura 19. Cambios alométricos y ontogénicos en el delfín tornillo (*Stenella longirostris*). La forma de la aleta a lo largo del desarrollo se muestra a la derecha (adaptado de Perrin, 1975).

Ontogenetic changes often need biological (hormonal) cues to trigger the process; these indicators may be based on environmental information, and the organism must have a system to translate environmental signals to a biological response (Smith-Gill, 1983; Stearns, 1989; Dewitt *et al.*, 1998). This system must be efficient, reliable and cost effective to be of selective advantage.

Unlike male spinner dolphins, where dorsal fin shape may reflect sexual maturity and is correlated to testis size (Perrin, 1972; Perrin and Mesnick, 2003), dorsal fins of the bottlenose dolphin would seem to have a small contribution to overall fitness compared to other morpho-physiological features; therefore, although the selection coefficient of the dorsal fin may vary among species, in the bottlenose dolphin it may be relatively low. Also, even when fin shape may be important in reproduction (due to blood vessels from fins to testis which help cooling sperm for viability) (Rommel *et al.*, 1994; Rommel *et al.*, 1999), no evidence is currently available to correlate fin shape (or size) and reproductive output in the species; and this may be significant only when male dolphins are sexually mature. Therefore, based on the best evidence at hand, an ontogenetic system to modulate dorsal fin shape does not seem cost effective in this species. Comparatively, the long-term accumulated effects of suboptimal dorsal fin shapes on swimming performance and thermal conduction capacity may potentially cause negative effects on swimming abilities and reproductive output. This would diminish individual fitness, allowing better adapted phenotypes to be more successful in reproduction (positive Darwinian selection).

2.5. Sexual dimorphism of dorsal fin

Since socially controlled plasticity may exist in a population (Gotthard and Nylin, 1995), sexual dimorphism may be very important in determination of dorsal fin phenotypic variability (Perrin *et al.*, 1991, Perrin 1994). Such variable patterns are present in fin shapes of dolphins; for instance, Perrin (1972) suggested that changes in dorsal fin shapes of spinner dolphins (*Stenella longirostris*) may have a sexual connotation, indicating sexual maturity (Figure 20).

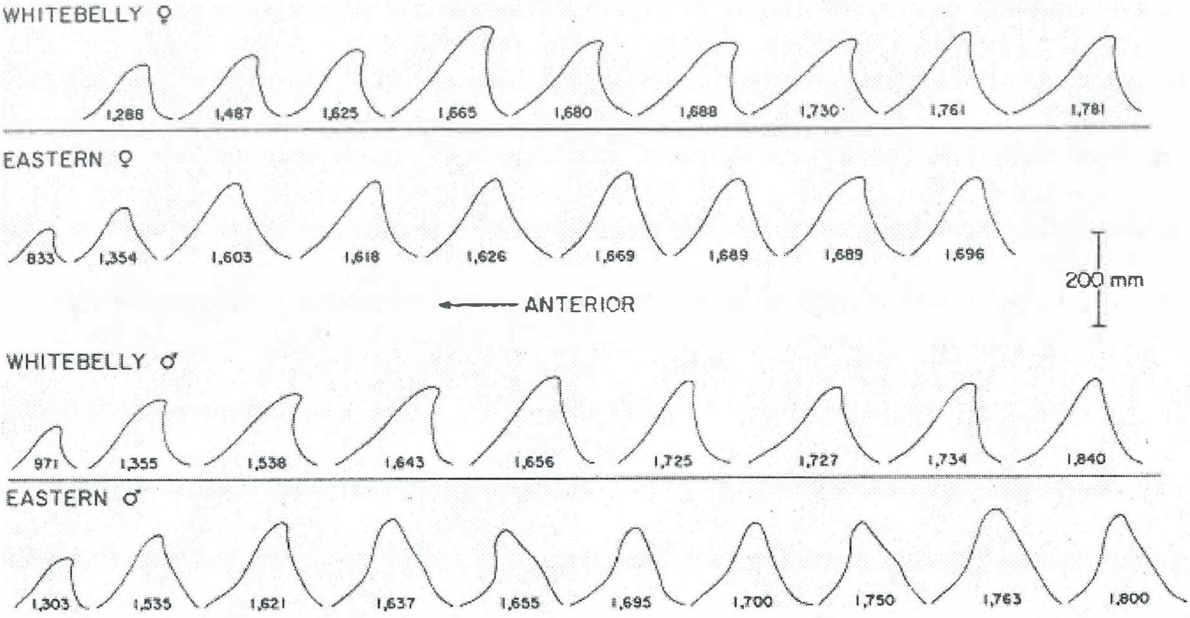

Figure 20. Developmental and sexual dimorphism in the dorsal fin of spinner dolphins (*Stenella longirostris*). Fin shapes are drawings from traces. Total body lengths (mm) are shown below fin contours (Adapted from Perrin, 1975).

Figura 20. Dimorfismo sexual y ontogénico en la aleta dorsal de delfines tornillo (*Stenella longirostris*). La formas de la aleta son los dibujos de los trazos. Las longitudes totales (mm) se muestran debajo de los contornos de la aleta (adaptado de Perrin, 1975).

Conspicuous changes in this trait may be related to structural and hydrodynamic constraints associated to a better performance during the competition for access to females;

also, they may represent a visual cue during sexual displays (Perrin and Mesnick, 2003). Perrin and Mesnick (2003) also found a correlation between dorsal fin shape and testis size in males of two spinner dolphin forms, indicating differences in mating systems (polygynous *vs.* polygynandrous). Dorsal fins in killer whales (*Orcinus orca*) are larger in mature males (Ford *et al.*, 2004). However, few studies have addressed sexual dimorphism in the bottlenose dolphin and the results are controversial; for instance, in the area of Sarasota (Florida, USA) reports from Tolley *et al.* (1995) indicate sexual dimorphism when analyzing total body length and dorsal fin height of coastal bottlenose dolphins. These changes have been tought to be the result of differential behavior; however, in the coasts of the Indian and Bannana rivers (Florida, USA), Hersh *et al.* (1990b) found the opposite; also, bottlenose dolphins along the Texas coastline did not show gender-based differences in either fin notching (number or damage) or proportional fin size (Weller, 1998).

2.6. Genetic assimilation

Much discussion is developing on the concept of genetic assimilation. Also known as the Baldwin effect (Baldwin, 1896), it suggests that environmental demands interact with a species gene pool. The suggested mechanism initially involves an environmental stimulus which promotes certain behaviors or traits. If useful, the trait becomes prevalent within the population, and those individuals with a genetic predisposition to it gain selective advantage over others. Thus, the trait becomes genetically assimilated. Therefore, a character that is normally expressed in certain environmental situations becomes fixed in a population, and it no longer requires environmental factors to be expressed (Pigliucci and Murren, 2003).

