Gray whales accomplish an annual migration which spans as much as 50° of latitude in the northeast Pacific Ocean. This migration links their summer high latitude feeding grounds with winter calving and breeding areas. The purpose of this study was to determine how adult females apportion their stored lipid reserves while away from their principal feeding areas to accommodate their own maintenance and locomotory needs while developing a fetus and transferring energy through lactation to support growth and maintenance of their calves.

Major components of this study included examinations of migratory swimming speeds and costs of transport, of calf growth and mortality rates, of metabolic and heat loss rates, of summer distribution patterns, and of the
magnitudes and utilization rates of maternal lipid reserves. The results of this study support the conclusions of other investigations that calf heat losses are similar to minimum observed metabolic rates, and that maintenance and lactation costs can be accommodated without winter feeding by all but the small adult females. It is suggested that present oceanographic conditions in the North Pacific Ocean support a larger gray whale population and allow very different gray whale feeding and migrating patterns than existed during the last glacial maximum.
LATITUDINAL DISTRIBUTION, CALF GROWTH AND METABOLISM, AND REPRODUCTIVE ENERGETICS OF GRAY WHALES, *ESCHRICHTIUS ROBUSTUS*

by

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LATITUDINAL DISTRIBUTION, CALF GROWTH AND METABOLISM,
AND REPRODUCTIVE ENERGETICS OF GRAY WHALES,
ESCHRICHTIUS ROBUSTUS

CHAPTER ONE

INTRODUCTION

The subject of this study is the gray whale, *Eschrichtius robustus*. It is a medium-sized mysticete whale which reaches maximum lengths of 15 m. Although this species is now completely restricted to the margins of the North Pacific Ocean basin, it has occupied the North Atlantic Ocean within historic times (Mead and Mitchell, 1984). The fossil record of gray whales is no more than 100,000 years old (Barnes and McLeod, 1984), and phyletic relations with other mysticete whales are uncertain, but they are sufficiently distinct to warrant separation into a monotypic family, *Eschrichtiidae*.

Like other large mysticete species, gray whales have experienced episodes of intense commercial exploitation during the last half of the 19th and early 20th centuries (Scammon, 1874; Rice and Wolman, 1971; Mitchell, 1979; Henderson, 1984; and Reeves, 1984). At present, two stocks (which may represent distinct populations, Rice and Wolman, 1971) of gray whales exist, and both are restricted to the North Pacific Ocean. The Korean stock inhabits coastal waters of the western North Pacific, and
is seriously depleted (Brownell and Chun, 1977). In contrast, the California stock of the eastern North Pacific has possibly recovered to its pre-exploitation population levels (Mitchell, 1979; Henderson, 1984), and now numbers 15-18,000 (Reilly, 1981). California gray whales are found in coastal waters in the eastern North Pacific Ocean from the Chukchi Sea in the north to the periphery of the Gulf of California (L. Findley and O. Vidal, pers. comm.). It is this eastern, or California, stock that is the subject of this study.

Some ecology of the species was reviewed recently in a compilation of papers (Jones, Swartz, and Leatherwood, 1984). Results of a year-long study of a captive gray whale calf, Gigi II, have been reported by Evans (1974). Rice and Wolman (1971) reported the results of a decade-long study of 317 migrating gray whales collected off the central California coast. These and other published works have made important contributions to our understanding of gray whale biology, yet major gaps remain. This study was initiated to examine the energetic basis for existing latitudinally distributed patterns of feeding, reproduction, and early calf growth in this highly migratory cetacean species.

Gray whales accomplish the most extensive annual migration of any mammal, covering 15,000-20,000 km. This migration spans as much as 50° of latitude and links summer feeding areas in the Bering, Chukchi, and Okhotsk
Seas with warmer breeding, calving, and assembling grounds along subtropical coastlines in winter (Gilmore, 1960). Gray whales commence fasting in late autumn as they leave their principal high latitude feeding areas to begin the southward migration. The stimulus for initiation of migration and fasting is not known, but development of winter sea ice and decreasing day length have been suggested as likely cues (Rice and Wolman, 1971). Gray whales continue to fast for several months as they draw on their stored lipid reserves to sustain them during their absence from the feeding grounds (Andrews, 1914; Pike, 1962; Rice and Wolman, 1971).

Prolonged fasting during long distance migrations to low latitudes in winter months is typical of large mysticetes. These migrations coincide with the reproductive cycle. Thus, calves, with their relatively thin insulative blubber layers and high surface:mass ratios, are born and remain in warm and often protected waters during their initial post-natal growth period (Irving, 1969; Rice and Wolman, 1971; Lockyler, 1981). The presumed adaptive advantages of being in warm waters to reduce thermoregulatory costs (especially for small individuals) while food is unavailable underlies much of the present thinking concerning the distribution patterns and resource needs of large baleen whales (e.g. Rice and Wolman, 1971). Yet the allocation of stored lipid reserves to meet various metabolic needs while fasting is
unresolved for any species of large cetacean.

Past attempts to evaluate metabolic functions of large unrestrained cetaceans have relied primarily on making anatomical measurements of dead individuals, then scaling with allometric relationships derived for smaller captive cetaceans or other mammals (Scholander, 1940; Kanwisher and Sundnes, 1966; Brodie, 1975, 1977; Lockyer, 1981). Large body size and attendant difficulties of captive maintenance have negated the controlled experiments needed to test the many simplifying assumptions employed in even simple metabolic models of mysticete cetaceans. However, in the past two decades, new and, for the most part, benign methods of studying large whales in their natural settings have gained wider acceptance.

Gray whales are a convenient species to study general metabolic functions of a mysticete whale. Large numbers of individuals migrate very close to shore throughout most of their geographic range. This general accessibility of gray whales in their natural habitat is enhanced by their occupation of shallow protected coastal lagoons in winter; and by the expression in some of those lagoons of a whale-initiated approach behavior (Gilmore, 1976) which allows a moderate amount of physical contact between whale and researcher without capture or restraint.

Gray whales occupy the small end of the range of body sizes encompassing those cetacean species entrained into
long-distance annual fasting migrations. Consequently, their migratory energy requirements are expected to closely match their anatomical capability to store lipids to meet those requirements. Although successive annual births occasionally have been noted (Jones, 1984; Yablakov and Bogoslovskaya, 1984), adult female gray whales typically give birth to a single calf in alternate years at the southern terminus of their migratory route (Rice and Wolman, 1971). Following birth, females transfer energy through lactation to their calves for several months. Thus, each lactating cow is linked to her calf through lactation as a single metabolic system that draws on the lipid depots of the cow for the energy needs of both until feeding resumes. It is this cow/calf metabolic system that is anticipated to be most sensitive to the limits of lipid storage in fasting animals, to the duration of the fasting period, and to the manner in which those limited energy reserves are apportioned during the fasting period.

This study was initiated to: 1) estimate the magnitude of energy demands gray whale calves make on their mothers prior to weaning for growth, thermoregulation, and maintenance; 2) to evaluate the effects of migrations to low latitudes on the rates of body heat losses, and to relate that to the observed pattern of latitudinal distribution of gray whale calves (and their mothers); 3) to construct an energy budget
which describes the energy costs of pregnant/lactating females while fasting, and 4) to speculate on the selective advantages of this form of extreme migratory behavior.

**MIGRATION**

The migratory timing and route of California gray whales has been described in general terms by Gilmore (1960) and by Pike (1962), although they lacked sufficient empirical data to clarify such subtleties as year to year or age and sex related variations in migratory timing. Gilmore, as well as Kellogg (1929) and Ichihara (1958), speculated that gray whales migrated directly across the Gulf of Alaska between Unimak Island and the Washington coast. However, Pike's (1962) hypothesis of a nearshore migratory route in the Gulf of Alaska has been confirmed recently by Braham (1984).

The general picture of the migratory timing was substantially improved by Rice's and Wolman's 1971 report of 317 gray whales taken as they migrated past central California. More recently, studies of migratory patterns have been conducted at the Aleutian Islands (55° N; Rugh, 1984), Oregon (45° N; Herzing and Mate, 1984), California (37° N; Reilly et al, 1983; and 36° N; Poole, 1984), and Laguna San Ignacio (28° N; Jones and Swartz, 1984). Collectively, these studies demonstrate that the migration is best described as two independent
annual cycles which exhibit considerable temporal overlap in the same geographic range (Fig. 1.1). Late pregnant females pass central California about two weeks ahead of other gray whales (Rice and Wolman, 1971), and are also presumed to depart the Bering Sea earlier (dotted line, Fig. 1.1). These same females, accompanied by calves, are also the last to leave Mexican lagoons the following spring (Jones and Swartz, 1984). Juveniles, adult males, and nonpregnant adult females start south later (although they overlap somewhat the earlier pulse of pregnant females) and remain for shorter periods in low latitudes during winter. Even in lagoons and adjacent coastal areas, most lactating cows with calves maintain a spatial separation from other age and sex groups by occupying the inner, more protected reaches of the lagoons until the other animals depart (Norris et al, 1983; Jones and Swartz, 1984).

On average, gray whales require about 55 days for the south migration from Unimak Pass. Time spent in winter lagoons varies by sex and reproductive condition. Females without calves are the first to leave after an average stay of no more than 30 days, and they are soon followed by adult males (Rice and Wolman, 1971). The average stay of females which arrive near term and leave with their calves is about 80 days. Patterns of lagoon use by immature animals are not well defined.
Fig. 1.1. General annual migratory patterns for pregnant/lactating females (dotted and slashed lines) and other gray whales (solid lines) between summer high latitude feeding areas and winter lagoons. Compiled from Rugh, 1984 (solid square); P. Hessing, pers. comm. (open square); Herzing and Mate, 1984 (open circles); Rice and Wolman, 1971 (open triangle); Poole, 1984 (solid circles); and Jones and Swartz, 1984. The E-W lines at 45° N indicate the range around the mode of passage time for 90% of the whales observed by Herzing and Mate (1984).
The thermal environment encountered by gray whales during this migration ranges from near \(0^\circ C\) along the edge of arctic pack ice in summer months (Fig. 1.2) to 17-20\(^\circ C\) in the well-mixed waters of winter lagoons and adjacent coastal areas (Fig. 1.2). The migratory patterns of Fig. 1.1 show that pregnant/lactating cows and their calves encounter given latitudes at somewhat different times than do other gray whale sex or age groups, and consequently experience different thermal regimes through much of the migration. A rough approximation of this difference can be made using published monthly mean sea surface temperature maps (e.g. Robinson, 1976) with Fig. 1.1 to calculate the number of degree-days experienced in each migratory pattern shown in Fig. 1.1. These calculations indicate that typical pregnant/lactating cows experience about 26\% more degree-days than do other gray whales (3400 vs 2700) during a complete annual migration.

**FEEDING**

Pregnant/lactating females remain in winter lagoon areas much longer than do other adults (Fig. 1.1), and they are away from their principal arctic feeding grounds nearly two months longer than other gray whales. The question of whether significant feeding occurs outside the principal arctic summer range continues to complicate attempts to evaluate energy budgets of "fasting" whales. So long as feeding does not occur, all energy demands of
Fig. 1.2. Annual water temperature curves at the surface (solid line) and at 30 m (dashed line) for the central Bering Sea (bottom) and the west coast of Baja California Sur (top). Redrawn from Robinson, 1976.
cow/calf metabolic systems must be accommodated solely at
the expense of the fasting mothers' lipid reserves.

Intensive feeding occurs in high latitudes during
summer months. There, feeding behavior has been confirmed
by direct observations (Zimushko and Lenskaya, 1970;
Braham, 1984; Wursig et al, in press), by observing their
record of bottom sediment disturbances (Oliver et al,
1983; Johnson and Nelson, 1984; Nerini, 1984), by analyses
of stomach contents of commercially harvested whales
(Zimushko and Lenskaya, 1970; Bogoslovskaya et al, 1981),
and by measurable differences in body girth between south-
and north-bound migrants (Rice and Wolman, 1971). In the
principal foraging areas of the Bering and Chukchi Seas,
feeding occurs almost exclusively in waters less than 70 m
deep which are underlain by dense infaunal crustacean
communities (Nerini, 1984). These communities are
dominated by several species of benthic amphipods in three
families; Ampeliscidae, Atylidae, and Lysianassidae
(Zimushko and Lenskaya, 1970; Nerini, 1984). Lactating
cows with their calves may occur more frequently in the
Chukchi than Bering Sea during late summer (S. Moore,
pers. comm.), possibly continuing the pattern of
segregation from other gray whales seen in lagoons and on
migration.

Pike (1962) and Rice and Wolman (1971) argued
convincingly from observations of empty stomachs in all of
190 southbound whales examined that feeding does not occur
during this portion of the migration. This argument is supported by a general lack of observed feeding behavior during the southbound migration despite more than a decade of intensive shore-based census efforts along southern and central California, Oregon, and the Aleutian Islands (Nerini, 1984).

Available evidence for substantial feeding in winter lagoons has been reviewed recently by Oliver et al (1983) and Nerini (1984). The few reports of apparent feeding are fragmentary, often anecdotal, and sometimes contradictory, for they are based largely on observations of behaviors which may suggest, but cannot confirm, ingestion of nutritionally useful 'food' items. These behaviors include intense 'working' of a small area for several tens of minutes (often with mud plumes visible at the surface), rapid circling or criss-crossing of areas occupied by schools of bait fish or shoaling crustaceans, stationary orienting into tidal or rip currents at lagoon mouths, surface skimming of slick lines, mouthing of kelp or eelgrass, and the presence of fecal material (Nerini, 1984). All of these indications of possible feeding have been reported for gray whales in or near the mouths of lagoons, but such observations are rare. Scammon (1874) examined several stomachs of animals taken in winter lagoons and found no animal prey. Oliver et al (1983) and Swartz and Jones (1981) found depauperate benthic crustacean faunae both in these lagoons and near their
mouths, even at sites where 'feeding' behavior had been observed. Norris et al (1983) suggested that some non-social behaviors observed in tidal rips near the entrance to Bahia Magdelena were dives to feed on pelagic euphausiids or galatheid crabs (*Pleuroncodes*). No stomach content samples are available to confirm that ingestion was occurring, nor were cows with calves seen participating in this behavior. Taken together, the evidence of stomach contents, behavior, and lack of appropriate prey indicates that substantial feeding in the vicinity of winter lagoons by many gray whales is uncommon, and is avoided almost entirely by lactating females.

Even less is known concerning feeding during the northward migration. Of 136 northbound whales taken mostly in February and March off central California, 134 had empty stomachs (Rice and Wolman, 1971). This sample included no lactating females. Mate and Harvey (1984) reported apparent feeding by about sixty cows with calves in late April along northern Baja California (30° N). Braham (1984) also reported nearshore feeding from Cape St. Elias to Kodiak Island in the Gulf of Alaska during the spring migration. The inshore route taken by northbound cows with calves (most are within one km of shore along central California) reported by Poole (1984) and Herzing and Mate (1984) may be influenced by the availability of shallow water benthic prey and the need
for some animals to resume feeding before arriving in the Bering Sea. Likely prey along the migratory route include amphipods (Oliver et al, 1983; J. Guerrero, pers. comm.), various mysids (Murison et al, 1984; J. Guerrero, pers. comm.), and ghost shrimp (Callianassa; Hudnall, 1985; H. Plewes, pers. comm). This limited evidence suggests that lactating females may feed at least intermittently as appropriate prey becomes available to them during what appears to be a slow grazing migration northward from their winter lagoons; and that most gray whales are probably doing some feeding by the time they reach southern Alaskan waters.

Nursing calves are expected to begin supplementing their diets with active consumption of benthic prey sometime before complete weaning occurs in mid to late summer (Rice and Wolman, 1971). Bottom-feeding behavior by a calf has been observed in early June along the Oregon coast (pers. obs.); and benthic feeding by calves during the north migration may contribute an unknown amount to their total energy intake before reaching the Bering Sea.

The inconclusive nature of the evidence regarding the intensity and magnitude of feeding, especially by lactating females and their calves, only emphasizes the need for a different approach to answer questions about migratory and reproductive energetics of gray whales. The approach taken in this study focuses on the development of a model to assess the fate of lipid stores of gray whales
during their annual migration away from summer feeding areas.

PROBLEM STATEMENT

How do fasting female gray whales apportion their stored lipid reserves during migrations away from their principal feeding areas to accommodate their own maintenance and locomotory needs while simultaneously transferring energy through lactation to support growth and maintenance of their calves?

This problem is addressed in seven papers which follow as separate chapters. Each chapter has been written to examine a particular component of the general problem. Relationships between each component are diagrammed in Fig. 1.3. Chapters Two through Five have been published or accepted for publication elsewhere, and are reprinted here by permission with slight changes to maintain consistency in format and unit usage.
Fig. 1.3. Chapter designation of the major components of this study.
CHAPTER TWO

SWIMMING VELOCITIES, BREATHING PATTERNS, AND ESTIMATED COSTS OF LOCOMOTION IN MIGRATING GRAY WHALES, ESCHRICHTIUS ROBUSTUS

ABSTRACT

This study was conducted to determine the swimming velocities and breathing patterns of south-migrating gray whales (Eschrichtius robustus) and to estimate their minimum costs of transport during migration. Swimming velocities and breathing patterns were monitored with theodolite techniques from a coastal vantage point on Point Loma, San Diego County, CA. Estimates of energy expenditures were based on observed breathing rates and on extrapolations from tidal lung volume and oxygen uptake measurements. The results of 74 whales monitored over 354 whale km yielded a mean velocity of 2.0 m/s and a mean breathing rate of 0.72 breaths/min. The regression of breathing rates on swimming velocities (V) by the method of least squares is best described by the equation, breathing rate = 0.5 + 0.024V^{3.0}. The calculated minimum cost of transport for a 11.5 m, 15.6 MT whale was 0.035 Watt·second·Newton−1·meter−1 at the observed mean swimming velocity of 2 m/s during the southward migration. The coefficient of total drag was estimated to be 0.046. Estimated rates of lipid depletion for a 11.5 m whale are...
equivalent to 5% of body weight per month if no supplementary food intake occurs for the 4- to 6-month period each year that gray whales are presumed to fast.

INTRODUCTION

The energy costs of long-distance annual fasting migrations of gray whales have been assumed to be partially compensated for by the energy savings accrued by spending winter months when suitable prey are less available in warmer, low-latitude waters (Rice and Wolman, 1971; Brodie, 1975). This assumption has been fundamental to our understanding of the distribution patterns and resource needs of large baleen whales, yet the way in which they allocate their stored lipid reserves to pay costs of locomotion, thermoregulation, and other physiological functions is unknown. A necessary step in evaluating any assumption concerning lipid utilization during migration is to determine the energetic costs of swimming for a whale over the migratory distance. The energetic cost of transport (COT) can be defined as the power (P) required to move a given body weight (W) at some velocity (V). Thus, in appropriate units, COT=P/WV. Tucker (1975) summarized the known minimum COT for a variety of swimming, flying and running animals. Conspicuously absent from Tucker’s summary were estimates of the COT for cetaceans or other swimming endotherms.

Like flying animals, swimmers typically have some
optimum velocity at which their COT is minimum (Schmidt-Nielson, 1972; Tucker, 1975; Alexander and Goldspink, 1977). Presumably, gray whales follow the pattern of other vertebrate swimmers. If so, the efficient use of lipid stores would require a mean migratory velocity similar to the swimming velocity at their minimum COT.

Models of hydrodynamic performance indicate that power requirements for submerged swimming by streamlined animals are proportional to the cube of the swimming velocity. Predicted performance for streamlined swimming vertebrates can be generalized by Eq. 2.1 (from Webb, 1975):

Eq. 2.1: \[ P = 0.5 \rho C_t A_t V^3 \]

where \( \rho \) = water density

\[ C_t = \text{coefficient of total drag} \]

\[ A_t = \text{total wetted surface area,} \]

\( V = \text{swimming velocity} \)

The magnitude of \( C_t \) is unknown for any species of large whale. The wetted surface area can be approximated as a function of body length, \( L \), and maximum girth, \( G \).

Published estimates of mean swimming velocities for southward migrating gray whales range from 1.5 m/s (Andrews, 1914) to 2.8 m/s (Cummings et al., 1968), with little discussion of the magnitude or cause of variability from these reported means.

This study was initiated to: 1) determine the mean
values and the magnitude of variability in swimming velocities of south-migrating gray whales; 2) describe the relationship between breathing rates and swimming velocities of south-migrating whales; and 3) estimate the minimum COT of migrating gray whales and to compare the swimming velocity at their minimum COT to observed migratory velocities.

METHODS

During late December and January of 1975 and 1976 and January of 1977, 1978, and 1979, southbound whales were observed from an elevated coastal vantage point atop Point Loma, San Diego County, California, (32°42' N) by the author and several student assistants. Southbound gray whales in large numbers can be easily observed from shore at numerous sites, particularly in California, during late December and January, as they swim steadily on courses generally parallel to shore. By this time, most late pregnant whales were presumed to have passed the study site on their way to Mexican calving lagoons (Rice and Wolman, 1971), leaving immature whales and nonpregnant adults as the principal subjects for observation. The location of the observation site selected for this study is within Cabrillo National Monument at an elevation of 111 m above sea level. This site provided a clear view to the west of migrating whales 2-5 km offshore. Weekdays were selected to avoid large numbers of weekend whale
watchers, both ashore and in boats at sea. Late afternoon sea surface glare restricted observations to morning or very early afternoon hours.

A surveying theodolite (Dietzgen model 6170) was used to determine the position of individual gray whales or whale groups. The theodolite was equipped with a 25x sighting telescope and horizontal and vertical vernier scales calibrated in degrees and minutes of arc. When a whale or group of whales was sighted to the north, the theodolite was used to establish the vertical angle between the observation site and the whale's position. At the same time, a compass angle of the whale's position was obtained and the time was recorded. This procedure was repeated several times as the whale or whale group proceeded south past the observation site. During dives, it was assumed that the whales were swimming in straight line between surfacing points. Corrections for surface current drift were not made as currents in the study area were generally less than 0.2 m/s and were quite variable in direction owing to tidal influences (T. Hendricks, pers. comm.).

The total number of observed exhalations for all whales in each group was counted by two observers using 7x binoculars and a 15x spotting telescope. The mean breathing rate for individual whales of each group was calculated by dividing the number of observed exhalations by the elapsed time and by the number of whales in the
A computer program was developed to convert elapsed time and theodolite angle data to map positions and mean swimming velocities between each map position and for the total observed distance. The positions of each whale group were then plotted on an outline map of the study area and the migrating path was drawn in (Appendix 1).

RESULTS

The results of the 1975 and 1976 series of observations indicated that the counted number of exhalations per whale decreased significantly (ANOVA, $\alpha = 0.05$) with group sizes larger than three. This was interpreted as an inability of observers to spot all exhalations in the larger groups. Subsequently, groups with more than three whales were ignored. As a result, our efforts were biased toward those whales swimming closer to shore and in smaller groups to improve the accuracy of our breathing rate determinations. There was no evidence at the 0.05 level of significance (ANOVA) that swimming velocity varied with group size.

Several criteria were established to select only those breathing rate--swimming velocity observations which were deemed to reflect uninterrupted, direct swimming behavior. Observations were rejected from further consideration in this study if: 1) the group size was larger than three; 2) the state of the sea surface was 3
or higher on the Beaufort scale; 3) the direction of swimming differed by more than $30^\circ$ from one segment of the observed path to the next (considered to be an unacceptably large course change; 4) measured $V$ in any segment of the observed path was less than 0.5 times or greater than 2 times the mean swimming velocity over the entire observed path (considered to be an unacceptably large velocity change; 5) the elapsed observation time was less than 15 min; 6) behavior such as courting, meandering, or breaching occurred; and 7) the whale group was followed by one or more boats at distances less than 100m.

A total of 137 southbound gray whales was observed over a distance of 661 whale·km during 91 whale·h of elapsed observation time. Of these, observations of 74 whales (354 whale·km) were considered acceptable for additional analysis according to the criteria listed above. The general results of these observations are summarized in Table 2.1.

Table 2.1. Summary of the total and acceptable observations of south-migrating gray whales.

