CENTRO DE INVESTIGACIÓN CIENTÍFICA Y DE
EDUCACIÓN SUPERIOR DE ENSENADA

POSGRADO EN CIENCIAS EN ECOLOGÍA MARINA

COST OF TRANSPORT OF MIGRATING GRAY WHALES (*Eschrichtius robustus*), ALONG COSTA AZUL, BAJA CALIFORNIA, MEXICO

TESIS
que para cubrir parcialmente los requisitos necesarios para obtener el grado de

MAESTRO EN CIENCIAS

Presenta:

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Ensenada, Baja California, agosto de 2006.

RESUMEN de la tesis que presenta **Samantha Rodríguez de la Gala Hernández**, como requisito parcial para la obtención del grado de MAESTRO EN CIENCIAS en ECOLOGÍA MARINA, Ensenada, Baja California, agosto de 2006.

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Costo de transporte de la ballena gris (*Eschrichtius robustus*) durante su migración en Costa Azul, Baja California, México.

La ruta migratoria de la ballena gris (Eschrichtius robustus) del Pacífico nororiental se traslapa con áreas usadas para actividades humanas. Esta interacción produce cambios en el comportamiento de las ballenas a nivel individual y poblacional. La velocidad de nado y el patrón de respiración son variables importantes en la evaluación de las reacciones de las ballenas a la perturbación industrial y tráfico de embarcaciones, pero poco se ha relacionado a problemas de gasto energético. El costo de transporte (CDT) es útil para monitorear los efectos de importancia biológica, como lo propuso la Comisión Ballenera Internacional (CBI).

Los objetivos de este trabajo fueron estimar la velocidad de nado (V) y la tasa de ventilación (TV) para las ballenas grises en migración (migración sur, migración al norte de ballenas sin crías y migración al norte de parejas madre-cría) en Costa Azul, Baja California, y generar un modelo general del costo de transporte para cada uno de los grupos. De Diciembre 2004 a Mayo 2005 se siguieron grupos de ballenas con ayuda de un teodolito (Topcon DT-102) para establecer su posición. Con ayuda de binoculares (7X50) se contaron los soplos y se registró el inicio y final de los avistamientos, así como los tiempos de las observaciones. La velocidad de nado se calculó con el programa T-Trak ($m\ s^{-1}$) y la tasa de ventilación como número de soplos por ballena por unidad de tiempo. Con esta última variable se calculó el costo de transporte (CDT) por medio de la tasa de consumo de oxígeno (Vo_2), el oxígeno extraído (FO_2) y el volumen de oxígeno intercambiado (V_T). Los resultados para la migración al sur ($V=1.9\ ms^{-1}$; TV=0.8 soplos/min; CDT=0.42 MJ $kg^{-1}m^{-1}$) fueron muy similares a los publicados por Sumich (1983). Las ballenas sin crías de la migración norte presentaron el CDT más bajo de los tres grupos ($V=1.8\ ms^{-1}$; TV=0.5 soplos/min; CDT=0.30 MJ $kg^{-1}\ m^{-1}$). Para las parejas madre-cría de la migración norte, la velocidad de nado fue la misma ($V=1.2\ ms^{-1}$) pero la TV y el CDT fueron calculados por separado. Para las madres se obtuvo una TV=0.5 soplos/min y un CDT=0.50 MJ $kg^{-1}\ m^{-1}$ y para las crías TV=0.7 soplos/min y CDT=0.63 MJ $kg^{-1}\ m^{-1}$. La diferencia de valores con relación a estas variables puede estar relacionada con el tamaño, estado fisiológico, características hidrodinámicas del medio o el tipo de actividad en que se encuentren los individuos.

Palabras clave: Costo de transporte, migración, *Eschrichtius robustus*, ballena gris, Baja California, México.

ABSTRACT of the thesis presented by **Samantha Rodríguez de la Gala Hernández**, as a partial requirement to obtain the MASTER OF SCIENCE degree in MARINE ECOLOGY, Ensenada, Baja California, México, August 2006.

Abstract approved by

Gisela Heckel Dziendzielewski, Ph.D.

Cost of transport of migrating gray whales, (*Eschrichtius robustus*), along Costa Azul, Baja California, México.

The migratory route of the eastern north Pacific gray whale (*Eschrichtius robustus*) overlaps with areas used for human activities. This interaction brings as a consequence a modification in behavior at individual and population levels. Swimming velocity and breathing pattern are important variables in the assessment of the reactions of whales to industrial disturbance and to boat traffic, but little has been linked to energetic cost issues. The Cost of Transport (COT) is useful to monitor the effects of biological importance, as proposed by the International Whaling Commission (IWC).

The objectives of this study were to estimate the swimming velocities (V) and breathing rates (BR) for migrating gray whales (southbound, northbound without calves, and northbound mothers with calves) at Costa Azul, Baja California, and to develop a general cost of transport model for each of these groups. From December 2004 to May 2005, whales were followed using a theodolite (Topcon DT-102) to establish their position. Binoculars (7X50) were also used to count whale blows, register the beginning and end of the sightings as well as the observation times. The swimming velocity was calculated with computer program T-Trak (m/s) and the breathing rate as the number of blows by whale by unit of time. The latter was used as the variable with which the cost of transport (COT) was estimated by means of oxygen consumption rate (Vo_2), oxygen extraction (FO_2) and tidal lung volume (V_T) calculations. Results for the southbound migrating whales ($V=1.9\ ms^{-1}$, BR=0.8 breaths/min; $COT=0.42\ MJ\ kg^{-1}m^{-1}$) were almost equal to those published by Sumich (1983). Northbound whales without calves showed the lowest COT of the three migrating groups ($V=1.8\ ms^{-1}$, BR=0.5 breaths/min; $COT=0.30\ MJ\ kg^{-1}m^{-1}$). Northbound mothers and calves had the same swimming velocity ($V=1.2\ ms^{-1}$), but BR and COT were calculated separately yielding for mothers BR=0.5 breaths/min; $COT=0.50\ MJ\ kg^{-1}\ m^{-1}$, and for calves BR=0.7 breaths/min and $COT=0.63\ MJ\ kg^{-1}m^{-1}$. The difference in numbers with respect to these variables may be related to the whales' size, physiological state, hydrodynamic characteristics of the enviroment or the type of activity in which they are engaged.

Key words: Cost of transport, migration, *Eschrichtius robustus*, gray whale, Baja California, México.

ACKNOWLEDGEMENTS

I would like to thank CICESE for accepting me in its Marine Ecology graduate program and for providing financial aid (PEM scholarship) to finish this research. Financial aid was provided also by the Consejo Nacional de Ciencia y Tecnología (CONACYT), Shell Mexico, S.A de C.V. and Energía Costa Azul, S. de R.L. de C.V.

My gratitude to Gisela Heckel for your important comments, but mostly, for all your patience along the way as a teacher, but more important, as a friend.

My special gratitude to James Sumich who guided me all the way through the cost of transport calculations and for making the effort of coming from San Diego to the comittee meetings.

My recognition to all the members of my comittee: Sharon Herzka, Oscar Sosa, Benjamín Barón and James Sumich for all their valuable, very polite, but straightforward comments to improve this manuscript (I enjoyed it).

This thesis would never have been possible without the help of valuable people who helped me in the field with data acquisition, and with whom I shared fun times: Luis Enriquez, Alejandra Baez, Denise Lubinsky, Nelva Victoria, Guadalupe Gómez, Ligeia del Toro, Nemer Narchi, Erick Bravo, Laura Barboza, Concepción García, Héctor Pérez, Ivonne Posada, Aileen Gaset, Esther Araiza, and Jorge López.

Thanks to Olga Flores for helping with the statistical analysis.

Thanks to Yolanda Schramm for the last physiology mini-discussion.

To my father (Francisco), mother (Alma) and sister (Caz), and the rest of my family!!!! All my love to you, without you I would have never survived here.

Thank you friends! Mark, Iris, Vane, Concha, Claris, Yoli, Ale, Li, Nemer and Erick, who have shared all my secrets, you made me realize that life without friendship is really boring, and for being there next to me always, I love you!!! To the rest of my friends who showed me “parties are an essential part of our scientific formation” (Galindo 2006). Héctor, Lucy, Fernando, Lorena, Luis, Julien, Manuel: thank you for accepting our self-invitations with a smile on your face; Silvia, Alicia and Lupis, Rodrigo (Poke), and Julio Candela for receiving us at his house. Salud!!!!!

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I. INTRODUCCIÓN

La ballena gris es la especie con distribución más costera de todos los grupos de ballenas (Pike, 1962). Recorre cada año entre 15,000 y 20,000 km de sus zonas de alimentación durante el verano en los mares de Chukchi y Bering, a sus sitios de reproducción en invierno en aguas mexicanas en Baja California, lo que se conoce como migración al sur, (Lagunas Ojo de Liebre, San Ignacio, Bahía Magdalena y aguas aledañas). Regresan en su migración al norte con una marcada separación en dos grupos, ballenas sin crías y parejas madres-crías, completando la migración más larga que ningún otro mamífero realice (Sumich, 1983) (Fig.5).

Los corredores migratorios por los que migra este misticeto se distribuyen cerca de la costa a todo lo largo de Norte América. Esto ha permitido la creación de flotas dedicadas a la actividad de avistamiento de ballenas y otros cetáceos, además del desarrollo de actividades turísticas a lo largo de la ruta migratoria. Estas actividades probablemente han influido a que estos corredores se hayan alejado de su posición original (por ejemplo en San Diego, California, EUA), lo que a su vez puede incrementar la demanda energética de las ballenas durante su recorrido y a la larga, ocasionar problemas en su historia de vida (IWC, 1993).

Por esto, en el año 2000, la Comisión Ballenera Internacional (IWC), organizó un taller para evaluar los efectos a largo plazo de la actividad de avistamiento sobre las poblaciones de cetáceos. Se propuso evaluar estos efectos con parámetros como la abundancia estacional y densidad de organismos en zonas donde se realizan actividades de avistamiento, patrones de uso del hábitat, medidas de fecundidad, tasas de sobrevivencia de crías por hembra y evidencias de heridas físicas o enfermedades. Sin embargo, el evaluar los efectos biológicos a largo plazo es complicado y como resultado de este taller se recomendó tratar de evaluar los efectos de importancia biológica con fines de regulación y manejo de las actividades de avistamiento de cetáceos. Se plantearon tres líneas de investigación: 1) medición del estrés fisiológico, 2) estudios poblacionales y 3) desarrollo de modelos matemáticos para evaluar los posibles efectos de ésta y otras actividades humanas en las poblaciones de cetáceos tomando el gasto energético como un indicador (IWC, 2001). El Costo de Transporte (CDT) se define como la fuerza necesaria para mover un peso determinado una cierta distancia a cierta velocidad (Tucker, 1975; Ec.4; Webb, 1975; Sumich, 1983; Berta y Sumich, 1999; Boyd, 2002). Durante la migración, la fuerza necesaria para recorrer una distancia es alta y determina que los animales viajen a una velocidad promedio en la que se maximiza el rango de desplazamiento con un mínimo CDT (Costa, 1999). La tasa metabólica puede expresar los requerimientos energéticos de los organismos y se ha podido calcular para pequeños mamíferos marinos, principalmente pinnípedos y odontocetos (Berta y Sumich, 1999; Boyd, 2002), sin embargo, pocas veces se ha medido para misticetos en vida libre. Aunque existen varias maneras de medir la tasa metabólica, la única que parece factible para las grandes ballenas es el monitoreo del patrón de respiración, ya que constituye una variable fácil de medir en campo, midiendo el consumo de oxígeno, con ayuda de parámetros como la fracción de oxígeno extraído, volumen de aire inspirado o exhalado por minuto y volumen tidal.

El patrón de ventilación de la ballena gris durante la migración es regular. Exhalan varias veces en una sucesión rápida de soplos alrededor de 3 a 5 minutos antes de levantar la aleta caudal, para iniciar un periodo de buceo que puede durar hasta 15 minutos. Este patrón de ventilación está estrechamente relacionado con la velocidad de nado (Fig.4; Sumich 1983; Würsig 1984; Berta y Sumich 1999), por lo tanto, un cambio en la velocidad implica un cambio en el patrón de ventilación (MBC, 1989). Para calcular la tasa de ventilación se divide el número de soplos por ballena por unidad tiempo (Sumich, 1983; Würsig *et al.,* 1984; Dorsey *et al.,* 1989).

Los mamíferos marinos presentan una capa de grasa alrededor del cuerpo que proporciona flotabilidad neutral, aislamiento y les otorga una forma hidrodinámica (importante para el ahorro de energía en cuestiones de termorregulación y locomoción). Aunado a esto, la oxidación de los lípidos que la conforman provee la energía necesaria para cubrir sus funciones fisiológicas (Pabst *et al*., 1999). Además, los mamíferos marinos presentan adaptaciones morfológicas y conductuales que les ayudan a reducir el costo de transporte en el medio que habitan.

Sumich (1983) calculó la velocidad de nado y la tasa de ventilación y propuso un modelo del costo de transporte para las ballenas en migración al sur frente a las costas de San Diego, CA. Sus resultados sugieren que el menor costo de transporte se da a una velocidad de 2.2 ms^{-1}, y se incrementa por abajo y por arriba de ésta; igual ocurre con la ventilación. El mismo autor sugiere además, velocidades menores para la migración norte comparadas a las del sur y propone como resultado de esto un mayor costo de transporte para este sentido de la migración (Fig.7).