Based on the frequency of character states among putative populations, and the low variability within localities, this mechanism may explain different fin shapes in different environments. However, assumptions for this mechanism are not yet demonstrated (dorsal fin as a plastic trait, which is heritable and that its actual shape is an adaptation). Accordingly, genetic separation between populations may be a prerequisite for genetic assimilation to occur, because gene flow would fade separation.

2.7. No adaptation or selection in trait (spandrels)

In order to detect evolutionary change it is necessary to have some knowledge of what the initial state of the trait was (Gould and Lewontin, 1979; Gotthard and Nylin, 1995); however, no fossil records are available to determine the ancestral condition of dorsal fins in this genus or how it has changed. It has been assumed that the dorsal fin was developed as an adaptation to aquatic life from terrestrial ancestors; and here I showed evidence suggesting that its shape may be the result of natural selection. However, Dewitt *et al.* (1998) argue that the differences being studied may not always reflect the causes believed to be under investigation; two examples of fast swimming dolphins with anti-tropical distribution and lacking dorsal fins might suit the case (*Lissodelphis borealis* and *L. peronii*).

Smith-Gill (1983) argues that environmental phenotypic variation of traits may only exist because the organism fails to adjust to environmental changes; thus variation might not be genetically based. Also, alleles may become fixed by drift in a small population in spite of natural selection, such that fixation for slightly deleterious alleles may be common if selection coefficients are small and if many genes are involved (Gould and Lewontin, 1979). Comparatively, random fixation for unfavorable alleles is rare in large populations, and if present, they may be extremely unstable (Stearns, 1989); thus maladapted phenotypes may not be successful in populations over generational scales.

Although direct cause-effect is yet to be demonstrated, evidence suggests that positive Darwinian selection, although very slow, may in fact rule the shape of the dorsal fin in bottlenose dolphin populations. Also, if hydrodynamic and thermal functions are in fact relevant selective pressures, fin polymorphisms may be ineffective in dealing with long-term disturbances. Therefore, populations might eventually evolve to suit specific environmental conditions (either variable or stable), thus switching prevailing phenotypes and may show a completely different geographic pattern of morphological variation (Caswell, 1983).

3. METHODS FOR ASSESSMENT OF DORSAL FIN PERFORMANCE

Dorsal fin anatomy has been detailed for a few cetacean species; although it has been assumed to provide hydrodynamic and thermoregulatory advantages, its functionality is not fully understood (Lang, 1966; Elsner *et al.*, 1974; Fish and Rohr, 1999; Meagher, 2001). Morteo (2003) reviewed dorsal fin morphology (size, shape, position) in 34 dolphin species (family Delphinidae), and could not find clear correlations with biological (total size-weight, characteristic swimming speed, dive duration) or ecological features (grouping habits, feeding habits, and distribution patterns); therefore, he concludes that the variables in the model may not be directly correlated to dorsal fin shape, because it may have acquired different functions through evolutionary divergence. Consequently, comparison between several populations of the same species may be a better approach to gain further insight into the possibility of these causal relationships. Quantitative analyses of dorsal fin shape exist for at least 19 different localities within the distribution range of the bottlenose dolphin (Weller, 1998; this study); therefore, these should be used for assessment of functionality.

3.1. Hydrodynamic performance

Hydrodynamic performance may be assessed by measuring drag and vortex formation by dorsal fins. Since experiments with living animals are difficult to accomplish, fiber glass casts may be obtained from dorsal fins of dead beached bottlenose dolphins; these casts may also be customized to suit representative fins from different localities. Since strandings of bottlenose dolphins may be rare in some areas (Bravo, 2003), and also, not much information regarding dorsal fins is regularly acquired through regular morphometry, fin shape models may be difficult to design on a 3-D basis. A preliminary analysis of cross sections (Figure 21) from dorsal fins of bottlenose dolphins (Morteo *et al.*, In progress) shows linearity among chord, maximum thickness, and shoulder position (Figure 22); therefore, reliable 3-D dorsal fin representations may be designed based only on fin contours or pictures such as those used in this research (Figure 23).

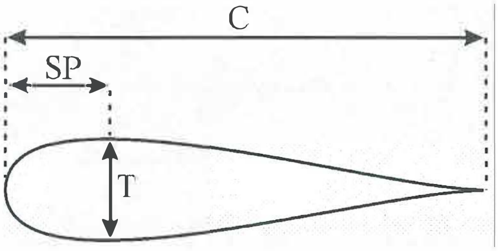

Figure 21. Upper view of the cross section of a dorsal fin. C=Chord (base length), SP=Shoulder position, T=Maximum thickness (from Fish and Rohr, 1999).

Figura 21. Vista superior de la sección de una aleta dorsal. C=Longitud de la base, SP=Posición del hombro, T=Máximo espesor (de Fish y Rohr, 1999).

