

BIOENERGETICS IN THE KILLER WHALE, ORCINUS ORCA

by

BIRGIT KRIETE

**B.Sc., Trent University, 1982
Honours B.Sc. Trent University, 1983**

**A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY**

in

**THE FACULTY OF GRADUATE STUDIES
DEPARTMENT OF ANIMAL SCIENCE**

We accept this thesis as conforming
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THE UNIVERSITY OF BRITISH COLUMBIA

August 1995

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Department of Animal Science

The University of British Columbia
Vancouver, Canada

Date August 28, 1995

ABSTRACT

A series of three papers is presented, each one related to the bioenergetics of killer whales, *Orcinus orca*. The first chapter describes how standard and realized metabolic rates were determined in captive killer whales by collecting respirations at different apneas and different activity states by training the animals to exhale into a funnel onto which a meteorological balloon was attached. These exhalations were analyzed for tidal volumes and respiratory gases; estimates of realized metabolic rates were based on activity budgets observed in the individual animals. Tidal volumes at rest were 2.7 to 4.2 times higher than those predicted by allometric equations, while estimated vital capacities are estimated to lie between 68% and 94% of the values predicted by allometric equations. Standard metabolic rates for the adult animals were similar to Kleiber's estimates (1.2 to 1.3 times Kleiber). Realized metabolic rates were between 2.7 and 2.9 times those of the whales' SMR, which are values similar to those of terrestrial mammals.

In the second chapter, food consumption and the influence of other factors such as pregnancy, lactation and water temperature on the food intake of captive killer whales, were examined. Food data were collected from the aquaria at which the animals were held and analyzed for caloric values on a daily basis. While food intake increased with age, differences in water temperature ranging between 7 and 23 °C had little or no effect on food intake. Pregnancy caused an increase in food consumption of 25% only during the last month of gestation, but food intake increased up to 100% with lactation. The best fit for feeding rate as a function of body weight was determined as: food intake (kg/d) = $0.277 M^{0.663}$, where

M = body mass in kg. A mean net assimilation efficiency of 0.73 was calculated by comparing food intake to energy expenditure measured by respiration analysis.

In the third chapter, realized metabolic rates were estimated in free-ranging killer whales along the Pacific West Coast of British Columbia and Washington. Swimming velocities and respiration rates were determined by tracking movements of whales using a theodolite and a loran. The relationship between swimming velocities and respiration rates showed an increase in respiration rate with increasing swimming speed for different age and sex classes of killer whales. These data were combined with metabolic rates determined by respiration analysis in captive killer whales during different activity states to estimate metabolic rates of wild killer whales during swimming (males: metabolic rate (kcal/kg/d) = $29.32 + 1.11V^{2.5}$; females: metabolic rate (kcal/kg/d) = $32.29 + 1.26V^{2.5}$). The minimum cost of transport for male and female killer whales occurred at 3.1 m/sec which corresponded to 0.18 and 0.20 kcal/kg/km. The drag that killer whales experience at different swimming velocities was calculated based on theoretical assumptions and suggests that drag is mainly laminar (males: 88% of the flow was laminar and 12% were turbulent; females: 89% of the flow was laminar and 11% turbulent).

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ACKNOWLEDGEMENTS

Many people have been part of and contributed to this research. Mike Bigg, David Shackleton and David Bain have been the inspiration to begin and finish this work. Their cooperative spirits put this work much further of where it would have been without them.

My colleagues in the field, David Bain, Tiana Colovos, Ralph Brandt, Lisa Berry, Vanessa Geary, A. Rus Hoelzel, Pam Stacey, Robin Baird, Linda Nichol, Patrick Kirby, and Paula Trost have spent months with me working in beautiful locations but not always under easy conditions. M.D. Lamont and Dale Pratt provided access to locations for the theodolite study. Colleen Howe and Bruce Gregory were always there to provide logistical support. The Whale Museum in Friday Harbor, WA, provided logistical help and Rich Osborne in particular helped with many aspects of the research on San Juan Island.

Without the trainers and researchers at the aquaria this research would not have happened. Jeremy Fitz-Gibbon, Doug Pemberton, Vic Biscaro and Klaus Michaelis of the Vancouver Public Aquarium in Vancouver, B.C., and Sonny Allen, Paul Povey, Jon Lawrence, Debbie Marin-Cooney, Amy Traxler and Terry Samansky of the Marine World Foundation in Vallejo, CA, were invaluable during all the months of collecting respirations from the whales and in searching for food data records as well as providing entertainment at all times. David Bain and Patty Gallagher Cates helped with all aspects of data collection at Marine World Africa/USA. Dave Bisso at the Sutter Solano Hospital in Vallejo, CA, permitted me the unlimited use of their blood-gas analyzer.

My committee at the University of British Columbia and Simon Fraser University was partly put together at the last minute. Many thanks go to Bill Milsom and Alton Harestad for their encouragement and help with the last draft.

Peter Olesiuk from the Pacific Biological Station in Nanaimo, B.C., Heinrich Binder of the University of Zuerich in Switzerland, Anne York from the National Marine Mammal Lab, Don Hood from the University of Alaska and David Bain were always available for discussions, statistical and mathematical help.

Many thanks to Horst Kriete for financial support during part of this research. The World Wildlife Fund Canada and the Anne Vallee Memorial Fund provided financial assistance for parts of this research. Equipment was donated by Micrologic and Humminbird.

This dissertation is dedicated to the memories of

Ute-Marie Dauelsberg Kriete

and

Michael Andrew Bigg

PREFACE

It has been a long-standing belief that marine mammals have metabolic rates that are significantly higher than those of terrestrial mammals of comparable size in order to maintain thermal homeostasis in cold aquatic conditions (Andersen 1965, Ridgway 1972, Brodie 1975, Schmidt-Nielsen 1984). The belief that marine mammals have elevated metabolic rates has existed for decades and even more so since Slijper (1979) published accounts of all the remnants of prey found in a killer whale's stomach. The increased heat loss in water compared to air was the main basis for suggesting higher metabolic rates in marine mammals. More recent studies (Lavigne *et al.* 1982, Yasui and Gaskin 1986, Innes *et al.* 1987) suggest, however, that marine mammals have metabolic rates similar to those of terrestrial mammals.

However, it is still difficult, or impossible to measure metabolic rates in most cetaceans. Logistic problems prevent direct measurements in the wild, so other methods have been used to estimate metabolic rates. Species held in aquaria can be used for measurements, but physiological measurements may differ somewhat from those of the species in the wild.

To shed some light on whether cetaceans, and in particular killer whales, *Orcinus orca*, have higher metabolic rates than do terrestrial mammals of similar sizes, this study attempts to determine how much food different age and sex classes of killer whales require. Three studies, two of them on killer whales in different aquaria, and one on free-ranging whales, were conducted independently of each other to test whether estimates of metabolic rates determined in each one of the methods was comparable with the results of

the other methodologies. If the estimates obtained by the different techniques are similar the methods can be conducted individually to estimate metabolic rates in killer whales.

The importance of this result is not only of academic interest because as humans continue to exploit and deplete the natural resources of the sea, conflicts between marine mammals and fisheries have become more frequent. For example, harbour seals (*Phoca vitulina*) are considered a problem because they remove fish from fishing gear and are believed to prey on valuable fish species (Beach *et al.* 1985, Olesiuk *et al.* 1990b) while California sea lions' (*Zalophus californianus*) depredation on a depleted winter-run of wild steelhead (*Oncorhynchus mykiss*) has led to temporary removal and relocation of the sea lions (Norberg and Bain 1994). Recently, the question of how much killer whales eat has become an important issue due to fishery conflicts with killer whales. Competition between salmon fisheries and killer whales has been an issue for several decades in British Columbia and Washington waters (Bigg and Wolman 1975, Bigg 1982). In Alaska, killer whale depredation on blackcod (*Anoplopoma fimbria*) in the longline fisheries has seriously financially harmed the fishery (Matkin 1988).

The first chapter reports the development of a technique to measure metabolic rates for killer whales in different activity states. Both standard (a low estimate of metabolic rate to sustain life) and realized (the energy necessary for standard metabolism plus daily activities) metabolic rates are estimated for different age and sex classes of killer whales using this technique.

In the second chapter, food data for the individual killer whales for which metabolic rates via respiration analysis were determined, as well as two other individuals, are

analyzed from the time they were available and trends of food consumption as a function of body mass are determined. Other factors such as season, water temperature and reproductive status are also examined to possibly affect food intake. Food consumption reported in this chapter and energy expenditure determined through respiration analysis in the previous chapter are compared and net assimilation efficiencies (NAE) are inferred. If the net assimilation values determined are similar to those reported in the literature for other marine mammals, then the NAE inferred and methodology used here can be assumed to be reasonable for killer whales.

In the third chapter, metabolic rates are estimated for free-living killer whales by analyzing the respiration rates of different age and sex classes as a function of swimming velocity. The cost of locomotion and most efficient swimming speed of male and female killer whales are determined. Data on respiration from captive whales are then combined with the respiration rates observed in the wild killer whales to convert respiration rates to metabolic rates. Realized metabolic rates are estimated using respiration rates and oxygen consumption from different activity states of captive animals and combining those data with daily activity budgets observed in wild killer whales.

Several others (Blake 1983, Lang 1965, 1966) mathematically estimated the drag different marine mammals encounter while swimming at different velocities. One of the leading thoughts has been that it is unknown how marine mammals can overcome drag, which, according to theoretical calculations, should be almost entirely turbulent.

According to Gray (1936), the power that would be required to overcome drag was greater than the maximum power available to cetaceans from their locomotor muscles. Here, an

attempt is made to estimate what percentages of drag are laminar and turbulent for killer whales swimming at different velocities. Several unknown parameters need to be assumed to fit laminar and turbulent curves to those determined for the cost of locomotion in killer whales. If drag is lower than expected, the animal would have to expend less energy for its daily moving activity, which in turn would decrease its realized metabolic rate.

By approaching the estimation of metabolic rates of killer whales from different perspectives, estimates can be compared to each other to test whether results are homogeneous. While some uncertainties and unknowns, such as exact body weight and growth rates, exist, assumptions and methodologies can be considered reasonable if similar results are obtained from the different studies.

Chapter 1: METABOLIC RATES IN CAPTIVE KILLER WHALES,

Orcinus orca

INTRODUCTION AND OBJECTIVES

Over the last 60 years, many studies have been conducted to measure the metabolic rates of animals. To compare metabolic rates among species, a baseline, the basal metabolic rate, has been established by studying animals of different sizes and creating a regression equation showing the relationship between heat production and body weight under standardized conditions (Brody 1945, Kleiber 1987). To meet standardized conditions during testing, animals must be physically and sexually mature, in a non-reproductive and post-absorptive state, in a calm psychological condition and resting in a thermal neutral chamber at temperatures at which no additional metabolic energy is necessary to keep the body at a constant temperature and metabolic rates are independent of environmental temperature (Brody 1945, Kleiber 1987, Worthy 1990).