<table>
<thead>
<tr>
<th></th>
<th>Total observations</th>
<th>Acceptable observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of whales</td>
<td>137</td>
<td>74</td>
</tr>
<tr>
<td>Total distance</td>
<td>661 whale·km</td>
<td>354 whale·km</td>
</tr>
<tr>
<td>Total elapsed time</td>
<td>91.0 whale·h</td>
<td>51.3 whale·h</td>
</tr>
<tr>
<td>Mean velocity</td>
<td>2.02 m/s</td>
<td>1.97 m/s</td>
</tr>
<tr>
<td>Mean breathing rate</td>
<td>not determined</td>
<td>0.72 breath/min</td>
</tr>
<tr>
<td>Mean group size</td>
<td>2.0 whales/group</td>
<td>1.6 whales/group</td>
</tr>
<tr>
<td>Mean distance/whale</td>
<td>4.8 km</td>
<td>4.8 km</td>
</tr>
</tbody>
</table>
The 74 acceptable paired breathing rate-velocity observations are plotted in Fig. 2.1. These observations fall into a rather narrow velocity range (1.2-2.8 m/s) around the mean of 2.0 m/s, because of the limitations of the listed criteria for acceptance. Whales swimming more slowly than 1 m/s were always engaged in courting, boat avoidance, or other complicating behavior. Only one whale was observed swimming faster than 3 m/s. It was closely followed by a boat and was clocked at 4.2 m/s (15.5 km/h) over a 2.2 km portion of its swimming path.

An analysis of the surfacing patterns of 11 individual whales observed in this study indicated that breathholds were of two distinct types (Fig. 2.2). Short breath holds of less than 1 min accounted for approximately two-thirds of the total. Most of the remaining breath holds were longer than 2 min. The dive patterns of four whales swimming at less than the overall observed mean of 2 m/s were compared with those of seven whales swimming faster than the mean (Table 2.2). Both groups had similar proportions of short breath holds (less than 1 min), but the mean duration of these short breath holds was greater for the faster group of whales (The probability (p) of this difference occurring by chance is $0.10 > p > 0.05$, ANOVA.). The faster whales achieved their overall higher breathing rates not by making more short dives but by decreasing the mean duration of their long
Fig. 2.1. Breathing rates and swimming velocities of south-migrating gray whales. ●, single whales; +, two-whale groups, △, three-whale groups.
Fig. 2.2. Frequency distribution of breath-hold durations, by 10-s time increments, for fast- and slow-migrating whales.

**Fast whales**
- # whales = 7
- # breath holds = 218

**Slow whales**
- # whales = 4
- # breathholds = 131
Table 2.2. A comparison of some breathhold characteristics of slow- and fast-swimming gray whales.

<table>
<thead>
<tr>
<th>Breath holds</th>
<th>slow whales (n=4)</th>
<th>fast whales (n=7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;60s</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>88</td>
<td>151</td>
</tr>
<tr>
<td>%</td>
<td>67</td>
<td>69</td>
</tr>
<tr>
<td>$\bar{X}(s)$</td>
<td>22</td>
<td>27</td>
</tr>
<tr>
<td>&gt;60s</td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>43</td>
<td>67</td>
</tr>
<tr>
<td>%</td>
<td>33</td>
<td>31</td>
</tr>
<tr>
<td>$\bar{X}(s)$</td>
<td>231</td>
<td>183</td>
</tr>
</tbody>
</table>

breath holds to just over 3 min. In comparison, the slower whales had a mean long breathhold duration of nearly 4 min. Again, the probability that this difference occurred by chance was $0.10 > p > 0.05$ (ANOVA).

Acceptable breathing rates for whales swimming at velocities less than 1 m/s could not be obtained in this study because of the complications of nonswimming behavior in slow-moving animals. Therefore, minimum breathing rates of five inactive adult gray whales ($\bar{X} = 0.50$ breaths/min) observed in Laguna San Ignacio (pers. obs.) were assumed to provide a reasonable estimate of minimum mean breathing rates for gray whales at $V = 0$. The mean breathing rate of acceptable observations was 0.72 breaths/min, with a range of 0.45-1.12 breaths/min.

A multiple regression F-test of the data in Fig. 2.1, comparing the breathing rate: swimming velocity regression below and above the mean swimming velocity, indicated a tendency toward curvilinearity ($F$ calc. = 1.41 with 1 and 71
df; the probability that the proportion of variance explained by some curvilinear function occurred by chance is $0.25 > p > 0.10$). A curvilinear function was fitted to the data shown in Fig. 2.1 with the following procedure. The breathing rate at $V = 0$ was assumed to be 0.5 breath/min. Means of breathing rates and swimming velocities were calculated for each 0.5 m/s velocity increment above 1.0 m/s. These five points (shown in Fig. 2.3) were analyzed with a least squares power curve fit procedure, which yielded Eq. 2.2:

$$\text{Eq. 2.2: breathing rate} = 0.5 + 0.024(V)^{3.0}$$

These points and the resulting curve are shown in Fig. 2.3. Equation 2.2 was tested against the data shown in Fig. 2.1. The results of the ANOVA test ($F_{\text{calc.}} = 39.35; F_{\text{crit.}} (2,71 \text{ d. f., } \alpha = 0.05) = 3.15$) indicate that a large and significant portion of the variance of breathing rate is explained by its regression on swimming velocity as described by Eq. 2.2. From Eq. 2.2, a crude estimate of the COT based on the mean number of breaths required for each km of distance travelled at different swimming speeds was calculated:

$$\text{Eq. 2.3: COT (in breaths/km) = }$$

$$\frac{\text{breathing rate (breaths/min) \times (1000 m/km)}}{V \text{ (m/s) \times (60 s/min)}}$$

The minimum COT of 5.7 breaths/km occurs at swimming velocities between 2.0 and 2.2 m/s (Fig. 2.3).
Fig. 2.3. Mean breathing rates and swimming velocities (*) for 0.5 m/s velocity increments with +1 s.d. shown as vertical and horizontal lines. Sample size is indicated above each mean. The least squares regression of breathing rate on swimming velocity (solid line) best fitted the mean breathing rate according to Eq. 2.2, with $r^2 = 0.99$. Dashed curve is COT calculated from the breathing rate:swimming velocity regression.
DISCUSSION

The results of this study indicate that the swimming velocities for southbound gray whales off Point Loma are representative of swimming velocities found by other investigators for the southward migration. The mean $V$ of 2.0 m/s obtained from this study agrees well with the value of 2.1 m/s calculated by Pike (1962) and by Rice and Wolman (1971) along the California coast. Their estimates were based on times of peak passage of the migrating population between widely separated shore counting stations.

The breathing rate:$V$ relationship of southbound gray whales, as expressed by Eq. 2.2, is consistent with $P:V$ relationships predicted by generalized hydrodynamic equations (Eq. 2.1). Additional lines of evidence support the concept that breathing rates of migrating whales unencumbered by other complicating behaviour or by reproduction are reasonable reflections of their total power requirements and, ultimately, of their COT. Unlike terrestrial mammals, regulated heat losses are handled via vascular radiators in the flukes, pectoral flippers, and other specialized surface regions of cetaceans, making evaporative cooling from the respiratory tract not only unnecessary but costly in terms of respiratory water losses (Schmidt-Nielsen et al., 1970). In addition, power requirements for swimming increase severalfold at water
depths less than three body diameters below the water surface because of surface drag effects (Hertel, 1966). Thus, there exists a strong energetic incentive for migrating whales to swim at depths below three body diameters (about 6 m for an adult gray whale) for several minutes, surfacing to breathe only as frequently as \( \text{O}_2 \) demands dictate. This is reflected in the marked distinction reported here between long and short breath holds (Fig. 2.2), as well as in the typical surfacing patterns exhibited by migrating gray whales: two-four successive blows 20-30 s apart followed by a dive of several minutes. The long dives appear to be an adaptive strategy which permits extensive swimming at depths below significant surface drag effects. The durations these long dives likely represent the practical limits for aerobic breath-hold diving by migrating gray whales, with maxima near 6 min for slow whales (\( V < 2 \text{ m/s} \)) and somewhat less than 5 min for fast whales (\( V > 2 \text{ m/s} \)).

The short breath holds are not of sufficient duration to swim long distances or to achieve and maintain for long dive depths below 6 m. It is suggested that the preferred short breathhold duration of 20-30 s is selected to maximize the utilization of \( \text{O}_2 \) from inspired air. Preliminary studies of \( \text{O}_2 \) utilization by active unrestrained gray whale calves in winter lagoons indicate that \( \text{O}_2 \) utilization increases to 10-12% of inspired air volume with increasing breathhold time to about 20-25 s.
At longer breath holds, little additional \( O_2 \) utilization is apparent. Thus, short breath holds apparently serve to achieve efficient rates of \( O_2 \) utilization, whereas long breath holds permit more efficient transport over migratory distances.

Breathing rates can be converted to approximations of actual rates of energy expenditure with estimates of tidal volume \( (V_t) \) as a function of body weight (Table 6.5) and of the fraction of \( O_2 \) extracted from inspired air \( (F_{O_2}; \text{Eq. 6.6}) \) made in Ch. 6. \( V_t \) of a typical 11.5 m, 15 MT gray whale nearing sexual maturity is estimated to be about 370 l, with 11.7% of that, or 43 l, representing utilized oxygen. At an average breathing rate of 0.72 breaths/min, the total daily \( O_2 \) consumption for such a whale is approximately \( 44.6 \times 10^3 \) l of \( O_2 \).

During this migration, energy is presumed to be derived from the oxidation of stored lipids. Ridgway (1972) reported that \textit{Tursiops} and \textit{Lagenorhynchus} lose muscle protein almost as rapidly as they do lipids during short-term fasting. For fasting periods extending over several months, however, lipid depots must be the principal energy reserve, for lipids not only contain more energy per gram than either protein or glycogen, but also yield more metabolic water when oxidized. The oxidization of each gram of lipid requires 2 l of \( O_2 \) and yields approximately 9.5 kcal (39.7 kJ) of energy. Thus, utilization of an estimated \( 44.6 \times 10^3 \) l of \( O_2 \) each
day by a migrating, fasting, 15 MT gray whale is equivalent to oxidizing 22.3 kg of lipid daily, resulting in the release of 212 x 10^3 kcal (0.9 x 10^6 kJ) of energy at a rate of 10.1 x 10^3 Watts.

Comparisons with other species of large whales are limited both by the paucity of information and by its manner of treatment. Brodie (1975) calculated surface related "resting" metabolic rates of 48 Watts·m^-2 for 20 m, 48 MT fin whales. These calculations also were based on estimated rates of lipid depletion. Brodie's metabolically active surface area (essentially the area of the inside blubber surface minus the fins and flukes) of an 11.5 m gray whale is 0.67GL (from Ch. 7) = 49 m^2. The daily energy ration of 0.9 x 10^6 kJ is equivalent to 206 Watts·m^-2 of body surface, substantially more than that calculated by Brodie (1975) for larger fin whales. Part of the discrepancy in these results can be assigned to differences in activity levels. Although Bennett and Ruben (1979) consider five- to ten-fold increases in O_2 consumption (and metabolic rate) typical for mammals going from resting to active states; a much smaller, but still apparent, increase in breathing rates is actually seen across the scope of gray whale activity observed in this study. Other differences may be attributed to the three-fold absolute difference in body size of the whales being compared and to the warmer, more tropical winter waters experienced by Brodie's fasting fin whales.
The validity of the estimated daily energy ration presented here is supported by other studies of Rice and Wolman (1971). They measured body girth decreases from 0.56L to 0.49L in gray whales (immature but older than one year) for the time period between south and north passages by central California (68 days). Body weights are calculated from these G values, L of 11.5 m, and Eq. 5.3 (Ch. 5). For the 11.5 m whale in the previous example, the 68 day southern portion of the migration costs about 11% of the body weight, or 0.16% (25 kg) each day. This independent estimate of lipid depletion rates differs by about 10% from the 22.3 kg daily lipid loss estimated from breathing rates, $V_t$, and $P_O_2$ values. The total drag coefficient, $C_t$, of Eq. 1.1 can be derived from the preceding estimate of power output ($10.1 \times 10^3$ watts at $V = 2.0$ m/s) and from the water density and body surface area:

$$\text{Eq. 4: } C_t = \frac{P}{0.5 \rho A_t V^3}$$

where $P = 13.8 \times 10^3$ watts

$$\rho = 1.025 \text{ g/cm}^3$$

wetted $A_t = 0.74GL = 53.8 \text{ m}^2$

$L = 11.5 \text{ m}$

$V = 2 \text{ m/s}$.

At these conditions, $C_t$ is 0.05. This is the only known estimate of $C_t$ available for baleen whales, and is about 1.6 times the turbulent $C_t$ values reported by Lang (1975) for three species of small streamlined odontocetes.
The calculated COT (Fig. 2.3) occurred at $V = 2.0-2.2$ m/sec. Using the terms and units of Tucker (1975), the minimum COT for a 15 MT whale swimming at 2.0 m/sec with an expenditure of $10.1 \times 10^3$ watts is 0.035 watt·sec·N$^{-1}$m$^{-1}$. Minimum costs of transport for other swimming endotherms of similar size are not available for comparison. However, Tucker found that reasonable projections of COT can be made over wide ranges of body sizes and taxonomic groups using similar modes of locomotion. Using these projections, Kawamura (1975) established a COT value of 0.01 watt·sec·N$^{-1}$m$^{-1}$ for a hypothetical 34 MT fin whale swimming in conditions of laminar flow at 10 knots (18 km/h). The minimum COT calculated for the 15 MT gray whale is about 2.6 times higher than that projected for a hypothetical fish of similar size, and about 3.5 times greater than Kawamura's fin whale estimate. The latter estimate was based on the assumption that fin whales, like dolphins, maintain conditions of laminar flow over their bodies at typical swimming velocities. At the swimming velocity and body length conditions given by Kawamura (5 m/s and 18 m), a fin whale has a Reynolds' number of about $9 \times 10^7$. In stable conditions, water flow over streamlined bodies becomes turbulent at Reynolds' numbers greater than about $5 \times 10^6$ (Webb, 1975). Thus, Kawamura's assumption of laminar rather than turbulent water flow leads to a serious underestimate of the actual COT of fin whales.
It is noteworthy that the speed at which the COT is minimum, (or at which the maximum swimming range is greatest), is nearly identical to the mean migration speeds of southbound gray whales found in this study and those determined by Rice and Wolman (1971) and Pike (1962). The energetic implications of migrating at speeds which minimize their COT and maximize their range, as southbound gray whales do, are obvious. Yet Pike (1962) suggested that northbound whales migrate about half as fast as they do going south. This slower northward migratory velocity was confirmed by observations of a radio-tagged whale (Mate and Harvey, 1984), with mean daily swimming velocities of this whale of 1.0 m/s along the California coast increasing to 1.5 m/s between Oregon and Unimak Pass. The COT in Fig. 2.3 indicates that gray whales making this slower northward migration in spring months incur a COT nearly double that experienced by southbound whales. The reasons for this seeming paradox of much higher COT during the latter portion of an extended fasting migration are not known. Supplemental feeding during the spring may explain partially the slower migrating speeds and higher COT incurred during the northward leg of this, the longest migration of any mammal.
CHAPTER THREE

GRAY WHALES ALONG THE OREGON COAST

IN SUMMER, 1977-1980

ABSTRACT

Gray whale distribution and relative abundance along the Oregon coast were studied during the summers of 1977-1980. Shore-based observations along the entire Oregon coast were made in 1977. In 1978-1980, detailed studies of whale distribution, activities, and body size were made along the central coast only; they were supplemented with observations from aircraft.

Twelve hundred thirty two summer sightings were made within 0.5 km of shore. Numbers of sightings varied considerably from day to day and from year to year, with maximum observed whale abundance estimated at 0.2-0.3 whales/km of shoreline for a 100 km portion of the study area in 1977 and 1978. Over one-half the whales were thought to be feeding; the remainder were traveling, usually parallel to shore. Body length was determined for 42 whales photogrammetrically. The majority of these summer whales were evidently subadults; calves and yearlings accounted for approximately 50% of the total.
INTRODUCTION

Gray whales migrate north from winter lagoons to their principal feeding grounds north of 60° in spring and early summer (Fig. 1.1). However, not all northward migrants leaving their winter grounds in Mexico proceed directly to the Bering Sea. Pike (1962) reported that a few gray whales remain as summer residents along the British Columbia coast. Rice and Wolman (1971) listed six summer sightings between Baja California and British Columbia. Additional published reports (Hatler and Darling, 1974; Patten and Samaris, 1977; Sprague et al, 1977; Sullivan et al, 1983; and Darling, 1984) and numerous unpublished reports indicate that summer occurrences of gray whales along much of the west coast of North America are more common than previously assumed. In response to a 1976 inquiry, gray whales were reported as sighted or stranded during summer in at least 24 coastal locations in California and Oregon. Subsequent studies of summer gray whales in 1977-1980 along the Oregon coast are the subject of this paper.

METHODS

Summer sightings are defined as those occurring between 1 June and 15 September in coastal waters. Beginning in June, 1977, fortnightly ground-based searches for summer gray whales were conducted from elevated
observation sites approximately 20 km apart between the Columbia River and the Oregon-California border (a distance of 450 km). Visual searches for whales (aided by 7 x 35 binoculars) were made from each site. The date, time, apparent activity, direction of travel, and number of whales were recorded. Body size estimates were made when possible. These observations were supplemented with opportunistic sightings made by Coast Guard personnel, park rangers, commercial and sports fishers, and other cooperators. The counts were adjusted to discount possible repeated sightings of the same whale(s) on the same day. No corrections for visibility or observer effort have been attempted.

The scope of the summer study area was narrowed in 1978 to 100 km of the Oregon coastline between the Siuslaw River (44°00' N.) and Government Point (44°51' N., Fig. 3.1) to obtain detailed information on site utilization, identification of individual whales, body length, and activities. Ground surveys in 1978 and 1979 were concentrated along the 25 km northern portion of the study area between Yaquina Bay (44°37' N.) and Government Point, where several coastal bluffs and headlands (named in Fig. 3.1) provided elevated observation sites for complete visual coverage. Cape Foulweather (44°46' N.), with an elevation of 140 m, was especially suitable for monitoring behavior and for obtaining information on size and identification of
Fig. 3.1. The 1977 (left) and 1978 (right) Oregon summer gray whale study areas.
individual whales. Ground surveys were discontinued in 1980.

During summer months of 1978, 1979 and 1980 aerial flights were made along portions of the Oregon coast. Helicopters of the U. S. Coast Guard (equipped with radar altimeters) or fixed wing aircraft were utilized as observation platforms. Determinations of body length were made from photographs taken from known distances with 35 mm high speed black and white film, 230 mm telephoto lens, and polarizing filter. Whales were usually photographed vertically from altitudes between 200 and 300 m when they surfaced to blow. For oblique photographs, the angle deviation from vertical was measured with a hand-held inclinometer and the correct camera-whale distance was calculated.

Additional photographs, using the same procedure, were taken from Cape Foulweather. Film negatives were examined under a 7x microscope. The standard length of the whale image was measured to the nearest 0.01 mm with an ocular micrometer. Body length was calculated with the following formula:

\[
L = \frac{I \times D}{F}
\]

where \( L \) = body length, m

\( I \) = whale image size on film, mm

\( D \) = whale to camera distance, m

\( F \) = camera lens focal length, mm
When a whale was photographed more than once, the lengths calculated from each photograph were averaged.

The relationship between body length and age of gray whales has been unresolved for some time (Rice and Wolman, 1971; Zimushko, 1970; Zimushko and Ivashin, 1980), principally because most studies are of large, sexually mature whales. A re-examination of the age:body length relationship of young gray whales (Ch. 5) indicates that calves in their first summer are shorter than 8 m, and yearlings are between 8 and about 9.5 m.

On 20 July 1978, a study was conducted to test the value of aerial surveys along more extensive reaches of coastline. Seven shore observers were positioned on vantage points along a 25 km long portion of the study zone (Yaquina River to Government Point). Concurrent with the observations from shore, seven sequential flights of approximately ten minutes duration each were made over the zone with a Cessna 180 carrying a pilot and an observer. Flight speed was 180 km/h at 500 m altitude. The observation strip was one km wide, established with calibrated marks on the wing strut. Four flights were made to the south over the shoreline (observed strip extending from shore seaward one km); and three flights were made to the north one km offshore (observed strip extending from the line of flight to shore).
RESULTS

Twelve hundred thirty two sightings of summer gray whales were reported from all sources along the Oregon coast between 1 June 1977 and 15 September 1980 (Appendix 2). Sixty percent of the 460 summer whales reported in 1977 were along the 100 km of coastline from the Siuslaw River to Government Point just north of Depoe Bay (44°00' to 44°51' N., Fig. 3.1), suggesting that they were either more numerous or were more easily seen there than along other portions of the Oregon coastline. Therefore, the 1978 shore surveys were limited to that region. Figure 3.2 illustrates the daily number of gray whale sightings from all sources between 1 June and 31 August of 1977 and 1978 for the northern (44°51' - 44°25' lat.) and southern (44°25' - 44°00' lat.) halves of that 100 km study area. Observer effort and weather conditions affecting whale visibility were not necessarily equivalent for 1977 and 1978, and statistical comparisons of the two summers cannot be made. However, the data in Fig. 3.2 do suggest that summer gray whales occurred more frequently in the northern half of the study area in 1978 than in 1977. The largest single-day count in 1977 (August 22) was 30 for the 100 km study area; in 1978, it was 19 (on July 30), yielding a maximum observed occurrence of 0.2-0.3 whales/km of coastline.

Ten complete shore surveys made along the 25 km
Fig. 3.2. Daily numbers of summer gray whales reported from all sources in 1977 and 1978 for the northern (44°51'-44°25' N.) and southern (44°25'-44°00' N.) halves of the 100 km study area. Each small vertical division represents 1 whale.
coastal section from Yaquina River to Government Point in 1978 and 1979 during half-day periods of acceptable visibility (at least 5 km) and sea state conditions (Beaufort 3 or less). All 10 surveys were conducted by the same observer. Whale counts for those surveys are listed in Table 3.1. During June and July, calves remained close to their mothers and were easily recognized. As summer progressed, calves wandered farther (often more than 200 m) from their inferred mothers, were seen alone more frequently, and thus were more difficult to identify as calves without independent estimates of their body lengths. Accordingly, the relative number of calves listed in Table 3.1 (32% of the whales sighted) is considered a conservative estimate, particularly for the

Table 3.1. Results of 10 acceptable ground surveys between Yaquina River and Government Point, Oregon, in 1978 and 1979.

<table>
<thead>
<tr>
<th>Date</th>
<th>calves</th>
<th>others</th>
<th>total</th>
<th>whales/km</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Jun 78</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>0.28</td>
</tr>
<tr>
<td>17 Jun 78</td>
<td>1</td>
<td>5</td>
<td>6</td>
<td>0.24</td>
</tr>
<tr>
<td>5 Jul 78</td>
<td>4</td>
<td>7</td>
<td>11</td>
<td>0.44</td>
</tr>
<tr>
<td>11 Jul 78</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>0.24</td>
</tr>
<tr>
<td>13 Jul 78</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1978 totals:</td>
<td>13</td>
<td>23</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>25 Jun 79</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>6 Jul 79</td>
<td>1</td>
<td>9</td>
<td>10</td>
<td>0.40</td>
</tr>
<tr>
<td>8 Jul 79</td>
<td>3</td>
<td>4</td>
<td>7</td>
<td>0.28</td>
</tr>
<tr>
<td>3 Aug 79</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td>6 Aug 79</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1979 totals:</td>
<td>5</td>
<td>16</td>
<td>21</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTALS:</td>
<td>18(32%)</td>
<td>39(68%)</td>
<td>57(100%)</td>
<td></td>
</tr>
</tbody>
</table>
latter part of the summer. The mean observed occurrence of 0.23 whales/km compares well with the highest occurrences (0.2 - 0.3 whales/km) seen along the 100 km section of coastline in 1977 and 1978.