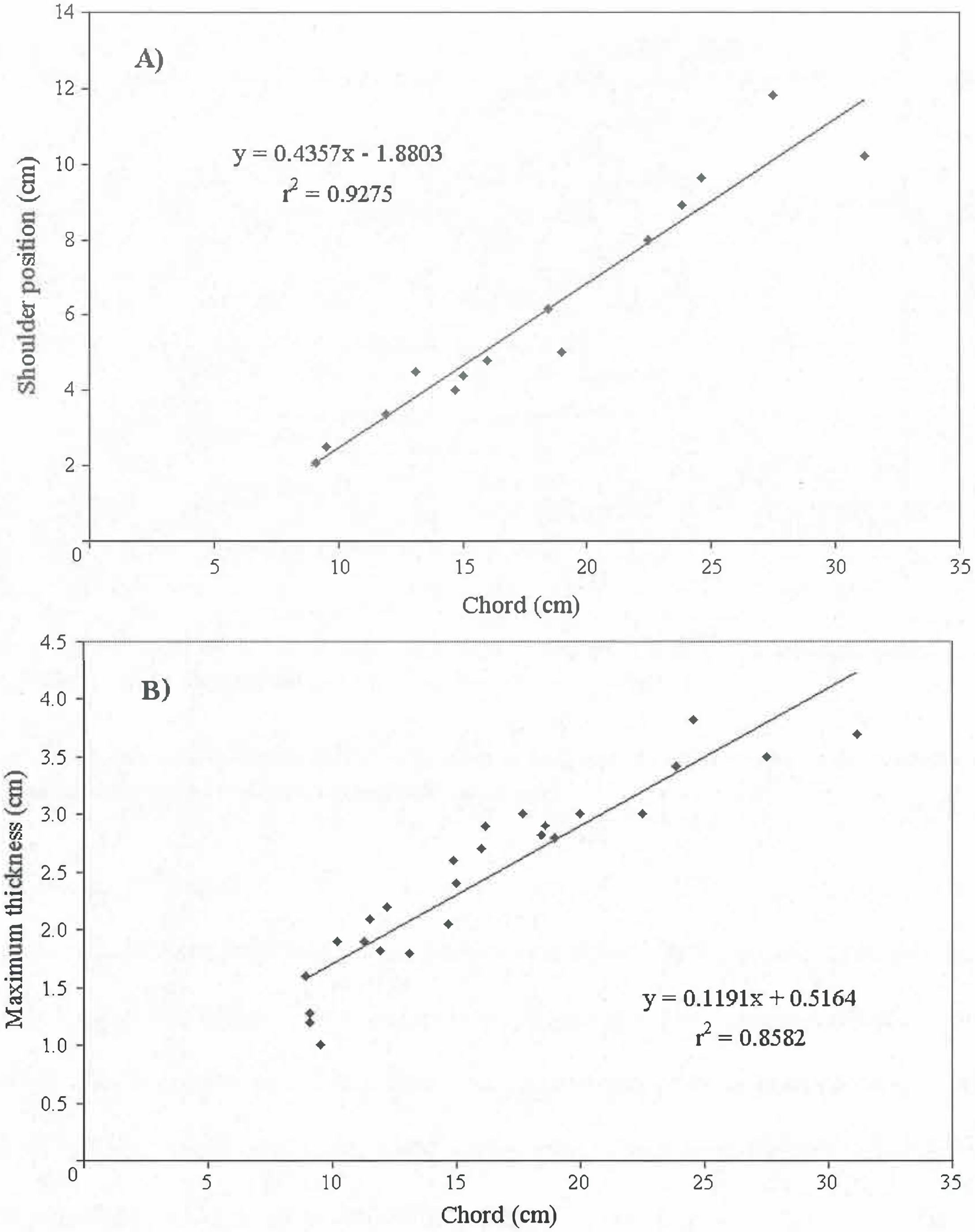

Figure 22. Linearity between hydrodynamic parameters in the dorsal fin of bottlenose dolphins. A) Chord *vs.* shoulder position and B) maximum thickness. (from Morteo *et al.*, In progress).

Figura 22. Linearidad entre los parámetros hidrodinámicos de la aleta dorsal en los tursiones. Longitud de la base *vs.* la posición del hombro y el espesor máximo. (de Morteo *et al.*, In progress).

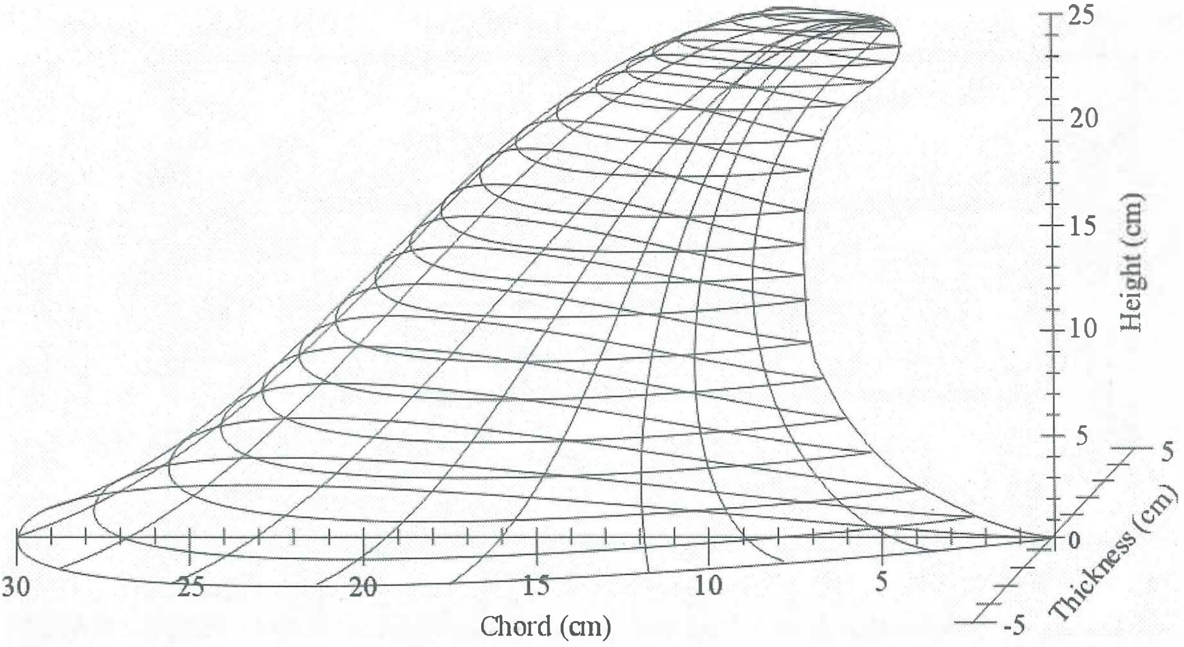

Figure 23. Example of a 3-D dorsal fin design based on a 2-D shape contour (adapted from Morteo *et al.*, In progress).

Figura 23. Ejemplo del diseño 3-D de una aleta dorsal basado en el contorno de la forma en 2-D (adaptado de Morteo *et al.*, In progress).

3.1.1. Vortex formation

A possible way to assess vortex formation is shown in Figure 24; it consists of cast models fixed to the bottom of a transparent acrylic container with inner walls to allow flux stability. The container would be filled with water impelled by a pump equipped with a diffuser to obtain a stable flow. Flow speed may be acquired through a mini ADCP (Acoustic Doppler Current Profiler) (Figure 24).