II. HIPÓTESIS

El costo de transporte de la ballena gris es mayor durante la migración al norte que durante la migración al sur.

III. OBJETIVOS

1. Calcular la velocidad de nado para tres diferentes grupos de ballenas: ballenas migrando al sur, y de la migración norte: ballenas sin crías, y parejas madres-cría.
2. Calcular la tasa de respiración para cuatro grupos de ballenas en migración: migración sur y migración norte (ballenas sin crías, madres y crías).
3. Con base en estimados de circunferencia, largo y masa corporal, estimar el volumen tidal, el volumen de aire por minuto, la fracción de oxígeno utilizado y la tasa de consumo de oxígeno, para cada ballena modelo.
4. Con base en la velocidad de nado, la tasa de consumo de oxígeno y estimados del peso corporal, calcular el costo de transporte (CDT) y aplicar un modelo para la migración de las ballenas hacia el norte y hacia el sur.

IV. MÉTODO

Costa Azul se localiza aproximadamente a unos 23 Km al noroeste de la ciudad de Ensenada, Baja California, México (Fig.8). Se realizaron salidas al campo durante las temporadas 2003 (abril y mayo), de diciembre 2003 a mayo de 2004 y de diciembre 2004 a mayo de 2005. El puesto de observación (31°59’19”N, 116°50’22”W) se ubicó a 59 m de altitud sobre el nivel del mar. El equipo de observación realizó un promedio de 6 horas al día con salidas tres veces a la semana en las temporadas 2003-2004 y 2004-2005, incrementándose a 5 a 6 días por semana de abril a mayo de 2005. Las observaciones se iniciaron a las 7 AM y finalizaron hasta que las condiciones ambientales lo permitían. Un grupo de ballenas se define como una agregación donde la distancia máxima entre los individuos es de menos de cinco longitudes del cuerpo (MBC, 1989). Un avistamiento se define como el seguimiento de una ballena solitaria o un grupo de ballenas; y se da inicio al observarse la primera señal de ballena y termina 15 minutos después de verse la última señal. Los avistamientos, no las ballenas individuales, fueron la unidad muestral básica porque es difícil distinguir el comportamiento de cada uno de los individuos en un grupo. Los grupos de ballenas se seguían con un teodolito electrónico (Topcon DT-102) que midió ángulos verticales y horizontales desde la plataforma hacia la ballena. Además se registró el tiempo de inicio y final del avistamiento, el número de soplos, la posición y comportamiento de las ballenas en una grabadora de microcassettes (IFAW *et al.,* 1995; Heckel *et al.,* 2001). Los registros se transcribieron en hojas de datos y después se creó una base de datos. Las condiciones ambientales que se tomaron en cuenta para lograr un avistamiento exitoso fueron: el viento y el estado general del mar (no mayor a *3* en la escala de Beaufort) (Jahoda *et al.,* 2003), el reflejo en el agua ocasionado por el sol, nubosidad, neblina y lluvia. Además se eliminaron: 1) grupos de más de 3 ballenas, 2) grupos de ballenas localizados menos de tres veces y 3) avistamientos donde la velocidad de nado entre dos puntos fuera mayor a 10 ms^{-1} (valor escogido arbitrariamente).

La velocidad de nado de los grupos de ballenas se calculó con el programa T-Trak con base en la distancia y el tiempo entre dos localizaciones sucesivas de las ballenas durante un avistamiento (Cipriano, 1990). Además de esto, se dibujó la trayectoria de cada avistamiento con el paquete *Surfer 8.01.* En cuanto al patrón de respiración, la variable de respuesta fue la tasa de ventilación (Sumich, 1983; Würsig *et al*., 1984; Dolphin, 1987; Dorsey, 1989).

Para el análisis exploratorio de los datos se utilizó estadística no paramétrica, después de probar la distribución no normal de los datos (Kolmogorov-Smirnov). Se utilizó una prueba de Kruskal-Wallis (K-W) para probar si existían diferencias significativas en la velocidad de nado y la tasa de ventilación entre los grupos en migración y una prueba *a posteriori* de rangos de Newman-Keuls (N-K) para ver entre cuáles grupos existían las diferencias (Neave y Worthington, 1988).

Se establecieron cuatro modelos diferentes de ballenas, una perteneciente a cada uno de los cuatro grupos que conforman la migración (migración al sur, ballena sin crías al norte, madres y crías), con base en medidas de longitud estimadas previamente por Perryman y Lynn (2002), y se calculó el peso para cada una con base en estimados de la circunferencia corporal (Ec. 9; Tabla I; Sumich, 1986).

Se calculó el intercambio gaseoso (V_T) para cada una, sin embargo, para las tres categorías de ballenas adultas se escogió el valor intermedio de 690 l ya que nos ayuda a evitar la distorsión asociada con las ballenas más robustas y más delgadas, y un V_T de 132 l para las crías (Tabla II). La fracción de oxígeno extraído por respiro (FO_2) se supuso un 11% del total de aire inspirado con base en mediciones previas (Sumich, 2001). Para las estimaciones del COT además de la velocidad de nado y tasa de ventilación, se calculó la tasa de consumo de oxígeno (Vo_2) (Ec.10) con base en el porcentaje de intercambio gaseoso (V_T) y estimaciones del porcentaje de oxígeno extraído por respiro (FO_2) (Fig.10). Siguiendo la ecuación de Tucker (1975; Ec.4), se calcularon los costos de transporte para cada grupo de ballenas grises en migración (Tabla VIII). Finalmente se hicieron dos gráficos por separado de la velocidad de nado contra la tasa de consumo de oxígeno (Fig.12) y la velocidad de nado contra el CDT (Fig.13).

VI. RESULTADOS

Se completaron un total de 132 días (904 horas) en campo de diciembre 2003 a mayo 2005. Se registraron 310 avistamientos de los cuales 179 se seleccionaron para análisis (Tabla III). De los dos sentidos de la migración, sur y norte, la literatura subdivide generalmente la migración norte en Fase A, compuesta por ballenas sin crías y Fase B, compuesta por las parejas madre-cría. Debido a la connotación temporal de la palabra “fase” y en vista de que durante el trabajo de campo se vio un traslape entre estas dos fases, en este trabajo se redefinió la nomenclatura con relación a los diferentes grupos de ballenas. Se cambió palabra “fase” por “grupo”, lo que antes se denominaba Fase A, será grupo de ballenas sin crías y lo que era Fase B, serán parejas madre-cría.

Se encontró que para los datos obtenidos en el 2003 durante los meses de abril y mayo (parejas madre-crías), no se registraron individualmente los soplos de las madres de los de las crías, por lo que estos datos se descartaron para los análisis posteriores.

Para la temporada 2003-2004, la velocidad de nado de las ballenas durante la migración al sur fue de 2.1±0.1 ms^{-1} (media ± error estándar). Para las ballenas sin crías se obtuvo una velocidad promedio de 1.5±0.1 ms^{-1} mientras que para las parejas madre-cría fue de 1.1±0.2 ms^{-1} (Tabla IV).

Se utilizó una prueba de K-W para probar diferencias en la velocidad de nado entre los grupos en migración. Se encontraron diferencias significativas entre los tres grupos (migración sur, ballenas sin crías de la migración al norte y las parejas madre-crías también de la migración al norte) (H=24.26, df=2, p=0.001, n=81). Tales diferencias se dan entre la migración sur y las ballenas sin crías al norte (p=0.02) y migración sur y las parejas madre-cría (p=0.0002) de la migración al norte. No se encontraron diferencias significativas entre las ballenas sin crías y las parejas madre-cría (p=0.05) (N-K), lo que puede deberse al tamaño de muestra relativamente bajo (n=24).

Para la temporada 2004-2005, la velocidad fue para la migración sur 1.9 ms^{-1}, para las ballenas sin crías al norte 1.8 ms^{-1} y para parejas madre-crías 1.2 ms^{-1}

(Tabla V). La prueba de K-W mostró diferencias significativas en la velocidad de nado entre los tres grupos (H=33.3, df=2, p=0.0001, n=94). La prueba *a posteriori* de N-K mostró estas diferencias entre la migración sur y ballenas sin crías al norte (p=0.0001) así como entre ballenas sin crías y parejas madre-cría (p=0.0001) de la migración al norte. En cambio, no se encontraron diferencias significativas entre las ballenas migrando al sur y las parejas madre-cría (p=0.2).

No se encontraron diferencias significativas en la velocidad de nado entre temporadas (2003-2004 y 2004-2005) de cada uno de los tres grupos: migración sur (U=788, p=0.2, n_1=57; n_2=32), ballenas sin crías de la migración al norte (U=166, p=0.1, n_1=13; n_2=36) y parejas madre-cría (U=109, p=0.2, n_1=11; n_2=26), lo que nos permitió juntar los datos.

La tasa de ventilación se calculó para los cuatro diferentes grupos de ballenas (migración sur, ballenas sin crías al norte, madres y crías por separado). La tasa de ventilación para la migración sur de la temporada 2003-2004 fue 0.6 ± 0.03 soplos/min (media±ES). Para las ballenas sin crías de la migración norte fue 0.5 ± 0.04 soplos/min y para las parejas madre-cría los soplos se contaron por separado. Para las madres se obtuvo una tasa de ventilación de 0.8 ± 0.2 soplos/min y para las crías 0.4 ± 0.1 soplos/min (Tabla VI). De acuerdo a la prueba K-W aplicada, hubo diferencias significativas (H=7.07, df=3, p=0.07, n=92) para la tasa de ventilación entre los cuatro grupos. Según la prueba *a posteriori* N-K se encontraron diferencias significativas entre ballenas al sur y madres (p=0.05), ballenas sin crías y madres (p=0.01) y madres y crías (p=0.01). No se encontraron diferencias significativas entre ballenas migrantes al sur y ballenas sin crías al norte (p=0.4), ballenas al sur y crías (p=0.5) y ballenas sin crías al norte y crías (p=0.7).

La tasa de ventilación para la migración al sur de la temporada 2004-2005 fue 0.8 ± 0.1 soplos/min (media±ES). Para las ballenas sin crías al norte la tasa de ventilación fue 0.5 ± 0.03 soplos/min, para las madres 0.5 ± 0.1 soplos/min y para las crías 0.7 ± 0.1 soplos/min (Tabla VII). La prueba de K-W mostró diferencias significativas (H=23.3, df=3, p=0.0001, n=119) entre los grupos de ballenas con respecto a la tasa de ventilación. Las diferencias encontradas (N-K) se dieron entre las ballenas al sur y las ballenas sin crías al norte (p=0.0002), ballenas al sur y madres (p=0.0005), ballenas sin crías y crías (p=0.01), madres y crías (p=0.03). No se encontraron diferencias entre ballenas al sur y crías (p=0.07) y ballenas sin crías al norte y madres (p=0.4).

La tasa de ventilación mostró diferencias significativas entre las dos temporadas dentro de cada grupo de ballenas migrantes al sur (U=535, p=0.001, n_1=57; n_2=32) y crías (U=63, p=0.01, n_1=11; n_2=25). No así para ballenas sin crías (U=205, p=0.5, n_1=13; n_2=36) y madres (U=97, p=0.1, n_1=11; n_2=26) de la migración al norte.

Los costos de transporte calculados para cada grupo en migración fueron para la migración al sur 0.42 MJ $kg^{-1}m^{-1}$ y para las ballenas sin crías de la migración norte 0.30 MJ kg^{-1} m^{-1}. Para las parejas madre-cría de la migración norte, el CDT fue calculado por separado. Para las madres se obtuvo un costo de transporte de 0.50 MJ kg^{-1} m^{-1} y para las crías 0.63 MJ kg^{-1} m^{-1}. Además, se calculó el intervalo del

CTD con base en ±0.1 ES de la velocidad de nado y la tasa de ventilación (Tabla VIII).

VI. DISCUSIÓN

La velocidad de nado para las ballenas migrantes al sur en Costa Azul, Baja California es de 1.9 ms^{-1}. Este valor concuerda con las velocidades medidas en las costas de San Diego y Ensenada (Sumich, 1983; Heckel, 2001). Para el grupo de ballenas sin crías de la migración al norte se obtuvo una velocidad promedio de 1.8 ms^{-1}, también comparable con las encontradas en la literatura. Para las parejas madre-cría no existen valores publicados y en este trabajo se obtuvo una velocidad promedio de 1.2 ms^{-1}.

Por muchos años se ha sabido que las ballenas migrantes al sur viajan a velocidades más altas que las que migran al norte, y se han propuesto varias hipótesis para tratar de explicar esta diferencia. Cambios en los niveles de hormonas reproductivas y la influencia de la corriente de California son dos de las más recurrentes.

Las bajas velocidades de nado de la migración al norte pueden deberse a la falta de reservas energéticas después del ayuno prolongado, además de que las ballenas que migran en este periodo se han visto involucradas en conductas sexuales, como cortejo, o alimentación oportunística (Pike, 1962; Poole, 1984).

Con relación a la tasa de ventilación se vio en este trabajo que las ballenas que migran hacia el sur nadan sin interrupciones, y presentan conductas, como saltos en la superficie característicos en la reproducción. La tasa de ventilación para este sentido de la migración (0.8 soplos/min) es similar a la obtenida por Sumich (1983) de 0.72 soplos/min.

Para la migración hacia el norte, las ballenas sin crías tuvieron una tasa de 0.5 soplos/min, que es comparable con la obtenida por MBC Applied Enviromental Sciences en un estudio de monitoreo realizado en 1987-1989, en donde la tasa de ventilación fue de 0.3-0.4 soplos/min para la misma categoría (MBC, 1989).