During the 20 July simultaneous ground/air study, the shore observers sighted 6 whales within the 25 km study zone during the aerial observation period. Four of the six whales were within 100 m of shore, and all six were located in surf or foam lines. No whales were seen from the air on any of the three flights one km offshore. Of the four flights over the shoreline, 0, 1, 3, and 1 whales were seen on successive passes (\( \bar{X} = 1.25 \) whales/pass; s.d. = 1.26).

In conditions of good visibility, five km was considered a practical maximum distance that gray whales could be reliably seen with binoculars under ideal conditions. Most of the sightings mentioned to this point were made within 500 m of shore. However, 14 reports of 27 whales 5 to 80 km offshore were received from Coast Guard personnel and fishing boat operators during 1977 and 1978. Water depths of these locations ranged from 50 to 2700 m. After 1978, efforts to contact these observers were discontinued.

Body lengths of 42 gray whales (Fig. 3.3) were determined using the photogrammetric technique. The precision of this technique was tested on a small whale photographed repeatedly from Cape Foulweather on 3 August
Fig. 3.3. Body lengths of 42 summer gray whales photographed, 1978-1980, plotted at dates of length determination. Age class assignment based on Ch. 5. C = calf, Y = yearling, M = inferred mother with calf, x = other.
1979. Five film negatives showed the entire animal clearly. From these, body lengths were calculated ($\bar{x}=7.78$ m; s.d.$=0.11$ m). Twelve of the 42 whales (29%) measured were less than 8 m and were judged to be calves. This percentage is very close to the 32% calves observed in ground surveys (Table 3.1). Seven additional whales (17%) were considered yearlings (Fig. 3.3).

**DISCUSSION**

In the past decade, summer gray whale sightings have increased appreciably at several locations along the west coast of North America. The large variation in observed abundance along the Oregon coast described here may, in part, reflect varying observer effort. Sightings were never common north of Lincoln City (45°10' N.), where strategic headlands are fewer. Reliable estimates of whale numbers along inaccessible stretches of coastline could not be obtained from the air, because nearshore whales are extremely difficult to detect against their typical backdrop of surf and sea foam.

The numbers of summer whales at any one coastal site varied considerably from day to day and from one year to the next, and showed no defined time maximum occurrence to compare with other areas along the west coast. Due to the limitations of weather, sea state, and coastal terrain on the visibility of summer whales, the abundances reported in this study (0.2-0.3 whales/km) along the central Oregon
coast are thought to represent fewer than the true number of whales. In another study of gray whales along a 40 km portion of the west coast of Vancouver Island, Darling (1984) found a maximum occurrence of 0.3 whales/km in July 1974 and 1976. In spite of the similar numbers of summer gray whales found for the Oregon and Vancouver Island locations situated over 500 km apart, it is premature to extrapolate these numbers to other west coast locations known to be frequented by summer whales. Consequently, it is not yet possible to indicate what fraction of the total whale population does not migrate to arctic waters in summer.

Although the principal activity of summer whales appears to be feeding, their prey is unknown. Gray whales in arctic feeding grounds forage on benthic infauna, particularly gammarid amphipods (Pike, 1962; and Rice and Wolman, 1971). These organisms occur in the Bering and Chukchi Seas in densities to 24,000 animals/m² (Zimushko and Lenskaya, 1970). The offshore sightings are intriguing in that 8 of the 14 occurred at sites where water depths exceeded 100 m, and 3 were in depths of 400 m or more. Gray whales seldom feed in arctic waters deeper than 70 m (Nerini, pers. comm). The presence of summer whales in deep water suggests that, if they are feeding on pelagic rather than benthic organisms, they are exploiting a range of prey broader than previously supposed.

Reilly (1984a) estimated the annual gray whale birth
rate to be no more than 14%, and the average annual mortality rate for all immature whales, 10%. However, it appears that mortality is much higher among calves (36%) and yearlings (27%) than for older immature animals (Ch. 4). Complications at birth, predation by sharks and killer whales, and severe storms may all contribute to high calf and yearling mortality (Morejohn, 1968; Rice and Wolman, 1971; and Baldridge, 1972). Thus, no more than 10% of the gray whale population during summer months are expected to be calves, and 8%, yearlings. A Chi-square test comparing the expected frequencies of calves (10%), yearlings (8%), and others (82%), with those actually observed (29%, 17%, and 54%) yielded:

\[
calculated \ x^2 = 55.8 \\
\text{critical } x^2 (\alpha = 0.05 \text{ with 2 d.f.}) = 5.99
\]

Both calves and yearlings contribute significantly more to the counts of summer gray whales along the Oregon coast than would be expected from a random sample. The numbers of calves suggest, by association, the presence of comparable numbers of lactating females, at least prior to weaning in late summer (Rice and Wolman, 1971). Moreover, approximately one-half of the whales in Fig. 3.3 larger than yearlings, including 3 of the 4 inferred females in the company of calves, are smaller than the mean length at sexual maturity (slightly over 11 m; Rice and Wolman, 1971). Thus, Oregon summer whales are predominantly immature or atypically small mature animals.
Summer whales may gain energetic benefits by cutting short their northward migration and foraging in Oregon rather than colder arctic waters. Also, summer feeding can commence earlier and continue later prior to the southward autumn migration. These benefits may be particularly crucial for calves and their mothers, as pregnant females are the first to leave the arctic feeding grounds at the end of summer (Rice and Wolman, 1971). Moreover, with their calves, they are the last to migrate north in spring (Sullivan et al, 1983; Poole, 1984; and Herzing and Mate, 1984).

The benefits of a shortened northward migration hinge on the availability of adequate sources of prey in temperate southern waters. Where food resources are available well south of their principal feeding grounds, some whales can be expected to exploit them for energetic advantage. Thus, the shallow inshore portions of the Oregon coast, at least, should be considered as a narrow southward extension of the arctic summer feeding grounds of the gray whale.
CHAPTER FOUR

JUVENILE MORTALITY IN GRAY WHALES

(ESCHRICHTIUS ROBUSTUS)*

ABSTRACT

Reports of 218 stranded gray whales from diverse sources for the period 1952-1981 were summarized and analyzed for evidence of juvenile mortality patterns. Frequency of observed strandings was highest in winter lagoons. Eighty seven per cent of the reported stranded animals were less than 10 m in length, and were judged to be first or second year class animals. Most first year mortality occurred in winter lagoon. In the migratory corridor, second year class mortality was higher. The results of this study suggest a steeply descending juvenile mortality curve for this species, to mortality rates approximating 0.010 after the second year.

INTRODUCTION

During the past two centuries, all species of large whales have experienced episodes of intense commercial harvesting. Although the gray whale (Eschrichtius robustus) has more nearly recovered to its pre-exploitation numbers than have other large cetacean species (Rice, 1981), whaling pressures through the first

*Co-authored with James E. Harvey, Oregon State University Marine Science Center, Newport, Oregon.
two decades of this century have left a relatively youthful population with few individuals which would be older than 40 years as of 1980 (the age of sexual maturity given by Rice and Wolman, 1971). Thus, the gray whale population probably had not achieved either a stable or a stationary age distribution during the last period (mid-1960s) for which abundant life-history data exist (Reilly, pers. comm.). Consequently, mortality of juveniles is expected to reflect their relative abundance and be higher in gray whales than in unexploited mammalian species with greater proportions of older animals.

Swartz and Jones (1983) estimated calf mortality rates from observed early mortality in winter calving lagoons (0.054) and from differences between lagoon recruitment estimates and shore-based counts of north-migrating cows with calves about three months later (0.310). Gray whale population models developed by Reilly (1984) include estimated annual birth rates of no more than 0.014 and generalized annual mortality rates ranging from 0.103 for animals less than five years old to 0.055 for adult animals (older than 11 years). With resolution at the scale of individual age classes, Caughley (1966) proposed that most mammalian populations will exhibit U-shaped mortality curves, with mortality high in very young age classes, then several classes with low mortality followed by mortality gradually increasing with age. Such mortality patterns have not been defined for any species
of large cetacean. Our purpose in this paper is to examine patterns of strandings to clarify estimates of natural mortality rates in juvenile age classes of this currently little-harvested cetacean species.

METHODS

Reports of stranded gray whales were solicited from the Smithsonian Institution’s Scientific Event Alert Network (S.E.A.N.) and from biologists along most of the migratory range of this species in the eastern North Pacific Ocean, including winter lagoons in Baja California and summer feeding areas in the Bering Sea. Information on date of death or stranding, location of stranding, standard body measurements, sex, and cause of death were requested. In most instances, the original stranding reports were not available to us. The location or condition of the stranded animal sometimes precluded gathering all of the information requested. Of 98 strandings reported from the Bering Sea (F. Fay, pers. comm.), most were sighted from aircraft, without subsequent examination of carcasses. Body lengths of these whales were either estimated or were not reported. Consequently, no useful inferences regarding age can be made. As only two additional strandings were reported from north of the U. S.-Canadian border, this report is limited to the coast from Washington south through Baja California Sur, Mexico.
Observations were mostly opportunistic, without systematic efforts to search for stranded animals. The stranding process itself may be selective for calves because larger, older animals migrate farther offshore during the northward migration than do calves with their mothers (Poole, 1984) and spend less time in semi-enclosed winter lagoons (Jones and Swartz, 1984). Conversely, calves decompose and are removed from beaches more quickly after death, and their carcasses may reach shore less frequently if death occurs before stranding. In areas of infrequent observations, differential decomposition rates of carcasses may distort the size or age frequency of the stranded animals actually observed. Influences of these biases on our data set are unknown, and so no corrections for them are made in our interpretations.

RESULTS

Two hundred eighteen dead gray whales were reported south of 49°N latitude from 1952 through 1981; 85% were reported after 1971 (Fig. 4.1). Sex of 59% (130) was reported. Females accounted for 45.4% (59), and males 54.6% (71) of those whose sex was identified. There was no evidence that the frequency of stranding was related to the sex of the animal ($X^2 = 0.554$, d.f.=1, $\alpha = 0.05$).

The frequency of strandings was highest in winter lagoons (25-28°N--32°), followed by the Southern California Bight (32-35°N--29°), then the Monterey-San
Fig. 4.1. Time distribution of stranding occurrences south of 49° N. Open bars represent winter lagoon strandings.
Francisco area (37°-40° N--22°), with the remainder scattered from northern California through Oregon and Washington. The latitudinal distribution of strandings by month reflects the general migratory movements of this species including summer-month strandings of animals remaining at latitudes well south of the U.S.-Canadian border (Ch. 3).

Most (87%) of the 189 stranded gray whales for which lengths were reported were less than 10 m in length (Fig. 4.2). Age-length relationships developed for juvenile gray whales (Ch. 5) were used to establish the relative frequencies south of 49° N. First-year animals were less than 8 m in length, and their lengths overlapped the 7-9 m length range of second-year animals. Animals whose lengths were between 7 and 8 m were assigned to year class one if stranding occurred after June, and to year class two if stranding occurred prior to July. Subsequent year classes cannot be distinguished reliably on the basis of body length alone. Only the period from 1977-1981 was used to estimate age-related mortality because those years included extensive observations both in winter lagoons and along the migratory corridor. These data are summarized in Table 4.1 for the 112 animals whose body lengths were measured and reported for 1977-1981.

Causes of death usually were not determined. Most winter lagoon strandings apparently occurred shortly after parturition, for reports of fetal folds and unhealed
Fig. 4.2. Body length distribution of stranded animals. Approximate mean lengths at birth, weaning, and sexual maturity are shown.
Table 4.1. Year class assignment of gray whales (from Ch. 5) stranded between 1977 and 1981 whose body lengths were measured.

<table>
<thead>
<tr>
<th></th>
<th>winter lagoons</th>
<th>migratory corridor</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st year class:</td>
<td>50 (45%)</td>
<td>17 (15%)</td>
<td>67 (60%)</td>
</tr>
<tr>
<td>2nd year class:</td>
<td>4 (4%)</td>
<td>26 (23%)</td>
<td>30 (27%)</td>
</tr>
<tr>
<td>older animals:</td>
<td>1 (1%)</td>
<td>14 (12%)</td>
<td>15 (13%)</td>
</tr>
<tr>
<td>total:</td>
<td></td>
<td></td>
<td>112 (100%)</td>
</tr>
</tbody>
</table>

Umbilici were common. Outside lagoons, 10 deaths (one calf and nine probable yearlings) were attributed to gear entanglement, usually fishing nets or float lines on crab or lobster pots. Six additional animals (five were probable yearlings) exhibited severe bite wounds, likely consequences of attacks by large sharks or killer whales, Orcinus Orca (Baldridge, 1972). Two deaths were attributed to collisions with boats (D. Patten, pers. comm.), one to a severe bacterial infection (R. Stroud, pers. comm.), and one to apparent starvation.

DISCUSSION

The steadily increasing numbers of strandings (Fig. 4.1) likely reflect the continuing increase of the gray whale population size (Reilly, 1984a) as well as increased observer effort and improved reporting effectiveness. This is particularly apparent for the post-1976 period in the Baja California winter lagoons.

Most (60%) gray whale mortality south of 49° N., as
indicated by the frequency of stranded animals (Table 4.1), is in the first year class, followed by 27% in the second year class. Nearly three-quarters of the first year mortality occurs within a few weeks of birth in winter lagoons. The frequency of observed strandings in the migratory corridor outside winter lagoons is actually higher for second year animals (23%) than for calves (15%). These yearlings, on their first solo migration, may be particularly vulnerable to the perils of gear entanglement and large predators. Whether these trends continue into higher latitudes in summer must await length measurements of whales stranded along Canada's west coast and in the Bering and Chukchi seas.

Reilly's (1984a) models of gray whale population dynamics accommodate the observed population increase over 13 years of south migration censuses from 1967-68 to 1979-80 with a combined juvenile mortality of approximately 0.600 by age 11. Our data (Table 4.1) indicate that juvenile mortality is concentrated heavily in the first two age classes. Even if all observed stranding mortality reported here is assigned only to juvenile age classes, 60% of this (0.360) occurs during the first year, and 27% more (0.162) the second year. This intense first and second year mortality (0.522) requires that, to achieve the same net survivorship at sexual maturity as proposed by Reilly (1984), all other juvenile year classes must have exceedingly low mortality
rates (about 0.010).

These data define a steeply descending left side of the U-shaped mortality curve predicted by Caughley (1966), but the stranding data presented in this paper show none of the expected increase of adult mortality in old age (large size) classes. Absence of larger stranded animals likely reflects both the current youthful age structure of the population and possible stranding biases of larger animals migrating farther offshore and remaining in winter lagoons for shorter periods.

Our estimate of calf mortality rates (0.360) is the same as the combined lagoon and early north migration mortality calculated by Swartz and Jones (1983). However, they attributed most calf mortality to post-lagoon losses rather than to mortality within lagoons as the data in Table 4.1 indicate. The low estimates of lagoon mortality by Swartz and Jones was based on absolute rather than relative counts of stranded carcasses, and so are sensitive to factors affecting both stranding and carcass detection. Although our results do corroborate their conclusion of high calf mortality prior to completion of their first northward migration, their assignment of the bulk of that mortality to post-lagoon losses is not supported by the distribution of observed calf strandings reported here.

The interpretations presented here must be tempered with caution, for even in years with high numbers of
observed strandings (Fig. 4.1), only about 3-5% of the total annual mortality predicted by Reilly (1984a) was observed as stranded animals.
CHAPTER FIVE

GROWTH IN YOUNG GRAY WHALES, (ESCHRICHTIUS ROBUSTUS)

ABSTRACT

Mean body lengths of gray whale calves were found to increase linearly from 4.6 m at birth to 7 m by weaning at six months. After weaning, rates of length increase diminish, with calves reaching 8 m by one year of age, and 9 m by two years. Evaluations of the weights of nine gray whales as functions of their measured lengths and girths reduce the emphasis placed on fast-induced seasonal variations in girth by Rice and Wolman (1971). From birth weights of just under one metric ton, calves double their weights by three months of age, and double again by weaning at six months.

INTRODUCTION

The long-distance annual migrations which characterize the life cycles of large mysticete whales have been explained as behavioral adaptations which place newborn calves in warmer low-latitude waters during their initial post-natal growth period (Rice and Wolman, 1971; Lockyer, 1981). Our understanding of the adaptive significance of these extensive migrations requires descriptions of the patterns of change in body dimensions in calves following birth, for these changes largely
define the magnitude of the energy demands that these calves place on their lactating mothers for growth and for thermoregulation during the lactation period. This study was initiated to evaluate existing information and compile new data regarding the pattern of change in body length and weight for young gray whales (*Eschrichtius robustus*).

Patterns of change with age in either body length or body weight are not well documented for very young members of any mysticete species (Lockyer, 1981). Studies of age:length and age:weight relationships in gray whales have been restricted to older, usually sexually mature, animals (Rice and Wolman, 1971; Zimushko and Ivashin, 1980). Without access to animals less than one year in age (excepting fetuses), Rice and Wolman (1971) hypothesized that gray whale calves grow to 8.0-8.5 m by weaning at seven months of age and 9.0-9.5 m by the end of their first year. Zimushko and Ivashin (1980) concluded from similar evidence that gray whale calves reach only about 7 m by weaning, and do not achieve 8.5 m until their second summer. The very different conclusions of these two studies give widely differing estimates of age-related body weights and consequently of energy intake required for calf growth during this period.

Methods used to determine ages of baleen whales have been based on counts of incremental growth layers found in baleen plates (Ruud, 1940, Ichihara, 1966), in ear plugs
(Rice and Wolman, 1971), and in tympanic bullae (Nerini, pers. comm.). Of these, only ear plugs have been studied extensively in gray whales. Following the terminology proposed by Perrin and Myrick (1980), each pair of adjacent light and dark layers is considered here as a single growth layer group (GLG). No gray whale ear plugs have been collected and examined with fewer than two GLGs. In the collection reported by Rice and Wolman (1971) were eight whales with two ear plug GLGs each, taken mostly in February and March. Their body lengths ranged from 8.6 to 9.9 m. Using their assumed weaning length of 8.0-8.5 m and derived relationships between the numbers of GLGs and rates of accumulations of ovarian corpora in sexually mature females, Rice and Wolman (1971) hypothesized that gray whales form two ear plug GLGs during their first year and a single GLG annually thereafter. Zimushko (1970) employed similar techniques with gray whales killed in Arctic feeding grounds, but concluded that two ear plug GLGs rather than one are formed annually. In a later study based on a larger sample size, Zimushko and Ivashin (1980) imply that a single ear plug GLGs is produced annually, without clarifying the discrepancy with either the earlier interpretation of Zimushko or with that of Rice and Wolman. These conflicting interpretations of age based on ear plug GLGs indicated that an independent method of establishing length:age relationships was needed to evaluate the time interval represented by one GLG in
young gray whales.

LENGTH:AGE RELATIONSHIPS

The pattern of gray whale fetal growth described by Zimushko and Ivashin (1980) and by Rice (unpubl. ms.) included logistic growth curves leading to mean birth lengths of about 4.6 m. Their estimates of natal body lengths were based on measurements of 55 near-term fetuses and of 13 neonates stranded in winter lagoons and nearby open coasts. Table 5.1 summarizes body length information for those late-term fetuses and for 78 neonates, including 65 additional stranded neonates from Ch. 4 which were not available to Rice or to Zimushko and Ivashin. All fetuses were measured in December and January (presumably 1-2 weeks prior to calving; Rice and Wolman, 1971), and all but 2 neonates in January and February. Although the January neonates are slightly shorter than late fetuses for the same month, the difference is not significant at $\alpha = 0.05$ (ANOVA, $F$ calc. = 1.49; 0.25 $> P > 0.20$).

Table 5.1. Summary of body lengths of gray whale late term fetuses and neonates (from Rice and Wolman, 1971; Rice, 1983; and Ch. 4).

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<tbody>
<tr>
<td>n</td>
<td>31</td>
<td>24</td>
<td>50</td>
<td>74</td>
<td>28</td>
<td>133</td>
</tr>
<tr>
<td>$\bar{x}$</td>
<td>4.65</td>
<td>4.63</td>
<td>4.50</td>
<td>4.55</td>
<td>4.60</td>
<td>4.58</td>
</tr>
<tr>
<td>s.d. of $\bar{x}$</td>
<td>0.40</td>
<td>0.29</td>
<td>0.46</td>
<td>0.39</td>
<td>0.73</td>
<td>0.49</td>
</tr>
<tr>
<td>range</td>
<td>3.6-5.5</td>
<td>4.1-5.3</td>
<td>3.5-5.4</td>
<td>3.5-5.4</td>
<td>3.5-6.3</td>
<td>3.5-6.3</td>
</tr>
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</table>
Rice (1983) suggested that the lack of apparent fetal growth between December and January reflects a prenatal "diapause" in gray whale fetal growth. The body lengths shown for February neonates probably represent late births, and not a continuation of the prenatal diapause following birth. Unhealed umbilicuses and fetal skin folds were often still obvious, indicating that death had occurred within a few days of birth. As all these late term fetus and neonate lengths are considered equally valid estimates of length at birth, they are pooled to provide a single estimate of mean birth length, 4.58 m.

Body lengths of 230 small and presumably young gray whales (arbitrarily limited to those less than 9 m long and obtained at known times throughout the year) are presented as a scattergram in Fig. 5.1. These lengths include measurements of small whales collected in the study reported by Rice and Wolman (1971), of small stranded animals (Ch. 4), of small whales measured from aircraft and elevated coastal headlands in Oregon waters with photogrammetric methods (Ch. 3), and of the pooled fetus and neonate measurements summarized in Table 5.1.

With the exceptions of late term fetuses and neonates, ages of the animals whose lengths are included in Fig. 5.1 are not known. For most, however, reasonable possibilities are few. A whale measured at 7.2 m in August, for example, must be either about 7 or 19 months of age (based on an assumed mean mid-January birthdate;
Fig. 5.1. Distribution of body lengths of 230 gray whales plotted against the month at which their lengths were determined. Means, standard deviations, ranges, and sample sizes of fetuses and neonates are shown for December, January, and February.
Rice and Wolman, 1971). The absence of measured animals less than 6 m after June in Fig. 5.1 suggests a general pattern of body length increase following birth in January at a mean length of 4.6 m. The lack of data points between about 6 and 7 m in length from December through May appears to represent a real hiatus in the length:age distribution, clearly separating first and second year classes. This is consistent with growth that would follow a mean mid- to late-January birth length of 4.6 m, and also is apparent in frequency distributions of body lengths of stranded gray whales (Ch. 4). This hiatus becomes indistinct by summer (Fig. 5.1).

For the following analysis, animals in Fig. 5.1 whose lengths are less than 7 m prior to May are assumed to be young members of the first year class. The body lengths of these calves and of the pooled fetuses are plotted in Fig. 5.2. Seven small animals (less than 8 m) measured with aerial photogrammetric methods and observed in the close company of adult sized animals (presumed to be their mothers, Ch. 3) were also assumed to be calves. Their lengths, as well as those of Gigi II (maintained in captivity between the ages of 2 and 14 months; Wahrenbrock et al, 1974), also are included in Fig. 5.2.

The age \(A_m\), in months) distribution of body lengths \(L,m\) shown in Fig. 5.2 traces a coherent pattern of approximately linear growth at least to weaning at seven months (Eq. 5.1):
Fig. 5.2. Length:age distribution of small gray whales from Fig. 5.1 assumed to be less than 6 months old (●), those in the company of an adult and measured photogrammetrically (○), Gigi II (G), and those with (2) and (3) ear plug laminae (from Rice and Wolman, 1971). Equation 5.1 defines the regression between 0 and 7 months; and \( L = 7.97 + 0.05(A_m) \) defines the regression between 20 and 38 months.
Eq. 5.1: \( L = 4.58 + 0.37A_m; \quad r^2 = 0.62 \)

The 95% confidence interval for the mean of predicted \( L \) at 3 months (5.69 m) is 5.35-6.03 m (based on Eq. 5.1 and the data points in Fig. 5.2).