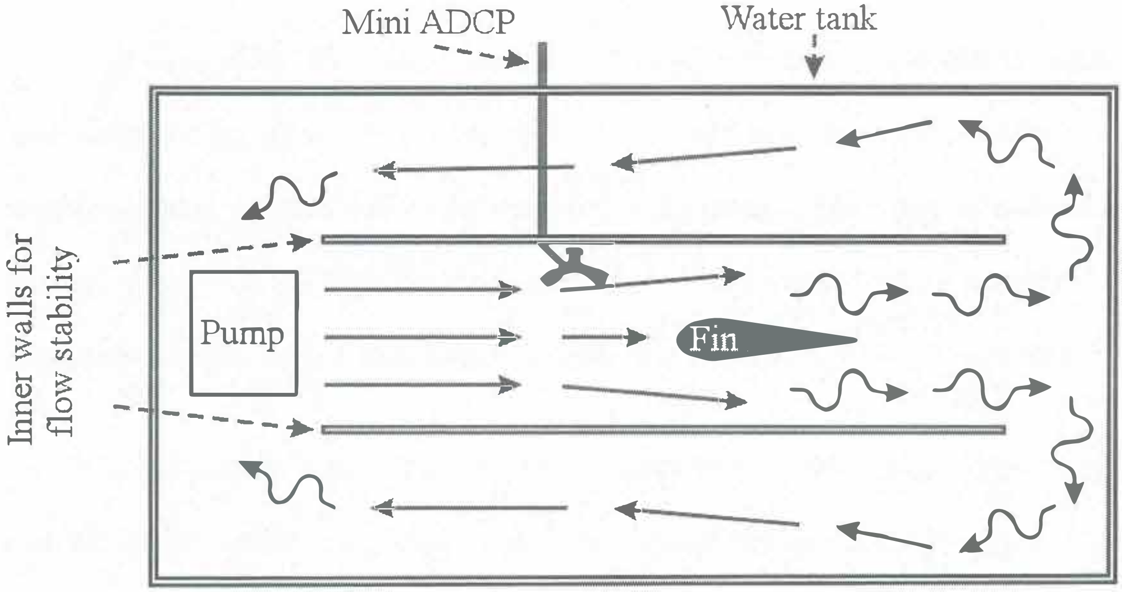

Figure 24. Upper view of the system for the evaluation of vortex formation by dorsal fins. Solid arrows indicate direction of water flow. ADCP=Acoustic Doppler Current Profiler.

Figura 24. Vista superior del sistema para evaluar la formación de vórtices con las aletas dorsales. Las flechas sólidas indican dirección de flujo de agua. ADCP= Perfilador Acústico de Corrientes por efecto Doppler.

To avoid limitations from airfoil bi-dimensional analogies (Fish and Rohr, 1999), particles would be placed through a range of depths to trace fluid motion (Figure 25-A). Images of flow dynamics would be obtained by a steady photographic camera placed above the container; these images may be analyzed through software like PIV Sleuth (Christensen *et al.*, 2000). Each experiment would be repeated on several occasions to obtain average graphic representations of the velocity fields (Figure 25-B); these would be generated for all fins to identify the areas of variation at different flow speeds and angles. Flow speeds would vary between the ranges of the species' swimming velocities (3 – 10 m s^{-1}) (Fish and Rohr, 1999). Efficiency of fin design will be evaluated by identifying the speed and angle at which the flow becomes turbulent.

Noise caused by fin's rigid surface and wall effects are a major concern for experimental design (Cincotta and Nadolink, 1992 cited in Fish and Rohr, 1999); since material structural stiffness will be the same for all fin models, this effect is assumed to be consistent throughout the experiments. However, the effect exerted by the container walls has to be analyzed to correct calculations, or may be corrected increasing container size.

Data generated from hydrodynamic experiments would be compared using parametric statistics. Velocity fields would be compared throughout spatial statistics in the form of variation ellipses (Emery and Thompson, 1997). Results could be related to sort term and long term environmental conditions at each study site to make inferences about the efficiency of dorsal fin design from each location.

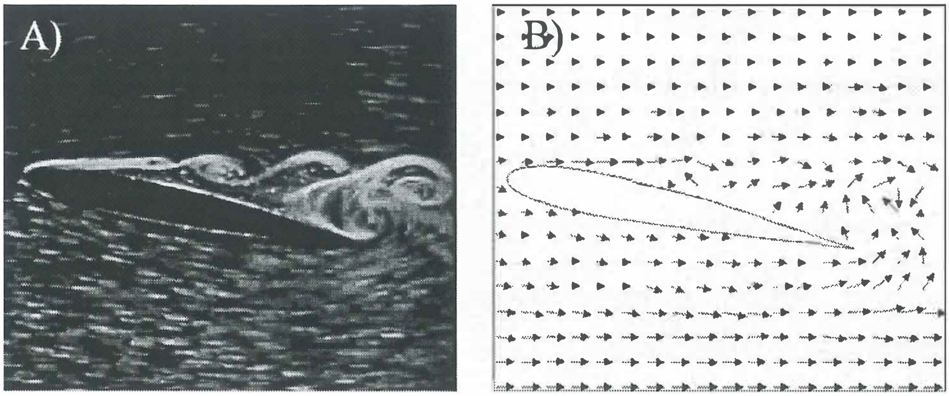

Figure 25. Cross section of a fin with a 5 degree angle through a stable flow (Upper view). A) Photograph of moving particles in the fluid. B) Simulation of the velocity field calculated by PIV Sleuth (Modified from Christensen *et al.*, 2000).

Figura 25. Sección de una aleta con un ángulo de 5 grados a través de un flujo estable (vista superior). A) Fotografía del movimiento de las partículas en el fluido. B) Simulación del campo de velocidad calculado por PIV Sleuth (Modificado de Christensen *et al.*, 2000).

3.1.2. Drag assessment

Drag can be measured with towing experiments; these have been used in a variety of marine organisms including bottlenose dolphins (Aleyev, 1977). The dorsal fin casts may be fixed over a mobile base, which would be placed on a track on the bottom of the same water tank from the previous experiment; the base would be attached to a dynamometer which would measure the resistance of the fin to a water flow impelled by a pump placed in front of the fin (Figure 26). Experiments would include all fins at different flow speeds and angles of attack. Efficiency of fin designs would be measured by evaluating its resistance over a range of different flow conditions. Once again, noise caused the by a fins rigid surface will be assumed to be consistent throughout the experiments; however, wall effects must be analyzed to correct calculations.