Kleiber's (1987) best fit regression for basal metabolic rates in terrestrial mammals is described as:

$$[1] \log_{10} \text{BMR} = 1.83 + 0.756 \log_{10} M \pm 0.05,$$

where BMR = basal metabolic rate in kcal/d, and M = body mass in kg.

This formula was approximated and simplified by Kleiber (1987) to:

$$[2] \text{ BMR} = 70 M^{0.75},$$

where BMR = basal metabolic rate in kcal/d, and M = body mass in kg.

To determine whether the animals are in a post-absorptive state, the respiratory quotient (RQ, the ratio of volume at STP of carbon dioxide produced to the volume of oxygen consumed) is measured. By simultaneously measuring both oxygen consumption and carbon dioxide production by the animal, the resulting RQ indicates the nutrient that has been metabolized (Schmidt-Nielsen 1990). Usually the RQ lies between 0.7 and 1.0. An RQ near 1.0 suggests primarily carbohydrate was metabolized while an RQ of 0.7 suggests that fat was the primary substrate. An intermediate RQ indicates that proteins or mixtures of two or three different classes of nutrients were being metabolized (Schmidt-Nielsen 1990). An RQ indicating the burning of fat shows the animals were in a postabsorptive state when measurements for basal metabolic rates were collected. In mammals, the time when the post-absorptive state is reached, changes depending on the type of feed and species, but is about 12 hours in rats (Kleiber 1987, Schmidt-Nielsen 1990).

When animals are in a thermal neutral chamber, metabolic rates are independent of environmental temperatures (Worthy 1991). Williams *et al.* (1991) estimated thermal neutral zones for bottlenose dolphins (*Tursiops truncatus*) and determined that the animals' core temperature did not change with water temperatures ranging from 3.6° C to 17.3° C,

while the animals' metabolic rates did not change with water temperatures ranging between 6 °C and 17.3 °C.

Because traditional methods for determining metabolic rates, such as placing animals into thermal neutral chambers, are impractical for large aquatic mammals, alternative approaches have been used in marine mammals. Metabolic rates of cetaceans, and in particular large mysticetes, have been estimated from lung volumes measured from harpooned or dead animals, with respiration rates determined from wild living individuals (Laurie 1933, Scholander 1940, Thompson 1961, Kanwisher and Sundnes 1965, 1966, Rice and Wolman 1971). The potential lung volume and oxygen consumption of the harpooned whales (litres of oxygen) was then converted to energy expenditure by assuming an energy equivalent for oxygen consumption (4.8 kcal/litre oxygen per breath, Brody 1945). Parry (1949) used seasonal variations in blubber thickness measured by whalers as an indicator of energy consumption, though his conclusions are questioned by Kanwisher and Sundnes (1966) for assuming a constant mammalian metabolic rate. Brodie (1975) used the net gain in oil during feeding, estimating the daily lipid ration, its catabolic value and approximated standard metabolic rates for rorquals in subtropical waters.

Well designed studies using double-labelled water have been conducted with pinnipeds (Costa 1987), but have been too expensive to apply to larger cetaceans. Therefore, metabolic rates have been determined in captive delphinids using indirect calorimetry, measuring the amount of oxygen used by the individual and converting this into equivalent energy utilized by the animal.

Lenfant *et al.* (1968) measured tidal volumes, the volume of air inhaled in a single breath, of a subadult female killer whale (*Orcinus orca*) while beaching her during the process of gas collection. Being beached may have decreased the animals' ability to exhale and inhale fully by as much as 20% due to the pressure of her weight out of the water (Wahrenbrock *et al.* 1974). Because training techniques and conditions for captive cetaceans have improved over the last 30 years, animals now can be trained so that respiratory gases can be collected with the whale at the water surface rather than beached at the bottom of the pool. Young animals do not have to be used because individuals have survived well into adulthood and are accessible for data collection. Kasting *et al.* (1989) collected respirations from one adult male and two subadult trained killer whales and analyzed the respirations for energy requirements. He also suggested higher metabolic rates for killer whales than for terrestrial mammals of similar sizes. However, he did not correct for the decreased respiration rates during absolute rest (see methods this chapter) and used estimated weights that were probably too low for the animals in question (see methods this chapter). Other metabolic studies on wild cetaceans have been inconclusive and researchers often assumed respiratory variables from other species, hence estimating metabolic rates indirectly from physiological data (e.g. Lockyer 1981a, 1981b, Yasui and Gaskin 1986).

Brodie (1975) suggested using the term "standard metabolism" or "maintenance metabolism" for cetaceans rather than basal metabolism. He argued that many cetaceans are negatively buoyant and must move in order to reach the surface to breathe. Brodie (1975) states that basal metabolic rate is therefore probably never attained by cetaceans,

and the cost of the minimal exertion required to move to the water's surface to breathe is inseparable from the animal's basal metabolism. However, killer whales are neutrally buoyant in the still water of an aquarium depending on how inflated their lungs are (D. Bain pers. comm.), so standard metabolic rates (SMR), which should be quite similar to BMR's, can be attained. Lockyer (1981a, 1981b) had similar concerns to Brodie's (1975). She stated that instead of measuring BMR, the resting metabolic rate (RMR) is more appropriate for whales and dolphins, because BMRs are measured under minimal metabolic energy expenditure which is rarely encountered in cetaceans. Lockyer further suggests that using the RMR, which according to Brody (1945) is the true BMR in adult terrestrial animals plus 15% for the expense in muscular effort necessary to move about to breathe, is an appropriate measure for metabolic rates in cetaceans. Peters (1989) also suggests using SMR to replace BMR in situations where the measurements are not necessarily minimal but when they are collected under standardized conditions to yield low values. The term "standard metabolic rate" (SMR) will be used for the animals reported in this paper.

In many of the early energetics studies marine mammals were determined to have higher metabolic rates than do terrestrial mammals of similar size (Kanwisher and Sundnes 1965, 1966, Sergeant 1969, Irving 1973, Kasting *et al.* 1989). These higher metabolic rates, with low metabolic scopes (the ratio of metabolic rates between maximal exertion and rest) were interpreted as being due to water drawing heat away from the body 25 times faster than does air, and to the animals needing to increase their metabolism to maintain a constant internal body temperature (Ridgway 1972). An

unfavourable (large) surface to volume ratio for smaller cetaceans was also suggested to elevate metabolic rates. More recently, other researchers (Olsen *et al.* 1969, Hampton and Whittow 1976, Lavigne *et al.* 1986; Innes *et al.* 1987, Worthy *et al.* 1987) rejected the idea that cetaceans have elevated metabolic rates. All pointed out that high rates in many of the past cetacean studies were calculated under environmental conditions different than those specified by Kleiber (1987), or that juvenile animals were used. They provided empirical data to show that metabolic rates of some marine mammals are comparable to those of terrestrial species, an indication that marine mammals are well adapted physically and physiologically to their marine environment. Some of these adaptations include a small surface to volume ratio and a thick blubber layer with a high lipid content for effective insulation, all of which allow cetaceans to have a thermal neutral zone under most normal ranges of water temperatures (Worthy 1990).

The opposing conclusions for marine mammal metabolic rates and scopes can be summarized relative to terrestrial mammals (Brody 1945, Kleiber 1987) as:

- a) high basal metabolic rates and low metabolic scopes, versus
- b) normal basal metabolic rates and normal metabolic scopes.

This study is intended to discriminate between these 2 hypotheses in the case of killer whales. Also, additional baseline data were collected to examine fundamental aspects of cetacean bioenergetics. Specifically, I collected data based on respiration analysis to:

- 1) determine respiration rates during rest, at moderate, and at high activity states,
- 2) determine daily activity budgets,
- 3) estimate standard metabolic rates and metabolic scopes, and
- 4) estimate daily caloric expenditures.

METHODS

Study Animals

Four different study animals were used for respiration collection and activity budget determination.: one adult male (Hyak, 20 years old at time of the study) and one subadult male (Finna, 11 years old at time of study) from the Vancouver Aquarium, Vancouver, B.C., as well as one adult female (Yaka, 21 years old at time of study) and one subadult female (Vigga ,11 years old at time of study) from Marine World Africa/USA in Vallejo, California.

Metabolic Rate Determination

Metabolic rates of killer whales were estimated by collecting respiratory gases after various apneas during different activity states. Tidal volumes, oxygen uptake and carbon dioxide production rates were determined, and standard metabolic rates and daily caloric expenditures were estimated. Respiratory quotients and the metabolic scope for each animal were determined. Standard metabolic rates were compared to Kleiber's (1987) equation on basal metabolic rates in mammals.

Several variables, described below, were collected and measured to determine metabolic rates. Metabolic rates were calculated by the generalized equation:

$$[3] \text{ MR} = \bar{x} * \text{Vol O}_2 * c,$$

where: MR = metabolic rate (kcal/d), \bar{x} = mean number of breaths per day, and Vol O₂ = mean litres of oxygen consumed per breath, c = conversion factor for litres of O₂ to kcal (1 litre of O₂ = 4.8 kcal, Brody 1945, Pike and Brown 1975).

a) Respiration Rate Determination

Respirations were counted and timed for a minimum of 15 min prior to sampling respirations for gas analysis to determine respiration rates at rest (Activity state 1) (activity states are defined below). Respirations at medium and high activity states (Activity states 2 and 3, respectively) were counted while the animals were involved in the activity state (i.e. approximately 15 min during a training session or during the show). Respiration rates were counted during two other activity states, nightly rest and extremely active behaviours (Activities states 0 and 4, respectively). These respiration rates were used only to determine metabolic scopes, therefore only the minimum and maximum respiration rates observed were used for metabolic estimates of standard and extremely active metabolic rates.