The early growth trajectory derived from Fig. 5.2 and described by Eq. 5.1 places calves at approximately 7 m in length by weaning in August. The pattern of growth after August is less apparent. Length measurements of Gigi II suggest an appreciable flattening of the growth curve late in the first year, possibly reaching 8 m by one year of age. Such a decrease in slope is also seen in larger mysticete species (Lockyer, 1976). The pattern of calf growth described by Eq. 5.1 and by measurements of Gigi II contradict the assumptions of Rice and Wolman (1971) that calves reach mean lengths of 8.5 m by six months of age; and by extension also negates their conclusion that 9-10 m long animals with two ear plug GLGs are only one year old. The simplest interpretation of the present data is that gray whales, like other species of large mysticetes, experience declining rates of length increase following weaning, and produce a single ear plug GLG annually. Consequently, the 9-10 m long animals listed by Rice and Wolman with two ear plug GLGs were more likely two years old rather than one. The body lengths of the animals with two and three ear plug GLGs are also shown in Fig. 5.2 at ages corresponding to two and three years, and a curve is projected through the means of their lengths.
WEIGHT:LENGTH RELATIONSHIPS

Body weights of whales typically are estimated from equations incorporating readily measured body dimensions (especially length) rather than from direct weighing (Omura, 1950, Ash, 1952, Lockyer, 1976). Rice and Wolman (1971) found significant decreases in maximum body girths (G, measured posterior to the pectoral flipper) between immature gray whales migrating south past central California (G = 0.56L; n = 28) and those going north 60-70 days later (G = 0.49L; n = 48). These temporary seasonal variations in girth of about 12.5% reflect annual fast-induced weight losses and indicate that the sensitivity of equations used to estimate body weights of gray whales are improved when girth is included as a variable. Rice and Wolman (1971) used an equation of the form:

Eq. 5.2: \( W = aG^2L \)

where \( a \) = an empirically derived coefficient = 38

\( W \) = body weight, kg

\( G \) = maximum body girth, m

\( L \) = standard body length, m

The value of the coefficient ‘\( a \)’ was derived from \( W, G, \) and \( L \) measurements of seven gray whales of which two were pregnant. With this derived co-efficient, Rice and Wolman used Eq. 5.2 to calculate weight losses experienced by gray whales of all ages between their north and south
passages past central California. They concluded that immature and non-pregnant adult gray whales incur weight losses of approximately 9-10% per month for the several month fasting portion of their winter migration.

Since the study of Rice and Wolman, several more young gray whales have been weighed. The G, L, and W values of these whales plus those originally reported by Rice and Wolman (1971, Table 2, p. 29) are listed in Table 5.2. The G/L ratios of the two pregnant females (#6 and #7), were about 15% larger than those of nonpregnant females and adult males (similar differences are also found between pregnant and nonpregnant Icelandic fin whales: Lockyer, pers. comm.); and animal #12 was extremely thin, with starvation a probable contributory

<table>
<thead>
<tr>
<th>Date</th>
<th>Sex</th>
<th>W, kg</th>
<th>G, m</th>
<th>L, m</th>
<th>G/L</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>20Jan68</td>
<td>F</td>
<td>900</td>
<td>2.15</td>
<td>4.75</td>
<td>0.45</td>
<td>neonate</td>
</tr>
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<td>9.65</td>
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<tr>
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<td>9.90</td>
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<tr>
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<td>11.72</td>
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<td>12.40</td>
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</tr>
<tr>
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<td>8.80</td>
<td>13.55</td>
<td>0.65</td>
<td>pregnant</td>
</tr>
<tr>
<td>19Aug36</td>
<td>F</td>
<td>31,470</td>
<td>8.48</td>
<td>13.35</td>
<td>0.64</td>
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</tr>
<tr>
<td>25Mar71</td>
<td>F</td>
<td>1,970</td>
<td>3.12</td>
<td>5.57</td>
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<td>Gigi II</td>
</tr>
<tr>
<td>18Nov71</td>
<td>F</td>
<td>3,450</td>
<td>3.62</td>
<td>7.20</td>
<td>0.50</td>
<td>Gigi II</td>
</tr>
<tr>
<td>03Mar78</td>
<td>M</td>
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<td>4.52</td>
<td>8.66</td>
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<tr>
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<td>7.81</td>
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<tr>
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<td>M</td>
<td>3,500</td>
<td>3.66</td>
<td>9.10</td>
<td>0.40</td>
<td>probable starvation</td>
</tr>
</tbody>
</table>

Sources: 1-7: Rice and Wolman, 1971
8-9: E. Wahrenbrock, pers. comm.
10: J. Harvey, pers. comm.
11-12: A. Geiger, pers. comm.
cause of death. Therefore, the measurements of these three animals were excluded from further evaluation. The weights of the remaining nine animals listed in Table 5.2 were analyzed as a dependent function of the independent variables G and L using a multiple regression method to obtain the equation for the least squares best fit. The resulting regression equation, simplified slightly to obtain integer exponents, is:

Eq. 5.3:  $W = 18.7GL^2; \ R^2 = 0.970$

For the same animals, Eq. 5.2 (Rice and Wolman, 1971) yields an $R^2$ value of 0.919.

These results indicate that gray whale body weights are defined almost entirely by length and girth dimensions, and are influenced more by changes in length than by changes in girth. Thus, Eq. 5.3 provides an improved basis over Eq. 5.2 for estimating $W$ from G and L measurements of immature and nonpregnant animals.

In combination with the length:age equation (Eq. 5.1) developed in the previous section, Eq. 5.3 is used to predict weights of calves as they age. Girth measurements of stranded calves are unreliable, for gas pressure from decomposition or the direct effects of the cause of death (i.e. starvation) often create serious distortions of normal body girth. Girth measurements of five live neonates are available: 0.49L, 0.50L, and 0.52L (Norris and Gentry, 1974), and 0.47L and 0.51L (Kooyman, pers. comm). These are very close to the mean girth of 0.49L
found for 54 near term fetuses (D. Rice, pers. comm.). Calves observed in winter lagoons in March are noticeably fatter than are January calves. Just after her capture at about two months of age, Gigi's girth was 0.60L, the same as when she was released one year later. Other immature gray whales must have similar girth measurements at the commencement of their southward fasting migration in November, for their mean girth is reduced to 0.56L by the time they reach central California a month later.

For the purposes of predicting rates of gray whale post-natal weight gain, it is assumed that the mean girth of calves at birth is 0.5L, increases to 0.6L by their third month when they depart the winter lagoons, and remains at 0.6L at least through their first summer. Thus, from typical birth weights of just under one metric ton, gray whale calves double their weight by three months of age, and nearly double that again to 3.5 metric tons by the time they are weaned in August of their first summer (Table 5.3). Support for these predictions comes from actual weights of Gigi II at 2.5 and 14 months of age.

Table 5.3. Calculated calf lengths and weights at age. Measured values of Gigi II in () from E. Wahrenbrock, pers. comm.

<table>
<thead>
<tr>
<th>Age, months</th>
<th>0</th>
<th>2.5</th>
<th>3</th>
<th>6</th>
<th>14</th>
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<td>Calculated L, m</td>
<td>4.6</td>
<td>5.5</td>
<td>5.7</td>
<td>6.8</td>
<td></td>
</tr>
<tr>
<td>Measured L, m</td>
<td></td>
<td>(5.5)</td>
<td></td>
<td>6.8</td>
<td>(8.2)</td>
</tr>
<tr>
<td>G/L</td>
<td>0.50</td>
<td>(0.60)</td>
<td>0.60</td>
<td>0.60</td>
<td>(0.60)</td>
</tr>
<tr>
<td>Calculated W, kg</td>
<td>910</td>
<td>1,870</td>
<td>2,080</td>
<td>3,530</td>
<td>6,190</td>
</tr>
<tr>
<td>Measured W, kg</td>
<td></td>
<td>(1,970)</td>
<td></td>
<td></td>
<td>(6,350)</td>
</tr>
</tbody>
</table>
which differ from predictions based on Eq. 5.3 by 5 and 3% respectively (Table 5.3), whereas Eq. 5.2 (of Rice and Wolman, 1971) overestimates the same weights by 16 and 17% respectively.

The implications of calculating body weights with Eq. 5.3 instead of Eq. 5.2 extend to adults as well. Fat whales at the end of summer are not as heavy, nor are lean whales weigh as small as previously suggested by Rice and Wolman (1971). Estimates of body weight losses attributed to lipid depletion during gray whale fasting migrations must be revised downward from 10% (Rice and Wolman, 1971) to about 6.5% of total body weight per month, as must estimates of energy production based on utilization of that lipid store (Ch. 2).
CHAPTER SIX

METABOLIC RATES OF FREE-SWIMMING GRAY WHALE CALVES
ESTIMATED FROM REMOTELY MONITORED VENTILATORY CHARACTERISTICS

ABSTRACT

A model of metabolic activity of gray whale calves is developed using ventilatory characteristics to estimate \( O_2 \) consumption. Breathing rates were derived from monitored breath hold times, and the fraction of \( O_2 \) extracted on each breath (\( F_{O_2} \)) was also found to be a function of breath hold time. Analyses of 110 time-flow rate recordings obtained in unrelated studies for two gray whale calves and one yearling indicated that tidal lung volume (\( V_t \)) can be predicted as a function of expiration duration (\( E_d \), in 0.01 s) and body length (\( L \), in m). Sound recordings of nearly 800 expirations of 32 unrestrained gray whale calves were made during the 1980 and 1981 winter seasons in Laguna San Ignacio, B. C. Sur, Mexico. With \( L \) estimated from age, \( V_t \) averaged 2.1% of body volume through the lagoon season. In combination with breathing rates and estimates of \( F_{O_2} \) based on the same ventilatory behavior, \( O_2 \) consumption on a breath-by-breath basis was calculated. Mean metabolic rate for neonates was 1.1 W/kg, and decreased in older calves. Observed aerobic scope was highest (about 4X) in neonates,
below the range of values typical for terrestrial mammals.

INTRODUCTION

Gray whale calves, *Eschrichtius robustus*, are born at the southern end of their long annual migratory
route. This long-distance migratory behavior for reproduction presumably is adaptive, as it places newborn calves in warm water of approximately 17-19°C (Fig. 1.2) throughout the winter lagoon season. However, no studies of metabolic rates or thermoregulatory capabilities have been conducted for calves of any species of large, highly migratory cetacean.

The purposes of this study are to: 1) measure the causes and magnitudes of individual variability in several ventilatory characteristics of young unrestrained gray whale calves, and to evaluate their potential applicability as predictors of O$_2$ consumption rates, and 2) to develop a general model of metabolic activity based on remotely monitored ventilatory characteristics of unrestrained gray whale calves during the three months following birth. Such a model is crucial to evaluating hypotheses concerning the evolution and maintenance of the extreme migratory behavior which characterizes the life cycle of this species.

Attempts to estimate metabolic rates of large and often inaccessible cetaceans often have become exercises in deduction and extrapolation, compounded by lack of
agreement on how well small manageable cetaceans serve as reasonable metabolic models of much larger ones. Estimating metabolic rates by scaling from experimentally derived values of smaller mammals (Scholander, 1940; Tenney and Remmers, 1963; Kanwisher and Sundnes, 1966; Rice and Wolman, 1971; Wahrenbrock et al., 1974), by estimating feeding rates and assimilation efficiencies (Brodie, 1975; Hinga, 1978; Lockyer, 1981), or by evaluating time-activity budgets or measuring turnover rates of injected labeled water (Hargrove and Gessaman, 1973) have been suggested as possible methods for establishing metabolic rates of whales. But all are either exceedingly difficult to apply to unrestrained animals or are inappropriate for active, feeding, growing gray whale calves which are usually visible only when they surface to breathe.

Use of ventilatory parameters to estimate metabolic rates of free-living homeotherms has met with mixed success (Stahl, 1967; Lasiewski and Calder, 1971; Hargrove and Gessaman, 1973; Leith, 1976; and O'Neil and Leith, 1980). One factor complicating this approach has been the dual roles of the respiratory surfaces of most homeotherms, functioning simultaneously as sites to facilitate gas exchange while providing extensive surfaces for evaporative cooling during periods of heat stress. Unlike terrestrial mammals, however, cetaceans regulate heat losses with vascular regulators in flukes, flippers,
and other specialized body surfaces (Parry, 1949; Scholander and Schevill, 1955; Elsner et al, 1974).

In this study, it is hypothesized that the thermoregulatory requirements placed on ventilatory mechanics are less in cetaceans than in nonaquatic homeotherms, and that breathing rates of cetaceans more closely reflect their rates of gas exchange. Hampton and Whittow (1975) reported a high positive correlation between breathing rates and rates of O₂ uptake in a captive Hawaiian spinner dolphin (Stenella longirostris: \( r^2 = 0.89 \), calculated from their Fig. 3, p. 196). In a study of south migrating gray whales (Ch. 3), relationships between breathing rates and swimming velocities were found to be consistent with predicted power: velocity relationships for swimming streamlined homeotherms. These observed relationships indicate that ventilation rates are mediated principally by breathing rates, and that breathing rates alone should provide reasonable relative indices of metabolic rates in migrating gray whales.

Estimates of oxygen consumption rates can be refined considerably if, in addition to breathing rates, tidal volumes (\( V_t \)) and fractions of extracted oxygen for each breath (\( FO_2 \)) also can be determined. Wahrenbrock et al (1974) reported mean \( V_t \) values of 2.0% of body volume (based on weight) and mean \( FO_2 \) values of about 11% for the captive gray whale, Gigi II, at 13 months of age.
Kooyman et al (1975) measured ventilatory flow rates and \( V_t \) of three temporarily restrained gray whale calves at ages less than 3 months, and reported mean \( V_t \) values from 2.1 to 2.5% of estimated body volume. In both studies, mean \( V_t \) values ranged from 57-64% of maximum \( V_t \) (Kooyman et al, 1975; Wahrenbrock, pers. comm.). No other \( V_t \) measurements of live, healthy mysticetes have been reported. Gray whale \( V_t \) values are appreciably lower than the maximum \( V_t \) values reported for killer whales, *Orcinus* (5.6% of body volume; Spencer et al, 1967), for pilot whales, *Globicephalus* (9.4%; Olsen et al, 1969) and for bottlenose dolphins, *Tursiops* (4.0%; Ridgway et al, 1969; and 8.9%; Kooyman and Cornell, 1981). All of these studies of captive or restrained whales were initiated principally as pulmonary function studies, and were not designed to provide effective measures of the variability anticipated from unrestrained animals functioning in typical environmental settings.

In a study of respiration in a trained, but free-swimming *Tursiops*, Ridgway et al (1969) reported \( \text{FO}_2 \) to be influenced by breathhold duration and depth of dive. Kolchinskaya et al (1980), also working with *Tursiops*, found three factors to be correlated with variations in ventilatory rhythm (including both breathing rate and breathhold pattern): activity level (reported as swimming speeds), time of day (presumably reflecting circadian cycles in feeding or other activities), and age
(or size). Tidal volume was found to be influenced by age (or size) and activity level (Kolchinskaya et al., 1980; Spencer, 1970, cited in Lockyer, 1981). No comparable studies of the causes of variability in ventilatory characteristics of mysticetes have been reported.

The general metabolic model developed here is based on the assumption that, in the thermally stable waters of calving lagoons, metabolic and heat loss rates are influenced principally by the magnitudes of and changes in body sizes and activity levels of the subjects (Schmidt-Nielsen, 1975; Wilkie, 1977; Calder, 1981). Assumed relationships of several ventilatory characteristics to size and activity are shown in Fig. 6.1. In this study each component of the proposed model is estimated or measured for gray whale calves between birth and the end of the lagoon season three months later; and an empirical equation for its prediction from body size, activity levels, and remotely monitored ventilatory characteristics is developed. From these equations, a model of the metabolic activity patterns of young gray whale calves is constructed and evaluated. Where feasible, assumptions incorporated into the model are validated using captive *Tursiops*. Heat losses and minimum required thermogenesis are addressed in the following chapter.
Fig. 6.1. General model of relationships between age and body size, activity levels, ventilatory characteristics, and metabolic rates of gray whale calves.
METHODS

Age and body size

Most gray whale calves are born in or near three major lagoon systems along the southern half of the west coast of Baja California Sur (25-28° N.). These lagoons are characterized by nearly stable wintertime water temperatures of 17-19°C, and include Laguna Ojo de Liebre, Laguna San Ignacio, and the large Bahia Magdalena complex. Calves occupy these lagoons with their mothers until late March or early April when they commence their northward migration. The earliest births are reported in early January and newborn calves are not seen after mid-February (Jones and Swartz, 1984). Most births occur in the last half of January, with variations in the mean date of birth of no more than two weeks from one year to the next (Rice et al., 1981). Lacking methods of establishing more precisely the birthdates of individual subjects, standardized ages are indicated as the number of days after January 1. Changes in body length and weight with age, based on an assumed mean birthdate of January 20 are described by Eqs. 5.1 and 5.3 (Ch. 5), and are modified as Eqs. 6.1 and 6.2 to accommodate standardized ages in days \( (A_d) \) after January 1:

\[
\text{Eq. 6.1: } L = 4.4 + 0.012(A_d) \\
\text{Eq. 6.2: } W = 18.7(G)(L)^2
\]

\( A_d \) in days, \( L \) and \( G \) in m, and \( W \) in kg
Study sites and subjects

Field studies were conducted in Laguna San Ignacio, Baja California Sur, Mexico, during the January-April lagoon seasons of 1978-1981. This lagoon was selected for its relatively small size (25x6 km), high wintertime density of gray whale calves (over 200 at each season's peak), and especially for the occurrence of a type of behavior nearly unique to this lagoon. This contact behavior, frequently termed "curious" or "friendly", is exhibited by a small number of calves and adults that can be approached, touched, and to varying degrees, manually manipulated without causing apparent distress. The animals used in this study were not restrained and were free to terminate contact any time. To avoid unsupported implications concerning the reason(s) for this behavior, it will be termed tactile behavior in this paper.

Breathhold and activity patterns

Breathhold times and breathing patterns of calves were determined by voice recording the expiration events of observed calves with a portable cassette tape recorder or by recording the expiration sounds of observed animals directly with a Uher model 4400 dual channel tape recorder and a Sennheiser model MK815U directional microphone. Voiced notes describing activity were made simultaneously. Tapes were later played back with a clock to obtain
breathhold times. Continuous observation periods of 10 min or 15 consecutive expirations were considered minimum acceptable time samples, and samples of 20-30 min were more typical. Mean breathhold times were calculated and histograms of the frequency distributions of breathhold times were constructed (Appendix 3) for each acceptable sample period to determine maximum breathhold times and frequency of breathholds greater than 60 s.

Activity patterns of calves were difficult to assess, for calves spend little of their time visible at the surface. Surface indications of activity could be observed only during daylight hours and in periods of relative calm (3 or less on the Beaufort scale of sea states). Therefore, in place of descriptive activity labels, a numerical activity level was assigned based on observable surface activity. For each breathhold observation period, the calf was assigned an activity level according to the following criteria:

Activity level 1: Except for blowing, little surface activity such as circling, splashing, fluke flopping, or direction or position changing. Always with a cow that is quiescent.

Activity level 2: More surface activity than level 1, or moderate continuous swimming speed, but without characteristics of level 3. Cow may be active or quiet.
Activity level 3: Repeated breaching or lunging by calf with bow wave and strong flukeprints (in quiet water), often with flukes thrown clear of water; or keeping pace with cow when she is forming a breaking bow wave.

Extraction of oxygen (FO₂)

A valve-and-balloon device, similar to that used by Wahrenbrock, et al (1974), was initially tested to capture expired lung gases for O₂ analysis as well as for measurements of Vₜ. Avoidance of this device by tactile calves subsequently led to a simplified gas capture system consisting of a 5 l latex meteorological balloon attached to a short section of rigid PVC pipe and valved manually with thumb and index finger (Fig. 6.2). Subsamples (2 to 5 l) of expired gases were obtained and sealed, then analyzed within 1 h of collection to reduce errors related to CO₂ diffusion from the collection bag (Kasch and Phillips, 1965). Each sample was passed through a drying column of silica gel, then over the sensing element of Servomex model OA150 polarographic O₂ analyzer calibrated to atmospheric O₂. Two readings were obtained; one when half the sample had passed through the analyzer, the other on completion, and the two were averaged and subtracted from 20.9% to obtain FO₂. Initially, FO₂ was not corrected for expired CO₂ to
Fig. 6.2. Expired lung gas sampler in use on a tactile whale.
permit direct comparisons with results obtained from *Tursiops* by Ridgway et al, 1969. Breathhold times prior to the sampled expirations were obtained from voice recordings made during the sampling session. All samples were obtained opportunistically from tactile calves exhibiting moderate levels of activity typical of contact situations, but atypical of the activity level criteria established in the preceding section.

**Tidal lung volume**

Direct capture of complete expirations for $V_t$ assessment was precluded by avoidance responses of tactile calves when the valve-and-balloon device was placed on their blowholes. However, three unpublished series of time:flow rate records of expirations of young gray whales initially obtained for other studies (Wahrenbrock et al, 1974; and Kooyman et al, 1975) made possible an alternative non-contact method for estimating $V_t$ of unrestrained calves on a breath-by-breath basis. Two series, obtained from calves estimated to be less than 3 months old, were provided by Dr. G. Kooyman; and another, of Gigi II at 13 months of age, by Dr. E. Wahrenbrock. These records were made by temporarily stranding the calves, fitting a laminar flow element type pneumotachograph over their blowholes and recording the time change in flow rates during expiration and inspiration.
The ventilatory flow rate:time curves were redrawn to a common scale. Tidal volumes were calculated by integrating the area under the flow curves with a computer driven graphics digitizer. Expiration durations (E_d) and peak expiratory flow rates (PEF) were derived from the same curves (Fig. 6.3a). All volumes are reported at ATPS, as the data needed to correct to STPS are unavailable. These data (listed in Appendix 4) were analyzed with least squares multiple regression techniques to determine the relationship between the E_d and PEF of each expiration and its V_t, as well as body length (L). The derived empirical equation was used for the prediction of V_t from independent estimates of E_d and/or PEF obtained from recordings of unrestrained calves' expiration sounds in the lagoon setting.

During the 1980 and 1981 seasons, expiration sounds of unrestrained calves were recorded throughout the lagoon season to obtain measures of their E_d. Recordings were made with the Sennheiser directional microphone on one channel of the two-channel tape recorder. Voiced notes regarding behavior, activity, and animal identification were recorded on the second channel. Clean recordings of expiration sounds could be made only during periods of calm or very light wind, and then only when microphone-calf distances were less than about 250 m. Minimum acceptable sample size of readable recordings for each calf was 10.
Fig. 6.3. Tidal volume ($V_t$), peak expiratory rate (PEF), of expirations. A from pneumotachograph traces, and B from oscilloscope traces of recorded expirations.
Preliminary visual inspection of time-frequency spectrographs of six calf expirations indicated that most of their acoustic energy was concentrated below 2500 Hz, with strong low frequency wind and water surface noise below 300 Hz. Therefore, recorded expiration sounds were passed through a Hewlett-Packard sound filter/amplifier with a low end frequency cutoff set at 300 Hz with 24 db/octave rolloff to reduce background noise. The filtered signal then was projected as a time-intensity image on an oscilloscope and permanent paper records of the signals were made (Fig. 6.3b). The duration of each expiration signal was measured with vernier calipers to a precision of 0.01 s. Inspiration amplitudes generally were much lower and yielded indistinct signals inadequate for analysis. They were therefore not considered in this study. Breathhold times preceding each expiration were obtained from the same recordings, and were noted to the nearest 1 s.

Captive *Tursiops* studies

Ventilatory characteristics of captive *Tursiops* were measured at the Naval Ocean Systems Center, San Diego, to test in controlled circumstances some of the methods and assumptions applied to gray whale calves in field settings. The animals used, with sex, weight, and standard length were: A (male, 255 kg, 308 cm), B (female, 173 kg, 243 cm), and C (female, 155 kg, 237 cm).
Expired lung gas samples of *Tursiops* were obtained from animals trained to hold a padded bitebar just under the water surface and expire on command into a water-filled gas collection dome (Fig. 6.4) after breath holds of 10-60 s (similar to the apparatus used by Ridgway et al, 1969). Subsamples (1 to 3 l) of the expired gas were collected in 5 l latex meteorological balloons and analyzed using an Applied Biochemistry Oxygen Analyzer calibrated to atmospheric O₂. Expired CO₂ was not determined, for absorption by sea water was expected to substantially, but unpredictably, reduce the CO₂ content of the samples. Samples were obtained from two animals during quiescent periods and from one of these immediately after 5 min periods of vigorous activity including rapid swimming, tailwalking, and jumping.