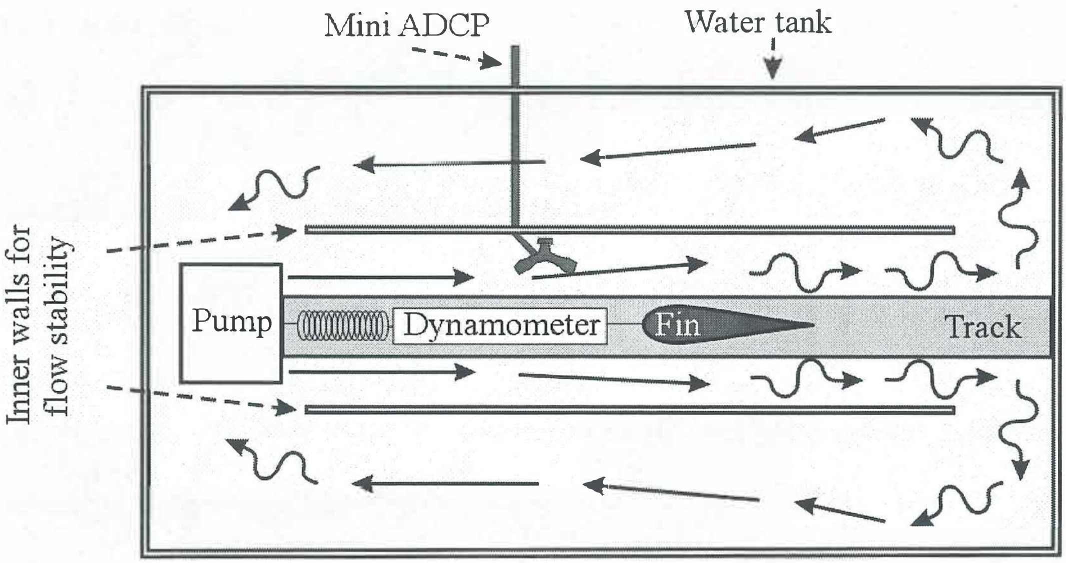

Figure 26. Upper view of the system for drag evaluation of dorsal fins. Solid arrows indicate direction of water flow. ADCP=Acoustic Doppler Current Profiler.

Figura 26. Vista superior del sistema para evaluación del arrastre en aletas dorsales. Las flechas sólidas indican dirección de flujo de agua. ADCP= Perfilador Acústico de Corrientes por efecto Doppler.

Another method to measure drag is free fall experiments; these have been used to measure dead drag in a variety of fish (Richardson, 1936; Gero, 1952; Blake, 1979a,b, 1981a,b). Two basic methods are employed to calculate distance-time curves: video and chronograph. Fiber-glass molds of different dorsal fins could be placed on the top of a water tank with a known depth; fins would be released and time will be recorded until it reaches the bottom (Figure 27).

According to Blake (1983) The equation of motion for a free falling fish body is:

$$m\, dU/dt = mg - kU^{n} \tag{Equation 1}$$

where, m is the mass of the object and the water perturbed due to its unstable movement (typically around 10-20% the mass of the object), and kU^{n} is the drag force. In practice, n ranges from 0-2, for $n = 1$:

$$U = mg/k\ (1 - e^{kt/m}) \tag{Equation 2}$$

and according to Stoke's law, the final speed (U_t) is:

$$U_t = mg/mk \tag{Equation 3}$$

for $n = 2$:

$$U = [(mg/mk)^{1/2} \tanh g] / (mg/mk) \tag{Equation 4}$$

and according to Newton's law :

$$U_t = (mg/mk)^{1/2} \tag{Equation 5}$$

From fish experiments it was concluded that time-distance curves are exact parabolas (e.g., $n = 0$). This implies that acceleration is constant and drag is independent of speed, and these are only achieved in a vacuum. Controversy has been generated upon the validity of these results through standard hydrodynamic equations of resistance (Richardson, 1936; Gero, 1952; Webb, 1975). However, based on a laminar boundary layer using the same Reynolds numbers, experimental results have been found to be close to theoretical values (Blake, 1979a,b, 1981a,b).

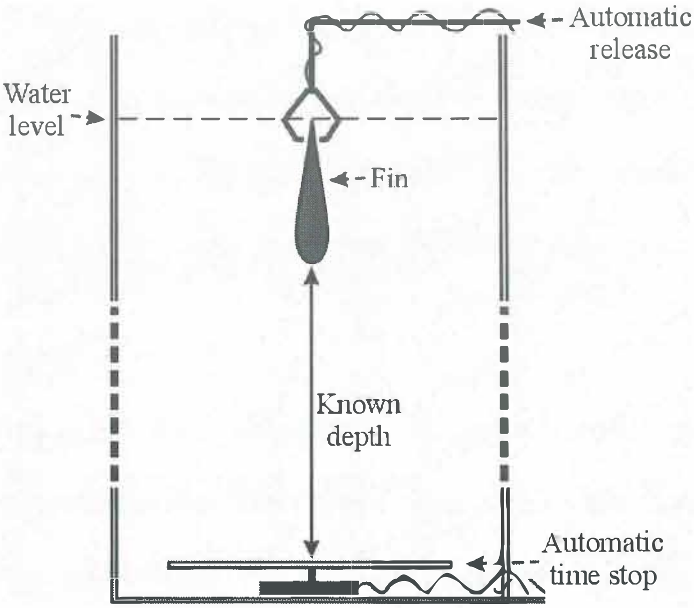

Figure 27. Front view of the system for drag evaluation of dorsal fins (adapted from Blake, 1983).

Figura 27. Vista delantera del sistema para evaluación del arrastre en aletas dorsales. (adaptado de Blake, 1983).

Considering that cross sections of dorsal fins resemble fish hydrodynamic bodies (Figure 21), a similar approach may be based on the same equations. However, the tank should be deep enough so the molds would reach terminal speed; if not, a possible solution would be diminishing the mass of the fin or changing water resistance by slightly modifying its density. Another concern would be that fins should be able to fall in the same position until the end of the experiment; this may be accomplished by manipulating the distribution of weight or by substantially increasing the mass of the fins.

3.2. Thermoregulation performance

Thermoregulation performance may be assessed by several approaches: observing heat distribution patterns in different fin shapes, direct measurements of heat flux, description of vascular anatomy and mathematical modeling. Most of these approaches involve experiments or must be validated with living animals; therefore, captive dolphins are invaluable sources of data under semi-controlled conditions.

3.2.1. Infrared imaging

Infrared imaging has been very useful to assess thermal patterns of cetacean appendages; this method provides direct spatial data on heat distribution across the fins; however, temperature differences between the body and the water, and changes in respiration and heart beat rates may affect measurements. Also, no information can be obtained under the water surface, and heat distribution patterns may be very variable among individuals (Cuyler *et al.*, 1992; Meagher *et al.*, 2002) (Figure 28). Therefore, such patterns must be analyzed for different individuals under the same experimental conditions and correlated to the underlying vasculature.