Tasas de ventilación para las parejas madre-crías han sido publicadas, pero no se han reportado valores para cada grupo por separado. Aún con todo esto es posible que los datos no puedan ser comparables a los obtenidos para animales en vida libre.

Con relación a las parejas madre-cría, durante el análisis de datos se constató un mayor número de soplos de la madre que de la cría. En campo se ve que por cada soplo de la madre, la cría ventila al menos de dos a tres veces, por lo que existe una duda acerca de la confiabilidad de los datos. Uno de los problemas que se enfrentan al observar las ballenas a la distancia, es que a veces los soplos de las crías no son evidentes o dependiendo de las condiciones de luz o de la posición de la ballena, se pueden confundir con los de sus madres.

Uno de los objetivos de este trabajo era comparar el valor de costo de transporte obtenido por Sumich (1983), con los obtenidos en este trabajo, utilizando el mismo modelo. Los resultados de su trabajo mostraron el CDT (0.160 kcal kg^{-1} m^{-1}) a 2.0 ms^{-1} con una tasa de ventilación de 0.72 soplos/min.

Tomando los datos de Sumich y aplicando el procedimiento que se utilizó en el presente estudio, se calculó el CDT de la migración al sur. El CDT obtenido para el área de San Diego (0.39 MJ kg^{-1} m^{-1}; datos de Sumich, 1983) (MJ=megajoules), es muy similar al obtenido para el área de Costa Azul en este trabajo (0.42 MJ kg^{-1} m^{-1}). La similitud de los costos de transporte en dos sitios diferentes y en diferentes años, puede significar que el costo de transporte es similar a lo largo de la ruta migratoria. Sin embargo, es necesario seguir realizando estudios de este tipo en diferentes sitios, y con diferente grado de perturbación a lo largo de ésta para que pueda complementarse.

Se ha propuesto que el costo de transporte para la migración al norte es el doble que para la migración al sur (Sumich, 1983). No obstante, en este estudio el valor más bajo se encontró para la migración al norte, en el grupo de ballenas sin crías (0.30 MJ kg^{-1} m^{-1}). La diferencia entre este valor y el obtenido para la migración al sur, se puede explicar por la velocidad y tasa de ventilación reducidas.

Las parejas madre-cría tienen requerimientos energéticos diferentes al resto de las ballenas, ya que la gestación y la lactancia son procesos energéticamente demandantes, que se reflejan en costos de transporte más altos (0.50 MJ kg^{-1} $m^{-1,}$ para las madres y 0.63 MJ kg^{-1} m^{-1} para las crías). Las hembras enfrentan esta situación de cuatro maneras diferentes: 1) incrementar el consumo de alimento antes de salir de sus áreas de alimentación, 2) movilización lipídica (convertir lípidos en vez de sintetizarlos), 3) compensación metabólica (reducción de gasto de energía en cuestiones no relacionadas a la producción de leche) y 4) tamaño corporal (tamaños grandes almacenan más lípidos) (Mellish *et al.*, 2000).

Durante la migración, las ballenas nadan en la superficie la mayor parte del tiempo. Nadar en la superficie aumenta la fuerza de arrastre 5 veces que nadar a una profundidad que sea 3 veces el diámetro corporal, como lo propone Hertel (1966), lo que podría significar mayores costos de transporte para las parejas madre-cría. En adición a este factor hidrodinámico, si un animal incrementa su nivel de actividad, la tasa de consumo de oxígeno se incrementa, si se llega a sobrepasar el límite (condición anaeróbica) se da la acumulación de lactato y CO_2 en la sangre y en los tejidos, lo que lleva a la fatiga y a la acidosis respiratoria y metabólica (Berta y Sumich, 1999). Si el proceso migratorio transcurre a la velocidad óptima, se ahorra energía, se minimiza la producción de metabolitos tóxicos y se maximizan las distancias recorridas (Beiwener, 2003).

Además de la locomoción, también se puede pérder energía en forma de calor en los procesos de termorregulación y de ventilación. Sin embargo, los mamíferos marinos tienen una gran variedad de mecanismos para controlar su temperatura y la cantidad de calor perdido es despreciable.

Aunque los costos de transporte obtenidos en este trabajo para la ballena gris migrando en Costa Azul se basan en estimados previos de muchas de las variables, a la fecha se basan en la mejor información disponible. El tener dos valores similares (Sumich 1983 y este trabajo) con respecto a la velocidad de nado y tasa de ventilación en diferentes áreas, en diferentes años (una diferencia de 20 años) y con un modelo de ballena diferente, puede ser indicador de la constancia de estas variables a lo largo de la ruta migratoria, y lo mismo ocurriría para el costo de transporte. Dos valores similares para el CDT, pudiera ser también el reflejo de la influencia de las mismas variables (velocidad de nado y tasa de ventilación). Sin embargo, esto es sólo una suposición, y es importante seguir con el desarrollo de trabajos similares, principalmente en áreas con diferencias marcadas entre ellas (topografía, con diferente grado de actividades humanas, condiciones oceanográficas, etc.) para tratar de establecer diferentes escenarios. Aunado a esto y debido a la dificultad que consituye el medir los parámetros ventilatorios para la ballena gris en vida libre, más aún en migración, las mediciones tomadas a crías en cautiverio y en las lagunas de reproducción constituyen los únicos valores disponibles. En la actualidad se están realizando trabajos (Sumich, com. pers.) con el objetivo de obtener medidas más precisas de las variables ventilatorias, como el volumen tidal (V_T), fracción de oxígeno extraído por respiro (FO_2) y la tasa de consumo de oxígeno (Vo_2) para la ballena gris, lo que puede llevar a un mejor estimado del CDT durante la migración de este cetáceo.

Por lo anterior, considero que los costos de transporte calculados para la ballena gris en el área de Costa Azul, al momento y con la información que existe disponible, pueden considerarse estimaciones confiables.

I. INTRODUCTION

1.1. Energy flow and metabolism

Energy budgets are the way in which an organism is able to balance the acquisition and loss of energy. The substrates and energy used by individuals to function are obtained from the food ingested, degraded and assimilated by metabolic processes (Costa, 2002). Substrate used for energy production is obtained from daily food ingestion or can be synthesized and stored by the organism in fatty tissue. Not all of the ingested food is absorbed and there are some losses due to excretion processes (Fig.1). The energy remaining following excretion is considered metabolizable energy. Metabolizable energy (ME) may be described by the following equation (Costa, 2002):

$$ME = IE - FE - UE \tag{1}$$

Where:

ME = metabolizable energy

IE = ingested energy

FE = feces excretion energy

UE = urine excretion energy

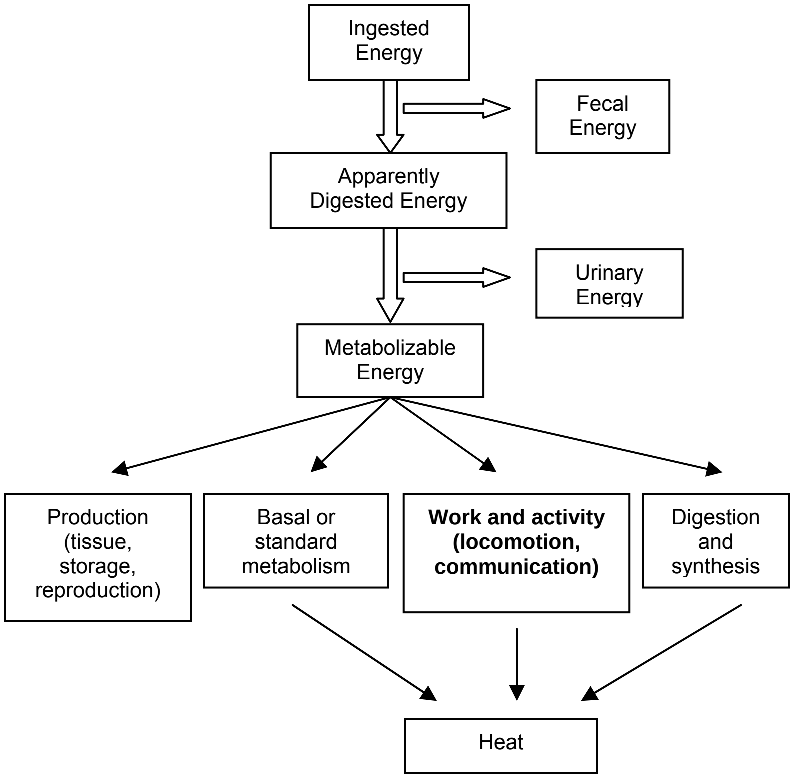

Figure 1. General energy flow model in mammals (Costa 2002).

Figura 1. Modelo general del flujo de energía en mamíferos (Costa 2002)

Metabolizable energy is the energy necessary to achieve work. It is the storage of chemical energy that is eventually lost as heat. The conversion of chemical energy into heat is defined as the metabolic rate (MR), and is measured as caloric energy consumption per time unit (Randall *et al.,* 2002).

The estimation of metabolic rate has been the subject of many studies, as it is one of the most important variables in ecology (Brown *et al*., 2004), since metabolism is the energy supplier for growth plus, it gives us information about the physiological and biological processes taking place within organisms, it can explain most of variation in ecological rates and helps us to understand the relationship between individuals and their environment (Costa, 2002).

Metabolizable rate can be expressed based on the corporal mass or corporal surface of the organism in an allometric equation that results from a lineal regression (Schmidt-Nielsen, 1984; Lavigne *et al*., 1986; Hunter *et al.*, 2000):

$$MR= B_0M^b \tag{2}$$

Where:

MR=metabolic rate

B_0= mass-independent normalization constant

M= mass

b= allometric scaling exponent (tipically b=0.75)

Measuring the metabolic rate is important to determine the energy expenditure of animals in the field. As for free-ranging oraganisms the measurement of the metabolic rate is complicated, the field metabolic rate is another practical way of estimation (FMR) (Costa, 2002). The field metabolic rate represents the daily metabolic costs associated to the species' behavior in the field. However, it can vary both under the influence of intrinsic and extrinsic factors, such as age and sex of the individual, repair and growth of tissues, internal (osmotic, electrical or mechanical) and external work (locomotion and communication). However, the metabolic rate is variable between species, even within the same species, and its variation in free-living organisms is not well known.

The field metabolic rate can be calculated in several ways including: 1) water marked with stable isotopes (Butler *et al*., 1997), 2) changes in corporal mass and 3) heart rate variation (Gordon *et al.,* 1968; Randall *et al.,* 2002). One of the most important is through estimates of O_2 consumption. This is relatively straightforward when animals can be enclosed in aquariums or laboratories, but in free-ranging marine mammals the rate of oxygen consumption can be measured only between dives, and the information generated during diving is lost (Randall *et al,* 2002).

Basal metabolic rates for mysticetes have never been measured in free-ranging animals. Sumich (1994) indicates their large size and the absence of a clear resting behavior, (although they can be observed floating on the surface or lying quiet at certain depth) are two of the main problems researchers face while trying to measure the metabolic rate of a large marine mammal (Lyamin *et al*., 2000). Of the various methods used for metabolic rate estimation, the only one that seems feasible for the large whales (for it constitutes a variable that is easy to evaluate in the field) is the monitoring of the breathing pattern. This involves estimating oxygen consumption by means of documenting the breathing rate and percentage of oxygen utilization, tidal volumes and oxygen ventilation per minute estimates (Prosser, 1973; Hainsworth, 1981; Sumich, 1983; Sumich *et al.* 2001).

In migrating gray whales that are fasting, the energy necessary to cover all physiological functions is obtained from body lipid oxidation. In addition, in marine mammals some lipids (tryacilglycerols) are stored in a layer around the animal´s body (fat layer or blubber; Fig.2) (Pabst *et al.,* 1999). Blubber serves as energetic reservoir and as insulation and helps the organism to achieve neutral buoyancy, thus eliminating the use of energy for support (Beiwener, 2003).

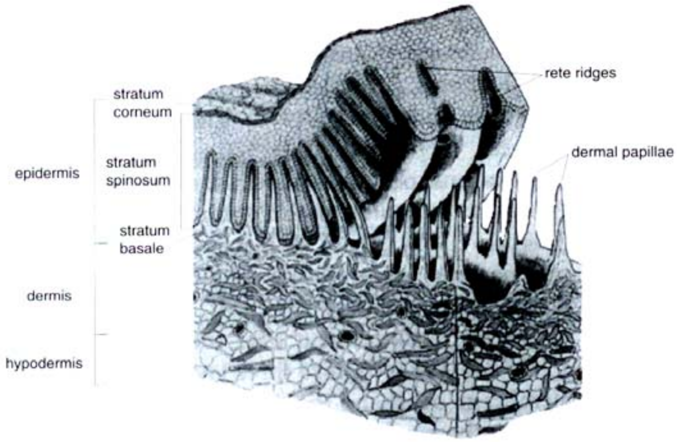

Figure 2. Transversal view of cetacean skin showing the epidermis, dermis and hypodermis (hypodermis=blubber) (Berta and Sumich 1999).

Figura 2. Vista transversal de la piel de un cetáceo mostrando la epidermis, dermis e hipodermis (hipodermis=capa de grasa) (Berta y Sumich 1999)

Blubber in addition, helps the organisms to achieve a smooth streamlined body, an important matter in relation to locomotory functions (Iverson, 2002), since several forces influence the way in which an animal moves in a fluid.