To compare observed frequencies of respirations during rest to those of terrestrial mammals, predicted respiration rates for the four killer whales were calculated from Stahl's (1967) allometric equation for mammals:

$$[4] \text{ Frequency of Respiration (breaths/min)} = 53.5 M^{-0.26},$$

where M = body mass in kg.

b) Daily Activity Budget Determination

The amount of time that the four killer whales spent in the different activity states was recorded throughout the days when breaths were collected, as well as during the early evenings at the Vancouver Aquarium and throughout the nights at Marine World. Activity budgets were estimated based on the number of hours Hyak and Finna spent in Activity states 1 and 3, while Yaka's and Vigga's daily activity budgets were separated into Activity states 1, 2, and 3.

c) Collection of Expired Air

During the fall of 1987, respiratory gases were collected from Hyak and Finna at the Vancouver Aquarium. From November 1988 to March 1989 and from September 1989 to November 1989, collections of respiratory gases were made from Yaka and Vigga at Marine World/Africa USA. To collect respiratory gases, an apparatus was built using 10 cm diameter PVC piping with two one-way valves for inhalation and exhalation (Figure 1). The bottom edge of the funnel was lined with soft foam to act as a seal when the apparatus was placed over the whale's blowhole to avoid the loss of exhaled air. Meteorological balloons, with a maximum capacity of 150 l, were attached to the exhalation tube(s) to collect the exhaled air. Two balloons were necessary for Hyak and Yaka because of the size of their tidal volumes. One-way valves were used in case the

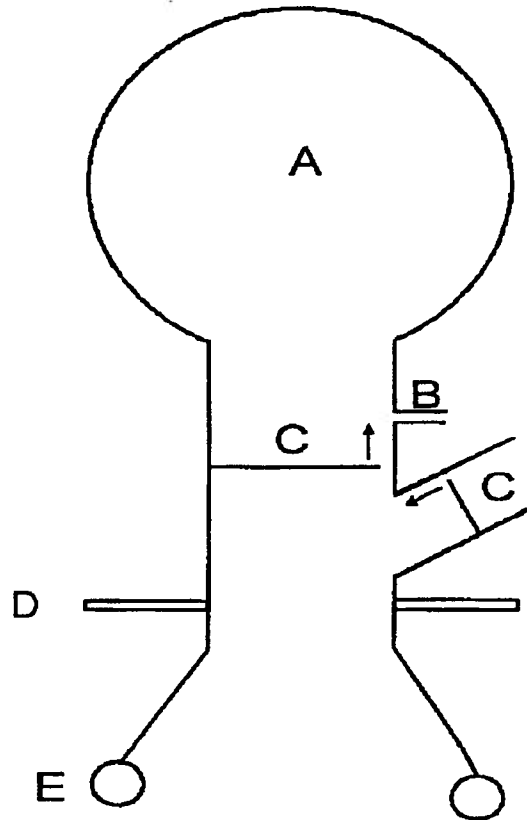


Figure 1. Apparatus used to collect expired air from captive killer whales, *Orcinus orca*. Body of apparatus is made from 10 cm diameter PVC pipe and a plastic funnel. A - Collection vessel (metereological balloon - 2 used for adult whales); B - Valve for collecting air samples for gas analysis; C - One-way valves; D - Handles to hold apparatus on whale's blowhole; E - soft foam seal around base of plastic funnel.

animal wanted to inhale immediately following the collection of respiratory gases and before removal of the funnel, or if it became frightened when the funnel was placed over its blowhole and it attempted to inhale. In this way, the animal could not inhale the air already collected in the balloon(s). A similar method of collecting respiratory gases was used by Spencer (1967) and by Kasting *et al.* (1989) for killer whales, and by Sumich (1983, 1986) for gray whale (*Eschrichtius robustus*) calves.

The whales were trained to accept the apparatus over their blowhole and to await a signal before exhalation. This procedure was intended to allow the researcher and trainer to control the duration of apnea. Samples were not used if an audibly noticeable amount of air escaped around the edges of the funnel or if the animal exhaled again after removal of the funnel and before inhaling.

Exhaled air was collected for tidal volume and respiratory gas analysis after three activity states operationally defined as:

Activity state 1: Resting for a 15 min period and at least 14 h after the last meal to meet conditions of post-absorptive state for standard metabolic rate determination.

Activity state 2: Light to moderate activity, involving a light training session, or swimming leisurely around the pool for at least 15 min prior to gas collection. Gas collections for Activity state 2 were always made after the animals had been fed at least once within the last 3 h.

Activity state 3: Immediately after the last activity of a show with high levels of activity, i.e. involving many breaches. Gas collections for Activity state 3 were always made after the animals had been fed at least once within the last 3 h.

For logistical reasons at the Vancouver Aquarium, collections of exhaled air were only possible after Activity states 1 and 3.

Two additional activity states were also defined, although no respiratory gases were collected due to the absence of training personnel. During these additional activity states, respirations of the individual whales were counted by an observer situated on a hidden platform after the training personnel had left for the day, i.e., in the evening and at night. The animals' behaviour during these periods ranged from 1 to 2 h of rest to more active behaviour (breaches) than that seen during shows. The two additional activity states were operationally defined as:

Activity state 0: Resting behaviour where the animals were stationary at the water surface for at least 15 min and appeared to be in the calm psychological state as described by Kleiber (1987). This was less than 14 h after the last feed.

Activity state 4: This activity state consisted of extremely active, "percussive" behaviours, consisting of breaches, tail and flipper slaps, and fast swimming. Activity state 4 sometimes occurred longer (>15 min) than similar behaviours during shows.

The difference between comparable behaviours seen during the day and night was that during night time no behaviour was requested of the whales and therefore the behaviour was spontaneous.

d) Tidal Volumes, Oxygen and Carbon Dioxide Ratios

After the whales exhaled through the funnel into the balloons, the collected gases were forced through a dry gas meter (calibrated with a Century 100H gas flowmeter) to determine the tidal volume. Tidal volumes were measured for each breath at each different activity state to determine if tidal volumes changed with activity state.

While the exhaled air was forced through the dry gas meter, four 60 ml gas samples of the exhaled air were drawn off with a syringe via a valve directly from the funnel. These samples were collected at equal intervals, i.e., after approximately 20%, 40%, 60% and 80% of the air in the balloon(s) had been forced through the dry gas meter, to get a mixed sample of exhaled air. These samples were analyzed for the difference of oxygen and carbon dioxide from atmospheric air after being corrected to standard temperature and pressure (dry). The mean value of oxygen and carbon dioxide present in the four samples was determined. In Vancouver, samples were analyzed both with a Beckman Carbon Dioxide Analyzer (LB-2) and a Beckman Oxygen Analyzer (OM-11). At Marine World, the samples were analyzed with an Instrumentation Laboratory System 1302 pH/blood gas analyzer provided by the Sutter Solano Hospital. All instruments used were calibrated before samples were run to minimize sources of variation and error.

Mean values of oxygen extraction, the oxygen available in the inhaled air, were

calculated for the three different activity states to relate the difference in oxygen extraction to differences in activity. Mean oxygen extraction at mean apnea during the different activity states was calculated as:

$$[5] \quad E_{O_2} = \left(1 - \frac{P_E O_2}{P_I O_2}\right) \times 100$$

where: E_{O_2} is the extraction of oxygen in %, $p_E O_2$ is the partial pressure (mm Hg) of the exhaled oxygen, and $p_I O_2$ is the partial pressure (mm Hg) of the inspired oxygen.

Carbon dioxide production by the whales was calculated as:

$$[6] \quad CO_2 \text{ Production} = (P_{E CO_2} - P_{ATM CO_2}) \times 100 / \text{Atmospheric Pressure}$$

where: CO_2 is the % of exhaled air produced by the animal, $P_{E CO_2}$ is the exhaled partial pressure (mm Hg) of carbon dioxide, $P_{ATM CO_2}$ is the partial pressure (mm Hg) of CO_2 in atmospheric air, and atmospheric pressure is in mm Hg..

Oxygen extraction and carbon dioxide production as a function of apnea were plotted for all animals in each activity state. A log-log transformed regression line, providing the best fit to the data, was fitted to the data. The amount of oxygen consumed, the amount of O_2 (l) taken into the body divided by apnea was calculated as a function of apnea and graphed.

Metabolic rates were calculated using:

$$[7] \quad \text{Mean Metabolic Rate} = (\text{Tidal Volume} \times [F_{I_{O_2}} - F_{E_{O_2}}]) / \text{apnea}$$

where: Metabolic Rate is in litres of O₂/s, tidal volume is in litres, F_{I_{O₂} is the fraction of inspired oxygen, F_{E_{O₂} is the fraction of oxygen in expired air, and apnea is measured in s.}}

To compare the killer whales' observed tidal volumes at rest and the animals' vital capacity, the maximum volume that can be inhaled in one breath (Peters 1989) which was operationally defined as the largest inhalation measured, to those of terrestrial mammals of similar sizes, predicted values for killer whales were calculated from Stahl's (1967) allometric equations:

$$[8] \quad \text{Tidal Volume at rest (ml)} = 7.69 M^{1.04},$$

where M = body mass in kg.

$$[9] \quad \text{Vital Capacity (ml)} = 56.7 M^{1.03},$$

where M = body mass in kg.

Ventilation rates were calculated for the killer whales from respiration rates and tidal volume and compared to Stahl's (1967) allometric equation for terrestrial mammals:

$$[10] \quad \text{Ventilation Rate (ml/min)} = 379 M^{0.80},$$

where M = body mass in kg.

e) Weight Estimates

To estimate caloric expenditures on a per kilogram basis, body mass was calculated using Bigg and Wolman's (1975) formula. This formula was derived from empirical data and was based on the actual weights of 32 live-captured and stranded killer whales:

$$[11] M = 0.000208 L^{2.577},$$

where: M is body mass in kg and L is total body length in cm.

Total body lengths for the captive animals were obtained by measuring from the tip of the rostrum to the notch of the flukes (Norris 1961). For the captive animals, 20% was added to the mass calculated by Bigg's and Wolman's (1975) formula. Data on actual weight measurements for animals in captivity (Heyning and Dahlheim, in press, J. Antrim, Sea World, pers. comm. and J. Fitz-Gibbon, Vancouver Aquarium, pers. comm.) showed that the whales were on average 20% (17%, 19% and 25%) above the weights calculated based on the whales' length (Bigg and Wolman 1975). Growth rates have also been reported to be faster in captivity and age of maturity is reached earlier than in animals in the wild (Asper *et al.* 1988, see also Chapter 2). The adjusted masses lie approximately one standard deviation (21.58% of the mean) above Bigg's and Wolman's (1975) study animals' masses.

f) Standard Metabolic Rate Estimates

Estimates for standard metabolic rates were made both with mean and maximum tidal

volumes. Minimum respiration rates collected during Activity state 0 were combined with oxygen consumption rates measured during Activity state 1. For further analysis, the oxygen data were applied to equation [3] to estimate SMR. The SMR was divided by the estimated mass of the whales to yield the animal's mass specific metabolic rate (kcal/kg/day).

To determine whether the data fit with those of terrestrial mammals, SMRs calculated for Hyak and Yaka, the two adult whales, were plotted on Kleiber's (1987) regression line of the relationship between the logarithms of metabolic rate and body mass of terrestrial mammals.

g) Daily Energetic Expenditure

Activity budget studies were conducted at Marine World over a period of 3 months to determine how much time the animals spent in different activity states. Measurements were taken in bouts of 15 min every hour over a period of 12 h two times a week (after Bain 1986), to relate respirations to activities. At the Vancouver Aquarium, nightly observations were not allowed, so observations were conducted from 06:30 until 20:30 for two days during the respiration collection study in October 1987. The number of hours spent in the different activity states for which respirations rates were collected was determined. Maximum tidal volumes were used for all calculations of metabolic rates. Mean respiration rates collected during Activity states 1, 2, and 3 were multiplied by the oxygen consumption per breath at the mean apnea measured during the respective activity state. The oxygen data were applied to equation [3] to estimate metabolic rates for

Activity states 1, 2, and 3. Daily metabolic rate can be estimated as:

$$[12] \text{ Daily MR} = (\text{Time}_{\text{Activity 1}} * \text{MR}_{\text{Activity 1}}) + (\text{Time}_{\text{Activity 2}} * \text{MR}_{\text{Activity 2}}) + (\text{Time}_{\text{Activity 3}} * \text{MR}_{\text{Activity 3}}),$$

where: Daily Metabolic Rate is in kcal/d, Time is in h/d, and the Metabolic Rate for the different activities is in kcal/h.