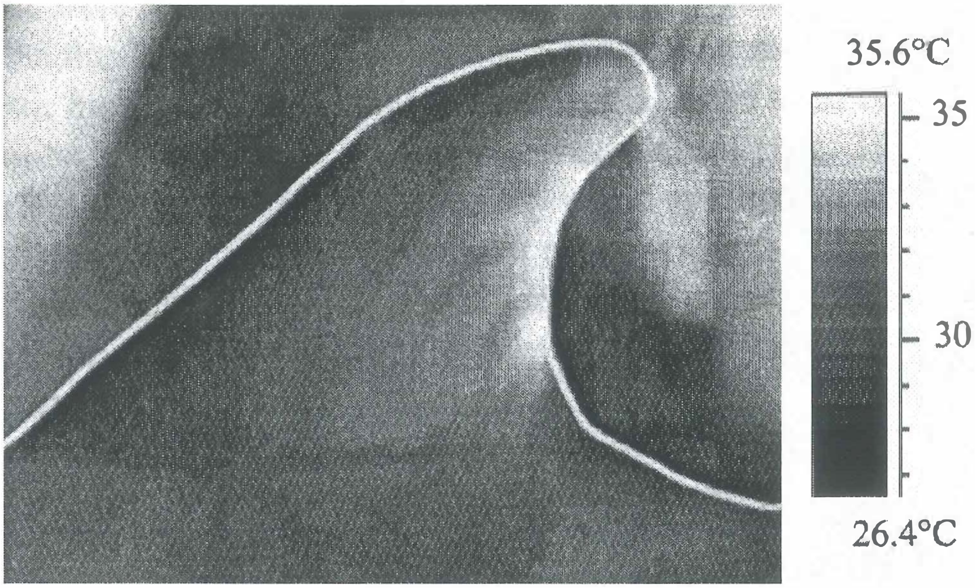

Figure 28. Infrared thermal image of a bottlenose dolphin dorsal fin (from Meagher *et al.*, 2002).

Figura 28. Imagen infrarroja de la aleta dorsal de un tursión (tomado de Meagher *et al.*, 2002).

3.2.2. Direct heat flux measurements

This method is based on heat flux transducers over the fin. Since the dorsal fin is a spatially heterogeneous thermal surface, transducers must be placed at least in three different areas; also, each area must have two transducers, one directly over a vein and the other away from it. Measurements on both sides of the fin are also recommended (Meagher, 2001; Meagher *et al.*, 2002) (Figure 29).

Air, water and internal body temperature must be monitored, as well as changes in respiration and heart beat rates (Rommel *et al.*, 1994; Meagher, 2001; Meagher *et al.*, 2002). In order to elucidate thermal patterns and identify anomalous measurements, several sessions must be performed for different individuals under the same experimental conditions. Once obtained standardized results, heat flux measurements may be correlated to the underlying vasculature.

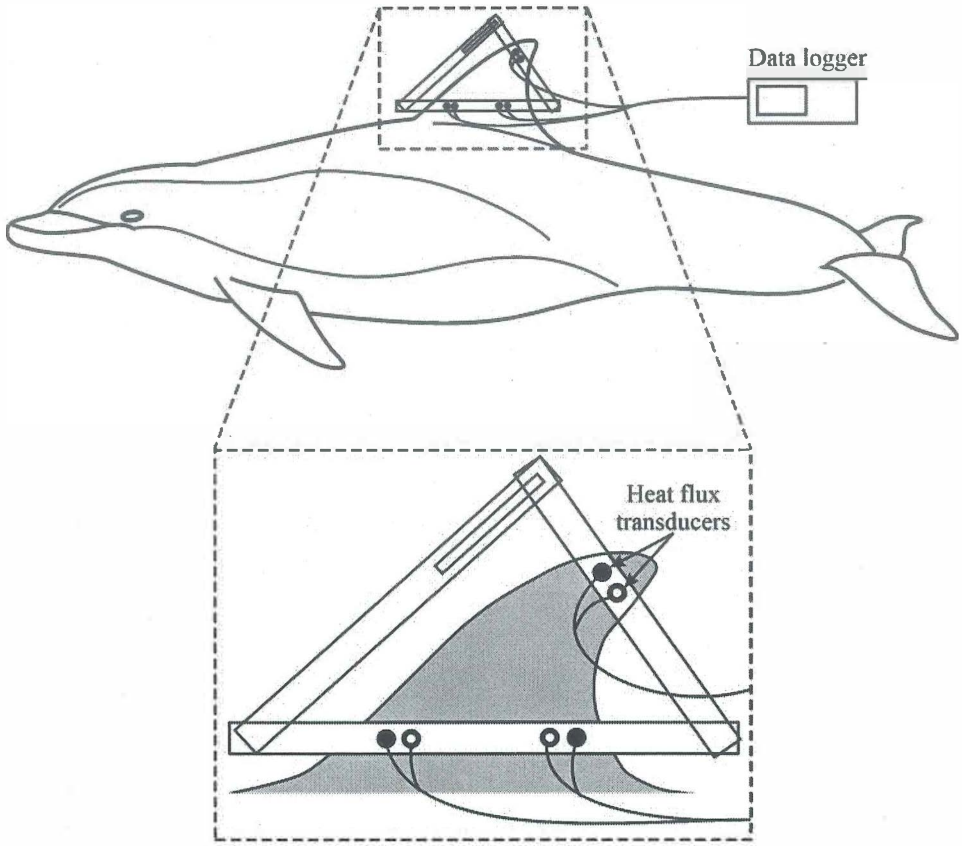

Figure 29. Schematic of the system for measuring heat flux in the dorsal fin. White transducers are placed directly over a superficial vein and black transducers are away from it. Both sides of the fin must be measured (adapted from Meagher *et al.*, 2002).

Figura 29. Diagrama del sistema para medir el flujo de calor en la aleta dorsal. Los transductores blancos se encuentran directamente sobre una vena superficial y los negros están lejos de ella. Deben medirse ambos lados de la aleta (adaptado de Meagher *et al.*, 2002).

3.2.3. Vascular anatomy

Dorsal fin vascular anatomy has been poorly studied and in some cases only with a limited number of specimens; however, it seems to vary individually and may be closely related to the patterns of thermal distribution over the appendages (Elsner, 1974; Meagher, 2001; Meagher *et al.*, 2002). The best way to describe the distribution of veins and vessels is by direct examination of cross sections of the appendages; however, strandings of dead dolphins may not be frequent and their fins may have been damaged or degraded through decomposition. Therefore, indirect and less accurate techniques are proposed to be used in dead and living dolphins; it is noteworthy that, in spite of being less precise, these are much faster and easier to apply.