1.2 Locomotion

Although marine mammals have several types of locomotion, the main movement mechanism for movement is without doubt swimming. Swimming results in the transfer of momentum from a part of the animal towards the environment and vice versa (Webb, 1988). This transfer of momentum is regulated by the physical properties of water and governed by important physical forces: gravity, inertia, drag (combination of friction and pressure of a fluid towards a body), thrust (weight of the liquid and opposite to the drag) and the viscous force (resistance of a fluid) (Berta and Sumich, 1999). The drag force has three different components that affect swimming: viscous drag (influenced by the swimmer´s surface area), pressure drag (influenced by the body streamlining) and wave drag (formed when the object moves at the air-water interface) (Costa, 1999).

Viscous force changes with temperature, decreasing with high temperatures while increasing in low ones (Vogel, 1994). The viscous force also influences the type of fluid around the swimmer´s body (turbulent, transitional or laminar), situation that can change the friction and pressure components of the drag force (Vogel, 1994). In marine mammals wave drag influences their swimming performance at the sea surface since it increases exponentially with velocity and body size because of the formation of diverging waves. It is extremely rare that organisms exceed this speed while swimming at the surface because of the extra energy required to swim faster (Fish, 1996). This may be the reason for individuals to exhibit the maximum swimming velocity below those speeds in which waves are generated (Hertel, 1966).

Marine mammal swimming is based on the thrust force which is highly efficient (Webb, 1988). It is originated by orienting the body or some corporal biofoil in a <30° angle to the direction of the fluid. In addition, the propellant structures of vertebrates (fins, legs, etc.) function in different ways depending on the type of habitat they live in and the intensity of the forces they have to overcome. These, combined with the oscillating movement pattern of the flukes along a sagittal plane (Webb, 1988) are adaptative features that allow cetaceans to reduce the cost of energy while traveling through the aquatic environment (Fish 1996) (Fig.3).

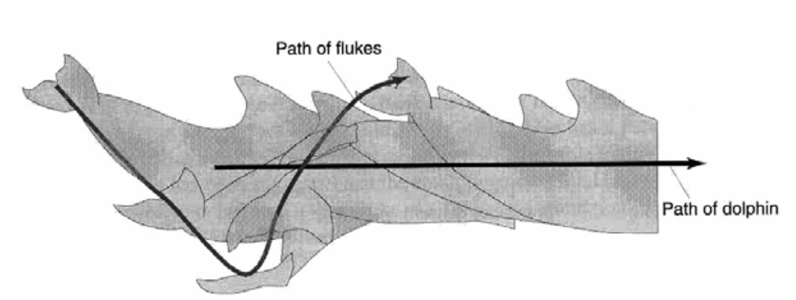

Figure 3. Cetacean propulsion (Berta and Sumich 1999).

Figura 3. Propulsión en cetáceos (Berta y Sumich 1999).

1.3 Breathing pattern

The breathing pattern in gray whales is related to their locomotion efficiency and speed. Sumich (1983) reported that for migrating gray whales individuals traveling at high speeds had higher breathing rates than those traveling slowly. Differences in the swimming speed also influence the breathing pattern, which also varies (MBC, 1989).

Whales are fast ventilating individuals, rising to the surface while moving to take a single breath. They also are considered long-diving animals (Kooyman, 1973). Divers such as the gray whale present special modifications in the respiratory and circulatory systems (Randall *et al.,* 2002). For example, cartilage reinforces the lungs to avoid their collapse and oxygen is storaged in blood and muscle (Berta and Sumich, 1999; Pabst *et al*., 1999; Randall *et al.,* 2002). The breathing pattern varies according to the species and the activity in which animals are engaged. In cetaceans, the respiratory cycle starts at the surface with a simple exhalation that constitutes the blow (formed by the contact between the warm air coming out of the lungs with the cold air in the environment) followed by a new inhalation. The size, shape and direction of the blow are characteristic of different species and can help to identify some species of whales at great distances in the field (Berta and Sumich, 1999). The breathing pattern of the gray whale during migration is relatively consistent, since individuals exhale several times in a fast succession of blows lasting around 3 to 5 minutes before raising the flukes to start a diving period that can last up to 15 minutes (Fig. 4) (Sumich, 1983; Würsig, 1984; Berta and Sumich, 1999).

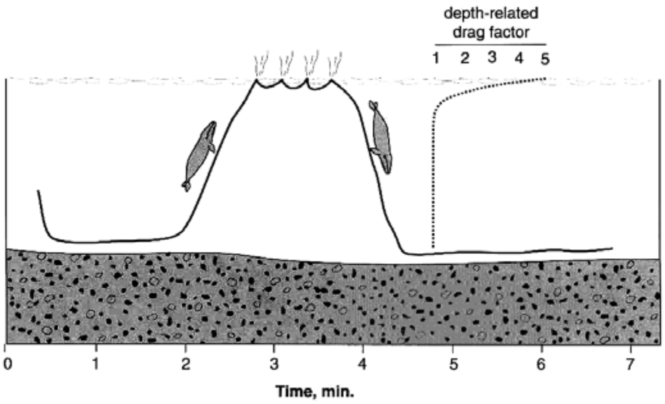

Figure 4. Apneustic breathing pattern of a migrating gray whale (Berta and Sumich 1999).

Figura 4. Patrón de ventilación de una ballena gris en migración (Berta y Sumich 1999).

1.4 Gray whale migration

Large-scale movements along the coast are rare in cetaceans, and gray whales are the only species to do so. Stern (2002) proposed the initiation of the gray whale migration may be associated to a change in foraging or some environmental factor such as the size of the ice cover. It has been discussed that probably they rely on landmarks and sea floor topography during migration, cues that would help them to follow the contour of the coastline along the same corridor every year (Stern, 2002); for the newborns it is thought that they have the chance to learn the route accompanying their mothers during their first returning northward trip to their summering areas (Pike, 1962).

Eastern North Pacific (ENP) gray whales travel 15,000 to 20,000 km from their summer feeding grounds in the Chukchi and Bering seas to their winter breeding grounds in Mexican waters (Laguna San Ignacio, Laguna Ojo de Liebre, Bahía Magdalena and surrounding waters) covering the longest annual migration acomplished by a mammal (Fig.5). The gray whale migration consists of a southbound and a northbound component (Poole, 1984). The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel *et al.,* 2001). Following southbound migrating whales, a first group of northbound migrating individuals (whales without calves: adults and juveniles of both sexes) can been seen from the coastal location of Costa Azul from February to May. Finally, a second group of the northbound migration (mother-calf pairs) passes Costa Azul from the first days of April until the third week of May (Fig. 6).

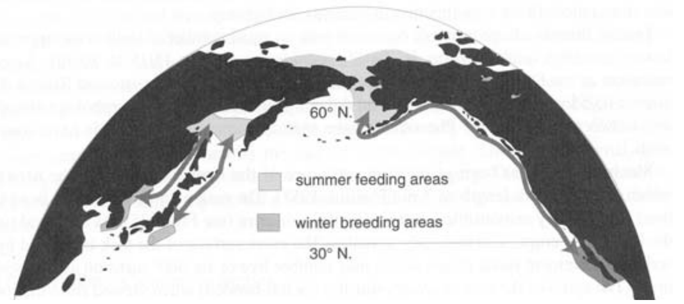

Figure 5. Migratory route Eastern North Pacific gray whale population (Berta and Sumich 1999).

Figura 5. Ruta migratoria de la población de ballena gris del Pacífico Nororiental (Berta and Sumich 1999).

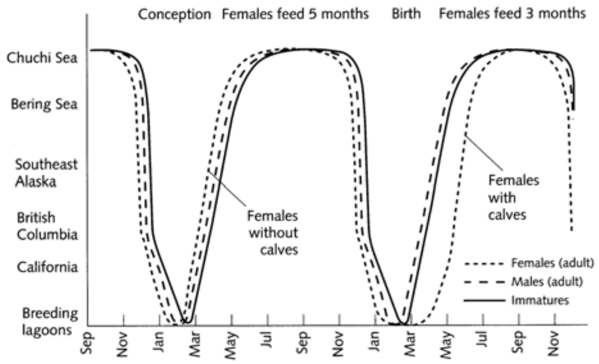

Figure 6. Migratory cycle of the gray whale (Berta and Sumich 1999).

Figura 6. Ciclo migratorio de la ballena gris (Berta and Sumich 1999).

1.5 Cost of transport: An indicator of biological importance

In 2000, the International Whaling Commission (IWC) organized a workshop in order to evaluate how long-term biological effects caused by whale watching activities on cetacean populations could be measured. The workshop participants proposed that the indicators could be the seasonal abundance and density of individuals in zones where sighting activities take place, habitat use patterns, fecundity and survivorship rates, and evidence of external wounds and disease. However, assessing long-term biological effects in cetaceans has not been demonstrated. Instead, the workshop participants suggested the possibility of measuring short-term effects as a means to model potential effects in the long-term (effects of biological importance), and proposed three research lines: 1) physiological stress measurements, 2) comparative population studies at different intensity levels of whale watching activities, and 3) the development of mathematical models based on energy expenditure estimates to evaluate the possible effects of human activities on cetacean populations (IWC, 2001). The gray whale migratory corridors are distributed closely along the coast of North America, which has motivated the establishment and rapid increase of whale watching and tourism activities. It seems that at least in San Diego, California, the corridor has shifted away from the coast, and this may have an influence in the increase of energy demand for whales by traveling a longer distance after months of fasting (IWC, 1993). An increased energetic cost during migration can lead to a lower reproductive rate, or to an increase in the number of strandings (IWC, 1993). Therefore, the estimation of cost of transport may be used to model and predict the effects of human activities on marine mammals. The results of this work will hopefully provide a baseline for future comparison and evaluation of the effects of whale watching and other human activities on gray whale migration.

1.6 Gray whale cost of transport

The necessary force to travel a certain distance can be high and may be one of the reasons that animals move at a mean speed that maximizes its range of movement with a minimum cost of transport (COT) (Costa and Williams, 1999). The COT is defined as the necessary power to move a certain weight over a certain distance at a particular speed (Tucker, 1975; Sumich, 1983; Berta and Sumich, 1999; Boyd, 2002), meaning that it is a function of body mass and swimming velocity:

$$COT = \frac{P}{WV} \tag{3}$$

Where:

P= power (energy expenditure; kJ)

W= weight (kg)

V= velocity (m s^{-1})

Hydrodynamic models prove that the power requirement for animals whose bodies have a hydrodynamic form (which is a "streamlined form, roundly bount at the front, tapered in the rear and round in cross section"; Berta and Sumich, 1999) is proportional to the cube of the speed (V^3). The equation, which predicts the performance of vertebrates with a hydrodynamic body, was described by Webb (1975):

$$P = (0.5\rho)(Ct)(Sw)(V^3) \tag{4}$$

Where:

P= power (energy expenditure; kJ)

ρ = water density (gr cm^{-3})

Ct = drag coefficient

Sw= wet surface (area; cm^2)

V= velocity (ms^{-1})

Organisms with a swimming mode based on the drag force and oscillating movements of the flukes, such as whales, have low COT values (Fish, 2000). Cost of transport for several species of pinnipeds, sirenians and some cetaceans have been determined. Most of the tested models show that the speed at which the COT is minimal ranges from 1.5 ms^{-1} to 2.2 ms^{-1} (Sumich, 1983; Boyd, 2002).

Breathing rates can be converted to energy expenditure (COT) by using oxygen as a practical measurement for the metabolic rate because the amount of heat produced for each liter of O_2 used during metabolism is relatively constant. An average of 4.8 kcal l^{-1} O_2 has been proposed as a measure for metabolic rate (Schmidt-Nielsen, 1979). Changing demands for the rate of O_2 consumption (Vo_2) by an organism are tightly related to changes in their breathing rates (*BR*; breaths/min), tidal volumes (V_T; volume of air exchanged in each breath), the percentage of O_2 extracted in each breath (FO_2) and body weight (*W*) (Hainsworth 1981; Sumich 1983). Besides these variables, it is necessary to estimate body girth (*G*) and mass (*M*) along with the swimming velocities. Sumich (1983) calculated the swimming velocity and breathing rate for the southbound migration of the gray whale at San Diego, California, USA, and based on these two variables plus the parameters mentioned above proposed the following cost of transport model for migrating whales (Fig.7).

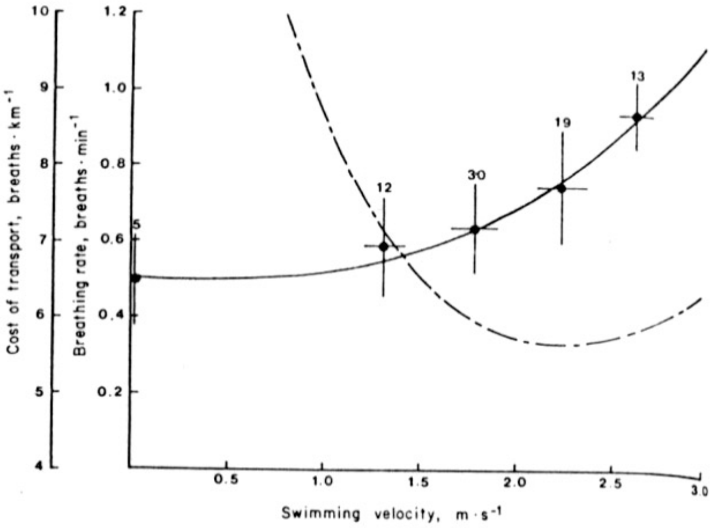

Figure 7. Swimming velocities, breathing rates and cost of transport (COT) values for southbound migrating whales observed at San Diego, California (broken line shows the COT, solid line the mean breathing rate) (Sumich 1983).