Ventilatory flow rates of two *Tursiops* were measured with a pneumotachograph consisting of a 17 cm diameter laminar element flow meter manufactured by Miriam Instruments, Inc., and provided by Dr. G. Kooyman, Scripps Institution of Oceanography. The apparatus and its operation are discussed by Kooyman et al (1975) and Kooyman and Cornell (1981). The system was calibrated by passing precisely measured volumes of dry air through the flow meter, recording the time:flow rate output signal, and integrating that signal to derive volume. Chart recordings of the amplified output signal were made with a Grass model 7B Polygraph and subsequently analyzed as for
Fig. 6.4. Schematic drawing of apparatus used to collect expired lung gases from captive *Tursiops*. Scale bar = 30 cm.
gray whales. Samples of expiratory/inspiratory cycles were obtained while the dolphins were held partially submerged in a restraint box. The pneumotachograph was placed snugly over the blowhole until an expiratory/inspiratory cycle occurred. At least one normal breathing cycle, without the pneumotachograph on the blowhole, was allowed to occur between sampled cycles. Simultaneous with the pneumotachograph recordings, the expiration/inspiration sounds were recorded on audio tape using the Sennheiser directional microphone placed approximately 2 m from the blowhole. This system also was used to record voiced data.

For each recorded expiration, $V_t$, $E_d$, and PEF were determined. Features of inspiratory flow traces were not measured, for the amplitudes of inspiratory sounds were too small to permit accurate determination of their durations. Durations and peak amplitudes (in arbitrary units) were obtained of the recorded audible signals of each sampled expiration as described for gray whales, as were durations of additional "normal" expirations without the pneumotachograph in place.

Linear regression equations and their coefficients of determination, determined by the method of least squares, are described by Sokal and Rohlf (1981), with statistical tables from Rohlf and Sokal (1981). Levels of significance ($\alpha$) in all tests are 0.05. Units conform to guidelines of the American Physiological Society for
respiratory mechanics units (Fishman, 1985) and of the International Union of Physiologists for metabolic and thermal physiology units (Bligh and Johnson, 1973).

RESULTS

Breathhold times and breathing patterns

Acceptable breathhold sequences from 78 calves, 39 in activity 1, 36 in activity 2, were logged, with a total of 2021 timed breath holds. Frequency distributions of calf breath holds for activities 1 and 2 during the first, second, and third months of the lagoon season (beginning 8 January) are shown in Fig. 6.5 and described in Table 6.1. Apparent in Fig. 6.5 is a strong mode at about 20 s in all Table 6.1. Summary statistics for calf breathhold patterns.

<table>
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<th>ACTIVITY 1</th>
<th>ACTIVITY 2</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>2</td>
</tr>
<tr>
<td>day</td>
<td>8-38</td>
<td>39-68</td>
</tr>
<tr>
<td># calves</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td># breathholds</td>
<td>290</td>
<td>202</td>
</tr>
<tr>
<td>mean breathhold, s</td>
<td>34</td>
<td>37</td>
</tr>
<tr>
<td>breathing rate, /s</td>
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<td>1.62</td>
</tr>
<tr>
<td>mean&lt;60, s</td>
<td>22</td>
<td>17</td>
</tr>
<tr>
<td>%&lt;60</td>
<td>84</td>
<td>76</td>
</tr>
</tbody>
</table>

ANOVA results comparing mean breathholds at activity 1 and 2 for each month.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>calculated F</td>
<td>18.75</td>
<td>2.10</td>
<td>0.06</td>
</tr>
<tr>
<td>critical F</td>
<td>4.23</td>
<td>4.45</td>
<td>4.26</td>
</tr>
<tr>
<td>degrees of freedom</td>
<td>1, 26</td>
<td>1, 18</td>
<td>1, 24</td>
</tr>
<tr>
<td>Accept or Reject H</td>
<td>R</td>
<td>A</td>
<td>A</td>
</tr>
</tbody>
</table>
Fig. 6.5. Frequency distributions of calf breathholds, in 10 s increments, for the first three months following birth (activity 1 = narrow bars, activity 2 = wide bars).
3 months and at both activities. Sixty seconds was arbitrarily selected to separate "short" from "long" breath holds. The frequency of short breath holds (less than 60 s) decreases from 92% of the total in the first month to about 77% by the end of the lagoon season as the maximum breathhold capacity increases from two to nearly three min. Means of breath holds less than 60 s are not significantly different at different activity levels (ANOVA, F=0.384, d.f.=1,72). Overall mean breathhold times at activity levels 1 and 2 do differ significantly for the first month, but not for the following two months (Table 6.1), and were found to increase significantly between the beginning and end of the lagoon season (Fig. 6.6 and Eq. 6.3, which describes the least squares regression of mean breathhold time with age, A_d).

Eq. 6.3: breathhold time = 24.3+0.25(A_d)

r^2=0.431; critical r^2=0.225(d.f.=73).

Inclusion of activity at levels 1 and 2 as a second independent variable in the regression reduces the proportion of unexplained variation by 11.6% (partial r^2= 0.116). Insufficient level 3 activity was observed to permit a comparable regression against time through the lagoon season. Mean breathing rate, in breaths/min, is 60/(mean breathhold time), or Eq. 6.4.

Eq. 6.4. breathing rate = 60/(24.3 + 0.25(A_d))
Fig. 6.6. Scattergram of mean breathhold durations of calves for the first 3 months following birth (solid circles = activity 1, open circles = activity 2).
gray whales

The fraction of O₂ extracted from inspired air was measured for 21 expirations from 10 tactile calves over a three year period between 4 March and 5 April in 1978 and 1981. Samples from very young whales born before March were not obtained, as calves seldom exhibited tactile behavior until late February when they are presumed to be at least one month old. Tactile calves frequently avoided the sampling device after it was placed on their blowholes, thus limiting the number of samples obtained. A maximum of 4 samples was obtained from one calf. Two additional values reported for Gigi II while in captivity at approximately the same age are also included (E. Wahrenbrock, pers. comm.). FO₂ values of the 23 samples were quite variable ranging from 4.5% to 12.5%. In Fig. 6.7, FO₂ values are plotted against values of breathhold duration preceding the sampled expiration, with the best least squares regression line fitting the data points described by Eq. 6.5:

Eq. 6.5: FO₂ = -1.58 + 3.364(ln(breath hold))

r² = 0.619; critical r² = 0.171; d.f. = 21

FO₂ values calculated with Eq. 6.5 using frequency weighted values of the 10 s breathhold increments shown in Fig. 6.5 (with activities combined for each month) are
Fig. 6.7. Scattergram of $F_O_2$ values plotted as a function of preceding breathhold time. Open circles are from Gigi II. Regression line is defined by Eq. 6.5.
listed in Table 6.2, and are compared to \( \text{FO}_2 \) values calculated from mean breath holds alone (calculated \( \text{FO}_2 \) for breathhold increments longer than 2 min were assigned values of 15\%). \( \text{FO}_2 \) based on mean breath hold consistently overestimates \( \text{FO}_2 \) calculated from frequency distributions of breath holds by 15-20\% (Table 6.2).

Table 6.2. Comparison of \( \text{FO}_2 \) calculated from frequency distribution of breathholds (b) with \( \text{FO}_2 \) calculated from mean breathhold only (a). Included for further comparison are similar data for calves during summer months (June-August) along the Oregon coast (Appendix 5).

<table>
<thead>
<tr>
<th>month</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean breathhold (activities combined)</td>
<td>29</td>
<td>35</td>
<td>48</td>
<td>56</td>
</tr>
<tr>
<td>( \text{FO}_2 ) (a)</td>
<td>9.7</td>
<td>10.4</td>
<td>11.4</td>
<td>12.0</td>
</tr>
<tr>
<td>( \text{FO}_2 ) (b)</td>
<td>8.3</td>
<td>8.3</td>
<td>9.6</td>
<td>9.6</td>
</tr>
<tr>
<td>( b/a )</td>
<td>0.86</td>
<td>0.80</td>
<td>0.84</td>
<td>0.80</td>
</tr>
</tbody>
</table>

Frequency distributions of breathholds are assumed to provide a more precise basis for estimating \( \text{FO}_2 \), but are more difficult to characterize than mean breath hold. To facilitate calculations of \( \text{FO}_2 \) from mean breathhold values alone, Eq. 6.5 is reduced by 17\% as Eq. 6.6.

\[
\text{Eq. 6.6: } \text{FO}_2 = -1.31 + 2.93 \ln (\text{mean breath hold}).
\]

**Tursiops**

The effects of interanimal and activity level differences on \( \text{FO}_2 \) were examined by collecting lung gases from 2 Tursiops (55 from A and 46 from C). Regressions of \( \text{FO}_2 \) on breathhold duration while
quiescent (approximately equivalent to activity levels 1-2 for gray whales) are presented in Fig. 6.8 (curves a and b). Also shown in Fig. 6.8 (curve c) are results obtained by Ridgway et al. (1969) for a smaller Tursiops (Tuffy, a 140 kg female) while breathholding at the water surface. The regression lines of all three animals while quiet are similar to each other and to the gray whale curve (Fig. 6.8, curve d) in both slope and intercept. However, FO₂ increases dramatically at higher activity levels. At short breath holds of 10-20 s, C extracted almost twice as much O₂ (curve e, Fig. 6.8) immediately following activity that included several tailwalks and jumps clear of the water than she did while quiet.

These FO₂ values have not been corrected for CO₂ content of expired air. Lacking R.Q. values for any of the 3 Tursiops, corrections can not be made. For gray whales, however, an R.Q. of 0.7 based on lipid metabolism can be assumed, and appropriate corrections for the volumes of CO₂ in expired air (Fishman, 1985) are combined with Eq. 6.6 to give Eq. 6.7:

Eq. 6.7: \( \text{FO}_2 = -1.48 + 3.05(\ln \text{mean breath hold}) \).

tidal lung volumes

\( V_t : E_d \) relationships of gray whales

Summaries of the three series of expiration flow rate
Fig. 6.8. Regression curves of $F_O_2$ as functions of prior breathhold for 3 *Tursiops* and gray whales (from Fig. 6.7). a = animal A, $r^2 = 0.81$; b = animal C, $r^2 = 0.50$; c = Tuffy (Ridgway et al., 1969), $r^2 = 0.96$; e = animal C (active), $r^2 = 0.66$; and d = gray whales, $r^2 = 0.62$. 
records of the two calves provided by Kooyman and of Gigi II (Wahrenbrock, pers. comm.) at 13 months of age are listed in Table 6.3. Scattergrams of expired $V_t$ against $E_d$ are plotted in Fig. 6.9. A multiple regression of the values in Fig. 6.9 yielded the least squares best equation, Eq. 6.8, demonstrating that the regression of $V_t$ on $E_d$ and $L$ explains a large and significant portion of the observed variation in $V_t$ (corrected to STPD).

$$\text{Eq. 6.8: } V_t = 0.0038 E_d^{1.55} L^{1.63}$$

$$R^2 = 0.940, \text{ critical } R^2 = 0.054, \text{ d.f. } = 2, 108$$

Table 6.3. Summary statistics of 3 series of time:expiration flow rate records. Courtesy Dr. G. Kooyman (calves #1 and #2) and E. Wahrenbrock (calf #3). All volumes at BTPS.

<table>
<thead>
<tr>
<th>calf #</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L$, m</td>
<td>4.77</td>
<td>5.78</td>
<td>8.07</td>
</tr>
<tr>
<td>$W$, kg (est or actual)</td>
<td>1015</td>
<td>1712</td>
<td>6150</td>
</tr>
<tr>
<td># expirations</td>
<td>63</td>
<td>21</td>
<td>26</td>
</tr>
<tr>
<td>$V_t$ mean, l</td>
<td>19.3</td>
<td>23.9</td>
<td>124</td>
</tr>
<tr>
<td>$V_t$ range, l</td>
<td>0.8-35.5</td>
<td>1.3-54.8</td>
<td>30-195</td>
</tr>
<tr>
<td>$E_d$ mean, .01 s</td>
<td>46</td>
<td>40</td>
<td>95</td>
</tr>
<tr>
<td>$E_d$ range, .01 s</td>
<td>9-82</td>
<td>14-91</td>
<td>32-130</td>
</tr>
<tr>
<td>PEF mean, 1/s</td>
<td>64</td>
<td>85</td>
<td>207</td>
</tr>
<tr>
<td>PEF range, 1/s</td>
<td>15-99</td>
<td>26-131</td>
<td>161-285</td>
</tr>
</tbody>
</table>

Curves for the three whales are fitted to the data in Fig. 6.9 according to Eq. 6.8 and the body length of each whale. When (PEF) is added as a third independent variable, the $R^2$ value increases to 0.991, with PEF accounting for most of the variation left unexplained by Eq. 6.7 (partial $R^2 = 0.850$). Thus, the 3 independent
6.9. Scattergram of $V_t$ (at BTPS) as a function of measured expiration duration for calves 1-3 in Table 6.3. Regression lines from Eq. 6.8.
variables, $E_d$, $L$, and PEF account for essentially all of the observed variation in $V_t$.

Field recordings of gray whale expiration sounds

Durations of expiration sounds from 32 calves, 14 in activity 1, and 18 in activity 2, were measured between days 9 and 97 of the lagoon season. Figure 6.10 illustrates the variation in mean $E_d$ with age of 793 expirations of acceptable quality, with a least squares linear regression curve fitted to the mean values in Fig. 6.10 and described by Eq. 6.9.

\[ E_d = 44.9 + 0.20(A_d) \]
\[ r^2 = 0.516, \text{ critical } r^2 = 0.126, \text{ d.f. } = 30 \]

Inclusion of activity as a second independent variable in the regression decreases the proportion of explained variation (partial $R^2 = -0.018$), so no further consideration is given to the effects of activity on $E_d$. For all 32 calves, $r^2$ values between $E_d$ and its preceeding breathhold was less than 0.07. The C.V. of each animal's mean $E_d$ value averaged 13.5%.

Equations 6.8, 6.9, and 6.1 are combined in Eq. 6.10 to predict mean $V_t$ throughout the lagoon season.

\[ V_t = 0.0033(44.9 + 0.20(A_d))^{1.55} \times (4.40 + 0.012(A_d))^{1.63} \]

A curve generated by Eq. 6.10 and substituting Gigi's actual length measurements for calculated $L$, is compared in Fig. 6.11 to 30 $V_t$ values reported by Wahrenbrock
Fig. 6.10. Scattergram of $E_d$ as a function of day. Means are indicated by solid circles for activity 1, horizontal bars for activity 2. Vertical bar represents ± 1 s.d. Regression line is described by Eq. 6.9.
Fig. 6.11. Comparison of predicted (line) and measured $V_t$ of Gigi at different ages.
(pers. comm) for Gigi over a period of nearly one year. Gigi's $V_t$ values, measured with a blowhole pneumotachograph, are similar to, but slightly and consistently lower than values predicted with Eq. 6.10 for unrestrained animals of the same size.

**Tursiops expiration features**

The combined results of 61 complete expiratory/inspiratory cycles from two *Tursiops* were used to determine the least squares regression between $E_d$ derived from flowmeter chart recordings ($E_{dc}$) and $E_d$ derived from recorded sounds ($E_{ds}$), Eq. 6.11.

Eq. 6.11: $E_{ds} = 0.940(E_{dc})$

$r^2 = 0.967$, critical $r^2 = 0.064$, d.f. = 59

These results confirm $E_{ds}$ as a precise estimator of $E_{dc}$, and no further distinction will be made between $E_d$ values derived from flowmeters and those from recorded expiration sounds.

$E_d$ values of 2 *Tursiops*, obtained from expiration sound recordings while the flowmeter was on the blowhole, are compared to durations of similar numbers of expirations without the pneumotachograph in place, but with the animal still in the restraint box. The results (Table 6.4) indicate that both animals took significantly shorter (and likely smaller) expirations when the flowmeter was on the blowhole than when off.
Table 6.4. Summary statistics of the durations of expiration sounds with and without the pneumotachograph in place for 2 *Tursiops*, A and B.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>on</td>
<td>off</td>
</tr>
<tr>
<td>n</td>
<td>25</td>
<td>17</td>
</tr>
<tr>
<td>range</td>
<td>.42-.54</td>
<td>.40-.65</td>
</tr>
<tr>
<td>mean</td>
<td>.45</td>
<td>.51</td>
</tr>
<tr>
<td>S.D.</td>
<td>.03</td>
<td>.05</td>
</tr>
<tr>
<td>difference in means, %</td>
<td>13</td>
<td>19</td>
</tr>
</tbody>
</table>

ANOVA test:
- d.f.: 1, 40
- calculated F: 32.9
- critical F: 4.08
- Accept or Reject H: R

PEF could not be predicted well from maximum amplitudes of 25 recorded *Tursiops* expiration sounds ($r^2=0.237$). As wind or distance induced variability in amplitudes of field recorded expiration sounds can neither be eliminated nor easily corrected, PEF is not considered further as a useful variable in this study.

Metabolic rates

Table 6.5 summarizes calculated growth and ventilatory characteristics and derived metabolic rate estimates of gray whales from birth to lagoon departure at three months. When corrected to STPD, estimated $V_t$ remains approximately 1.8% of body weight throughout the lagoon period. Metabolic rate calculations assume that lipids are the sole oxidative substrate, requiring 2 l of $O_2/g$ of lipid and releasing 4.7 kcal (19.8 kJ)/l of $O_2$. 
Table 6.5. Summary of calf ventilatory and metabolic characteristics.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Eq. #</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days, after 1 January</td>
<td>6.1</td>
<td>15</td>
<td>45</td>
<td>75</td>
<td>105</td>
</tr>
<tr>
<td>L, m</td>
<td>6.2</td>
<td>4.58</td>
<td>4.95</td>
<td>5.32</td>
<td>5.69</td>
</tr>
<tr>
<td>W, kg</td>
<td>6.3</td>
<td>28</td>
<td>36</td>
<td>43</td>
<td>51</td>
</tr>
<tr>
<td>br. rate, 1/min</td>
<td>6.4</td>
<td>2.1</td>
<td>1.7</td>
<td>1.4</td>
<td>1.2</td>
</tr>
<tr>
<td>Fo2, %</td>
<td>6.7, 6.3</td>
<td>8.7</td>
<td>9.5</td>
<td>10.0</td>
<td>10.5</td>
</tr>
<tr>
<td>Eq! 0.01 s</td>
<td>6.9</td>
<td>48</td>
<td>54</td>
<td>60</td>
<td>66</td>
</tr>
<tr>
<td>mean Vt, l</td>
<td>6.10</td>
<td>15.8</td>
<td>21.6</td>
<td>29.3</td>
<td>36.9</td>
</tr>
<tr>
<td>Vt/W, x100</td>
<td>6.8x6.4</td>
<td>33.2</td>
<td>36.7</td>
<td>40.8</td>
<td>44.3</td>
</tr>
<tr>
<td>MV, 1/min</td>
<td>2.9</td>
<td>3.5</td>
<td>4.0</td>
<td>4.7</td>
<td></td>
</tr>
<tr>
<td>MVxFO2</td>
<td>4157</td>
<td>5021</td>
<td>5760</td>
<td>6698</td>
<td></td>
</tr>
<tr>
<td>O2 use, 1/day</td>
<td>2.08</td>
<td>2.51</td>
<td>2.88</td>
<td>3.35</td>
<td></td>
</tr>
<tr>
<td>M MR</td>
<td>19.5</td>
<td>23.6</td>
<td>27.1</td>
<td>31.5</td>
<td></td>
</tr>
<tr>
<td>Watts</td>
<td>948</td>
<td>1145</td>
<td>1313</td>
<td>1527</td>
<td></td>
</tr>
<tr>
<td>Watts/kg</td>
<td>1.06</td>
<td>0.95</td>
<td>0.83</td>
<td>0.74</td>
<td></td>
</tr>
</tbody>
</table>

Wiegart, 1976). Calculated metabolic rates of the 32 animals included in Fig. 6.10 are shown in Fig. 6.12, and are compared to mean metabolic rate (MMR) values from Table 6.5. MMR increases about 61% as body weight increases 227% between birth and 3 months. Weight corrected MR for neonates is slightly less than 1 W/kg, and decreases in older animals. Minimum observed metabolic rates (MOMR) of neonates (Fig. 6.12) is about 500 watts, or 0.5 W/g. Observed aerobic metabolic scope (Fig. 6.12) is about 4 fold in neonates.

DISCUSSION

Consistent patterns in gray whale ventilatory behavior can be identified and characterized almost
Fig. 6.12. Scattergram of calculated metabolic rates of 32 calves (solid circles), and MMR for 0, 1, 2, and 3 months of age (open squares) from Table 6.5.
completely by measuring mean and maximum breathhold times and percentage of breathholds less than 60 s. These are predictable aspects of the ventilatory rhythm of calves which change with age; and time trends of these variables continue to midsummer of the calves' first year when they become statistically indistinguishable from those of adults (Appendix 5). The observed decrease in breathing rates with increasing age is a consequence both of decreasing frequency of breathholds less than 60 s and of increasing maximum breathhold times. Maximum observed breathhold times are about two min for neonates and three min for three month old calves. Within these limits, the actual breathhold pattern exhibited seems to be functions both of the $O_2$ needs of an animal and of its underwater activity obligations, such as suckling or swimming, which require breathholding.

The numerical activity scores used in this study are of little practical value, for they exhibit no statistically significant relationship to breathing rate after the first month, nor to $E_d$ at any age. The appropriateness of criteria used for activity ranking seems to diminish as calves get older, for such ranking appears to become a self-confirming exercise: Animals exhibiting higher breathing rates appear to the observer to be more "active", and are ranked accordingly. As most observable surface behavior of calves is related to ventilation, breathing rate itself seems to be the best
available numerical indicator of activity intensity.

Ventilatory patterns of whales in working activities which require submergence (such as suckling, foraging, or swimming) are expected to evolve in ways which provide adequate supplies of \( O_2 \) while minimizing time spent at the sea surface. Efficient extraction of \( O_2 \) is accomplished with rapid uptake of \( O_2 \) during the first 20-25 s of each breathhold (Fig. 6.7). This is accomplished with a breathing pattern marked by a well defined mode in breathhold frequency at about 20 s for calves of all ages (Fig. 6.5). This 20 s breathhold mode also exists for migrating adults (Ch. 2) and for foraging calves and adults outside winter lagoons (Appendix 5).

The similarity of \( F_{O_2}: \)breathhold time curves between gray whale calves and *Tursiops* (Fig. 6.8) suggests that similar patterns of oxygen uptake exist in other cetacean species, but confirmation is still needed. Intense activity in *Tursiops* dramatically increases \( F_{O_2} \) (Fig. 6.8, curve e). Comparable increases were found by Spencer (1970, cited in Lockyer, 1981) in *Orcinus* (6-8% at rest to 15-18% at high activity levels), and similar increases also should be expected in other cetaceans at high activity levels. However, unrestrained gray whale calves exhibit much narrower apparent ranges of activity in winter lagoons; they are seldom quiescent, nor, as noted by the near absence of observed level 3 activities, do they often engage for long in high activity
behaviors.

The coefficient of determination of the 23 gray whale $F_0_2$:breathhold values, derived from 11 animals over a three year period, is intermediate in magnitude between those for individual sets of samples from 2 quiescent *Tursiops* (Fig. 6.8, curves a and b). Thus, intercalf $F_0_2$ variations are of approximately the same magnitude as are breath to breath variations of a single *Tursiops*. These results, in combination with the narrow range of observed normal activities of gray whale calves in their winter lagoon, support the use of Eq. 6.5 or 6.6 as a reliable basis for predicting mean $F_0_2$ in unrestrained gray whale calves from breathhold times alone.