The metabolic rate calculation is given in equation [3]. Metabolic rates for the different activity states were also calculated on an hourly basis.

Metabolic Scope

The increase in metabolic rate between rest and maximal exertion was determined for the four whales used for this study by extrapolating how many times higher the maximal rate of oxygen consumption is compared to the standard metabolic rate (Schmidt-Nielsen 1984). In addition, metabolic scopes for the four study animals were determined for the activity states (1 and 3) for which gas analysis was possible.

Respiratory Quotient

Respiratory quotients were determined for each exhalation measured for each individual. This ratio [mols of CO₂ produced divided by the mols of O₂ consumed (Kleiber 1987)] indicates whether fat, protein or carbohydrates were burnt. Respiratory quotients were averaged by activity states for all individual whales combined.

RESULTS

Respiration Rates

Respiration rates and ranges differed for each killer whale in each activity state (Table 1). Respiration rates between Activity states 1 and 0 decreased by 61% for Hyak, by 51% for Yaka and Finna, and by 40% for Vigga. Spencer *et al.* (1967) observed respiration rates of an undisturbed, confined adult male (total length = 656 cm, weight estimate = 3414 kg) and determined that the animal's average respiration rate at rest was 1.06 breaths/min. This is similar to Hyak's respiration rate during Activity state 1 (1.02 breaths/min).

Respiration rates during Activity state 4 were between 16% and 40% higher than during Activity state 3 (Table 1). The whales' frequencies of respiration during rest (Activity state 0) were between 11.8 to 14.8 times lower than that predicted from allometric equations.

Rest periods were longer and continuous during the night, lasting up to 2 h, while rest periods during the day were shorter and intermittent, lasting only up to 30 min.

Apnea and Tidal Volume

Apnea could be controlled by the trainer and researcher only after Activity state 1 and for the short apneas (<30 s) after Activity states 2 and 3. The whales determined maximum apnea duration for Activity states 2 and 3 because they did not seem willing to

Table 1. Summary of respiratory data from four captive killer whales.

Animal	Activity	n	Apnea Range (s)	Mean Tidal Volume (l)	Range (l)	Standard Deviation (l)	Mean Respiration Rate (breaths/h)	Range Respiration Rate (breaths/h)	Standard Deviation
Hyak	0	-	-	-	-	-	24	-	1
	1	35	15 - 149	211.5	153.5 - 254.5	21.0	61	42.8 - 87.8	9.8
	3	15	24 - 50	205.5	82.0 - 258.5	42.1	84	62.1 - 90.0	4.2
	4	-	-	-	-	-	100	-	3.6
Finna	0	-	-	-	-	-	30	-	0.6
	1	35	10 - 120	94.5	40.0 - 133.0	22.7	61	35.0 - 82.0	12.6
	3	22	8 - 40	61.9	26.0 - 91.5	19.6	90	81.8 - 100.0	7.8
	4	-	-	-	-	-	109	-	3.5
Yaka	0	-	-	-	-	-	30	-	-
	1	21	10 - 119	97.5	54.0 - 149.0	26.6	61	43.9 - 97.3	14.1
	2	13	10 - 90	78.0	50.5 - 114.0	19.5	100	72.0 - 102.9	2.8
	3	12	14 - 46	102.6	75.5 - 135.0	17.3	129	97.3 - 156.5	5.3
4	-	-	-	-	-	180	-	-	
Vigga	0	-	-	-	-	-	36	-	-
	1	10	28 - 115	32.8	16.0 - 42.0	7.4	60	45.0 - 100.0	6.4
	2	9	28 - 44	41.3	30.0 - 55.0	8.5	72	60.0 - 90.0	3.3
	3	15	15 - 39	42.5	17.5 - 60.0	12.2	138	109.1 - 156.0	4.2
4	-	-	-	-	-	160	-	-	

hold their breaths for extended periods after exercise (Table 1). For collections of exhalations during Activity state 1, the durations of apnea ranged from 10 to 149 s, while the range of apnea after Activity state 2 was limited from 10 s to 48 s and from 8 s to 46 s after Activity state 3.

Tidal volumes were tested for variation with individual and activity state using a 2-way ANOVA (Table 2). A significant individual effect and interaction term were found; it appeared that whether there was any difference between tidal volume and activity state depends on the individual. Tukey's test for multiple comparisons (Zar 1984), using 187 cases and 10 groups of observations, showed that only Finna's tidal volumes were significantly different between the two activity states (Table 3). Tukey's multiple comparisons test (Zar 1984) was used to determine if differences exist in tidal volumes between individuals, when engaged in the same activity. All tidal volume comparisons were significantly different from each other except for Finna's and Yaka's volumes in Activity state 1, and Finna's and Vigga's tidal volumes in Activity state 3 (Table 4).

Tidal volumes at rest were determined for the animals from this study using Stahl's (1967) allometric equation. The mean tidal volumes measured for the four whales were between 1.3 and 4.2 times those of predicted values, while the whales' maximum tidal volumes measured were between 1.3 and 5 times the predicted tidal volume at rest. In both cases Vigga's differences in tidal volume from predicted values were at most half that for the other three whales (Hyak, Finna and Yaka). Comparing the whales' vital capacity to predicted values (Stahl 1967) and assuming tidal volume is 80% of the vital capacity as has been determined for other cetacean species (Irving *et al.* 1941, Olsen *et al.* 1969,

Table 2. Two-way ANOVA to test for variation of tidal volume among individual whales between Activity states 1 and 3.

Source	Sum of Squares	DF	Mean Squares	F-Ratio	Significance Level
whales	589846.043	3	196615.348	355.488	p < 0.0001
activity states	1212.842	1	1212.842	2.193	p = 0.141
whales * activity states	11121.132	3	3707.44	6.702	p < 0.0001
Error	86834.561	157	553.086		

**Table 3. Differences in tidal volume (l) for individual whales in different activity states (see Table 1 for sample size, SD and ranges) from Tukey's test for multiple comparisons.
NS = not significant**

Animal	Comparison between Mean Tidal Volumes		Significance Level
Hyak	Activity State 1	Activity State 3	NS
	211.46	205.50	
Finna	Activity State 1	Activity State 3	p < 0.003
	94.48	61.86	
Yaka	Activity State 1	Activity State 2	NS
	97.54	78.04	
	Activity State 1	Activity State 3	NS
	97.54	102.63	
	Activity State 2	Activity State 3	NS
	78.04	102.63	
Vigga	Activity State 1	Activity State 2	NS
	32.80	41.20	
	Activity State 1	Activity State 3	NS
	32.80	42.50	
	Activity State 2	Activity State 3	NS
	41.20	42.50	

Table 4. Significance of differences in tidal volumes between individual whales in the same activity state. NS = not significant

Animals	Activity State	Significance level
Hyak and Yaka	1	p < 0.001
	3	p < 0.001
Hyak and Finna	1	p < 0.001
	3	p < 0.001
Hyak and Vigga	1	p < 0.001
	3	p < 0.001
Finna and Yaka	1	NS
	3	p < 0.001
Finna and Vigga	1	p < 0.001
	3	NS
Yaka and Vigga	1	p < 0.001
	2	p < 0.01
	3	p < 0.001

Ridgway *et al.* 1969), Hyak's, Finna's and Yaka's vital capacities are between 68% and 94% of the values predicted from the allometric equation (Stahl 1967), while Vigga's vital capacity was only 35% of the predicted value from Stahl's allometric equation for vital capacity. Values for observed ventilation rates are between 0.26 and 0.32 those of predicted values.

Respiratory Gases

The extraction of oxygen and production of carbon dioxide were graphed as a function of apnea for the four individual whales (Figures 2-5, Table 5). Both oxygen extraction and carbon dioxide production were related to the duration of time between breaths (apnea). The different significant regression lines for oxygen extraction were compared to each other. Within individuals, slopes between activity rates were compared (Table 6). All slopes were significantly different, except those for Finna (Activity states 1 and 3). However, the intercepts were statistically different. Between individual whales, matching behaviour states were compared by using Tukey's test for multiple comparisons (Zar 1984). For Activity state 1, Yaka, Finna and Hyak were all significantly different from each other. For Yaka, Activity state 3 was significantly different from the other two activity states. For Hyak, Activity states 1 and 3 were also significantly different. All other comparisons tested were not significantly different from each other.

Comparisons among mean oxygen consumption and carbon dioxide production at mean apnea, based on mean tidal volumes for different activity states, showed that O₂ consumption and CO₂ production for Finna were lower at Activity state 3 than during

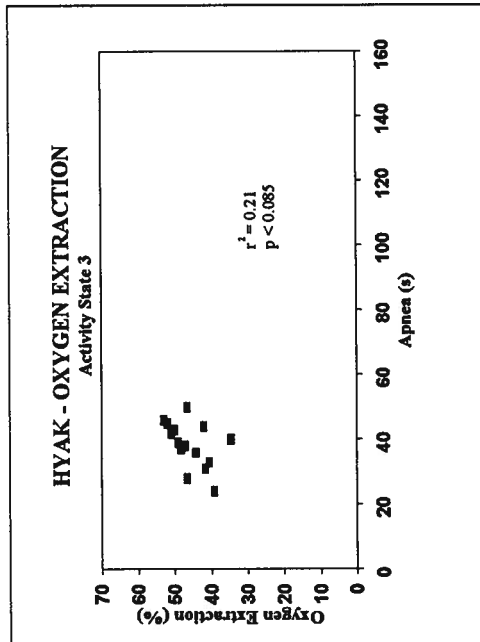
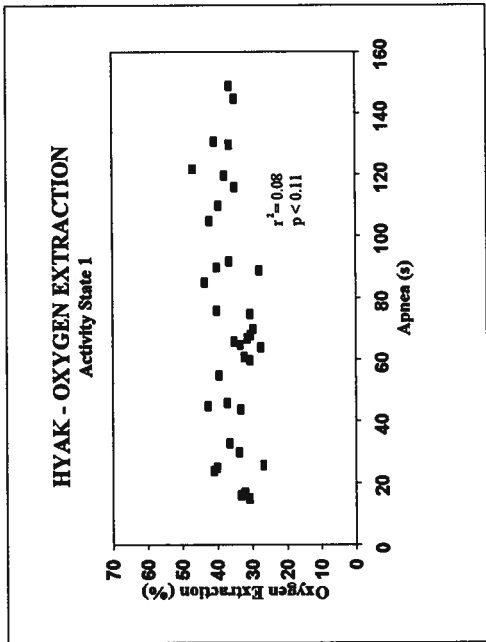
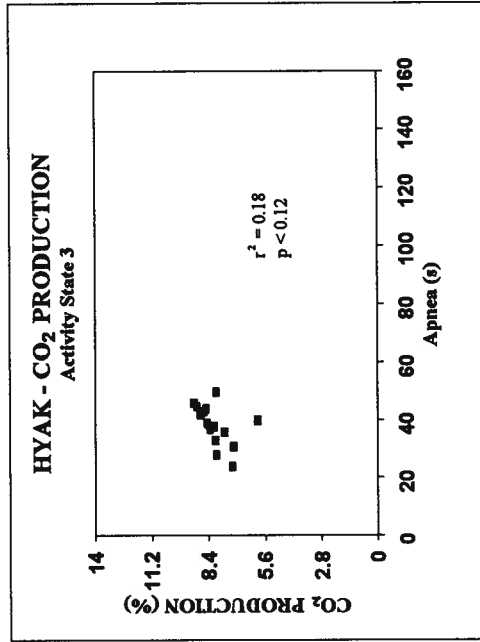
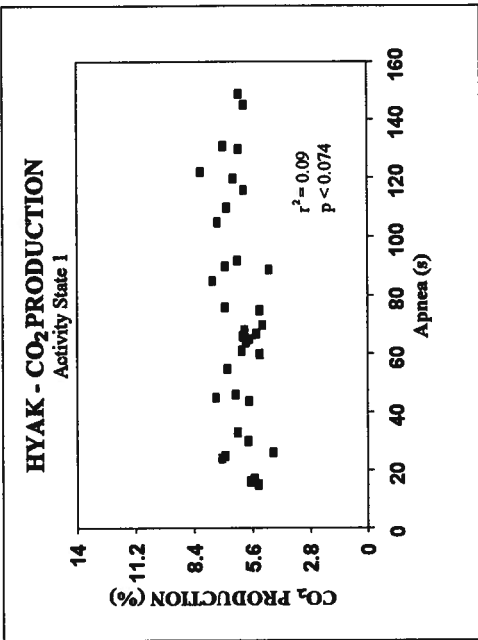