Figura 7. Velocidad de nado, tasa de ventilación y costo de transporte (CDT) para la migración al sur de la ballena gris en San Diego, California (la línea fragmentada representa el CDT y la continua la tasa de ventilación) (Sumich 1983).

The results of his work showed that the swimming velocity at which the COT is minimum is 2.0 ms^{-1}, and tended to increase at lower and higher velocity. This model suggests that at swimming velocities lower than 2.2 ms^{-1}, as during the northbound migration (also observed by Heckel, 2001); the COT may be higher than during the southbound migration (Sumich, 1983).

II. HYPOTHESIS

The cost of transport of gray whales is higher during the northbound than during the southbound migration.

III. OBJECTIVES

1. To measure the swimming velocity for three different groups of migrating gray whales: southbound, northbound without calves and northbound with calves (mother-calf pairs).
2. To calculate the breathing rate for the four different groups of whales (southbound whales, northbound whales without calves, mothers and calves)
3. To calculate based on girth, length, and body mass estimates the oxygen tidal volume, minute ventilation volume and consumption rate for each group of whales.
4. To model the cost of transport (COT) of south- and northbound migrating whales based on the swimming velocity, oxygen consumption rates and weight estimates.

IV. METHODS

4.1 Field work

The site where observations were performed, Costa Azul, is located about 24 km northwest of Ensenada, Baja California (Fig.8). Observations from land were conducted in April and May 2003, from December 2003 to May 2004, and again from December 2004 to May 2005.

Figure 8. Baja California map showing the study area: Costa Azul (discovery initiatives 2005).

Figura 8. Mapa de Baja California mostrando el área de estudio: Costa Azul (discovery initiatives 2005).

The study site (31°59'19"N, 116°50'22"W) was 59 m above mean sea surface level. According to Würsig *et al*. (1991), this height allows for the reliable measurement of the location of whales with a theodolite and the accurate estimation of swimming speeds and direction. The absence of visual obstacles such as vegetation and construction contributed to the choice of location.

The observation team consisting of two observers spent an average of 6 hours a day performing observations on Friday, Saturday and Sunday. Effort was increased by a further 2 or 3 days per week in April and May 2005. Observations started at 7 AM and continued as long as environmental conditions allowed. The environmental conditions to take into consideration for a successful sighting are: sea surface state below 3 in the Beaufort scale (Jahoda *et al.,* 2003), glare on the water caused by the sun, clouds (% of cover), fog and rain. Reilly *et al.* (1983) used these criteria to define a visibility scale: 1) Excellent, 2) Very good, 3) Good, 4) Fair, 5) Poor and 6) None. In our case we only followed groups of whales with good visibility or better. The observation effort was terminated when sighting conditions were poor (above visibility code 4 according to Reilly *et al.*, 1983).

A group of whales is an aggregation in which the maximum distance between individuals is less than five body lengths (MBC, 1989). A sighting is defined as the monitoring of a solitary whale or group of whales. It starts with the first signal of the presence of a whale (usually the observation of a blow or part of the body) and finishes 15 minutes after seeing the first signal. Sightings were considered the sampling unit; individual whales were not the sampling unit because it is difficult to distinguish the behavior of individuals within a group. Once a sighting commenced, one of the observers followed its movements with the theodolite while the second observer used 7x50 binoculars and a chronometer to record the start and finish time, number of blows and the theodolite angles which are important for the subsequent calculation of swimming speed and breathing pattern (IFAW *et al.,* 1995). Data were dictated to a micro cassette recorder (Heckel *et al*. 2001). Recordings were later transferred to data sheets and captured on a computer database.

The theodolite was used to measure vertical and horizontal angles (in degrees from the true north) between the platform and the whales. After reviewing the literature, it was decided to select the data based on the following criteria:

1) Groups with more than 3 whales where discarded because blows are difficult to count in large groups. Sumich (1983) reports a decrease in the number of blows as the group size increases, which may be due to lack of experience of the observers.

2) Groups of whales with less than three theodolite positions were eliminated.

3) Observations were eliminated when swimming speed between two points was higher than 10 ms^{-1}, an unreasonably high value for gray whales.

4.2 Data analysis

The swimming speed ($m\ s^{-1}$) of whale groups was calculated with the computer program T-Trak (Cipriano 1990). Swimming speed estimates are based on the distance traveled and the time elapsed between two successive locations of whales during a sighting. The program requires the station’s position on a map, the height of the theodolite platform above sea level, the position of a horizontal zero reference on a map, and data on changes in sea level (tidal fluctuations) as a function of time.

In addition, tracks were plotted on maps for each sighting using the package *Surfer 8.01* (Golden Software, Inc., 2002) (Fig.9). Only sightings that showed realistic tracks (whales travel in a relatively straight line) were selected for further analyses.

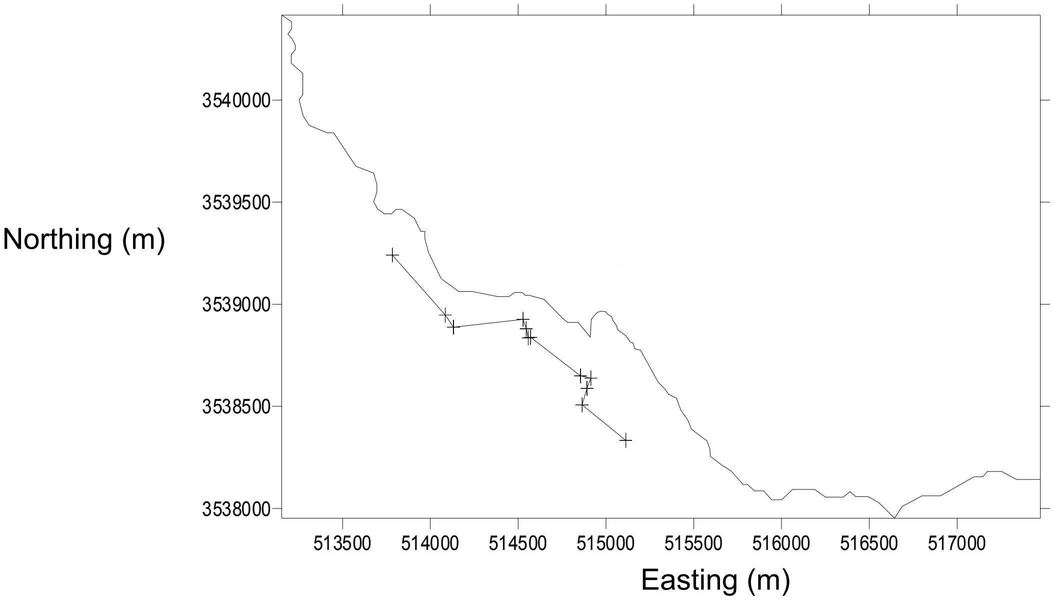

Figure 9. Example of a realistic track. Northbound migration mother-calf pair in the study site. Each ‘x’ represents a theodolite fix.

Figura 9. Ejemplo de una trayectoria realista. Pareja madre-cría de la migración norte en el área de estudio. Cada “X” representa una posición del teodolito.

The breathing rate (number of blows per whale per minute) was chosen as the response variable for each sighting (Sumich 1983; Würsig *et al.* 1984; Dolphin 1987; Dorsey 1989).

Exploratory data analysis was performed and since the assumptions necessary for parametric tests (sample size, normal distribution) were not met, non-parametric statistics were used. A Kolmogorov-Smirnov test showed that data were not normally distributed.

A Mann-Whitney *U* test for two independent samples was used to evaluate whether there were differences in swimming velocity and breathing rate between whales without calves observed during phase A (mid-February to end of March) and phase B (April and May), previously defined as northbound without calves and mother-calf migration phases.

A Kruskal-Wallis (K-W) test was used to test for significant differences between swimming velocities and breathing rates among the different migration groups (southbound and northbound: whales without calves, mother and calves). To identify which groups were different from each other with respect to both variables, a Newman-Keuls (N-K) range test was performed (Neave and Worthington 1988).

Another Mann-Whitney *U* test to test for differences in swimming velocity and breathing rates between the two seasons for the same migrating group was performed.

Cost of transport (COT=P/WV) values were estimated for the two main types of whales (adults and calves). For an average adult whale, an average length of 12.5m (range 11.2-13.9m) was used to represent the southbound, northbound whales without calves and mothers, while for migrating calves an average length of 7m (range 5.5-8.1m) was used (Perryman and Lynn 2002). Mean girth measurements were conducted on stranded and free-ranging whales. Based on the average known lengths of adults (12.5m) and of migrating newborn calves (4m), the girth/length ratios were estimated: 0.6L (G=0.6L=60% of body length) for southbound non-pregnant whales, 0.55L for whales without calves during the northbound migration, 0.5L for mothers and 0.6L for calves (Sumich 1986b).

Body masses of gray whales were calculated as a function of their girth (G) and length (L). To estimate the mass (M) of a non-pregnant whale, the following best-fit equation was used (Sumich *et al.* 2001):

$$M = 21.4\ G\ L^2 \tag{9}$$

Where:

M = Mass (kg)

G= Girth (m)

L= Length (m)

Mass (kg) was estimated using (Eq.9) for the four groups of whales: southbound whales weigh 25000 kg, northbound whales without calves 22000 kg, mothers 20000 kg, and calves 4400 kg (Table I):

Table I. Estimated body girth (G), body length (L) and body mass (M), for all gray whale migrating groups at Costa Azul, 2004-2005 season.

Tabla I. Circunferencia (G), longitud total (L) y masa corporal (M) de los grupos migratorios de ballena gris en Costa Azul, temporada 2004- 2005.

Migration group		Girth (m)	Length (m)	Mass (kg)
Southbound	21.4	7.5	12.5	25000
Northbound whales without calves	21.4	6.9	12.5	22000
Northbound mothers	21.4	6.3	12.5	20000
Northbound calves	21.4	4.2	7	4400

Body mass estimations are important to calculate tidal lung volumes (V_T). Sumich *et al.* (2001) estimated the tidal lung volume for a captive gray whale calf. He reported a V_T range from 2.9% to 3.4% of the body mass (kg) when $G = 0.55L$. Here, the mean V_T of 3% was chosen for further calculations, and although these are calf values, they were applied to adult whales because no other direct measurements are available (Sumich, pers. comm.). For our purposes, we used a V_T value of 690 l based on the intermediate mass value for the three categories of adult whales listed on Table II, to avoid the distortion associated with the fattest or thinnest whales, and a V_T value of 132 l for calves (Table II).

The amount of air ventilated per minute (air l min^{-1} = Vmin) can be estimated based on breathing rates and tidal lung volumes. Oxygen extraction for each breath (FO_2) measured in a captive gray whale (Sumich *et al.* 2001) exhibited a variation between 4.2% and 18%. Most values fell around 11%; therefore, we used an FO_2 of 11% for all cases.

Rates of oxygen consumption (Vo_2) were estimated as follows (Prosser 1973):

$$Vo_2 = (Vmin)\ (FO_2) \tag{10}$$

Based on the oxygen consumption equation (Eq.10), Vo_2 values were estimated as 61 l min^{-1} for southbound whales, 38 l min^{-1} for northbound whales without calves, 38 l min^{-1} for mothers and 10 l min^{-1} for calves (Table II).

During migration it is assumed that energy is obtained by the oxidation of stored lipids (Sumich 1983). To estimate how much lipid (kg) a whale burns every day, it is necessary to know the daily oxygen consumption (Vo_2/day). To oxidize 1 gr of lipid that releases 9.5 kcal or 39.5 kJ of energy (Power=P), 2 l of O_2 are required (Hainsworth 1981). Power values are summarized in Table II. Finally, to calculate COT, the power obtained (energy expenditure) was divided by the product of each group´s swimming velocity and the appropiate body mass estimates for each group of whales (Eq. 4).

Table II. Oxygen consumption rates for all migrating gray whale groups at Costa Azul, 2004-2005 season. BR=breathing rate, V_T=tidal lung volume, V_{min}=oxygen volume per minute, FO_2=oxygen extraction per breath, Vo_2=oxygen consumption rate, P=energy expenditure, power.

Tabla II. Tasa de consumo de oxígeno de los grupos migratorios de ballena gris en Costa Azul, temporada 2004-2005. BR=tasa de ventilación, V_T=intercambio gaseoso, Vmin=volumen de oxígeno por minuto, FO_2=extracción de oxígeno por soplo, Vo_2=tasa de consumo de oxígeno, P=gasto energético, fuerza.