X-ray photography has been used for this purpose, at least in bottlenose (Elsner, 1974; Morteo *et al.*, In progress) and Pantropical spotted dolphins (*Stenella attenuata*) (F. Townsend [7] Pers. Comm.). In spite of its low resolution, major vasculature can be easily observed; for instance, dorsal fin X-ray images from two bottlenose dolphins are shown in Figure 30 (a=Atlantic, b= Pacific); note that the major veins across the fin are closer to eachother in the Atlantic bottlenose dolphin; since water is generally warmer in that region, a more profuse vascular pattern may be needed to better dissipate heat (Morteo *et al.*, In progress). New digital X-ray equipment may have better resolution and may be adjusted to scan across skin layers in the same way as a tomography. However, this equipment is very expensive and in most cases not suitable for field use given it size, thus the dolphins may have to be transported to the X-ray facilities.

Alternatively, ultrasound equipment is less expensive and portable devices are very common among the veterinary staff of wildlife parks in captive facilities. No experiments or observations are currently available to validate this method; therefore, several experiments should be made with living and dead animals to assess its reliability.

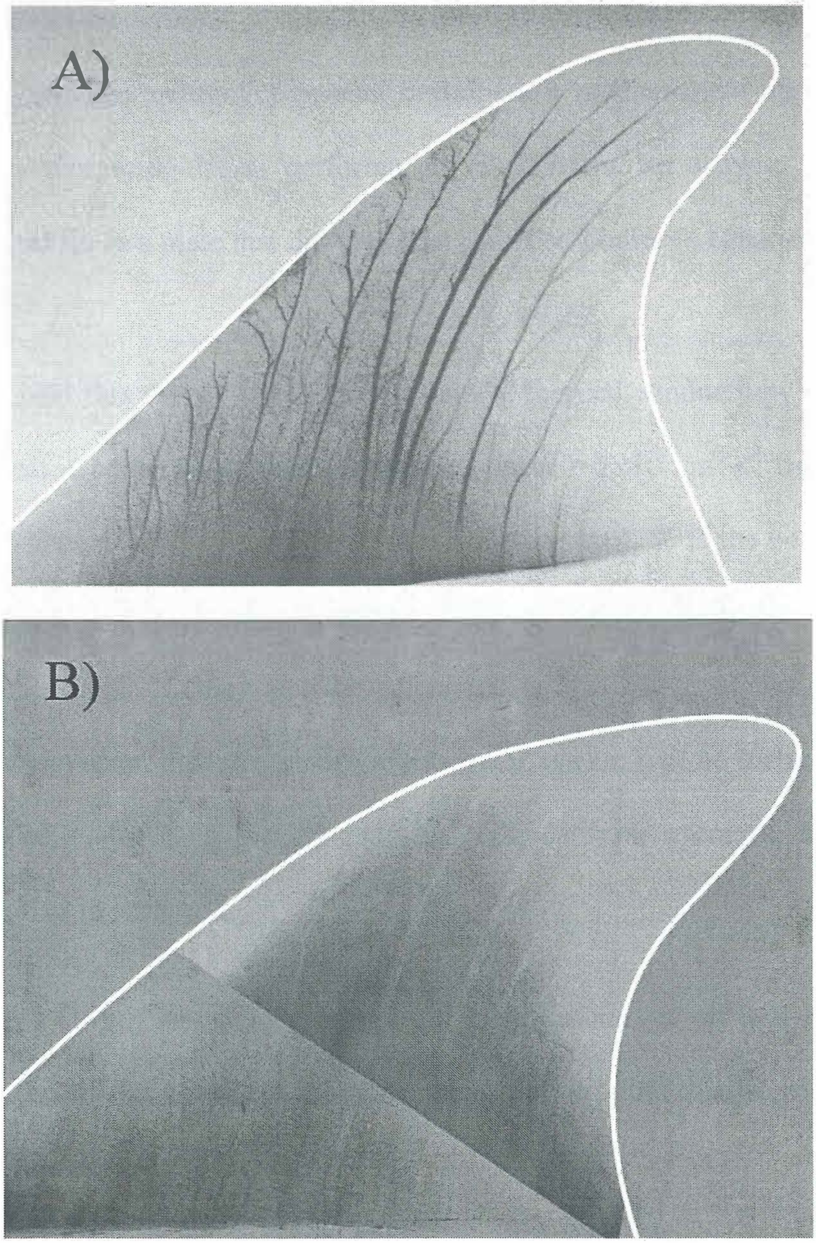

Figure 30. X-ray images showing the vascular anatomy of two dorsal fins. The white line has been added to outline the contours of the dorsal fins A) Digital X-ray from Atlantic bottlenose dolphin (from F. Townsend [7]); B) Traditional X-ray from Pacific bottlenose dolphin; the latter image was composed by two sets of X-ray plates (from Morteo *et al.*, In progress). Note that the distance between major veins is larger in the Pacific dolphin.

Figura 30. Radiografías que muestran la anatomía vascular de dos aletas dorsales. La línea blanca se ha agregado para delinear los contornos de las aletas. A) Radiografía digital de un delfín del Atlántico (F. Townsend [7]); B) Radiografía tradicional de un delfín del Pacífico; la segunda imagen se compone de dos juegos de placas de radiografías (tomado de Morteo *et al.*, En progreso). Note la mayor distancia entre las venas principales del delfín del Pacífico.

3.2.4. Mathematical modeling

Once the vascular anatomy has been described, a mathematical approach may be useful to assess thermoregulation performance in different fin shapes. This approach assumes the dorsal fin as a plate that diffuses heat based on Fourier's equation:

$$Q_t = K \cdot S\ (T_c - T_a)/L \qquad \text{(Equation 6)}$$

where Q_t is the heat flux (W m^{-2}), k is the constant of thermal conductivity of the material for which the heat is being transmitted (connective tissue = 1x10^{-7} m^2 s^{-1} from Bowman *et al.*, 1975 in Hokkanen, 1990), S is the area of the surface (m^2), T_c is the body temperature (~37 °C), T_a is the environmental temperature (°C), and L is the distance (m) between T_c and T_a (Marshall, 2002). L may also be calculated as the length of the countercurrent thermal exchange system; thus the underlying vascular system will be included as the heat source. Values of T_a for each locality may be obtained from averages, minimums and maximums reported in literature.

Hokkanen's (1990) model may be used to make inferences on heat generation and redistribution. The model considers the appendages as two-dimensional plates, solved in rectangular coordinates:

$$\nabla^2 T + H / k = (1/\alpha) \partial T / \partial t \qquad \text{(Equation 7)}$$

where T is the temperature profile of the appendage (°C), H is the rate of heat generation for unit of volume (W °C^{-1} m^{-3}), α and k are thermal diffusivity (0.57 W K m^{-1}) and conductivity (1x10^{-7} m^2 s^{-1}), respectively, and t is the lapsed time. Values of H may be analyzed considering the time of heat distribution from the source (countercurrent system) to the borders of the appendage. Values of Q_t and H may be examined through analysis of variance (ANOVA) for the different dorsal fin types.