Figure 2. Oxygen extraction and carbon dioxide production as a function of apnea for Hyak in different activity states.

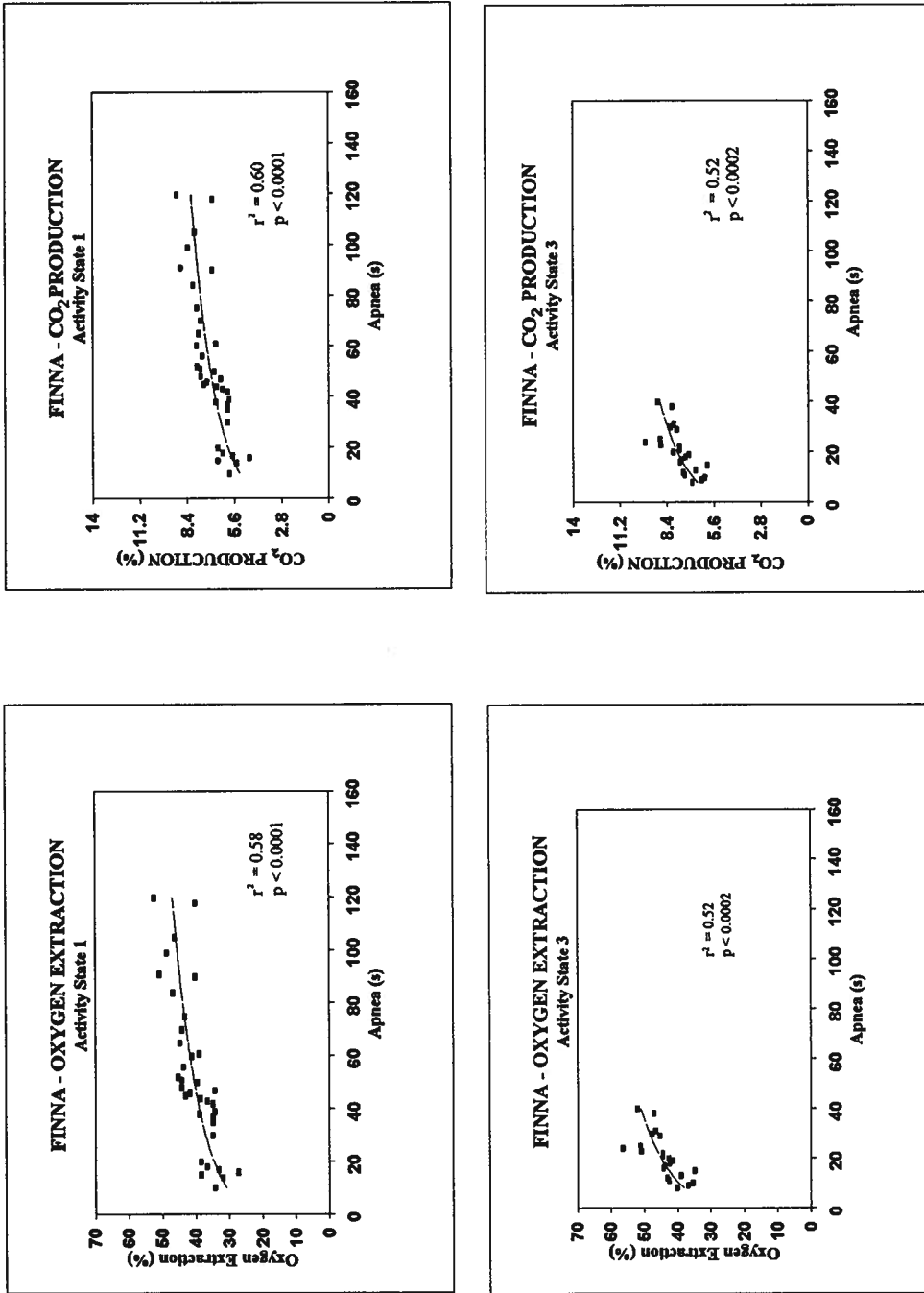


Figure 3. Oxygen extraction and carbon dioxide production as a function of apnea for Finna in different activity states.

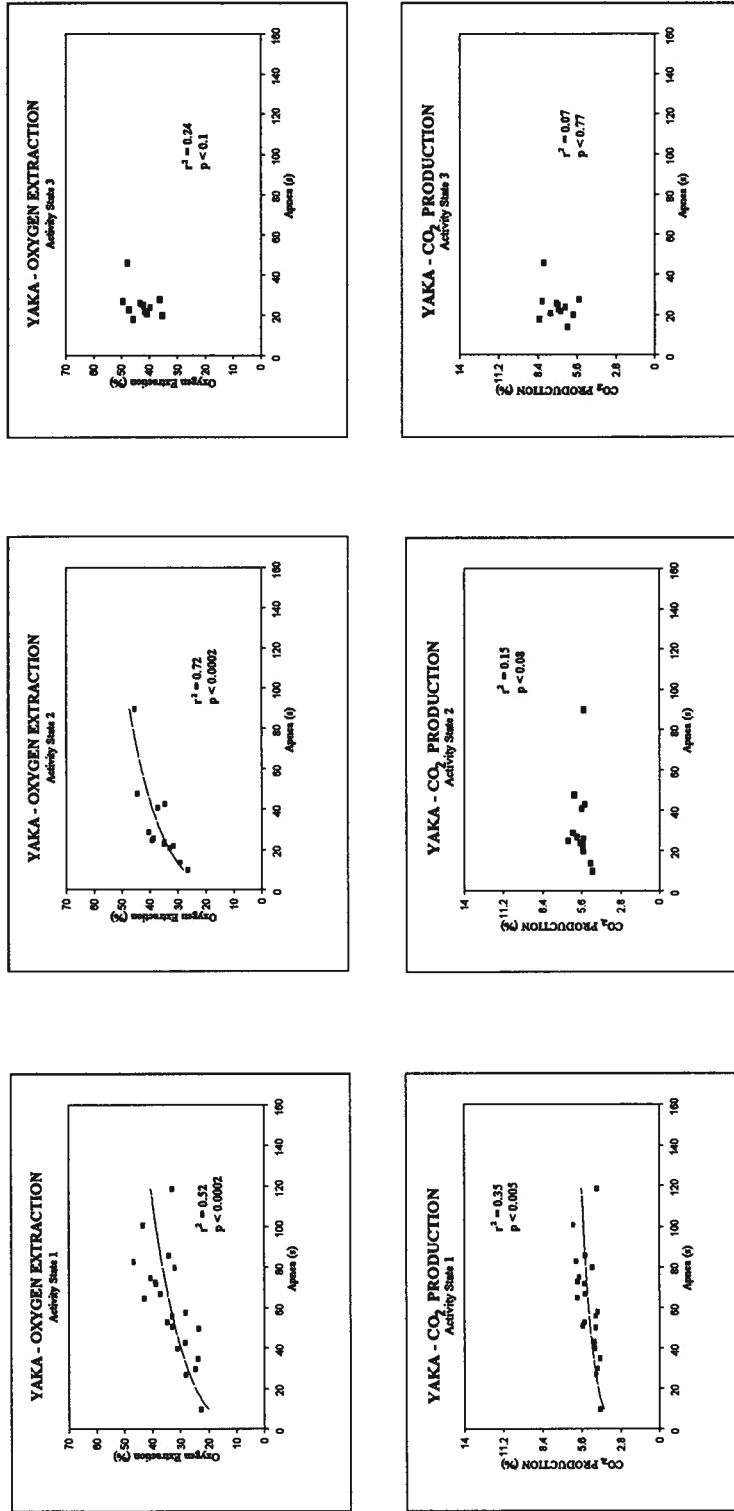


Figure 4. Oxygen extraction and carbon dioxide production as a function of apnea for Yaka in different activity states.