Migration group	BR (breaths min^{-1})	V_T (3% of body W)	V_{min}	FO_2 (%)	Vo_2 (lt min^{-1})	Energy Expenditure P (kJ min^{-1})
Southbound	0.8	690	552	11	61	1119
Northbound whales without calves	0.5	690	345	11	38	750
Northbound mothers	0.5	690	345	11	38	750
Northbound calves	0.7	132	92	11	10	200

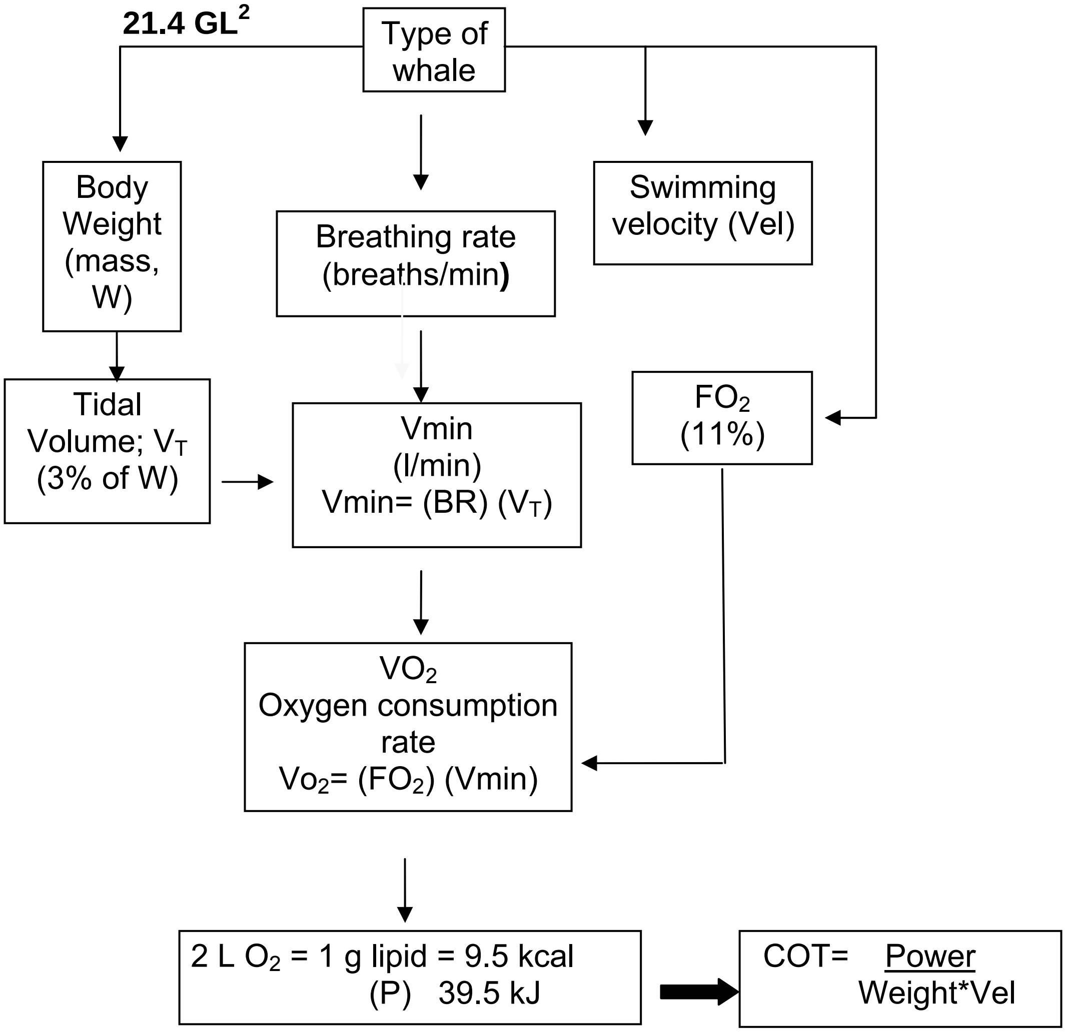

Figure 10. General scheme for the calculation of COT for migrating gray whales.

Figura 10. Esquema general del cálculo del CDT para las ballenas grises en migración.

V. RESULTS

5.1 Observation effort

A total of 132 days (904 hours) was spent in the field between December 2003 and May 2005. A total of 310 sightings was recorded and 175 were selected for analysis based on the previously mentioned criteria (Table III).

Table III. Observation effort and sightings at Costa Azul, Baja California, México.

Tabla III. Esfuerzo de observación y avistamientos en Costa Azul, Baja California, México.

Season	Effort (days)	Effort (hours)	Total sightings	Analyzed sightings
Dec 2003-May 2004	59	348	162	81
Dec 2004-May 2005	73	556	148	94
Total	132	904	310	175

5.2 Exploratory data analysis

According to the literature, the northbound migration is divided into Phase A (adult and juvenile whales without calves, from mid-February to end of March) and Phase B (mother-calf pairs, April and May) (Poole 1984; MBC 1989). The migration of whales without calves tends to end before the mother-calf pair migration starts, and this was expected to occur in Ensenada by the end of March (Heckel *et al.* 2001).

During this study, however, we observed that whales without calves (most of them solitary and sometimes in duos) continued to be observed during April and May, when mother-calf pairs were migrating also. For this reason the temporal connotation of “phase” was changed. Instead different “groups” of migrating whales will be refered to: southbound whales, northbound whales without calves (instead of Phase A) and northbound mother-calf pairs (instead of Phase B).

Data obtained in April and May 2003 of the northbound mother-calf pair migration were not used because blow counts of mothers and calves were not separated.

5.3 Swimming velocity

For the 2003-2004 season, swimming velocity of southbound whales was 2.1 ± 0.1 ms^{-1} (mean ± standard error), and of northbound whales without calves 1.5 ± 0.1 ms^{-1}, whereas mother-calf pairs averaged 1.1 ± 0.2 ms^{-1} (Table IV).

Table IV. Swimming velocities (ms^{-1}) for all migrating gray whale groups at Costa Azul, 2003-2004 season. SE=Standard Error of Mean.

Tabla IV. Velocidad de nado (ms^{-1}) de los grupos migratorios de ballena gris en Costa Azul, temporada 2003-2004. SE=Error estándar de la media.

Migration group	*n*	Median	Mean (± SE)	Min	Max
Southbound	57	1.9	2.1±0.1	1.0	5.2
Northbound whales without calves	13	1.5	1.5± 0.1	0.9	2.2
Northbound, mother-calf pairs	11	0.8	1.1±0.2	0.4	2.5

A Kruskal-Wallis test was performed to test for significant differences in swimming velocity between the data corresponding to southbound, northbound whales without calves and northbound mother-calf pairs for the 2003-2004 migration season. Results showed significant differences between the swimming velocities among the three migration groups (H=24.26, df=2, p=0.001, n=81). To learn which group was different from the others, a Newman-Keuls non-parametric multi-range *a posteriori* test was performed. The results of the test showed significant differences in swimming velocity between southbound whales and northbound whales without calves (p=0.02), as well as with mother-calf pairs of the northbound migration (p=0.0002). There were no significant differences between northbound whales without calves and mother-calf pairs (p=0.05).

For the 2004-2005 season, southbound mean swimming velocity averaged 1.9 ± 0.1 ms^{-1} (mean±SE), northbound whales without calves 1.8 ± 0.1 ms^{-1} and mother-calf pairs 1.2 ± 0.1 ms^{-1} (Table V).

Table V. Swimming velocities (ms^{-1}) for all migrating gray whale groups at Costa Azul, 2004-2005 season. SE=Standard Error of Mean.

Tabla V. Velocidad de nado (ms^{-1}) de los grupos migratorios de ballena gris en Costa Azul, temporada 2004-2005. SE=Error estándar de la media.

Migration group	*n*	Median	Mean (± SE)	Min	Max
Southbound	32	1.9	1.9± 0.1	1.0	2.6
Northbound whales without calves	36	1.7	1.8±0.1	0.7	2.7
Northbound, mother-calf pairs	26	1.2	1.2± 0.1	0.5	2.1

The Kruskal-Wallis test for the 2004-2005 season data showed significant differences in swimming velocities between southbound, northbound without calves and mother-calf pairs (*H*=33.3, df=2, *p*=0.0001, *n*=94). The Newman-Keuls test for the 2004-2005 data showed significant differences between southbound and mother-calf pairs (*p*=0.0001), and between northbound whales without calves and mother-calf pairs (*p*=0.0001). The test showed no significant differences between southbound whales and whales without calves of the northbound migration (*p*=0.2).

A Mann-Whitney *U* test was performed to test for differences in swimming velocities between the two years of observations (2003-2004, 2004-2005). There were no significant differences in southbound whales (U=788, p=0.2, n_1=57; n_2=32), northbound whales without calves (U=166, p=0.1, n_1=13; n_2=36) or mother-calf pairs (U=109, p=0.2, n_1=11; n_2=26).

5.4 Breathing rates

The mean breathing rate for southbound whales at Costa Azul for the 2003-2004 season was 0.6 ± 0.03 breaths min^{-1} (mean±SE). Northbound migrating whales without calves had a breathing rate of 0.5 ± 0.04 breaths min^{-1}. For mothers the breathing rate was 0.8 ± 0.2 breaths min^{-1}, while calves had a mean of 0.4 ± 0.1 breaths min^{-1} (Table VI).

Table VI. Breathing rates (breaths/min) for all migrating gray whale groups at Costa Azul, 2003-2004 season. SE=Standard Error of Mean.

Tabla VI. Tasas de ventilación (soplos/min) de los grupos migratorios de ballena gris en Costa Azul, temporada 2003-2004. SE=Error estándar.

Migration group	*n*	Median	Mean (± SE)	Min	Max
Southbound	57	0.5	0.6±0.03	0.2	1.1
Northbound whales without calves	13	0.5	0.5±0.04	0.2	0.8
Northbound mothers	11	0.6	0.8±0.2	0.4	2.3
Northbound calves	11	0.4	0.4±0.1	0.2	1.1

A Kruskal-Wallis test showed significant differences in breathing rates between southbound whales, northbound whales without calves and mother-calf pairs (*H*=7.07, df=3, *p*=0.07, *n*=92). The Newman-Keuls test showed significant differences in the breathing rate between southbound whales and mothers (*p*=0.05), northbound whales without calves and mothers (*p*=0.01) and mothers and calves (*p*=0.01). No significant differences were found between southbound groups and northbound whales without calves (*p*=0.4), southbound whales and calves (*p*=0.5) and northbound whales without calves and calves (*p*=0.7).

The mean breathing rate for the 2004-2005 season southbound migration was 0.8 ± 0.1 breaths min^{-1}, which was the highest value of all groups. Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths min^{-1}, mothers 0.5± 0.1 breaths min^{-1} and calves 0.7 ± 0.1 breaths min^{-1} (Table VII).

Table VII. Breathing rates (breaths/min) for all migrating gray whale groups at Costa Azul, 2004-2005 season. SE=Standard Error of Mean.

Tabla VII. Tasas de ventilación (soplos/min) de los grupos migratorios de ballena gris en Costa Azul, temporada 2004-2005. SE=Error estándar.

Migration group	*n*	Median	Mean (± SE)	Min	Max
Southbound	32	0.8	0.8±0.1	0.2	1.6
Northbound whales without calves	36	0.4	0.5±0.03	0.2	0.9
Northbound mothers	26	0.5	0.5±0.1	0.1	1.2
Northbound calves	25	0.6	0.7±0.1	0.2	1.7

The Kruskal-Wallis test showed significant differences among the four groups (H=23.3, df=3, p=0.0001, n=119). The Newman-Keuls tests showed differences between southbound and northbound whales without calves (p=0.0002), southbound whales and mothers (p=0.00005), northbound whales without calves and calves (p=0.01) and mothers and calves (p=0.03). The groups with no significant differences were southbound whales and calves (p=0.07) and whales without calves and mothers (p=0.4).

Unlike swimming velocity, breathing rates showed significant differences between years of observation (2003-2004, 2004-2005) for southbound whales (U=535, p=0.001, n_1=57; n_2=32) and northbound calves (U=63, p=0.01, n_1=11; n_2=25). This was not the case for whales without calves (U=205, p=0.5, n_1=13; n_2=36) and mothers (U=97, p=0.1, n_1=11; n_2=26) during the northbound migration.

After running all the statistical tests and reviewing all data, it was decided not to use the 2003-2004 data because they were considered unreliable and could have affected further analyses. The unreliability of the data may have been due to the lack of experience of the observers in the field. The low mean breathing rate for calves (0.4 breaths min^{-1}) during the 2003-2004 season is not a realistic number since young animals are known to have higher breathing rates than adults (Gagliardi and Rusconi, 1997), and whales are not an exception. The resulting number could be due to misidentification of individuals or because some blows were missed during field observations. Furthermore, sample size was much smaller during 2003-2004 than in 2004-2005.