The presence of metering devices on the blowholes of *Tursiops* resulted in shorter $E_d$ (and smaller predicted $V_t$) values (Table 6.4). Although comparable data are not available for gray whales, Fig. 6.11 suggests a similar response from Gigi. This apparent hesitancy by *Tursiops* to expire normally into a blowhole metering device creates some uncertainty about how well values of $V_t$ measured with such devices reflect normal $V_t$ values, and reinforces the need for a non-contact method for estimating typical $V_t$. As $V_t$ is largely a function of $E_d$ for animals of the same length (Eq. 6.8), analyses of recorded expiration sounds provide an appropriate method for determining $E_d$ and for estimating $V_t$ of unrestrained calves on a breath by breath basis.
without contacting or otherwise unduly interfering with their normal behavior. The data in Fig. 6.11 confirm the validity of this technique through at least 1 year of age if L is known (L is not a linear function of age after about six months; Ch. 5).

Stahl (1967) reported a general relationship between $V_t$ and body size of mammals, described by the equation:

$$V_t = aW^{1.04},$$

or Eq. 6.12 for gray whale calves (corrected to STPD):

$$\text{Eq. 6.12: } V_t = 0.014W^{1.04}$$

Mean $V_t$ values for gray whales are near 2% of $W$, and are less than 50% of the weight-relative $V_t$ values reported for Orcinus (Spencer et al, 1967) or Tursiops (Kooyman and Cornell, 1981). Kooyman and Cornell trained their subject to expire maximally, giving $V_t$ values which were essentially equal to vital capacities (8.9% of body weight). Ridgway et al (1969), also reporting on a Tursiops trained for maximal expirations, obtained much lower maximum $V_t$ values of 4% of body weight. Ridgway and Harrison (in press) suggest that the observed differences for Tursiops is genetically related; the Pacific Tursiops used by Kooyman and Cornell is a deeper diver with a higher hematocrit and hemoglobin than the Atlantic variety used by Ridgway et al. Kolchinskaya et al (1980) found typical Tursiops $V_t$ values to be about 50% of maximum $V_t$ (no details are given regarding methods of $V_t$ measurement). Spencer (1970) reported
30-56% increases in $V_t$ of Orcinus during periods of high activity. It is expected that discrepancies between published $V_t$ values of different species will diminish as methods of measurement and levels of subject activity become more comparable.

Total blood $O_2$ capacity of Gigi was determined to be 13 ml $O_2$/kg of body weight (Gilmartin et al, 1974). If the same relationship is valid for neonates, this represents about 12 l of $O_2$, or nearly a 4 min supply at utilization rates of 2.9 l/min (Table 6.5). The actual normal aerobic breathhold capacity will be somewhat less due to incomplete unloading of oxyhemoglobin during aerobic breathholds, and probably is closer to the maximum breathholds observed in neonates of about 2 minutes. Kooyman et al (1980) found that less than 3% of dives of Weddell seals exceeded the aerobic limits of this species, and suggested that maintenance of an aerobic diving schedule may be an adaptation widespread in diving reptiles, birds, and mammals; as longer breathhold excursions into anaerobiosis require longer surface recovery times and leave less time available for submerged work.

Minimum observed metabolic rate (MOMR) is related to $W$ by: $\text{MOMR} = aW^{0.75}$ (Hainsworth, 1981). The value of \('a\' (with MOMR in Watts) is about 3.4 for terrestrial placental mammals (Kleiber, 1961; Gordon et al, 1972). Reported values of MOMR for small marine mammals range
from 1-3 times higher than terrestrial mammals of equivalent body weight (Kooyman et al., 1981), but it is difficult to establish standardized thermal and behavioral conditions which encourage interspecies comparisons or comparisons between captive and unrestrained animals. A 68 kg Hawaiian spinner dolphin (*Stenella longirostris*) had a calculated 'a' value of about 2.8 (Hampton and Whittow, 1975). This animal was thought to be close to its minimum critical environmental temperature, and O\textsubscript{2} consumption rates yielding 'a' values of greater than 5 were typical when the animal was permitted to swim freely. At the other extreme of cetacean body sizes, Lockyer (1981) made estimates of 'resting' metabolic rates for blue and fin whales, using field observed breathing rates, assumed R.Q. of 0.82, assumed FO\textsubscript{2} of 10%, and lung capacities scaled from W. Derived values of the coefficient 'a' ranged from 4.7 for a 30 ton fin whale to 7.9 for a 122 ton blue whale. Calculated metabolic rates of gray whale neonates (Fig. 6.12) yields Eqs. 6.13 and 6.14:

Eq. 6.13: \[ MMR = 5.8W^{0.75} \]

Eq. 6.14: \[ MOMR = 2.7W^{0.75} \]

Maximum aerobic capacity of neonates appears to be at least 4 times MOMR (Fig. 6.12). This is about 8 times estimated BMR, and compares well with the 5-10 fold range of aerobic scopes typical of terrestrial mammals (Bennett and Ruben, 1979). Gray whale calves have hemoglobin
concentrations and weight relative blood volumes (13-14 g/100 ml and 61-81 ml/kg; Gilmartin et al, 1974) that are typical for mammals (Hainsworth, 1981). Thus, their derived blood O\textsubscript{2} capacity of 13 ml/kg is unexceptional among mammals (blood O\textsubscript{2} capacities as high as 40 ml/kg have been reported for Weddell seals; Kooyman et al, 1981), and is reflected in their limited aerobic scope and apparent maximum aerobic breathhold capacity of only 2-4 min. It is tempting to suggest that the aerobic scope of gray whale calves is restricted because thermogenic demands in small animals require a higher MOMR floor, and that they maintain some moderate level of activity almost constantly. This is consonant with lagoon observations of calf activity, but can be justified with calculated metabolic rates only if MMR rather than MOMR are most indicative of long term minimum metabolic requirements. This topic is addressed in more detail in the following chapter.

In summary, sea-surface expressions of breathing activities are the most common and certainly the most easily observed behaviors of unrestrained gray whales, providing our principal window on other more generalized aspects of gray whale behavior. The techniques described here, based on obtaining high quality recordings of expiration sounds from which measures of breathhold times, mean breathing rates, and E\textsubscript{d} are derived, provides a realistic method for evaluating the magnitudes of
individual and interanimal variations of the ventilatory characteristics listed in Fig. 6.1.
CHAPTER SEVEN

ESTIMATES OF MINIMUM BODY HEAT LOSSES
IN GRAY WHALE CALVES

ABSTRACT

Blubber samples from stranded neonate and subadult gray whales were obtained for lipid analysis and heat flux determinations. Blubber thicknesses and body surface areas of these and other stranded gray whales were mapped. Mean blubber thickness is 0.008L and mean surface area is 0.67GL regardless of length (L). Ventilatory heat flux is estimated from $V_t$ and breathing rate values from Ch. 6.

Blubber lipid content ranged from 1 to 62%. Blubber thermal conductivity was negatively and significantly correlated with blubber lipid content. Surface heat flux measurements were made on unrestrained calves two months old. Thermal conductivity values calculated for live calves were substantially lower than those derived from excised blubber samples. Estimates of minimum required thermogenesis for neonates in 18°C winter lagoon water are similar to estimates of minimum observed metabolic rates developed in Ch. 6. By three months of age, healthy gray whale calves should experience no thermogenic deficit anywhere within the migratory range of this species.
INTRODUCTION

The adaptive value of winter migrations to low latitudes depends on how surrounding water temperatures influence the magnitude of calves' thermal losses during their winter postnatal period in winter lagoons. Behaviors which reduce heat losses and related thermogenic requirements in calves offset a portion of the energetic costs needed to accomplish these extensive migrations, and reduce demands on the fasting mothers' lipid reserves which serve as the common and limited pool of stored energy from which both members of the cow/calf metabolic system draw during the three-month lagoon period.

The purpose of this study is to estimate the magnitude of body heat losses and consequent required thermogenesis for body temperature maintenance of gray whale calves during the first three months following birth. During this time, they remain in or near warm shallow lagoons along the west coast of Baja California Sur, Mexico (Rice et al, 1981; Jones and Swartz, 1984).

Heat losses from gray whale calves are expected to vary markedly with changes in behavior, physiologic condition, and body size (Tracy, 1972). Still, some consistent minimum thermal leakage through body and gas exchange surfaces must occur despite insulative blubber layers, peripheral vasoconstriction and vascular counter-current systems, and apneustic breathing patterns.
It is this unregulated minimum rate of heat loss which will be assessed and compared to the calves' metabolic activities and their available energy pool.

Heat losses representing the collective leakage of cetacean heat conserving systems are influenced by fewer conditions than those typically applied to analyses of heat losses from terrestrial or aerial homeotherms (for example, Leuck et al, 1975, used a set of 17 simultaneous partial differential equations to describe thermal losses of the California sea lion in water and in air). Cetaceans rely on controlled peripheral blood flow from the body core to the skin and appendages for heat conservation or loss (McGinnis et al 1972). For gray whales, a simplified heat transfer system can be represented as a body core of elevated and nearly constant temperature surrounded by an insulative shell of blubber and skin of measurable thickness, all submerged in a water medium of lower and predictable temperature and high heat capacity. During ventilation, air at ambient temperature is drawn into this body core, then warmed to core body temperature and humidified before being expired. Any ingested food, excepting milk for nursing calves, also must be warmed from ambient to core temperatures.

The macroscopic structure of gray whale blubber resembles that described by Parry (1949) for fin whales. Gray whale "blubber" consists of a distal pigmented epidermis usually less than one cm thick overlying a thin
dense mat of dermal fibrous connective tissue. Proximally, the dermal connective tissue is replaced by increasing amounts of adipose cells, and merges indistinctly into the hypodermis. The hypodermis is mostly adipose cells interspersed with scattered bundles of connective tissue, and extends several cm to a sharp interface with the body musculature.

Unlike terrestrial homeotherms whose insulation typically overlies vascular circulation to the skin, the insulating blanket of cetacean blubber is penetrated by vascular beds to the base of the epidermis (Parry, 1949). Consequently, minimum heat flux, achieved when peripheral vasoconstriction is greatest, is independent of maximum heat flux achieved during periods of heat stress. It is this minimum heat flux \( H_0 \) that is the focus of this study.

\( H_0 \) through body surfaces is a function of the thermal conductivity \( k \) of the blubber when radial blood flow through the blubber is minimized, the thickness of that blubber \( d \), the conducting body surface area \( A_D \), and the temperature difference between body core \( T_C \) and ambient water \( T_W \). These variables are related by Hardy's Law (Eq. 7.1) to describe steady state heat flux from a body (Strunk, 1971):

\[
\text{Eq. 7.1: } H_0 = k(A_D)(T_C - T_W)/d
\]

- \( H_0 \) in Watts
- \( k \) in Watts cm\(^{-1}\)\(\circ\)C\(^{-1}\)
A\textsubscript{d} in m
\[ d \text{ in cm} \]
\[ T\text{\textsubscript{w}} \text{ and } T\text{\textsubscript{c}} \text{ in } ^{\circ}C \]

Parry (1949) reported a single k value of 21 for a section of fin whale blubber; and a k value of 16 can be inferred from a thermoregulatory study of a Hawaiian spinner porpoise (Hampton and Whittow, 1976; and C. Whittow, pers comm.). Brodie (1975) and Lockyer (1981) made estimates of H\textsubscript{c} in fin whales of different sizes using the thermal conductivity value obtained by Parry (1949) and different correction factors to adjust for differences between blubber from live and dead animals. No other studies of heat flux in large cetaceans have been reported, although there have been several for small toothed whales (Kanwisher and Sundnes, 1966; McGinnis et al, 1972; Hampton and Whittow, 1976).

It is assumed that the thermal conductivity (k) of whale blubber varies inversely with its lipid content; but in no studies reported to date have both k and blubber lipid content values been measured for the same blubber sample. Ackman et al (1975) and Lockyer et al (1984) reported large seasonal variations in lipid content of the blubber of fin whales (38-69%), with most of the fluctuation occurring in the inner (proximal) half of the blubber. The lipid content of gray whale blubber also presumably varies with their annual feeding/fasting cycle of this species, but confirming evidence is needed.
Rice and Wolman (1971) found that blubber thicknesses of adult gray whales measured at standard midlateral positions are about 1.0-1.3% of body length (L), and they do not vary significantly between early and late stages of their fasting cycle. They suggested that "body fat" is utilized preferentially over blubber lipids during fasting, causing a decrease in body girth and blubber volume, but no significant decrease in blubber thickness. Blubber thicknesses of 4 dead neonates, varying from 0.007-0.010L, were reported by Eberhardt and Norris (1964). Curran and Asher (1974), using ultrasonography, found d to be 0.010 in Gigi II when she was one year old. Patterns of blubber thickness variation over the body away from the standard sampling site have not been reported, nor have dimensions necessary for calculating body surface areas of gray whale calves.

The migratory timing and route of gray whales are well documented (Ch. 1, see Fig. 1.1). The thermal environment encountered by gray whales during this migration can be approximated from the monthly means of sea surface temperatures (Fig. 1.2.). This is especially true for winter lagoons, where tidal and wind mixing of those shallow water bodies essentially eliminates vertical temperature stratification and large short-term temporal variations. Air humidity and wind speed, radiative heat loss, and postural adjustments are all variables which can be ignored without imposing serious error on calculations.
of $H_0$ from cetaceans. To estimate $H_0$, a model of steady state minimum heat losses from gray whale calves is developed, based on patterns of change in anatomical dimensions ($d$, $A_b$, and $L$), on measurements of blubber $k$ from both live and dead animals, and on estimates of $T_w$ during their winter lagoon occupation period.

Evaporative heat losses from skin are not of consequence, but those from respiratory surfaces are. The simplicity of their upper respiratory tract geometry of gray whales permits rapid exchange of lung gases and allows little recovery of respiratory heat or water (Hainsworth, 1981). This simplicity also facilitates estimation of respiratory heat losses from ventilation rates calculated in Ch. 6.

METHODS

Recently dead neonates and other subadult gray whales stranded in Laguna San Ignacio, Baja California Sur, Mexico ($27^\circ$ N.), and along the coasts of California, Oregon, and Washington provided excised blubber samples for lipid analysis and heat flux measurements. Blubber thicknesses at dorsal, ventral, and midlateral positions, and body girth dimensions of these animals were measured at several equally spaced positions along the length of the body, and standard measurements were recorded. Body surface areas ($A_b$) and mean blubber thicknesses ($d$) were calculated as functions of $L$ and $G$. 
Flippers and flukes account for about 11% of the total body surface area, but are equipped with vascular heat exchange systems capable of reducing heat losses to negligible levels (Scholander and Schevill, 1955; Elsner et al, 1977). Independent vasomotor control of blood flow to appendages and to the body wall has been demonstrated for the bottlenose porpoise (Hampton and Whittow, 1972), harbor porpoise (Kanwisher and Sundnes, 1965) and Hawaiian spinner dolphin (McGinnis et al, 1972). Consequently, the areas of these appendages are subtracted from the total body surface \(A_t\) to derive the thermally active body surfaces \(A_b\) that are insulated by blubber.

Sections of fresh blubber (0.5 m x 0.5 m and extending from the skin surface to body musculature) were excised from midlateral sites posterior to the pectoral insertion of stranded whales, and either were used immediately or were frozen for later lipid content analysis and thermal conductivity determinations. Gross lipid content of cross-sectional blubber subsamples (about 50 g each) were determined by extraction with alcohol-ether solvent in a laboratory blender and evaporation under vacuum to constant weight following a procedure modified from Entenman (1957).

Surface heat flux values of excised blubber sections were determined with an RdF brand ribbon shaped self-generating transducer-type heat flux sensor. The sensing area was 1.6 x 2.5 cm built into a flat 2.5 x 3.8
cm sensing head 0.03 cm thick. The signal output was
factory calibrated at 1 mVolt = 71.5 Watts/m², and was
monitored with a digital voltmeter. Blubber sections,
including the pigmented epidermal/dermal layer, of
measured thickness were placed between matching 30 cm
diameter flat aluminum plates, one maintained at about
35°C with a 25 watt heat source, and the other held at
0°C with a water/ice heat sink (Fig. 7.1). The
generated thermal gradient was maintained until heat flux
reached equilibrium (2-5 h, depending on the thickness of
the blubber section). Temperatures of the heated and
cooled blubber faces were monitored with 2 YSI bead
thermoprosbes. With the heat flux sensor and thermoprosbes
centered on the blubber section faces, the diameter of the
system was sufficiently large to permit edge heat losses
from the sample to be ignored (J. Pinto, pers. comm).
Values of k are derived from Eq. 7.1.

Measurements of heat flux from live calves were made
during March of 1978 and 1981 in Laguna San Ignacio in
conjunction with studies on ventilatory mechanics and
metabolic rates. The choice of subject animals for these
heat flux measurements necessarily was limited to the few
tactile whales that approached our skiff and tolerated
contact with the heat flow sensor. The sensor described
in the previous paragraph was mounted on a 2 m long PVC
wand and was placed flat on a submerged portion of a
calf's skin until sensor equilibrium was reached (about
Fig. 7.1. Schematic diagram of apparatus used to measure thermal conductivity (k) of blubber.
Skin surface temperatures were assumed to be equal to ambient water temperatures ($T_a$), which were determined at the time of heat flux measurement with an alcohol thermometer. A $T_c$ of 36°C is assumed, based on comparisons with other large cetacean species (Lockyer, 1981) and the finding by McGinnis et al (1972) that subcutaneous tissue temperatures of two species of dolphins varied only about 1°C despite an experimentally induced 10°C decrease in water temperature.

In steady state conditions, air inspired from just above the sea surface is the same temperature as $T_a$, and is saturated with water vapor (Sverdrup, 1970). Equations describing heat required to warm inspired air from $T_a$ to $T_b$ (36°C, Eq. 7.2) and to evaporate water to maintain saturation of inspired air at $T_c$ (Eq. 7.3) were derived empirically from published tabular values (Weast, 1969).

**Eq. 7.2:** $H_a$ (cal/l) = 11.304 - 0.350$T_w$ + 0.001$T_w^2$

**Eq. 7.3:** $H_e$ (cal/l) = 23.840 - 2.021$T_w$ - 0.018$T_w^2$

These equations are combined as Eq. 7.4 to calculate ventilatory heat loss ($H_v$):

**Eq. 7.4:** $H_v$, cal/l = 35.140 - 0.371$T_a$ - 0.016$T_w^2$

With appropriate values for $k$, $A_p$, $d$, and $H_v$ established, estimates of minimum total heat loss are made for gray whale calves at different ages and experiencing differing ambient water temperature regimes.
RESULTS

Body girth and blubber thickness patterns were mapped for three dead neonates and two stranded larger subadults before the effects of decomposition distorted these dimensions. Changes in girth and the means of dorsal, lateral and ventral blubber thicknesses along the body length are plotted as % of L in Fig. 7.2. Maximum girth (G) is about 0.5L, and occurs at midlateral positions in the middle third of the body, which are also the sites of maximum blubber thickness. The pattern of girth variation along the length of the body (Fig. 7.2) was used to estimate \( A_b \). Mean \( A_b \) is 0.67GL (slightly more robust than the simple two-cone model suggested for fin whales by Brodie, 1975). Blubber thickness varies from high values of about 0.010L in the region of maximum girth to about 0.004L on the tail stock and portions of the head. Overall mean \( d \) is 0.008L, regardless of body length. A 4.6 m neonate therefore exposes a body surface of about 7.1 m\(^2\) underlain by blubber averaging 3.7 cm thick.

Blubber lipid content was determined for 12 samples from 7 animals, 3 neonates, 2 yearlings, and 2 adults. Heat flow values for excised blubber sections of 6 animals were measured and are listed in Table 7.1 (with lipid content and information needed to calculate \( k \) with Eq. 7.1). In Fig. 7.3, the \( k \) values of each blubber sample is plotted against its corresponding lipid content. The
Fig. 7.2. Variation of girth and blubber thickness of stranded gray whales along the body length. Relative positions of the blowhole (b) and pectoral insertion (p) are indicated.
Fig. 7.3. Relationship between conductivity (k) and lipid content of excised blubber samples. Solid circles = neonates; open circles = older animals; a = k value for fin whale (Parry, 1949); b = k value for spinner porpoise (C. Whittow, pers. comm.); and c = highest reported blubber lipid value for a gray whale (Table 7.1).
Table 7.1. Summary of lipid contents and calculations of k for excised blubber samples of gray whales. N = neonate, Y = yearling, and A = adult.

<table>
<thead>
<tr>
<th>Date</th>
<th>Age</th>
<th>L, m</th>
<th>d, cm</th>
<th>% lipid</th>
<th>Tc-Ta</th>
<th>K calc.</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 Jan 80</td>
<td>N</td>
<td>4.4</td>
<td>4.9</td>
<td>7</td>
<td>29.1</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>14 Jan 81</td>
<td>N</td>
<td>4.2</td>
<td>4.2</td>
<td>11</td>
<td>-----</td>
<td>----</td>
<td>air-filled fold</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.0</td>
<td>3</td>
<td>17.5 28</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.5</td>
<td>4</td>
<td>16.3 30</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.0</td>
<td>5</td>
<td>----   ND---- air-filled fold</td>
</tr>
<tr>
<td>16 Jan 81</td>
<td>N</td>
<td>4.3</td>
<td>4.0</td>
<td>38</td>
<td>16.6</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>03 Mar 78</td>
<td>Y</td>
<td>8.7</td>
<td>7.8</td>
<td>33</td>
<td>24.0</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>23 Jun 81</td>
<td>S</td>
<td>9.3</td>
<td>5.8</td>
<td>1</td>
<td>----</td>
<td>ND-----</td>
<td>air-filled fold</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7.3</td>
<td>1</td>
<td>19.2 33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.6</td>
<td>1</td>
<td>16.1 21</td>
</tr>
<tr>
<td>5 Mar 76</td>
<td>A</td>
<td>12.1</td>
<td>5.8</td>
<td>39</td>
<td>26.0</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>1 Feb 79</td>
<td>A</td>
<td>-----</td>
<td>ND----</td>
<td>62</td>
<td>------</td>
<td>ND-----</td>
<td></td>
</tr>
</tbody>
</table>

least squares regression of the 8 data points in Fig. 7.3 is described by Eq. 7.5:

Eq. 7.5: \( k = 29.30 - 0.32(\%\ \text{lipid}) \); \( r^2 = 0.618 \)

\( r^2 \) crit. = 0.500; d.f. = 1, 4; = 0.05

A significant amount of the observed variation in \( k \) is explained by its regression on blubber lipid content.

Twelve surface heat flux measurements were obtained from tactile calves (Fig. 7.4). Values of \( k \) were calculated using Eq. 7.1, age:L equations from Ch. 6, and d values based on d:L relationships shown in Fig. 7.2.

\( T_a \) for all 12 measurements was 18-19°C. The most consistent and generally the lowest heat flux values were obtained in the region posterior to the insertion of the pectoral flipper, yielding a mean \( k \) of 11.6 (s.d. = ±1.6). This is about 70% of the minimum \( k \) value determined for excised blubber samples (Table 7.1). The data in Fig. 7.2
Fig. 7.4. Values, means, and s.d. of $k$ obtained from 4 tactile calves, listed by general anatomical position. Vertical lines group individual calf values.

<table>
<thead>
<tr>
<th>Value</th>
<th>Mean</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>33.6</td>
<td>13.3</td>
<td></td>
</tr>
<tr>
<td>24.4</td>
<td>13.1</td>
<td></td>
</tr>
<tr>
<td>16.2</td>
<td>12.9</td>
<td></td>
</tr>
<tr>
<td>10.7</td>
<td>10.5</td>
<td></td>
</tr>
<tr>
<td>9.1</td>
<td>10.0</td>
<td></td>
</tr>
</tbody>
</table>

Mean: $\bar{x} = 18.8 \pm 10.2$

Mean: $\bar{x} = 11.6 \pm 1.6$
suggest that d is least variable there, and consequent errors based on incorrect estimates of d for live calves are apt to be less there than for other anatomical regions.