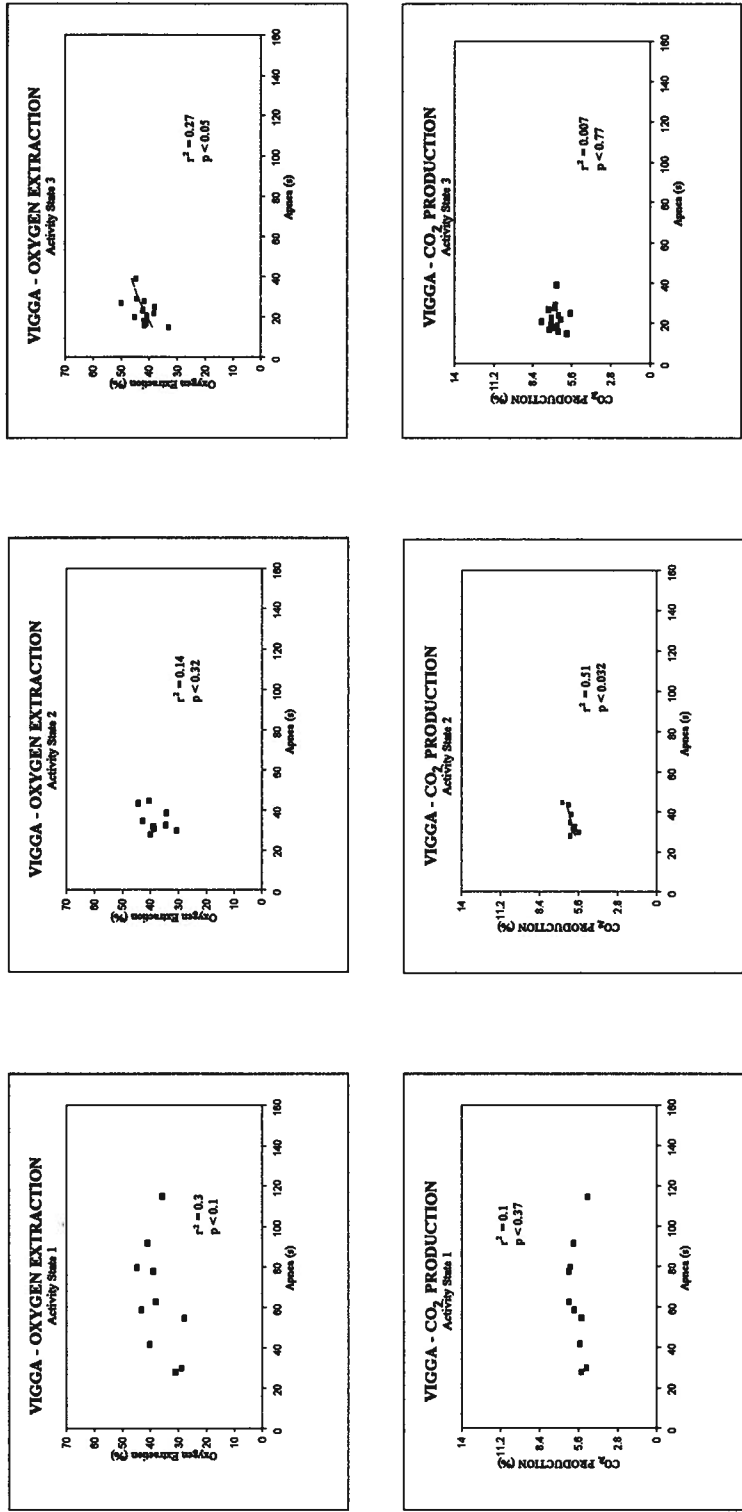


Figure 5. Oxygen extraction and carbon dioxide production as a function of apnea for Viggia in different activity states.

Table 5. Regression equations and statistics for the relationship between oxygen extraction and apnea and carbon dioxide production and apnea in four killer whales.

Animal	Activity State 1					Equation CO ₂ production	r ²	Significance Level	Standard Error intercept	Standard Error slope
	Equation Oxygen extraction	r ²	Significance Level	Standard Error intercept	slope					
Hyak	log O ₂ =3.32+0.06*log apnea	0.08	p < 0.11	0.14	0.04	log CO ₂ =1.57+0.06*log apnea	0.09	p < 0.074	0.13	0.03
Finna	log O ₂ =3.04+0.17*log apnea	0.58	p < 0.0001	0.09	0.03	log CO ₂ =1.27+0.17*log apnea	0.6	p < 0.0001	0.09	0.02
Yaka	log O ₂ =2.36+0.28*log apnea	0.52	p < 0.0002	0.15	0.06	log CO ₂ =1.09+0.13*log apnea	0.35	p < 0.005	0.10	0.04
Vigga	log O ₂ =2.80+0.20*log apnea	0.3	p < 0.1	0.15	0.11	log CO ₂ =1.49+0.06*log apnea	0.1	p < 0.37	0.09	0.06
Animal	Activity State 2					Equation CO production	r ²	Significance Level	Standard Error intercept	Standard Error slope
	Equation Oxygen extraction	r ²	Significance Level	Standard Error intercept	slope					
Hyak	-	-	-	-	-	-	-	-	-	-
Finna	-	-	-	-	-	-	-	-	-	-
Yaka	log O ₂ =2.78+0.24*log apnea	0.72	p < 0.0002	0.09	0.05	log CO ₂ =1.53+0.06*log apnea	0.15	p < 0.19	0.08	0.04
Vigga	log O ₂ =2.73+0.26*log apnea	0.14	p < 0.32	0.12	0.24	log CO ₂ =1.03+0.22*log apnea	0.51	p < 0.032	0.04	0.08
Animal	Activity State 3					Equation CO production	r ²	Significance Level	Standard Error intercept	Standard Error slope
	Equation Oxygen extraction	r ²	Significance Level	Standard Error intercept	slope					
Hyak	log O ₂ =2.81+0.28*log apnea	0.21	p < 0.085	0.11	0.28	log CO ₂ =1.25+0.23*log apnea	0.18	p < 0.12	0.10	0.14
Finna	log O ₂ =3.27+0.18*log apnea	0.52	p < 0.0002	0.09	0.18	log CO ₂ =1.51+0.18*log apnea	0.52	p < 0.0002	0.09	0.04
Yaka	log O ₂ =3.10+0.20*log apnea	0.24	p < 0.1	0.11	0.12	log CO ₂ =1.57+0.12*log apnea	0.07	p < 0.41	0.13	0.14
Vigga	log O ₂ =3.16+0.19*log apnea	0.27	p < 0.05	0.08	0.09	log CO ₂ =1.83+0.03*log apnea	0.007	p < 0.77	0.08	0.08

Table 6. Comparison of slopes of oxygen extraction as a function of apnea between different activity states for two killer whales.

Animal	Activity States	q	Significance Level
Finna	1 and 3	1.46	$p < 0.2^*$
Yaka	1 and 2	3.37	$p < 0.005$

***The intercept tested significantly different ($t = 8.22$, $p < 0.001$).**

Activity state 1 (Table 7). The mean value of the tidal volume probably underestimates normal tidal volumes. It was assumed that maximum tidal volumes better reflect normal tidal volumes than mean tidal volumes do. As a result of these assumptions, the values of the maximum tidal volumes of the killer whales are used for all further calculations (Table 8). Mean oxygen extraction at mean apnea during different activity states for the four killer whales showed that oxygen extraction increased between 14.4 % and 25.3% between Activity states 1 and 3 (mean = 20.3%) (Table 9).

The rate of oxygen consumption was graphed as a function of apnea (Figures 6-9). Changes in oxygen consumption with apnea as a function of activity state showed that:

- a) more oxygen is used at higher activity states than at lower activity states;
- b) the difference in oxygen consumption generally increases with increasing apnea; and
- c) the rate of increase in the differences declines with increasing apnea.

Mean oxygen extraction during the mean apneas observed for the different activity states increased with an increase in activity.

Standard Metabolic Rates

Standard metabolic rates, estimated both with mean and maximum tidal volumes, were calculated from equation [3] and compared to estimates of Hemmingsen (1960), Stahl (1967), McAlister (1981), Kleiber (1987) and Kasting (1989) (Table 10), although only estimates based on maximum tidal volumes are discussed here (see previous assumptions). Predicted estimates of basal metabolic rates from regression equations by Kleiber (1987), Hemmingsen (1960) and Stahl (1967) were lower than those measured for three of the

Table 7. Comparison between mean apnea and mean oxygen consumption and carbon dioxide production at mean tidal volumes for different activity states for four killer whales.

Animal	Oxygen Consumption (l/breath)			Carbon Dioxide Production (l/breath)		
	Activity State 1	Activity State 2	Activity State 3	Activity State 1	Activity State 2	Activity State 3
Hyak	74.5	-	96.8	13.0	-	17.0
Finna	39.3	-	31.6	6.8	-	5.0
Yaka	32.6	29.7	44.9	5.0	4.5	7.3
Vigga	12.1	17.3	18.3	1.9	2.7	2.9

Table 8. Comparison between mean apnea and mean oxygen consumption and carbon dioxide production at maximum tidal volumes for different activity states for four killer whales.

Animal	Oxygen Consumption (l/breath)			Carbon Dioxide Production (l/breath)		
	Activity State 1	Activity State 2	Activity State 3	Activity State 1	Activity State 2	Activity State 3
Hyak	91.0	-	121.8	15.8	-	21.3
Finna	55.3	-	67.8	9.6	-	11.7
Yaka	49.8	56.8	65.3	7.6	8.5	10.6
Vigga	22.1	25.2	25.8	3.4	4.0	4.1

Table 9. Mean oxygen extraction at mean apnea during different activity states for four killer whales.

Animal	Oxygen Extraction (% O /breath)		
	Activity State 1	Activity State 2	Activity State 3
Hyak	35.2	-	47.1
Finna	41.6	-	51.0
Yaka	33.4	38.1	43.8
Vigga	36.8	42.0	43.0
mean	36.8	40.1	46.2

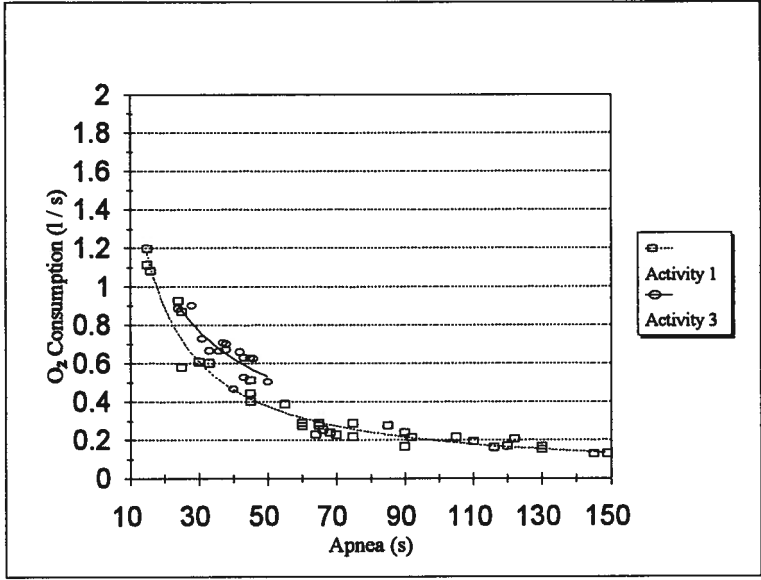


Figure 6. Rate of oxygen consumption as a function of apnea for Hyak for Activity states 1 and 3.

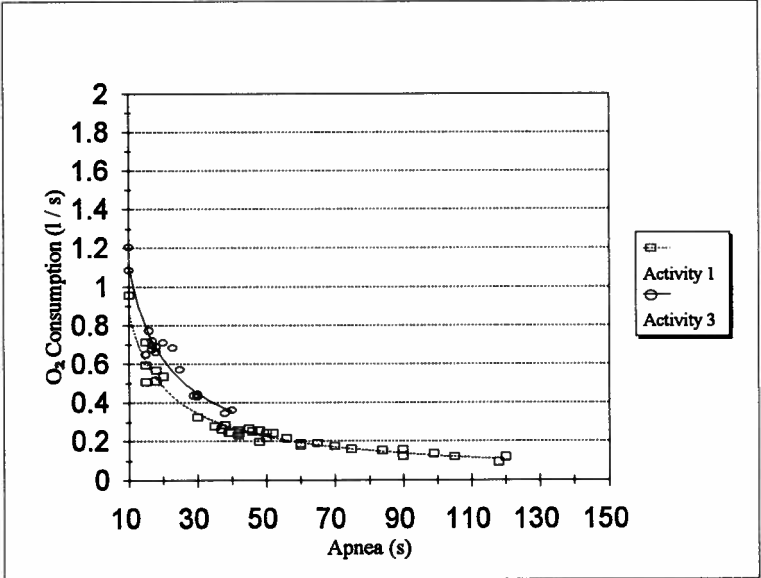


Figure 7. Rate of oxygen consumption as a function of apnea for Finna for Activity states 1 and 3.