After testing differences, 2004-2005 data were plotted in breathing rate-velocity plots (Fig.11):

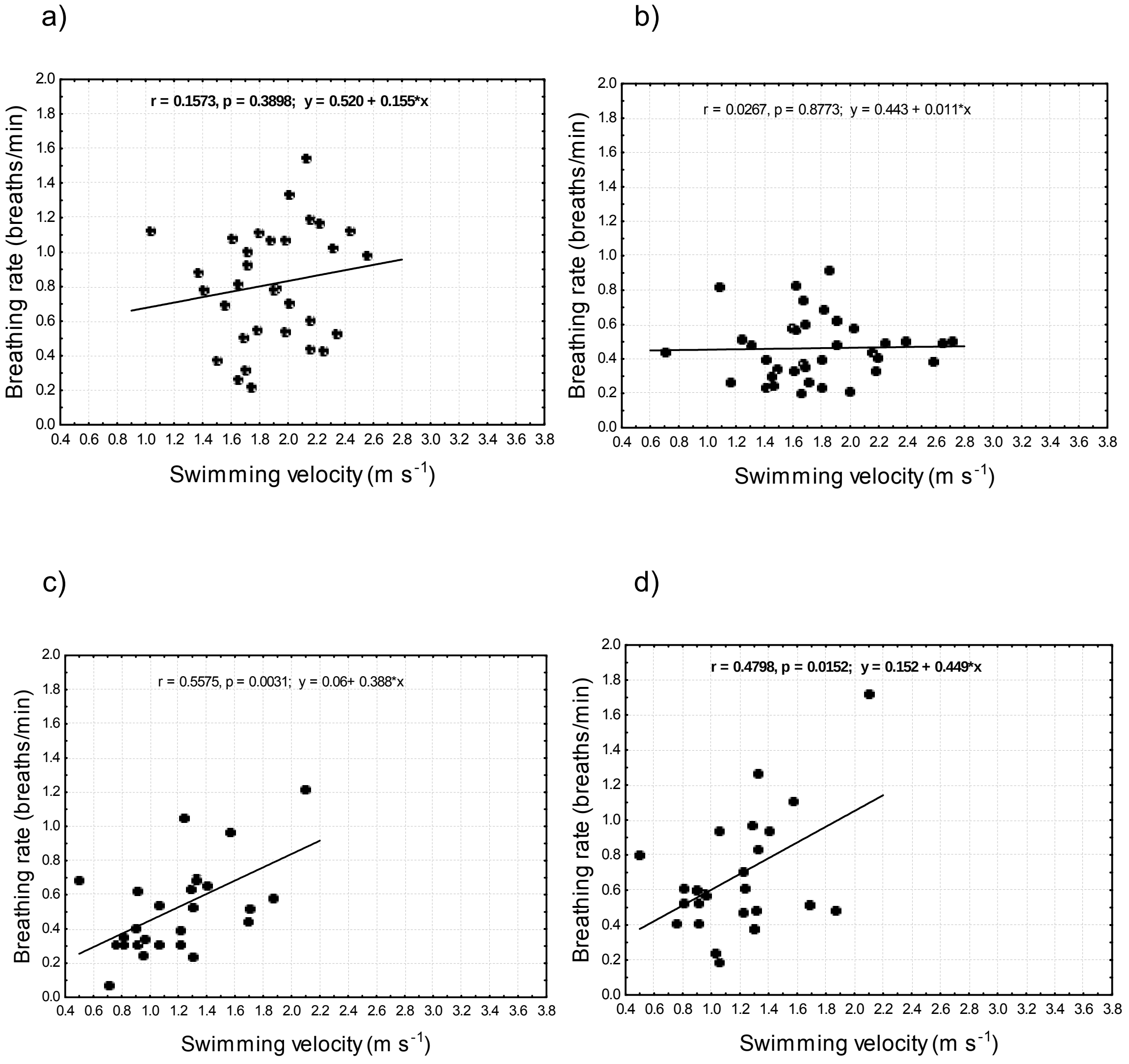

Figure 11. Swimming velocity and breathing rates for migrating gray whales observed at Costa Azul, Baja California, Mexico, 2004-2005 season. a) southbound whales, b) northbound whales without calves, c) northbound mothers and d) northbound calves.

Figura 11. Velocidad de nado y tasa de ventilación de ballenas grises migratorias en Costa Azul, Baja California, México, temporada 2004-2005. a) migración al sur, b) migración al norte de ballenas sin crías, c) migración norte madres y d) migración norte crías.

There was not sufficient evidence to prove relationship between swimming velocity and breathing rate in southbound migrating whales. This may be due to the different types of whales in this group (age, sex, reproductive and physiological state). In addition, northbound whales without calves did not show a significant relationship between these two parameters either. This migrating group exhibits a high variability in their behavior, which may be the reason for the lack of a relationship (Heckel *et al.* 2001).

In contrast, relationships of mothers and calves were significant, probably because these data comprise one single age group. Further, they had similar correlation coefficients (p<0.05, r=0.56 and r= 0.48, respectively; Figs.11c and 11d), probably because the mother adjusts her pace and ventilation to her calf.

5.6 Cost of Transport (COT)

The calculated COT following Tucker´s (1975) equation (Eq.4) for each migrating gray whale group was: 0.42±0.1 MJ $kg^{-1}m^{-1}$ (MJ=megajoules) for southbound migrating whales, 0.30±0.1 MJ $kg^{-1}m^{-1}$ for northbound whales without calves, 0.50±0.1 MJ $kg^{-1}m^{-1}$ for mothers and 0.63±0.1 MJ kg^{-1} m^{-1} for calves (Table VIII).

Table VIII. Cost of transport (COT) for all groups of migrating gray whales at Costa Azul, 2004-2005 season. BR=breathing rate. COT [min-max]=based on the mean ± SE of the breathing rate and swimming velocity. SE=standard error.

Tabla VIII. Costo de transporte (COT) de los grupos migratorios de ballena gris en Costa Azul, temporada 2004-2005. BR=tasa de ventilación. CDT [min-max]= basado en la media ± SE de la tasa de ventilación y la velocidad de nado.SE=error estándar.

Migration group	BR (breaths min^{-1}) (mean±SE)	Swimming velocity (ms^{-1}) (mean±SE)	COT (MJ $kg^{-1}m^{-1}$) (mean±SE)
Southbound	0.8±0.1	1.9±0.1	0.42±0.07
Northbound whales without calves	0.5±0.03	1.8±0.1	0.30±0.04
Northbound mothers	0.5±0.1	1.2±0.1	0.50±0.07
Northbound calves	0.7±0.1	1.2±0.1	0.63±0.04

After all the calculations the relation between swimming velocity, oxygen consumption rate (Vo_2) and COT were plotted. Because of the difference in scales these results were plotted in two different graphs (Figs.12-13).

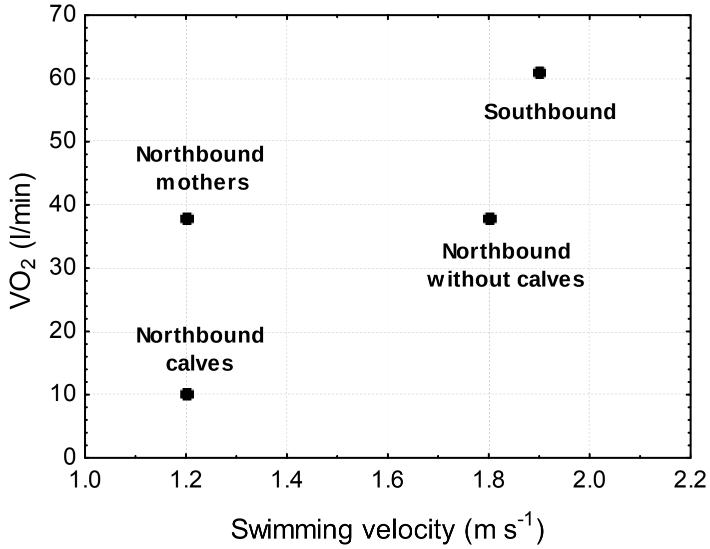

Figure 12. Mean swimming velocities and oxygen consumption (Vo_2) for all migrating gray whale groups at Costa Azul, Baja California, Mexico, 2004-2005 season.

Figura 12. Velocidad media de nado y tasa de consumo de oxígeno (Vo_2) de los grupos migratorios de ballena gris en Costa Azul, Baja California, México, temporada 2004-2005.

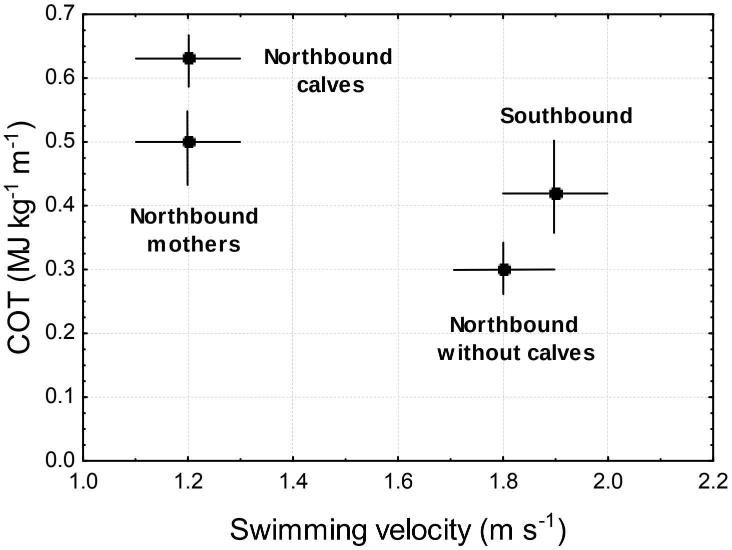

Figure 13. Swimming velocities and cost of transport (mean ± standard error) for all migrating gray whale groups at Costa Azul, Baja California, Mexico, 2004-2005 season.

Figura 13. Velocidades de nado y costo de transporte (media ± error estándar) de los grupos migratorios de ballena gris en Costa Azul, Baja California, México, temporada 2004-2005.

VI. DISCUSSION

Kleiber (1975) established some criteria for the measurement of the basal metabolic rate. Individuals have to be post-absorptive, thermoneutral, adults, in any reproductive state and they should display a resting behavior. These conditions can be controlled in individuals contained in enclosed areas, but in free-ranging animals this is difficult or impossible to do. Some of these conditions are present in gray whales, but not all of them. Even the range of their thermoneutral zone is not known. During the northbound migration they have been seen feeding opportunistically, although the number of prey they consume while migrating is negligible compared to the amount of amphipods they consume in high latitudes (Nerini, 1984). For southbound migrating whales no feeding behavior has been reported (Poole, 1984), so it can be assumed to be post-absorptive. However, not all the whales of the southbound or northbound migration are adults; they are always mixed in different age classes, and as a consequence the reproductive state of individuals is variable. This brings as a consequence differences in their swimming velocities and breathing rates, in addition to differences in their energy demands during migration.

Because most marine mammals (including gray whales) do not fulfill the conditions proposed by Kleiber to measure the metabolic rate, the most practical way to do this is to estimate the field metabolic rate (FMR).

6.1 Swimming velocity

The swimming velocity of southbound migrating whales at Costa Azul, Baja California was 1.9 ms^{-1}. This value agrees with 2.1 ms^{-1} calculated by Pike (1962), 2.0 ms^{-1} obtained by Sumich (1983), and 2.1 ms^{-1} published by Heckel *et al.* (2001). For northbound migrating whales without calves at Costa Azul, mean swimming velocity was 1.8 ms^{-1} which is comparable to 1.4 ms^{-1} measured by Heckel *et al.* (2001) in Ensenada, and 1.5 ms^{-1} reported by Mate and Urbán (1996) for northbound migrating whales. For mother-calf pairs the mean velocity of 1.2 ms^{-1} reported here is the first estimate for this group.

It has been known for many years that southbound migrating whales travel at higher speeds than northbound whales, and many theories have been proposed to explain the difference. Altough both groups are composed of individuals of different age classes (therefore size), the difference may lay in the separation of groups in the northbound migration, which leads to a difference in behavior. Southbound whales may travel faster as a result of an increase in the level of reproductive hormones they experience during the breeding season, therefore having a motivation and incentive to get there first (Heckel *et al.* 2001). However, this is only a hypothesis that would have to be confirmed with further studies. In addition, southbound migrating whales do not stop at any time for feeding.

The slower swimming of the northbound migrating whales may be due to the lack of energy reserves they have after several months of fasting (Heckel 2001), and Sumich (1983) suggested that supplemental feeding may be another explanation.

They have been seen involved in sexual behavior resembling courtship that may slow them down, but there is not any indication of copulation (Heckel 2001).

Northbound whales without calves may also be composed of different group sizes. Mate and Harvey (1984) registered a range of 1 to 18 whales in a group. In contrast, whales from this group observed at Costa Azul were mainly solitary, although sometimes they travel in pairs. In another attempt of monitoring the swimming speed Mate and Urbán (1996) radio-tracked one of these whales and their results suggest a constant overall swimming velocity of 2.0 ms^{-1}.

Mothers experience the highest depletion of lipid reserves during the northbound migration, since they have to nurse their calves and need to have enough energy to cover all their basic needs. This could lead to lower swimming velocities. Calves have a very different behavior than their mothers. As in any other young, their curiosity is highly developed, and they often engage in milling conduct in kelp beds and interact with other cetaceans when they encounter them. In addition, sometimes mother/calf pairs stop to rest and nurse when opportunity arises (Pike 1962).

Southbound swimming velocities do not appear to change in the total range of migration, but northbound velocities are reported to be very variable along the route, with higher velocities as they get closer to their feeding grounds (MBC 1989, Heckel *et al.* 2001).

Another hypothesis that has been discussed to explain the swimming velocity differences between southbound and northbound migration is related to the California Current System (CCS) (Heckel *et al.* 2001). This system is composed by three flows: the California Current (CC), the Inshore Current (IC, sometimes-called Davidson Current) and the California Undercurrent (CU) (Lynn and Simpson, 1987). As the CC flows to the Equator most of the year it would be valid to hypothesize that this would help the southbound whales to move faster in comparison to the northbound whales that have to swim against it. However, the IC flows poleward along the coast and is strongest from October to December when the whales are heading south. The equatorward flow of the CC is strongest at Ensenada from February to April, when gray whales migrate north. Therefore, they swim against the current during most of the migration, at least off the coasts of California and Baja California. In conclusion, the hypothesis of swimming velocity differences in relation to ocean circulation has been rejected (Heckel *et al.* 2001).