In order to better approximate real values, fins must be scaled to real dimensions. Some of the fin dimensions (commonly height and width) may be obtained from morphometric data, thus the remaining measurements of fin shape may be calculated from trigonometry according to Morteo *et al.*, (In progress) and the results of this research.

CONCLUSIONS

- Photographic procedures and digital measurements of dorsal fins in this study proved to be very useful and accurate to assess morphological differences in bottlenose dolphins.
- Dorsal fin of bottlenose dolphins along Mexican coasts showed certain degree of polymorphism and restricted local variability.
- Dorsal fin polymorphisms were useful for discrimination among localities and were geographically structured at different spatial scales (local and regional).
- Dorsal fin shape may be related to behavioral, physiological and anatomical responses due to environmental differences.
- Dorsal fin differentiation and discriminatory power may be regulated by space-time dependent factors (environmental, biological, genetic).
- Correlation between morphological and molecular data is needed to assess geographic trends and the genetic mechanisms that regulate dorsal fin shape must be addressed.
- Dorsal fin hydrodynamic and thermoregulatory performance must be evaluated in order to reveal the possible adaptations based on its shape (functional design).

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APPENDIX A

CONFOUNDING FACTORS AND SOURCES OF VARIATION

In accordance to the characteristics of the species and the methods used in this research, it is considered that the following aspects can affect the interpretation of results:

1) If individuals analyzed do not belong to the same species

Due to the high degree of polymorphism in the bottlenose dolphin, up to 20 nominal species and subspecies have been described; however, at the moment only *Tursiops truncatus* and *T. aduncus* have been formally recognized. The latter is present only in the coasts of South Africa, in the Indian Ocean and the west coast of Australia (Wells and Scott, 1999; Reeves *et al.*, 2002). For this reason, it is more likely that only specimens of *T. truncatus* were included in this study.

2) If individuals analyzed belong to different ecotypes

The morphological differences among ecotypes could introduce artificial variability, thus the possible separation between two populations would be underestimated. The possibility of this effect was evaluated by reviewing the residence degree (or site fidelity) of individuals (only when reported in literature). Additionally, since study sites are coastal areas, it was assumed that individuals were more likely to belong to the coastal ecotype.

It is important to mention that concerns have been expressed on the intrusion of oceanic animals to coastal zones in this area. Walker (1981) morphologically distinguished both forms based on stranded specimens along the coasts of Baja California; also, individual and genetic exchange has been previously reported in other areas (Hoelzel *et al.*, 1998), thus increasing genetic and phenotypic variability. Most studies report that 99% of coastal dolphins distribute within the first kilometer offshore, and water depths in these areas are below 20 m (Caldwell, 1955; Leatherwood, 1975; Würsig y Würsig, 1979a, b; Sandoval, 1987; Baylock, 1988; Ross *et al.,* 1989; Cockroft *et al.,* 1990; Van Waerebeek *et al.*, 1990; Kenney, 1990; Wiley *et al.*, 1994; Defran *et al.*, 1999; Morteo, 2002; Torres *et al.*, 2003). The narrow continental shelf off the coast of Baja California may provide better access to coastal locations for offshore dolphins. This process might not be recent, since it is suspected that coastal populations were founded by offshore dolphins (Natoli *et al.*, 2004). No evidence is currently available on genetic exchange between coastal and offshore ecotypes in this region; although the information in this study supporting isolation between inshore and offshore dolphins is limited, results on local variability suggest that, at least with the analyzed data, this is not likely to occur.

3) Growth allometries

Perrin (1975) found that during growth, some dolphins may display changes in the size of appendages and the dorsal fin can even move along the body. Although these changes do not imply a change in fin design, they could be a result of hydrodynamic and/or thermal adjustments, which would modify the function of the dorsal fin during development (Amano and Miyazaki, 1993 in Fish and Rohr, 1999). For example, it has been suggested that young animals may be at disadvantage when swimming (Fish and Rohr, 1999). Since animals cannot be aged from pictures, the methods in this study may have introduced variability into the analysis. This effect was reduced by using pictures of animals previously judged as sexually mature in the field; this implies that animals are not actively growing and allometric changes (if present) are minimum. Data for further assessment could potentially come from marine mammal stranding network databases and dolphinaria.

4) Temporal coverage

A time related bias may occur because most catalogues contained information from less than three years (Table I); thus, temporal changes on greater scales may not be reflected in the analysis (Perrin *et al.*, 1994). This is important when considering multi-annual migration patterns and shifts in environmental conditions such as ENSO and PDO. For instance, although there is no strong evidence on seasonality in dolphin movements along the Southern California Bight (USA), Defran *et al.* (1990) documented changes in distributional patterns during the 1982–1983 ENSO event; where dolphins moved to the north following shifts in prey and went back to their historical geographic limit. Dolphins are known to avoid severe temperature changes (Wells *et al.*, 1999) moving to places where prey abundance and availability is sufficient to cover their food requirements and where they can reproduce. Therefore, the trends reported in this research may vary through time.

5) Statistical trends and sample size

This concern comes from the statistical nature of the data set analyzed here. Previous research (Weller, 1998) on bottlenose dolphin's dorsal fin morphology over a wider geographic scale showed normally distributed ratios. Given the distribution of ratios for the populations in this study (not normal even when log-transformed), the question of adequate sample size was in order. Except for Bahia de los Angeles, sample size analyzed here was larger than the minimum estimated from local variability. This minimum was consistent among localities. In addition, pooled data over regions also yielded not normally distributed ratios (K-S, $p<0.01$); therefore, it is believed that the distribution of ratios for dolphins in Mexican coasts could reflect regional trends more than sample size effects.

6) Photo-identification success and sample size

Photo-identification studies often individualize less than half the observed dolphins (Würsig and Würsig, 1977; Würsig and Jefferson, 1990); this means that photographic records contain only those individuals that had conspicuous marks and came close enough to the boat to be photographed. In addition, the criteria used in this study to maintain image quality restricted even more the available data. Except for Bahia de los Angeles, and the Upper Gulf of California, the analysis included only a small proportion (< 50%) of these catalogs. Therefore, although randomly selected, since a very low quantity of animals was represented in samples, local phenotypic variability could be underestimated. As a comparison, Perrin *et al.* (1991) used a minimum sample size of 25 individuals to assess morphological variation of spinner dolphins (*Stenella attenuata*); however, their fin shape assessment averaged only 13 samples. Analysis of morphological variability within putative populations (Figure 7) showed that at least in this study, sample size was enough to account for most of local variability, thus in the end sample size was not a great concern.