In table 7.2, values for L, G, W, A_b, and d are listed for gray whales calves at 0, 3, and 6 months of age. From these values and an assumed $T_a$ of 18° C, total surface heat flux (ignoring appendages) is

Table 7.2. Body dimensions and calculated surface heat losses (watts) of gray whale calves using $K$ values of 12 and 18 and $T_w = 18° C.$

<table>
<thead>
<tr>
<th>Age, mo</th>
<th>0</th>
<th>3</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>L, m</td>
<td>4.6</td>
<td>5.7</td>
<td>6.8</td>
</tr>
<tr>
<td>G/L</td>
<td>0.50</td>
<td>0.60</td>
<td>0.60</td>
</tr>
<tr>
<td>W, kg</td>
<td>910</td>
<td>2080</td>
<td>3530</td>
</tr>
<tr>
<td>$A_b$, m²</td>
<td>7.0</td>
<td>13.1</td>
<td>18.6</td>
</tr>
<tr>
<td>$A_b/W \times 100$</td>
<td>0.77</td>
<td>0.63</td>
<td>0.53</td>
</tr>
<tr>
<td>Mean $d$, cm</td>
<td>3.7</td>
<td>4.6</td>
<td>5.4</td>
</tr>
<tr>
<td>Blubber volume, l</td>
<td>259</td>
<td>603</td>
<td>1004</td>
</tr>
<tr>
<td>$H_o$, Watts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at $k = 12$</td>
<td>385</td>
<td>579</td>
<td>698</td>
</tr>
<tr>
<td>at $k = 18$</td>
<td>577</td>
<td>862</td>
<td>1047</td>
</tr>
</tbody>
</table>

$k$ values of 12 (the mean of the post-pectoral measurements of live calves) and 18 (approximately the lowest $K$ values found for excised blubber). Ventilatory heat flux ($H_v$. Table 7.3) is calculated for 0, 3, and 6 month old calves using Eq. 7.5, ventilation rates from Table 6.5, and data on ventilation rates of feeding calves in Oregon coastal water in summer (Appendix 5).
Table 7.3. Calculated ventilatory heat losses of gray whale calves at 3 different ambient temperatures and at 0, 3, and 6 mo of age (from Eq. 7.5).

<table>
<thead>
<tr>
<th>Age, mo</th>
<th>0</th>
<th>3</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minute vent., 1/min</td>
<td>38.4</td>
<td>51.2</td>
<td>83.8</td>
</tr>
<tr>
<td>$H_v$, Watts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at $18^\circ$ C</td>
<td>60</td>
<td>80</td>
<td>140</td>
</tr>
<tr>
<td>at $10^\circ$ C</td>
<td>80</td>
<td>100</td>
<td>180</td>
</tr>
<tr>
<td>at $2^\circ$ C</td>
<td>90</td>
<td>120</td>
<td>200</td>
</tr>
</tbody>
</table>

DISCUSSION

The data in Fig. 7.2a indicate that reasonable estimates of $A_b$ can be obtained from measures of $G$ and $L$; and that standard measures of $d$ provides good indices of overall mean $d$. Although the details of how blubber thickness varies radially, around the circumference, or along the length of the body are not yet completely defined, overall mean $d$ can be approximated from $0.8(\text{standard } d)$ (Fig. 7.2b).

The value of $k$ is significantly effected by blubber lipid content (Fig. 7.3). If gray whale blubber lipid content varies according to anatomical position, as it does in fin whales (Ackman et al, 1975; Lockyer et al, 1984), the insulating character of the blubber blanket is more complex than the model presented here. For the purposes of this discussion, it is assumed in the absence of such details that the lipid content of gray whale blubber (and of its associated $k$ value) underlying $A_b$ is uniform over the entire body.

Several possible explanations exist for the
discrepancy between k values estimated from live animal heat flux and the generally higher values measured from excised blubber samples, even though the latter samples completely lack radial blood flow. First, the assumption that $T_c = 36^\circ$ C may be incorrect. If $T_c$ at the muscle/blubber interface is actually lower in gray whale calves (even though it is not in smaller toothed whales; McGinnis et al, 1972), k values estimated from live heat flux measures will be higher than those calculated in Table 7.1. The blubber samples available for both k and % lipid determinations (Table 7.1) fall into two groups (Fig. 7.3); those with less than 10%, and those with 30 to 40% lipid. Only one of the animals (1Feb79) listed in Table 7.1 is known to have died accidentally (from collision with a ship). It was an adult, and its blubber lipid content was 62% in March (well into its winter fast). The others may have suffered some nutritional deficit prior to death, and for those almost devoid of blubber lipids, starvation was likely a contributory cause of death. Cellular modification of blubber tissues associated with such extreme lipid depletion may also effect the insulative quality of the blubber in a manner that is independent of lipid content. Thus, the usefulness of determining more blubber k values from stranded and possibly starved animals with abnormally low blubber lipid contents must be questioned. As it is unlikely that blubber samples from healthy calves will ever be available
for k determinations, it is suggested that future emphasis be placed on measuring heat flow rates from live calves.

If the blubber lipid content of the 1Feb79 whale (62%, Table 7.1) is typical of healthy gray whales (as it is for 'fat' fin and humpback whales; Ackman et al, 1975; Lockyer et al, 1984), then k values of such blubber, predicted from the regression in Fig. 7.3, should approximate the minimum K values near 10 obtained from live animals at about two months of age. Appreciable fattening of calves is visibly apparent between birth and 2 mo. (mean G increases from 0.5L to 0.6L; Ch. 5). It is presumed that much of the increase in G during the first two months following birth is accompanied by a length-proportional thickening of the blubber blanket as well as an increase in blubber lipid content.

The data presented in Fig. 7.4 suggest that an assumed minimum k value of 12 is the best available estimate for calves older than 2 mo. Lacking data on the lipid content of blubber at birth, a higher value of 18 (corresponding to a lipid content of about 35%, or approximately the highest lipid value of any neonate listed in Table 7.1) is selected for neonates. With these k values, the data in Tables 7.2 and 7.3, and an assumption of blubber homogeneity over the body, approximations of minimum steady-state thermal leakage experienced by calves can be calculated. Plotted in Fig. 7.5 are estimates of total heat losses for calves at
Fig. 7.5. Comparison of predicted total heat loss and metabolic rates with age. Fine solid lines = water temperatures; heavy solid line = predicted MMR; and heavy dashed line = MOMR.
birth, 3, and 6 mo. in three different water temperatures: 18° C (typical winter lagoon temperatures), 10° C (representative of summer temperatures at midportions of the migratory range), and 2° C (summer Bering/Chukchi Sea temperatures). These estimates are compared to metabolic rates at those ages, estimated from Eqs. 5.1, 5.3, 6.13, and 6.14.

The comparisons between estimated rates of heat loss and metabolic rates shown in Fig. 7.5 indicate that, for neonates, required minimum thermogenesis in 18° C lagoon water is similar to estimate of MOMR made in Ch. 6, lending some support to the concept that a restricted aerobic scope for gray whale calves is necessary to maintain a higher MOMR base. Heat generated by neonates at MMR levels appears to be sufficient to accommodate minimum heat losses expected in water temperatures of about 10° C.

By three months (the age of lagoon departure), the increased thickness and lipid content of the blubber assumed for these calculations, as well as decreased breathing rates, limit heat losses to the same levels as those calculated for neonates despite a near doubling of \( A_b \). During the lagoon period, the metabolic rate increases about 70% (Fig. 7.5), so that even minimum metabolic rates are nearly adequate to accommodate 10° C temperatures by the time lagoon departure at 3 mo. of age occurs. The 95% C.I. for estimates of L at 3 mo. are
5.35-6.03 m (Ch. 5). By that age, even animals at the small end of this size range should be capable of countering heat losses experienced in 2°C water at MMR levels. Calves older than 5 to 6 mo. appear to experience no thermogenic deficit anywhere in the migratory range of this species, even at MOMR. It follows that little thermogenic advantage is achieved even by small calves by remaining in warmer waters along the migratory route during summer rather than returning to the Bering or Chukchi Seas (as suggested in Ch. 3).

These remain tentative conclusions, based as they are on several assumptions regarding blubber distribution and its lipid content. Despite these limitations, some general statements can be made about the general processes of heat retention in gray whale calves. From the calculations presented in Fig. 7.5, some margin apparently exists between minimum thermogenic needs of healthy calves and their calculated MMR. Actual heat losses may be somewhat higher (e.g. losses from flukes, flippers, mouth lining, and tongue are not included in the estimates presented here), but not so high that they couldn’t be accommodated by MMR levels of heat production. However, if MMR is maintained to support adequate thermogenesis, the selective advantage of being born in warm lagoon waters is apparent. For calves smaller or thinner than normal, or for offspring of small mothers with limited lipid reserves, the benefits of these warm lagoons in
reducing body heat losses may be essential to their survival by allowing them to ration the lipid reserves of their mothers until substantial feeding is resumed some time after leaving the lagoons. The magnitude of those reserves is the subject of the next chapter.
CHAPTER EIGHT
ENERGETICS OF LACTATION IN GRAY WHALES

ABSTRACT

The magnitude of the lipid store available to support lactation by fasting female gray whales is estimated from time changes in body girth dimensions and oil yields reported by Rice and Wolman (1971), and from calculated body weights. Adult females have significantly thicker blubber than do adult males at the same length. Girth/length ratios vary from 0.7 in late pregnant females to less than 0.5 four months later. "Fatness", as measured by girth/length ratios, is not significantly correlated with blubber thickness. All observed seasonal variation in girth/length ratios can be accounted for by utilization of lipids from non-blubber sites.

Energy expenditures of mature females during migration and while in winter lagoons are estimated by comparing calculated lipid reserves of pregnant and nonpregnant females at three different body lengths. These estimates indicate that maintenance and lactation costs can be accommodated by fasting adult females without supplementary feeding.

INTRODUCTION

The purpose of this chapter is to integrate the
results of the previous 7 chapters into a comprehensive picture of how gray whales use their lipid reserves to accommodate the costs of late pregnancy and early lactation while fasting. These cycles of annual fasting and biannual reproduction are overlain on the migratory pattern of gray whales, which commences as a directed movement away from feeding areas at the very time that energy requirements for reproduction are peaking. This migratory pattern promotes resource exploitation by reproducing females over a wider geographic range, while the reproductive cycle permits individual females to invest food resources collected over two summer seasons into their reproductive efforts.

From this study, some generalizations will emerge regarding the biology of lipid metabolism in this and other species of large fasting whales which experience similar reproductive and migratory cycles. It is the period while away from principal feeding grounds that is the focus of this study, for during most of that time, these animals must rely on lipid stores which have been accumulated during the previous summer and fall months.

**THE LIPID STORE**

The magnitudes and patterns of utilization of lipid stores are estimated from analyses of product yields of harvested whales and of patterns of change in external indicators of general nutritive condition. The most
detailed set of morphometric data available for gray whales is from 317 whales collected under Special Scientific Permits of the U. S. Bureau of Commercial Fisheries between 1959 and 1969 (Rice and Wolman, 1971). These whales were collected between Dec. 1 and Apr. 10 off the central California coast (37.5° to 38.0° N.), and were examined and processed at Richmond, California. Some of these data are listed in Appendix 6, and make possible indirect evaluations of lipid stores available for different sex and size classes and reproductive conditions at several stages of the migratory cycle. Date of kill, standard body length (L), girth at maximum circumference (G), and blubber thickness (d) taken at a midlateral point opposite the dorsal hump are listed according to migration direction, sex, and condition of maturity. These measurements are directly comparable to those used in earlier chapters of this study.

Rice and Wolman (1971) reported decreases in weights calculated from girth and length measurements during the fasting migration. Yet the most obvious lipid depot, the blubber, did not show significant changes in thickness between early and late stages of the migration. Rice and Wolman suggested that body girth, not blubber thickness, was the best available indicator of nutritive condition, or fatness, of a whale. They did not explain how substantial annual changes in girth could occur inside a blubber blanket of relatively constant thickness. This
potentially important phenomenon has received little
attention even though similar patterns occur in fin whales
(C. Lockyer, pers. comm).

To test the conclusions of Rice and Wolman, and to
examine other relationships in the data of Appendix 6,
least squares regression statistics were computed for the
variables L, G, d, and day, for immature and mature
animals of both sexes (Table 8.1). Girth (G) and blubber
thickness (d) increase with increasing body length (L), so
length-relative values of each (G/L and d/L) were also
tested. The variable 'day' was calculated for time trend
analyses as the number of days after December 1. The
sampling period extended from early December to early
April.

Table 8.1. Summary body dimensions and of correlation
coefficients for the listed regressions, by maturity and
sex class, using the data in Appendix 6 (from D. Rice and
A. Wolman, pers. comm.).

<table>
<thead>
<tr>
<th></th>
<th>all females</th>
<th>nonpregnant females</th>
<th>immature females</th>
<th>all males</th>
<th>immature males</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>146</td>
<td>95</td>
<td>33</td>
<td>165</td>
<td>43</td>
</tr>
<tr>
<td>XL</td>
<td>12.3 m</td>
<td>12.0 m</td>
<td>11.1 m</td>
<td>11.6 m</td>
<td>10.6 m</td>
</tr>
<tr>
<td>XG</td>
<td>5.6 m</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xd</td>
<td>15.0 cm</td>
<td>14.7 cm</td>
<td>13.1 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xd/L</td>
<td>1.22</td>
<td>1.23</td>
<td>1.22</td>
<td>1.13</td>
<td>1.17</td>
</tr>
<tr>
<td>XG/L</td>
<td>0.52</td>
<td></td>
<td></td>
<td>0.53</td>
<td></td>
</tr>
</tbody>
</table>

Regressions correlation coefficients

<table>
<thead>
<tr>
<th></th>
<th>all</th>
<th>nonpregnant</th>
<th>immature</th>
<th>all</th>
<th>immature</th>
</tr>
</thead>
<tbody>
<tr>
<td>L v. day</td>
<td>0.025NS</td>
<td>0.054NS</td>
<td>0.058NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d/L v. day</td>
<td>0.137NS</td>
<td>0.021NS</td>
<td>0.030NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d/L v. L</td>
<td>0.113NS</td>
<td>0.132NS</td>
<td>0.408S</td>
<td>0.358S</td>
<td></td>
</tr>
<tr>
<td>d v. L, L</td>
<td>0.185NS</td>
<td>0.228NS</td>
<td>0.411S</td>
<td>0.389S</td>
<td></td>
</tr>
<tr>
<td>d v. L</td>
<td>0.574S</td>
<td>0.574S</td>
<td>0.184S</td>
<td>0.059NS</td>
<td></td>
</tr>
</tbody>
</table>
These results support the conclusions of Rice and Wolman (1971) that fast induced weight losses are reflected by decreasing G/L values through the fast (Fig. 8.1), but not by changes in length-relative blubber thickness (d/L was not significantly correlated with day). Also, no significant time related bias ("gunner's bias") for different sized animals through the season is apparent. Two additional useful conclusions can be drawn from these regression analyses. First, 'fat' whales (those with large G/L values) do not necessarily have proportionally thicker blubber (d/L is not significantly correlated with G/L). Second, sexually mature females have significantly greater length-relative blubber thicknesses than do males. This difference is detected in two regressions. First, in all three classes of females, d is strongly correlated with L, but is only weakly so in males. When d is standardized to L, d/L is significantly negatively correlated with L in males (Fig. 8.2), but is not with L of any class of females. Apparently, as males approach maturity, blubber thickness ceases to keep pace with increases in L. Second, for large sexually mature whales, differences in d/L between females and males is substantial and significant (Table 8.2; with sex as a second independent variable, partial F = 48.72, d.f. = 2.307; F crit. = 3.04; P<<<0.001).
Fig. 8.1. Regression of immature gray whale G/L values with time during winter \((G/L = 0.60 - 0.001\text{day})\); \(r^2 = 0.573\). Day count begins on 1 December. Open circles = females; solid circles = males. Open square = \(X \pm 1\) s.d. for pregnant females. Means of adult nonparturient females and adult males fall on the regression line shown here for immature whales. Data from D. Rice, pers. comm.
Fig. 8.2. Regressions of $d/L$ with $L$ by sex. For clarity, data points for males only are plotted. The slope of the regression for females is not significantly different than 0. Regression for males is: $d/L = 1.972 - 0.072(L)$. 
Table 8.2. Comparison of d/L values for gray whales with L>12 m (includes 53 of 55 pregnant females). Data from D. Rice and A. Wolman, pers. comm.

<table>
<thead>
<tr>
<th></th>
<th>s-bound males</th>
<th>n-bound males</th>
<th>s-bound females</th>
<th>n-bound pregnant females</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>28</td>
<td>22</td>
<td>20</td>
<td>49</td>
</tr>
<tr>
<td>$\bar{x}$ d/L</td>
<td>1.08</td>
<td>1.08</td>
<td>1.28</td>
<td>1.22</td>
</tr>
<tr>
<td>s.d.</td>
<td>0.12</td>
<td>0.13</td>
<td>0.14</td>
<td>0.11</td>
</tr>
<tr>
<td>s-bound</td>
<td>n-bound</td>
<td>s-bound</td>
<td>n-bound</td>
<td></td>
</tr>
<tr>
<td>males</td>
<td>females</td>
<td>pregnant</td>
<td>females</td>
<td></td>
</tr>
</tbody>
</table>

These sex-related differences in d/L have implications both for thermoregulation and for lipid storage. Until gray whales reach 10 m in length and near maturity, d is approximately 0.0125L, and sex related differences in the thickness of the insulative blubber are not apparent. At lengths greater than 10 m, d/L values in males decline (absolute values of d remain near 13 cm, regardless of length) but continue to increase in thickness in females as L increases.

The larger d/L values of mature females must reflect the greater energy investment required by females for successful reproduction. This difference in blubber volume between males and females can be calculated from $A_b \times \text{mean } d$ (0.008 L, from Ch. 7). For $L = 12.5$ m, the sex related difference in d creates only a slight change in girth (0.56 in males v. 0.57 in females), but represents an additional 0.7 m$^3$ of blubber. If the blubber is 60% lipid with a specific gravity of 0.9 (Ch. 7), then medium sized (12.5 m) nonpregnant females have about 0.4 MT (metric tons) more blubber lipids than do males of the same length.
Historical records of 19th Century and modern gray whale catches provide some information on resultant oil yields. But, as whales usually were not processed individually, it is impossible to extract anything more than average yields per whale with limited regard to size, sex, or reproductive condition (R. Reeves, pers. comm; D. Rice, pers. comm.). Scammon (1874) reported mean oil yields of 4160 l (35 bbls.) from the blubber of each whale taken in winter months in Laguna Ojo de Liebre (Scammon's Lagoon). Average females were 12.2-13.4 m in length, with whales over 13 m regarded as large. One ´large´ whale (no length given) yielded 6,500 l (55 bbls.). A large pregnant female ($L = 14$ m, $G = 0.65L$) has a blubber volume of 11,300 l. To yield 6,500 l of oil, it must have a lipid content of 57%. This lends support to the assumption made in Ch. 7 that blubber of healthy gray whales contains about 60% lipids.

Rice and Wolman (1971, Table 5) reported greater oil yields (about 8400 l, or 70 bbl. per whale) from southbound, mostly late pregnant, whales than did Scammon. The higher oil yields reported by Rice and Wolman can be accounted for by better methods of oil extraction, including visera and bone as well as blubber for processing, and using fat, late pregnant females. The oil yield data of Rice and Wolman (1971) are not listed for individual whales, but hypothetical individuals typical of those collected can be reconstructed from the published
data of Rice and Wolman (Table 8.3). Most of the northbound whales were males, and were shorter and much thinner than the pregnant females making up the southbound sample. The difference of nearly 1.4 m in mean L exaggerates the apparent difference in oil yields between the south- and north-bound samples. Total W has been recalculated using Eq. 5.3 \( (W = 18.7GL^2) \) for northbound animals. For pregnant whales, the same equation form (Eq. 8.1), with a different coefficient derived from actual weights of the two pregnant whales listed in Table 5.2 is used:

\[
\text{Eq. 8.1: } W_{\text{preg}} = 20.9GL^2
\]

Table 8.3. Reconstruction of lipid and muscle distribution in south- and north-bound gray whales. Data in top 5 rows from Rice and Wolman, 1971, Table 5.

<table>
<thead>
<tr>
<th></th>
<th>southbound</th>
<th>northbound</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>( \bar{X}L ), m</td>
<td>12.62</td>
<td>11.23</td>
</tr>
<tr>
<td>Calc. weight, MT</td>
<td>31.66</td>
<td>12.86</td>
</tr>
<tr>
<td>extracted oil, MT</td>
<td>7.56</td>
<td>2.50</td>
</tr>
<tr>
<td>Meat, MT</td>
<td>4.69</td>
<td>1.53</td>
</tr>
<tr>
<td>( \bar{X}G/L )</td>
<td>0.64</td>
<td>0.49</td>
</tr>
<tr>
<td>new W</td>
<td>26.22</td>
<td>13.01</td>
</tr>
<tr>
<td>W-(fetus &amp; tissues), MT</td>
<td>24.72</td>
<td></td>
</tr>
<tr>
<td>&quot;nonpregnant&quot; G/L</td>
<td>0.59</td>
<td>0.49</td>
</tr>
<tr>
<td>Blubber volume, m³</td>
<td>8.89</td>
<td>4.61</td>
</tr>
<tr>
<td>Blubber wt, MT</td>
<td>8.44</td>
<td>4.38</td>
</tr>
<tr>
<td>Blubber wt/W, %</td>
<td>32.2</td>
<td>33.7</td>
</tr>
<tr>
<td>lipid wt/W, %</td>
<td>28.8 +5.4 for musc</td>
<td>19.2</td>
</tr>
<tr>
<td>Meat wt/W, %</td>
<td>17.9</td>
<td>11.8</td>
</tr>
</tbody>
</table>

From W of pregnant animals, 1.5 MT is subtracted to account for the estimated mass of the near term fetus and associated membranes (Rice and Wolman, 1971). In Table

---
8.3, the following are calculated: blubber volume, blubber weight (specific gravity = 0.9), percentage of W for blubber, lipid, and meat (which was removed without lipid extraction). The remainder included the skeleton, visera, and other unseparated tissues which were rendered for oil. Assuming blubber of the fat southbound whales to be 60% lipid, 67% of the extracted oil is from blubber (8.44 MT x 60% x 7.56 MT) and 33% is from other tissues (except muscle).

Despite possible variations in procedures used for removing and processing of these tissues, these data are useful for reconstructing and describing the lipid distribution in and utilization by average south- and north-bound whales. Between south and north passages, W decreases in proportion to G (given equal L), but blubber weight remains essentially the same percentage of W. The decrease of total lipids from 29% of southbound to 19% of northbound W can be accounted for entirely by lipid from muscle, bone, and visera, without involving blubber lipids. The 34% loss of muscle mass which also occurs during the fast, likely represents utilization of muscle lipids (Arai and Sakai, 1952, report lipid contents of baleen whale meat as high as 31%). This analysis indicates that, at least for the portion of the migration south of central California, blubber retains the same thickness and can retain the same lipid content while G decreases in response to lipid loss from nonblubber
deposition sites.

Late pregnant females do not have thicker blubber than nonpregnant females (Table 8.2), yet their lipid stores must support their own maintenance costs and, through lactation, provide energy for growth and maintenance of their offspring during the last month of pregnancy and the first few months following birth. In gray whales, as in fin whales (Lockyer, pers. comm.), the fundamental morphometric difference between late pregnant and nonpregnant mature females is expressed in G. Off central California, 55 late pregnant females collected during the south migration had mean G/L values ($\bar{X} \pm $ s.d.) of 0.66(±0.04) (calculated from Fig. 8 of Rice and Wolman, 1971). Like immatures (Fig. 8.1), mature males and non-pregnant mature females pass central California on the south migration with mean G/L = 0.56. Extrapolated back about one month, mean G/L must be about 0.60 when these animals depart the Bering Sea. No northbound lactating females were collected, and the short (35 day) time span of pregnant female collections precludes regressions of G/L on day (such as in Fig. 8.1). But if migration related reductions of G in pregnant females resemble those of other gray whales, pregnant females must depart the Bering Sea with mean G/L values near 0.7. The lack of differences in G/L values between southbound males and nonpregnant females indicates that fattening for pregnancy occurs only during the summer preceding parturition.
With G and L values extrapolated back to the start of the southward migration, body weights of pregnant and nonpregnant whales of differing lengths can be compared to estimate the magnitude of the potential lipid store available to pregnant females to support the costs of late pregnancy and early lactation while fasting. Rice and Wolman (1971) found that 25% of females are sexually mature at L = 11.0 m and 50% at 11.7 m. In Table 8.4, W is calculated for L = 11.0 m (considered a small mature female), 12.5 m, and 14.0 m (a very large female) at the start of the southward migration. Body weights of mature nonpregnant females are estimated using Eq. 5.3, and of pregnant females are estimated using Eq. 8.1.