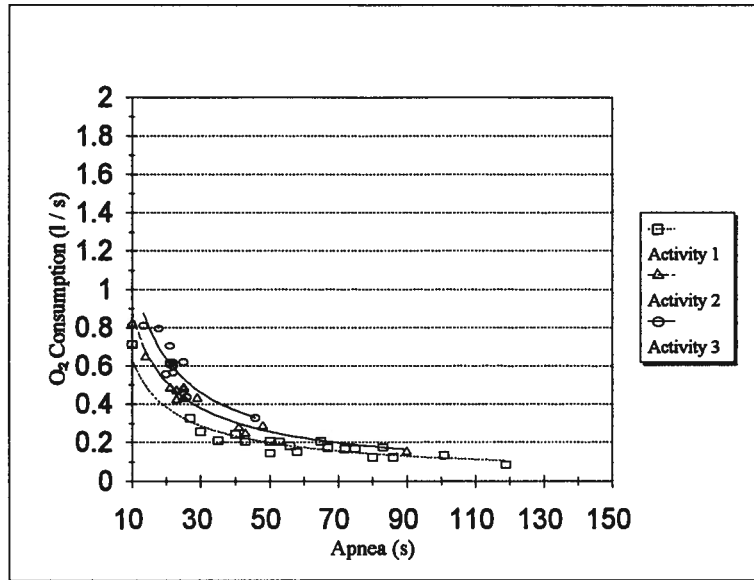


Figure 8. Rate of oxygen consumption as a function of apnea for Yaka for Activity states 1 through 3.

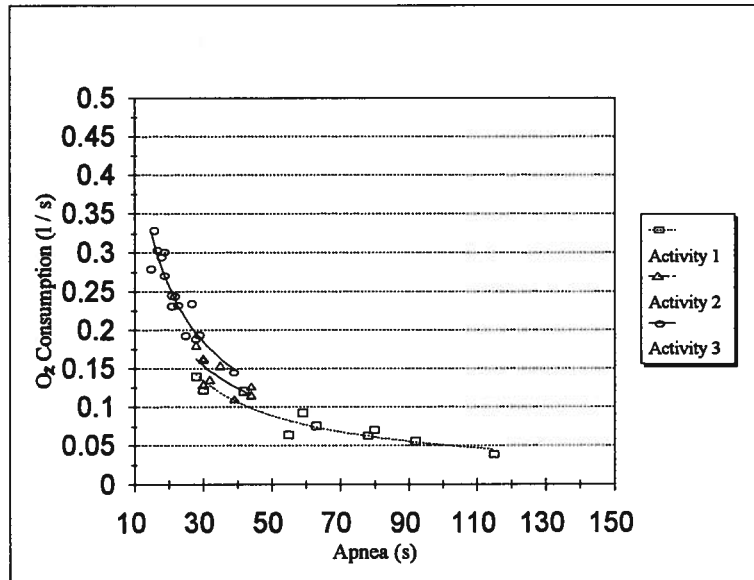


Figure 9. Rate of oxygen consumption as a function of apnea for Vigga for Activity states 1 through 3.

Table 10. Estimates (kcal/kg/d) of standard (SMR) and basal (BMR) metabolic rates for killer whales

	SMR (THIS STUDY) (MEAN TV)	SMR (THIS STUDY) (MAXIMUM TV)	BMR (KASTING et al. (1989))	BMR (McAlister) (1981)	BMR (KLEIBER) (1987)*	BMR (Hemmingsen) (1969)*	BMR (Stahl) (1967)*
HYAK	9.8	11.2	25.9	15.6	8.45	10.2	10.5
YAKA	7.1	10.9	-	17.8	9.19	11.1	11.4
FINNA	9.0	12.1	29.4	17.8	9.19**	11.1	11.4
VIGGA	6.8	8.7	-	20.3	9.99**	12.1	12.4

TV = Tidal Volume

*Estimates derived from general equation

**Animal did not fit Kleiber's criteria

four killer whales in this study. Hyak's estimated standard metabolic rate is 1.3 times the value predicted by Kleiber (1987) for an animal of his size, while Yaka's estimated standard metabolic rate is 1.2 times that predicted by Kleiber (Table 10). Though not directly comparable because Finna is a subadult, his standard metabolic rate is 1.3 times Kleiber's estimate, while Vigga's is 0.87 times Kleiber's estimate.

For the two adult killer whales, Hyak and Yaka, the standard metabolic rates were plotted on Kleiber's metabolic regression line (Figure 10).

Activity Budgets and Estimated Daily Caloric Expenditures

Caloric expenditure varied among individuals and among activity states (Table 11). Daily caloric expenditures for individual killer whales depended on the amount of time the animals spent in different activity states (Tables 12 and 13).

Metabolic Scopes

Minimum estimates for metabolic scopes were calculated for respiration rates and caloric expenditure (Table 14). The first column is based on measured metabolic rates for Activity states 3 and 1, and the second column is based on extrapolated values for Activity states 4 and 0.

Respiratory Quotients

Pooled estimates on respiratory quotients for the four animals only changed slightly throughout the day, ranging from 0.79 before feeding in the morning to 0.82 in the

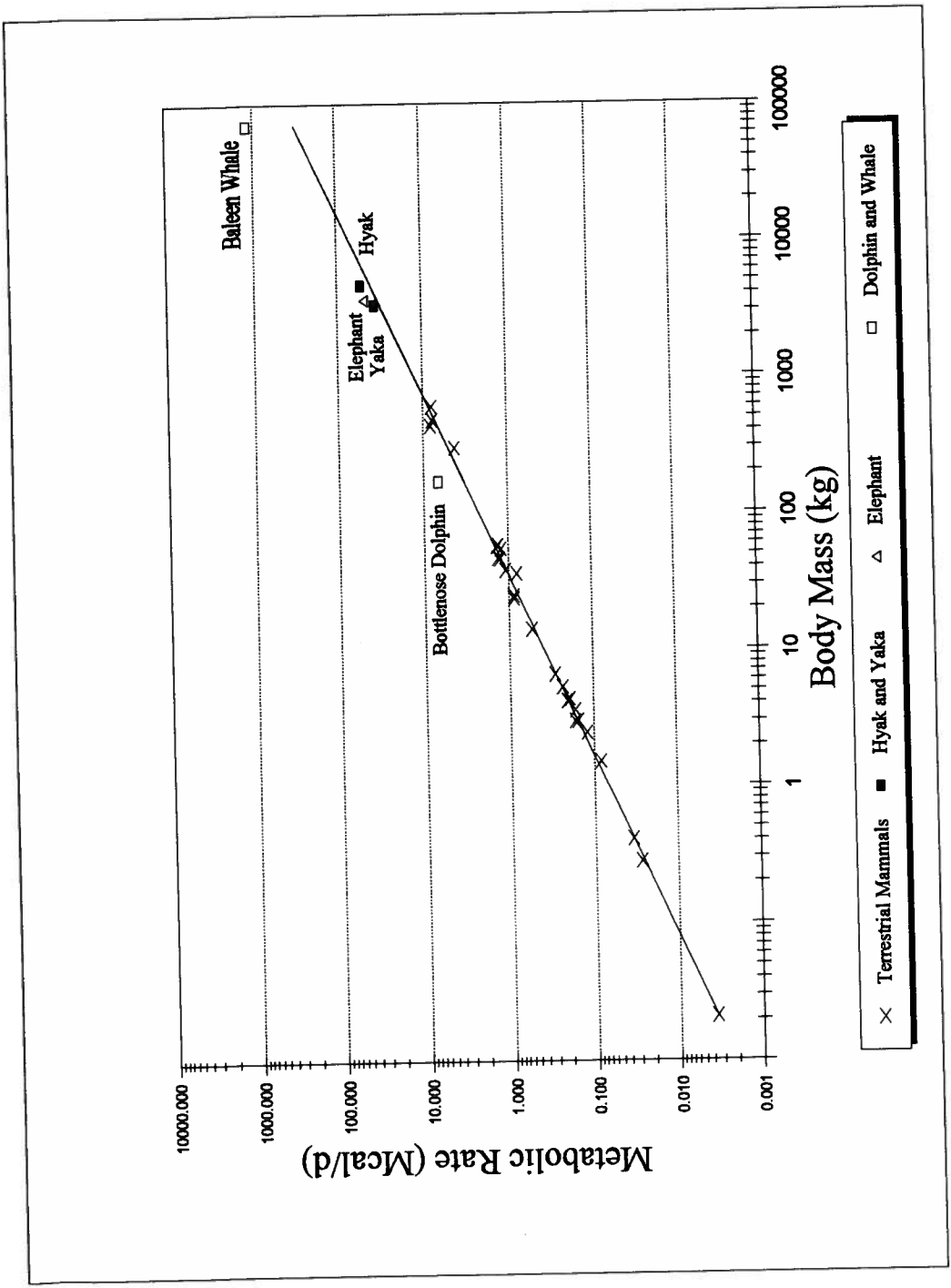


Figure 10. Metabolic rate as a function of body mass of mammals (after Kleiber 1987).

Table 11. Hourly caloric expenditure of four killer whales in different activity states.

	kcal/h			kcal/kg/h		
	Activity 1	Activity 2	Activity 3	Activity 1	Activity 2	Activity 3
Hyak	5502.6	-	10,270.9	1.17	-	2.19
Finna	3402.4	-	4232.8	1.00	-	1.26
Yaka	3060.1	4378.0	7662.8	0.91	1.30	2.28
Vigga	1483.3	1875.9	3599.4	0.62	0.78	1.50

Table 12. Average number of hours spent in different activity states by four killer whales.

	Activity 1	Activity 2	Activity 3
Hyak	22	-	2
Finna	16	-	8
Yaka	8	12	4
Vigga	7	12	5

Table 13. Daily energetic expenditure of four killer whales.

	kcal/d	kcal/kg/d
Hyak	141,600	30.2
Finna	88,301	26.3
Yaka	107,669	32.0
Vigga	50,891	21.2

Table 14. Metabolic scopes of four killer whales based on respiration rates and caloric expenditures.

	Respiration Rates		Caloric Expenditure	
	Activity 3/1	Activity 4/0	Activity 3/1	Activity 4/0
Hyak	2.1	4.2	1.4	5.0
Finna	2.9	3.6	1.5	3.8
Yaka	3.6	6.0	2.1	6.0
Vigga	3.5	4.4	2.3	4.6

afternoon after several feedings throughout the day (n=187; standard deviation ranged from 0.075 to 0.06). The differences in values of the respiratory quotients between morning and afternoons were statistically insignificant and did not reach the value of 0.7 (at which the burning of fat would be indicated) in the morning after the night-time fast. Therefore, the burning of fat alone 14 h after the last feed was not conclusively indicated.