6.2 Breathing rates

Several studies have taken the breathing rate as an essential variable with which to determine the cost of transport. Dolphin (1987) links the breathing pattern with diving behavior of humpback whales (*Megaptera novaeangliae*) in Alaska. Dorsey *et al.* (1989) measured the breathing pattern as a means to evaluate the reactions of bowhead whales (*Balaena mysticetus*) to industrial activities in the Beaufort Sea. Jahoda *et al.* (2003) proposed breathing rate, diving sequences, swimming speed, and travel direction of fin whales (*Balaenoptera physalus*) as indicators for whale watching disturbance in the Mediterranean Sea. In addition, different values for the breathing rate have been reported for migrating gray whales (Sumich 1983; Poole 1984; MBC 1989).

In this study almost all whales passing Costa Azul during the southbound migration swam without interruptions during this study; however, sometimes they had surface displays such as breaches. Breathing rate for southbound migrating whales in this work (0.8 breaths min^{-1}) is similar to the 0.72 breaths min^{-1} obtained by Sumich (1983). For northbound whales without calves we recorded a mean of 0.5 breaths min^{-1}, which is similar to the results of a gray whale monitoring study from 1987-1989 that reported 0.3-0.4 breaths min^{-1} for the same group (MBC 1989).

Mother-calf pairs breathing rates also have been published, but no values are available for each group individually. Mate and Harvey (1984) measured mother-calf pair breathing rates in Laguna San Ignacio and estimated 0.68 breaths min^{-1}. We expected to observe higher breathing rates for calves, since their ventilation rate should be higher than in adults, as Norris (1977) reported for calves in Laguna San Ignacio. However, those breathing rates were measured directly in enclosed areas such as breeding lagoons and aquariums. It is possible that data may not be applicable to free-ranging animals because of the stress caused to the individual while placing the pneumotachograph to do the measurements. In 1965, a gray whale calf was captured (Gigi I) for a study in San Diego, and in 1971 a second calf was brought too (Gigi II). Investigations proved that ventilation varied with activity intensity averaging 2-5 breaths min^{-1} (Wahrenbrock *et al.* 1974). However these numbers may differ considerably from whales during migration with respect to all groups.

6.3 Cost of Transport (COT)

One of the aims of this work was to compare the southbound COT obtained by Sumich (1983) with the the one obtained during this study. Although there were some differences, the parameters used were the same. Sumich (1983) registered the blows of 5 adult gray whales in Laguna San Ignacio assuming they were in resting conduct (this means V=0), to calculate energy expenditure. He also assumed a 0.5 breaths min^{-1} basal breathing rate and estimated both the breathing rate and swimming velocities for groups of whales every 0.5 ms^{-1} increment and grouped individuals in relation to their swimming speeds. In this study the sample size was not enough to do the same.

Breathing rates combined with tidal volume and oxygen consumption gives the energy necessary to oxidyze lipids and therefore generate power for different functions, such as locomotion. Sumich (1983) also created a general COT model based on the number of breaths required for each kilometer of traveled distance at different speeds for southbound migration whales. The results of his study suggested that the lowest COT (0.160 kcal kg^{-1}m^{-1}) for southbound migrating whales takes place at a swimming velocity of 2.2 ms^{-1} and a breathing rate of 0.72 breaths min^{-1}. However, at the time Sumich estimated this COT the value of some of the parameters were not known and had to be assumed, such as the V_T and the fraction of O_2 extracted for every ventilation cycle. In addition, the dimensions of whale models used were slightly shorter (11.5 m) and the body mass was smaller (15,000 kg) than those estimated in this investigation. Sumich's study site was in San Diego, during other sampling years (1975, 1976, 1978 and 1979) and he obtained a more substantial data sample. Plus, he used parametric statistics for the data analysis and reported the results in kcal.

As an additional effort to use Sumich's data (1983), the COT was calculated with this study's methodology for the whale model he proposed and taking his published numbers. The COT value obtained (0.39 MJ $kg^{-1}m^{-1}$) for southbound migrating whales in San Diego (data from Sumich, 1983) was quite similar to the value obtained for Costa Azul (0.42 MJ $kg^{-1}m^{-1}$). Deriving similar COT values for two different sites and years is not rare since they are the result of the same variables used to estimate them (breathing rate and swimming velocity). It can also indicate that the COT values along the entire migratory route are similar. However, this is only an assumption, and it is necessary to do more similar studies, mainly in areas with different characteristics (different topography, various degrees of human activities, oceanographic conditions, etc.) and try to set different possible scenarios. However, care should be taken with respect to these results. Southbound migration is composed by whales of different age and sex classes, as well as different physiological states (males, juveniles, pregnant and non-pregnant females, and occasionally some premature calves). These differences are very likely to cause some variation in COT estimates for this part of the migration in comparison to northbound whales, where at least one group is clearly identified and separated: mother-calf pairs.

The COT for the northbound migration (whales without calves) was proposed by Sumich (1983) to be almost the double than that for the southbound pulse. In contrast, the lowest COT value estimated in this study belongs to northbound whales without calves (0.30 MJ $kg^{-1}m^{-1}$). This is due to the lower swimming velocity and lower breathing rates. It is also reasonable that whales without calves have lower values than northbound mothers. Mothers have the highest energy loss during migration of all adults' whales (0.50 MJ $kg^{-1}m^{-1}$). In contrast to males or non-lactating females, their fat layer is reduced after many months of fasting and maternal care (Iverson 2002). It has been recorded that female gray whales require the oxidation of 3.2 Tm (metric tons) of their total lipid reserve (considered to be 4.4 metric tons) to feed their young and for their own cost of maintenance during the winter (Berta and Sumich 1999). Finally, the highest COT was estimated for calves (0.63 MJ $kg^{-1}m^{-1}$) in this study. Tucker (1975) proposed COT values for runners, flyers and swimmers belonging to different taxonomic groups and of all sizes as a function of their body mass; the result of this comparison yielded higher COT values for small animals (Hainsworth 1981; Beiwener 2003). This result agrees with the higher COT value obtained for the calves, the smallest animals in our data set. Some of these values may need to be changed to accommodate new V_T values as data from further research are gathered. Actually, investigations regarding to respiration variables are in progress, and this will facilitate a more accurate estimation not only of V_T, but also of the percentage of oxygen extracted per breath (FO_2) and oxygen consumption rates (Vo_2) which may lead to a better estimation of the cost of transport during the longest annual migration any mammal accomplishes.

Mother-calf pairs swim at the surface constantly, as the calf is not yet prepared to take long dives (no flukes are observed out of the water, a sign of the absence of long diving periods). In addition these whale pairs have different power requirements than the rest of the whales; gestation and lactation are considered the most expensive energetic activities for any female mammal. As gray whale calves are weaned at about 7-8 months after birth, they rely on their mothers' energy reserves to grow and build their own fat layer, obtaining all the lipids they need from their mother´s milk. Gray whale milk is mainly composed of 30-50% fat, 40-53% water, 9-15% protein and 1.2-2.1% minerals (Oftedal 1997). This has raised interesting questions as to how energy stores are allocated in mothers and calves. Mothers maintain their metabolism while fasting during the migration route when they are nursing their young. A mother´s ability to fast while lactating is related to the size of her energy reserve store and its utilization rate. There have been four principal ways in which the females can manage their energy requirements: 1) increase food consumption, 2) mobilize energy stores so that lipid turnover takes place rather than lipid synthesis, 3) metabolic compensation (the reduction of expenditure in other processes not related to milk production) 4) size - larger females can eat more, and as a consequence store higher amounts of lipids. Since the gray whale does not eat while migrating the first strategy is not used by mothers during migration, but they eat more than other whales on their feeding grounds before they give birth. They also store nutrients in different tissues during the feeding season to later mobilize them into milk. Metabolic compensation in inactive animals is common, but it had not been investigated in a fasting active organism until Mellish *et al.* (2000) studied the grey seal (*Halichoerus grypus*). Their results suggest females use metabolic compensation to deal with energetic costs of lactation. Perryman and Lynn (2002) evaluated the condition of migrating gray whales by photogrammetric analysis, measuring the length and width of the individuals (girth). During the southbound migration, they found marked differences between the early migrating whales, which were larger and wider than later southbound whales. They assumed they were pregnant whales, and that the rest of the whales, including non-pregnant females, were slender. Pregnant whales have a 0.7L (girth:length ratio) while non-pregnant females have a 0.6L at the time they leave feeding grounds, diminishing by the time they get to the breeding lagoons (Sumich 1986a). This implies that pregnant females eat more to increase their fat supply during their stay in northern latitudes to be able to accomplish their southbound trip while supporting their own metabolic cost and to nurse their calves. Once in the lagoons, when the calves are born, they remain there until the calf has gained enough fat weight to support its long northbound trip.

During migration, all the whales swim at the surface to breath. The drag force increases as much as 5 times as at depth. This could be another reason for the higher COT during the northbound migration of mother-calf pairs. Energy power input at the surface to overcome the wave drag force is related to swimming velocity, viscosity and body size. Hertel (1966) examined this by towing a dolphin-shaped model at different depths at the same velocity, and found that drag increased until the model was placed at a depth three times its body diameter under the surface. This is because when an object moves at a depth sufficiently away from the sea surface or the sea floor, wave drag is minimized. Williams and Kooyman (1985), did similar tests with a model of a harbor seal (*Phoca vitulina*), obtaining similar results. In relation to direct observation of free-ranging animals, Hays *et al.* (2001) used satellite telemetry and recorded the submergence duration and depth distribution of green turtles (*Chelonia mydas*) during migration, showing they travel at a preferred depth during the entire route as a means of minimizing their cost of transport by reducing drag. This strong background suggests gray whales do the same, swimming three body diameters under the surface, coming up to breath only when necessary.

In addition to this hydrodynamic constraint, if an animal moves faster, Vo_2 increases, eventually reaching a maximum when oxygen stores begin to deplete. When this happens a change to anaerobic metabolism takes place. Oxygen consumption exceeds its supply. An accumulation of lactate and CO_2 in blood and tissues starts leading to acidosis and fatigue (Berta and Sumich 1999; Beiwener 2003). This may be one of the reasons why all organisms have an optimum locomotion speed as a means of energy saving, for it minimizes the energy expenditures and maximizes the travel distance.

Besides locomotion, energy loss may occur by thermoregulation and ventilation (loss through heat). Marine mammals have a broad variety of mechanisms to control body temperature making the heat loss minimum even negligible. Marine mammals' internal temperatures range from 36ºC to 38ºC. The maintenance of a high and constant temperature may increase the energy expenditure. To avoid this problem, marine mammals are capable of regulating their loss of heat through several adaptations. First, their large bodies cool off slower than small ones (volume: surface area ratio). Thus, the area by where the heat is lost is smaller compared to the volume (Berta and Sumich 1999; Pabst *et al.* 1999). Additionally, marine mammals have compact bodies with short or absent extremities so that the surface in contact with the external environment is reduced. Second, the presence of the fat layer insulates the body. Third, the presence of a circulatory vessel network that links veins with arteries. This system of blood vessels is called the "miraculous network" ("*rete mirabilia*") and can be found mainly in the extremities, This system works as a countercurrent heat exchange in which the internal heat is transported by the blood to the body surface and can accomplish two functions as an heat insulator or if necessary heat conductor when heat needs to be lost (Berta and Sumich 1999; Pabst *et al.* 1999; Boyd 2002).

Ventilation is also accompanied by warming of the inspired air and a heat loss during expiration but again heat loss by respiratory evaporation in marine mammals has been estimated from 6%-10% of the total body heat (Sumich 1986a; Silva 2004). In relation to body size, tidal volumes and percentage of oxygen extracted per breath are high when swimming at the surface. However, compared to terrestrial mammals of similar size the volume of oxygen per minute is 25% to 50% lower. This lower volume suggests that for marine mammals including the gray whale, the loss of heat by this route is small, again, in relation to their body size. As the Vo_2 volume increases in an exponential way in relation to the effort and velocity, physiological demands are also extremely low (Elsner 1999).

VII. CONCLUSIONS

- Swimming velocities for the gray whale migration agreed with the values found by other authors for both migration directions. The similar values may suggest these results as the optimum swimming speeds for the gray whale. In this study, the southbound migration was the fastest, with 1.9 ms^{-1} in comparison to the northbound migration (whales without calves: 1.8 ms^{-1} and mother-calf pairs: 1.2 ms^{-1}). Although many hypotheses for these differences have been proposed, none of them have been tested.
- The breathing rate for the southbound migration in this study was 0.8 breaths min^{-1}, which is almost the same as that measured by Sumich (1983; 0.72 breaths min^{-1}). The slight difference is possibly due to the differences in the mass of the whales compared.
- Breathing rates of northbound migrating whales are the first estimates ever accomplished. Breathing rates for migrating mothers and calves were calculated separately because of the size differences. Calves had higher breathing rates when compared to the adults, as expected.
- The cost of transport (COT) published by Sumich (1983) matches the value found in this work for southbound migrating whales. However, care needs to be taken around these numbers if they are to be used as an indicator of the effects of biological importance of human activities on the gray whale population. Southbound and northbound migrations are composed by

different age and sex classes, as well as physiological states of whales, which certainly influences the COT values.

- The COT model (Sumich 1983) predicted higher COT values with under and above 2.2 ms^{-1} swimming velocities. Following this statement, COT during the northbound migration should be almost double than for the southbound migration. This could not be confirmed in this research. On the other hand, higher COT in small animals is common, small sizes have higher energy costs as proposed by Tucker (1975), and this coincided with the higher COT of calves in this investigation.

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