Table 8.4. Comparison of estimated weights, migratory energy costs, and lipid stores for pregnant (P) and nonpregnant (NP) females at L = 11.0, 12.5, and 14.0 m. Mean swimming velocity (V) is 2.0 m/s.

<table>
<thead>
<tr>
<th>L</th>
<th>P</th>
<th>NP</th>
<th>P</th>
<th>NP</th>
<th>P</th>
<th>NP</th>
</tr>
</thead>
<tbody>
<tr>
<td>G, m</td>
<td>7.7</td>
<td>6.6</td>
<td>8.8</td>
<td>7.5</td>
<td>9.8</td>
<td>8.4</td>
</tr>
<tr>
<td>A, m²</td>
<td>62.7</td>
<td>53.7</td>
<td>80.9</td>
<td>69.4</td>
<td>101.5</td>
<td></td>
</tr>
<tr>
<td>Swim power, 55 days watts x 10⁷</td>
<td>11.8</td>
<td>10.1</td>
<td>15.3</td>
<td>13.1</td>
<td>19.1</td>
<td>16.4</td>
</tr>
<tr>
<td>Lipid equiv., MT</td>
<td>1.41</td>
<td>1.21</td>
<td>1.82</td>
<td>1.56</td>
<td>2.29</td>
<td>1.96</td>
</tr>
<tr>
<td>H, MT</td>
<td>0.24</td>
<td>0.24</td>
<td>0.24</td>
<td>0.24</td>
<td>0.24</td>
<td>0.24</td>
</tr>
<tr>
<td>W, MT at lagoon</td>
<td>17.82</td>
<td>13.72</td>
<td>26.68</td>
<td>20.35</td>
<td>37.61</td>
<td>28.83</td>
</tr>
<tr>
<td>Fetus and memb., MT</td>
<td>1.50</td>
<td>1.50</td>
<td>1.50</td>
<td>1.50</td>
<td>1.50</td>
<td>1.50</td>
</tr>
<tr>
<td>Maint., in lagoon, in lipid equiv., MT</td>
<td>1.76</td>
<td>0.56</td>
<td>2.28</td>
<td>0.72</td>
<td>2.86</td>
<td>0.91</td>
</tr>
<tr>
<td>Difference in W, MT</td>
<td>1.40</td>
<td>3.26</td>
<td>5.33</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
MIGRATORY COSTS

Energy costs for the 55 day south migration can be calculated using Eq. 2.1 (Power = 0.5 \( p \ C_t \ A_t \ V^3 \)). The estimate of the coefficient of total drag, \( C_t \), is 0.046 from the addendum to Ch. 2. Mean migrating velocities of 2.0 m/s are assumed for the south migration (Ch. 2). Total body surface area, \( A_t \), including flippers and flukes, is calculated from 1.11(A_b) = 0.74GL (Ch. 2). When migratory velocities are the same for all three animals, differences in costs of locomotion are directly proportional to differences in G and L. G decreases somewhat during the migration, and mid-migratory G/L values of 0.67 for pregnant and 0.57 for nonpregnant females are used to calculate migratory costs for 11.0, 12.5, and 14.0 m females (Table 8.4).

The heat increment of gestation (\( H_g \)), due to additional fetal metabolic demands, is not known for gray whales, but an approximation can be obtained from Eq. 8.2 (modified from Brody, 1968):

\[
\text{Eq. 8.2: } H_g \text{ (in MJ)} = 18.4(\text{fetal birth } W)^{1.2}
\]

The last 55 days of the one year gestation uses the equivalent of 0.24 MT of lipids for a 0.9 MT fetus. Rice (1983) has shown that a prenatal diapause in fetal growth of about one month occurs between December and January (which accounts for much of the south migration). Thus, most fetal growth occurs prior to the female departing the
Bering Sea, and any additional growth occurring during the south migration is considered negligible.

LAGOON COSTS

Pregnant and nonpregnant females arrive at the lagoon in early winter (approximately two weeks apart; Fig.1.1; Rice and Wolman, 1971) with the body weights listed in Table 8.4. Differences in body weight between pregnant and nonpregnant whales of the same length range from 4.10 MT in small (11 m) females to more than twice that in large (14 m) females. In spite of this two-fold difference in excess tissue reserves, energy investments related to parturition and lactation must be approximately the same for all females, regardless of their size. Even small mature females, to maintain levels of fecundity comparable to those of larger females, must either bring to the calving lagoons lipid reserves adequate to meet the demands of lactation, or must supplement those reserves by feeding. Therefore, the focus of this analysis will be on the small pregnant females whose lipid reserves are most restricted.

Soon after lagoon arrival, pregnant females give birth to a 0.9 MT fetus (Table 5.3), which, with associated extrafetal membranes and fluids, immediately decreases maternal weight by about 1.5 MT. After subtracting the weight of the fetus and associated tissues, calculated post-parturition G/L values range from
0.59 for 11 m females to 0.63 for 14 m females. These females therefore begin lactation as fat as nonpregnant females are when they leave the Bering Sea nearly two months earlier. The remaining differences in W between pregnant and nonpregnant females of comparable lengths (ranging from 2.60 MT to 7.20 MT, Table 8.4) are available to support lagoon maintenance and lactation costs.

Lagoon maintenance

After reaching calving and breeding lagoons, behaviors of pregnant and nonpregnant females differ greatly. Pregnant females are the first to arrive in January (Rice and Wolman, 1971; Jones and Swartz, 1984), and remain for the next 80 days. Nonpregnant females usually remain for about one month, and are the first to depart on the northward migration (Rice and Wolman, 1971). Pregnant females generally are less active than on migration, often exhibiting prolonged periods of inactivity, but may experience compensating metabolic rate increases due to the extra costs of lactation. Harvey and Mate (1984) reported long-term monitoring of breath holds of 7 radio-tagged lactating females (minimum breath holds/whale = 342; mean = 1465 breath holds/whale) in Laguna San Ignacio, and found mean breathing rates of 0.62 breaths/min. This value is about 86% of the mean breathing rate found in south migrating whales (from Fig. 2.3). It is used here to approximate metabolic costs for
lagoon maintenance for late pregnant/lactating females during their 80 day lagoon stay ((80 days x migratory costs)/(55 days x 86%)). Maintenance for nonpregnant females is also calculated as 86% of their migratory metabolic rate ((30 days x migratory costs)/(55 days x 86%)). This is subtracted from the lipid store available at lagoon arrival to obtain an estimate of the energy available to support lactation (table 8.4).

Lactation

For the 80 days following birth that lactating females remain in lagoons, their calves each add about 1.1 MT to their birth weight of 0.9 MT. During this time, calf G/L increases from 0.5 to 0.6 (Table 5.3), likely reflecting fattening in all major sites of lipid deposition. As the increase in G/L by calves closely mimics (in reverse) the change in G/L experienced by older gray whales between southward and northward passages by central California (Fig. 8.1), the temporal changes observed in lipid content of adults between south and north migrations (Table 8.3) provides the best available model for estimating the energy equivalent of tissue growth accomplished by calves. As older whales must do each summer, lean neonates are presumed to increase their total lipid content from 19% to 34% of W and total muscle from 12% to 18% of W by the age of 3 mo (Table 8.3).
remainder includes water, bone, and connective and other specialized tissues. Thus, 46% of the added weight of 1.1 MT is assumed to be lipid and 23% muscle. About 22% of baleen whale muscle is protein (Arai and Sakai, 1952), representing about 5% of the added weight.

Calculations of the energy value of postnatal tissue growth are summarized in Table 8.5. The average energy value of 20.4 MJ/kg calculated for postnatal growth is somewhat less than the 26.5 MJ/kg determined for grey seals (Halichoerus grypus) of the North Atlantic (Fedak and Anderson, 1982). Like gray whales, grey seals raise their pups to weaning on lipid-rich milk (near 50%; Amoroso et al, 1951) while the mother is fasting. Grey seal pups have postnatal growth efficiencies to weaning of 75% (calculated from data in Fedak and Anderson, 1982).

Table 8.5. Computation of energy values of postnatal tissue growth from lean (L) at birth to fat (F) 80 days later in gray whales.

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<th>% of body increase</th>
<th>% of energy increase, equiv. of increase, MJ/kg</th>
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Zenkovich (1938) listed the following constituents for gray whale milk:

lipids = 53%
protein = 6%
ash = 1%
water = 40%

The caloric value of gray whale milk is calculated as 22.4 MJ/kg, using the energy equivalents listed in Table 8.5 for lipid and protein. This value is essentially the same as reported for grey seals (Fedak and Anderson, 1982). The lipid and protein requirements calculated for postnatal gray whale growth (46% and 5%, Table 8.5) are provided in milk in almost precisely those proportions.

During their 80 day lagoon stay, calves add 1.1 MT (at 20.4 MJ/kg), worth $22.4 \times 10^3$ MJ, to their weight while metabolizing an additional 252 kg of lipids ($10.0 \times 10^3$ MJ) for their own maintenance (Table 6.5). Thus, each calf requires $32.4 \times 10^3$ MJ from its mother during its lagoon stay, at an average growth efficiency of 69%. This energy requirement is equivalent to 1430 kg of milk containing 758 kg of lipids (46% x 1100 kg + 252 kg), 86 kg proteins, 15 kg soluble minerals, and 571 kg of water. Non-water milk products (lipid, protein, and minerals) total 859 kg (0.86 MT).

Water transferred through milk can be obtained as a by-product of maternal maintenance metabolism. As an example, small pregnant females are estimated to use 1.8 MT of lipids for their own maintenance while in the lagoon (Table 8.4), and produce 1.9 MT of metabolic water (1 g of lipid yields 1.07 g $H_2O$ when oxidized; Hainsworth,
1981). At typical lagoon air temperatures of \(18^\circ\text{C}\), water losses incurred by ventilatory evaporation to obtain the \(3.8 \times 10^6\) l of \(O_2\) needed to oxidize 1.8 MT of lipid is about 50% of that produced (Eq. 7.3), leaving nearly one MT of water available for other uses, including milk production.

Measured and predicted changes in G/L, derived from Fig. 8.1 and Table 8.4, for an 11 m female are shown in Fig. 8.3 for a complete two year reproductive cycle. The wintertime reduction in G/L of females larger than 11 m is less extreme. The limits for minimum G/L values are not known, but one lean stranded juvenile (G/L = 0.40; Table 5.2) died of apparent starvation with its blubber completely depleted of lipids (Ch. 7). Typical minimum G/L values must be between 0.40 and the mean of 0.49 reported for northbound whales at central California by Rice and Wolman (1971). A minimum G/L value of 0.45 is selected for Fig. 8.4, although questions about the incidence of feeding after lagoon departure makes this estimate of minimum G/L uncertain.

**SUMMARY**

Energy budgets for small and large sexually mature female gray whales are summarized graphically in Fig. 8.4. For small (11 m) females, about 60% of the reserves estimated to be available for lactation (Table 8.4) must be transferred to offspring by the end of the lagoon
Fig. 8.3. Time variation in G/L for a small mature female through a complete 2 year reproductive cycle. Solid circles indicate mean values reported by Rice and Wolman, 1971; open circles are from weight predictions in Table 8.4. Dashed line indicates uncertainty of minimum G/L after lagoon departure.
Fig. 8.4. Graphic representation of relative body weights and sizes of lipid reserves for large and small females listed in Table 8.4. Lipid equivalent energy costs are shaded. Note change in scale between adults and calves.
season. For large (14 m) whales, this value decreases to less than 20% of the reserves estimated to be available. The projected weight losses experienced by large females are sufficiently small to support at least occasional successive (and successful) annual pregnancies (as noted by Jones, 1984; and Yablakov and Bogoslovskaya, 1984).

The results of these calculations indicate that even smaller pregnant gray whales enter their calving lagoons with energy reserves sufficient to support themselves and their calves' growth and metabolic needs for 80 days without supplementary feeding. However, it also appears that smaller lactating females, with nearly two-thirds of their reserves gone by the time of lagoon departure, must initiate some level of foraging sometime after departing their winter lagoons on the 75 day northward migration. The amount of supplementary food expected to be required differs greatly, and larger lactating females could refrain completely from feeding until re-entering the Bering Sea in June. But for smaller lactating females and their growing calves whose collective lipid reserves would otherwise be exhausted before they regain their principal arctic summer feeding grounds, the shallow nearshore portions of the gray whale migratory corridor along the west coast of North America may provide crucial, albeit limited, food resources. These conclusions are consistent with observations that: 1) females with calves migrate north past California later, more slowly, and in shallower
water than do other gray whales (Sullivan et al, 1983; Poole, 1984); and 2) some gray whales also remain in shallow coastal waters along parts of the west coast of North America during summer months (Darling, 1984; Oliver et al, 1983; Hudnall, 1985; Ch. 3). Most of those gray whales spending summer months along the Oregon coast were feeding, and were predominantly juveniles and calves presumably attended by their mothers (about 30% of each, Ch. 3). The relationship between present day intensive summer feeding in polar waters and supplementary feeding in the northward migratory corridor is considered in the concluding chapter.
CHAPTER NINE

SUMMARY OF CONCLUSIONS

Within the past ten thousand years, gray whales ranged widely in coastal waters of both the North Pacific and North Atlantic Oceans. Like other species of large mysticete whales, modern gray whales now forage intensively in high latitudes during summer months, fattening for a winter fast while migrating to lower latitudes. Gray whales differ from other mysticetes, however, by grazing almost exclusively on benthic prey species which occur in dense beds in the shallow portions of polar seas.

The annual migration of gray whales (Fig. 1.1) is south in fall, commencing with late pregnant females, who are soon followed by other adults and immature whales. This migration places most members of the population in warm subtropical coastal waters or protected lagoons for some part of the winter while their shallow, high latitude feeding grounds are covered by winter sea ice. This migratory pattern is integrated with an annual alternation of summer feeding and winter fasting, and a biennial cycle of reproduction by females.

The observed mean swimming velocity (2 m/s) of the south leg of the migration corresponds to the calculated velocity at which the migratory costs of transport are minimized (and their migratory range maximized).
Breathing patterns exhibited by southward migrants incorporate periods of submerged swimming (below surface drag effects) which appear to approach the limits of their aerobic capacity. These prolonged dives are followed by surface bouts of several closely spaced breaths to replenish O₂ stores. The power required for adults to migrate at 2 m/s is about 2 times Kleiber's (1968) prediction of BMR for mammals of that size (Ch. 2).

Soon after entering winter lagoons, pregnant females give birth to offspring having mean weights of nearly 1 MT (3-7% of nonpregnant maternal weight). During the 80 days spent in winter lagoons, calves more than double their birthweight with a growth efficiency of nearly 70%, at an energetic cost to their mothers of 32,400 MJ (equivalent to 860 kg, or 60% of the maternal tissue stores calculated to be available to support lactation in small mature females). Despite the general conclusion that lactating females do little or no foraging in winter lagoons, they remain there with their calves for 1-2 months after other gray whales have departed for northern feeding grounds.

The northward migration of gray whales occurs in shallow nearshore waters along most of the west coast of North America. Opportunistic feeding during the north migration is possible for all whales, but some maintenance feeding during migration seems mandatory for smaller lactating females with their calves, and possibly for juveniles which also have limited capacities for storing
lipids. It is principally these calves (and their mothers) and juveniles that are most commonly observed in mid-migratory latitudes during summer months. These individuals are not numerous, but they are exploiting limited prey which may nonetheless provide crucial supplements to depleted lipid reserves. The relatively high apparent mortality (27%) of yearling mortality occurring in the migratory corridor (Ch. 4) suggests that, as is typical for many mammals, critical survival problems exist during the first year following weaning.

Consistent and predictable aspects of several ventilatory characteristics of calves in winter lagoons indicate that rates of oxygen consumption can be predicted well from breathing rates, breathhold times, and measures of the duration of individual expirations (Ch. 6). These conclusions also support an assumption made in Ch. 2 that breathing rates alone are reasonable relative indices of oxygen consumption rates (and power output rates) of migrating whales not involved in other complicating behaviors. The results of Ch. 6 indicate that gray whale adults and calves are not unusual among mammals in their mean values of tidal lung volumes or their weight related rates of energy expenditure. The observed aerobic scope is narrower (4x) in comparison to most terrestrial mammals (5-10x), but is typical of other marine mammals.

Minimum rates of total neonate heat losses in winter lagoon waters appear to be adequately accommodated by MOMR
at birth, and the ratio of heat loss to heat production improves through the lagoon season. By the time of lagoon departure, calves have grown and fattened sufficiently to accommodate $10^\circ C$ water temperatures with MOMR, and polar waters by the time they are 5-6 months of age. For healthy adults, body heat retention seems not to be a problem anywhere in the geographic range of this species.

If the winter lagoon waters offer thermal advantages only to very young calves, as the conclusions of Ch. 7 suggest, why do gray whales persist in returning each winter with very little deviation in their migratory schedule? The lagoons themselves have been temporally transient features through evolutionary time, with both global changes in sea level and local isostatic adjustments affecting the position of the shoreline. Even so, some comparable embayments likely existed during the last glacial maximum (LGM, 18,000 years before present) when sea level was about 150 m below its present stand (Imbrie et al, 1983). According to Imbrie et al (1983, their fig 12.4a), only the portion of the west coast of Baja California from 24° to 28° N., including essentially all the modern calving and breeding lagoons, had the same winter sea surface temperatures during the LGM as now. Coastal reaches to the north of the lagoon region experienced substantial cooling in comparison to the present as a direct result of northern glacial processes. South of the present lagoons, altered surface
current flow also produced lower coastal water temperatures.

With the shift of polar and subpolar waters southward during the last glacial maximum, migrations accomplishing a temperature range comparable to the present one would have been much shorter (to 50-55° N. in the North Pacific and to 45° N in the North Atlantic, where isotherms were even more compressed; Imbrie et al, 1983). The migratory pattern of eastern North Pacific gray whales may have been anchored in the thermally stable present winter lagoon region for long periods of time, while areas used for feeding swept across broad latitudinal ranges in response to climatically induced changes in the extent of sea ice.

All of the shallow sea floor areas presently used by and accessible to gray whales were inaccessible during the LGM. The shallow portions of the Bering, Chukchi, and Okhotsk Seas now used intensively for summer foraging were either drained of water during the last glacial maximum, or they were completely icebound. Thus, the extensive prey assemblages presently exploited by gray whales either did not exist or were unavailable to gray whales during the LGM. Most of the present continental shelves in both the North Pacific and North Atlantic Oceans were also exposed above sea level, leaving much narrower continental shelves than exist at present. An examination of bathymetric charts of the North Pacific indicates that an
area less than 10% of that presently being grazed was available then. Similar patterns of shallow area drainage and ice blockage existed in the North Atlantic in the Georges and Grand Banks areas (extensive shallow regions possibly capable of supporting the type of benthic foraging now exhibited by gray whales).

The strong contrast between present and LGM oceanographic conditions in both the North Pacific and North Atlantic Oceans leads to the conjecture that gray whales may be thriving just now because a particularly fortuitous set of environmental circumstances exists in polar seas during this (and possibly earlier) interglacial periods, but which disappears during glacial maxima. The present foraging flexibility expressed by gray whales feeding in the migratory corridor suggests that they always have been food generalists, but have specialized temporarily into a narrow ecological niche to capitalize on a food resource which is abundantly available during this present interglacial sea level stand. During glacial advances and consequent sea level lowering and polar sea exclusion by sea ice, this resource disappears or at least becomes unavailable to gray whales.

Gray whales exhibit evolutionarily conservative feeding structures, especially the relatively small head with few extensible throat pleats; and short, coarse baleen, which seem to make them poor competitors with other mysticete whales for pelagic food resources in high
latitudes. The present abundance of shallow water benthic prey not exploited by any other whale species permits gray whales to avoid such competition. The distribution and feeding patterns that we presently see in the migratory corridor during summer months may represent fairly well the summer behavior of most gray whales during the LGM.

With our present understanding of oceanographic conditions in the North Pacific Ocean during the LGM, one can speculate that, in comparison to present situations, annual migrations of gray whales were shorter (to only 50-55° N), and that relatively more foraging occurred along the shallow portions of the west coast of North America for a greater variety of prey species during a longer summer feeding period. Population responses to food resources insufficient to support the rates of either juvenile growth or of seasonal fattening of adult females defined in this study may have included older ages for the onset of sexual maturity and a longer period between successive pregnancies than the present average of two years. Consequently, it seems probable that, at least in the North Pacific Ocean, substantially fewer gray whales could have been supported by the benthic resources of limited shallow coastal reaches accessible during the LGM than at present.
REFERENCES CITED


APPENDICES
Appendix 1. Example of plot map of migratory route past Point Loma. Elapsed times and mean velocities between each point are shown.
Appendix 2. Oregon coast gray whale sightings, June, 1977 to August 1980.  a = date; b = time; c = degrees and minutes N. latitude; d = km offshore; e = # adults; f = # calves; g = # others or unknown size; h = direction (N = north, S = south, C = circling, U = unknown); i = behavior (S = swimming, F = feeding, U = unknown); j = observation platform (F = fixed wing aircraft, H = helicopter, blank = shore or boat).

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Appendix 3. Example of breathhold histogram with ventilatory parameters listed.

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36, 10, 5, 8, 13, 16, 48, 14, 56, 15, 7, 67, 20, 9.

DAY: 2    ACTIVITY: 2    NO. LE 60 SEC: 31
MONTH: 2   TOTAL DURATION: 927    MEAN LE 60 SEC: 20.9
YEAR: 81   BREATH HOLDS: 35    NO. GT 60 SEC: 4
TIME: 1220  MEAN BREATH HOLD: 26    MEAN GT 60 SEC: 70.8
DAYS: 33   BREATHING RATE: 2.27    NO. GT 2 MIN: 0

BREATH HOLD TIMES, IN 5-SEC. INCREMENTS

TYPE 1 FOR ANOTHER RUN, 2 TO END
Appendix 4. Measurements of individual ventilatory cycles of three gray whale calves. \( V_t \) in l, \( E_d \) and \( I_d \) in 0.01 s, and PEF and PIF in l/s.

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FEEDING CALVES

NO. OF BREATH HELDS: 284

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MEAN BREATH HOLD: 56 s
MEAN LE 60 SEC: 16 s
NO. ANIMALS: 11

FREQUENCY DISTRIBUTION (%) OF BREATH HOLD TIMES, IN 10-SEC. INCREMENTS
Appendix 5 (cont.).

FEEDING NON-CALVES

NO. OF BREATH HOLDS: 222
MEAN BREATH HOLD: 58 s
% LE 60 SEC: 65%
% LT 4 MIN: 3%
NO. ANIMALS: 8

FREQUENCY DISTRIBUTION (%) OF BREATH HOLD TIMES, IN 10-SEC. INCREMENTS

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BREATHHOLD TIME, MIN.
Appendix 5 (cont.).

TRAVELLING NON-CALVES

NO. OF BREATH HOLDS: 128  MEAN BREATH HOLD: 91 s
% LE 60 SEC: 48%  MEAN LE 60 SEC: 34 s
% GT 4 MIN: 5%  NO. ANIMALS: 6

FREQUENCY DISTRIBUTION (%) OF BREATHE HOLD TIMES, IN 10-SEC. INCREMENTS

BREATHEHOLD TIME, MIN.
Appendix 6. Body dimensions of gray whales taken off central California (data from Rice and Wolman, 1971, and D. Rice, pers. comm.), listed by date of take and by sex.

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