DISCUSSION

Tidal Volumes and Respiration Rates

Stahl (1967) scaled respiratory variables in mammals and expressed them as allometric equations. The differences in tidal volumes between Stahl's predicted and measured values in this study may be primarily due to relatively uniform tidal volumes across activity states in the killer whales studied. The large exchange of air per breath allows for the longer respiratory intervals observed (Irving *et al.* 1941, Olsen *et al.* 1969, Ridgway *et al.* 1969). In turn, the long respiratory intervals lead to reduced ventilation rates by allowing extraction of a larger proportion of the oxygen in inspired air (Figures 6-9). While a large tidal volume relative to vital capacity does not necessarily indicate that oxygen extraction will be large, a large oxygen extraction and a large tidal volume relative to vital capacity will extend the respiratory interval significantly. These observations appear to indicate a fundamentally different relationship among respiratory parameters than that observed in terrestrial mammals, who breathe more frequently and do not extract as much oxygen as marine mammals (Stahl 1967, Schmidt-Nielsen 1990). While lung

volumes in marine mammals have been reported to be very similar to those of terrestrial mammals (Bryden 1988), tidal volumes at rest in these study animals are a larger fraction of the lung volumes compared to terrestrial mammals, resulting in a more complete exchange of respiratory gases. Tidal volumes in terrestrial mammals at rest are a small fraction (1/6 to 1/7) of vital capacity (Schmidt-Nielsen 1984, 1990), but tidal volumes are higher during exercise than during rest (Stahl 1967). This was not observed in killer whales.

While lung volume and oxygen uptake rates in killer whales are similar to those predicted by allometric equations established using data from terrestrial mammals (Stahl 1967, Kleiber 1987, Bryden 1988), equations for respiratory variables should be used with caution when applying them to mammals that have evolved specialized behaviours and physiological adaptations for life in a marine environment.

At night, the whales were observed to be in their calmest state and during rest had lower respiration rates than those counted during the day in Activity state 1 (D.E. Bain, pers. comm.). The behaviour was very similar to that observed in Activity state 1, namely hanging at the water surface, but the respiration rate was noticeably lower, and the duration of rest was longer.

Bain (1986) and Ray *et al.* (1977, 1986) also noticed a reduction in respiration rates during night-time rest periods in other captive killer whales during 24-h respiration and behaviour observations. Decreased respiration rates during rest periods in wild killer whales have also been observed (Osborne 1986).

Reasons for the increased respiration rates at rest during the day relative to night-time

are difficult to interpret, but one possible explanation is that the whales are in a different emotional state once people are active around the pool. Anticipation of feeding and show times may be one of the factors contributing to the elevated respiration rates observed in all whales, although the physical behaviour (hanging at the water surface) was the same during rest behavior at night and during the day.

Apnea and Observed Rates of Oxygen Consumption

Innes and Lavigne (1991) criticize Kasting *et al.* (1989) for not collecting consecutive breaths from which to predict oxygen consumption. This criticism, of course, applies to this study as well. Innes and Lavigne (1991) state that, as a result, Kasting *et al.* (1989) were not justified in assuming that the relationship between oxygen consumption and apnea duration was determined in a steady-state, resting condition. They claim that the expected relationship between oxygen extraction and apnea duration should be linear, and not curvilinear as suggested by Kasting *et al.* (1989) and as reported here.

Using a large sample of respiration collections should eliminate the bias that could occur by collecting single respirations. The possibility of collecting data at a consistent breath during the respiratory cycle, which is characterized by a sequence of breaths separated by short apneas, followed by a single long apnea, should also be eliminated. Breaths were collected at a variety of points during the respiratory cycle, but it is not known whether this eliminated the bias of collecting single breaths.

Using Lenfant *et al.*'s (1968) data on the partial pressure of oxygen in the lung at exhalation, and information on the basic chemistry cited by Peters (1983) that flux rate is

proportional to the partial pressure difference between the lungs and the blood, several arguments can be proposed to show that the relationship between oxygen extraction and apnea duration is curvilinear in killer whales:

- a) When the whale inhales initially, there is a large difference in oxygen partial pressure between the lungs and the blood. As a result, the oxygen flux from the lung to the blood is high; and
- b) The high flux depletes oxygen in the lung which reduces the flux rate.

Once the flux rate drops below that required to maintain the animal's metabolic rate, the use of oxygen stores in the body, such as in the muscle, would be initiated. This model accounts for the curvilinear and not linear nature of the data. Innes and Lavigne (1991) proposed a linear fit in which the intercept reflected the mean oxygen debt at the end of apnea, and the slope reflected metabolic rate. However, the metabolic rate they inferred would require nearly 120 s to build up the debt indicated by the intercept, whereas Kasting *et al.* (1989) and I found that mean apnea was approximately 60 s for Hyak, the largest of my study whales. Thus attempts to fit a straight line such as proposed by Innes and Lavigne (1991) are unlikely to reflect the true relationship between oxygen consumption and apnea.

While, after any breath in the respiratory cycle, a decrease in the concentration of oxygen in the lungs relative to atmospheric oxygen is experienced, most of the oxygen depleted air gets exchanged during the first breath. As oxygen diffuses into the blood, the

rate of oxygen flow from the lungs to the blood decreases as the gradient between the oxygen level in the blood and atmospheric oxygen declines.

Regardless of the model chosen, over the range of apneas tested there is little difference in the mean rate of oxygen uptake between the log-log model used in this study and a linear fit model with an appropriate intercept, such as that proposed by Innes and Lavigne (1991).

Three trends can be interpreted from the oxygen extraction as a function of apnea curves:

- a) For a given apnea, oxygen consumption per ml of tidal volume is consistently higher at higher activity states.
- b) Within each activity state, oxygen consumption rate declines with an increase in apnea.
- c) The rates of oxygen extraction are higher immediately after a breath than are those later on; this trend was consistent for all individuals in all activity states.

Oxygen consumption increased with increasing activity state. Hewlett (1970) reports similar results for Skana, a female killer whale of similar size to Vigga. Skana's tidal volumes ranged from 50 to 60 l every 20 to 60 s. She consumed 3 to 4 l of O₂/min at rest, and this increased to 9 l of O₂/min at a mean tidal volume of 78 l. These oxygen consumptions are the equivalent of 9.94 to 13.3 kcal/kg/day at 3 to 4 l of O₂/min, and the animal used 29.8 kcal/kg/day at 9 l of O₂/min. This latter level was similar to Activity state 3 in this study.

Estimated Standard Metabolic Rates

To allow interspecific comparisons among different species, the data in Activity state 1 were collected as closely to Brody's (1945) and Kleiber's (1987) criteria as possible. These criteria state that in order to collect comparable data on metabolic rates, the animals have to be in a calm and relaxed physiological and psychological state, in a post-absorptive condition and be placed in a thermoneutral chamber. Only healthy, sexually and physically mature animals, neither pregnant nor lactating, can be considered. Hyak and Yaka both fit these criteria, except that they were possibly not in the same calm psychological state in which they were during night-time observations, hence their respiration rates were corrected to those observed during Activity state 0. The water temperature in the pools in which the animals live is probably well within the animals' thermal neutral zone (Chapter 2 and see Williams *et al.* 1991).

Schmidt-Nielsen (1979) determined that the moving metabolic rate of terrestrial mammals rises in direct proportion to velocity for walking and running from a velocity of almost zero to maximum. The BMR is lower than the intercept of the regression line calculated for the moving metabolic rate as a function of velocity. Schmidt-Nielsen (1979) called this metabolic rate at zero velocity the "basal metabolic rate plus postural costs" because the body needs to be held in an erect running position. Taylor *et al.* (1970) approximated this as 1.7 times the basal metabolic rate. Metabolic rate in Activity state 1 is approximately two times the basal metabolic rate and may reflect an analog to postural cost.

Comparing the whales' metabolic rates at night-time rest to Kleiber's (1987) data it is

obvious that all the animals in this study except for Vigga have slightly higher metabolic rates than the terrestrial mammals investigated by Kleiber (1987).

Kleiber (1987) predicts the basal metabolic rate of an animal Hyak's and Yaka's size to be 25% and 16% lower, respectively, than was measured in this study. However, by using oxygen consumption values from Activity state 1 and replacing respiration rates from Activity state 0 it is likely that the resting metabolic rate was overestimated. It is possible that not just the respiration rate was lower during Activity state 0, but the oxygen consumption rate was lower as well.

Taking Brodie's (1975) and Lockyer's (1981a, 1981b) arguments about using standard or maintenance metabolism for cetaceans into consideration instead of estimating basal metabolism, it is to be expected that killer whales' standard metabolic rate might be slightly elevated relative to that of terrestrial mammals' standard metabolic rates.

Estimates of basal metabolic rates made by Kasting *et al.* (1989) using the same technique used in this study were more than two times higher than metabolic rates estimated for the killer whales in this study. McAlister (1981) estimated BMR for marine mammals of different sizes based on food consumption of captive cetaceans and also suggested higher metabolic rates than the estimates for killer whales in this study. The values of these study animals' standard metabolic rates are within the ranges predicted for mammals and are even below that of a terrestrial mammal of comparable size. Comparing Yaka's SMR to that of an elephant (Benedict 1938) which is almost identical in size, shows that this killer whale has a metabolic rate (10.9 kcal/kg/d) 18% lower than the elephant (13.3 kcal/kg/d). McNab (1986) states that BMRs of terrestrial carnivores

average 1.47 times Kleiber's general prediction but this is not considered to differ markedly from other mammals. Ridgway (1972) also states that a high protein diet alone can contribute considerably to a high metabolic rate. Metabolic rates of the killer whales studied here can therefore be considered to be similar to those of other mammals.

Kasting *et al.* (1989) employed the same technique as used here for respiration collection, but obtained substantially different results. Their estimated mass-specific metabolic rates are 2.3 times higher than those determined in this study. Primary causes of the difference about standard metabolic rates were the activity state and the weight of the animals. While Kasting *et al.* (1989) used respiration rates counted during the day, this study exchanged reduced respiration rates observed during night time rest for respiration rates counted during rest periods during the day to estimate standard metabolic rates. Body weights in Kasting *et al's* (1989) report are 23% lower than the weight for killer whales used in this study. Minor differences exist in respiration rates during Activity state 1, tidal volumes and possible oxygen uptake, and while two of the killer whales that he examined were sexually mature, they were not physically mature (Duffield and Miller 1988, Innes and Lavigne 1991). Brody (1945) found that the resting metabolic rates of growing terrestrial mammals can be up to twice the BMR of adults. However, Kasting *et al.* (1989) used the data from both mature and immature animals to develop a regression equation predicting basal metabolic rates for differently sized killer whales.

Estimated Daily Caloric Expenditures

The two adult animals, Hyak and Yaka, had daily caloric expenditures which were

between 2.7 and 2.9 times those of the animals' standard metabolic rates. This is comparable to published data for terrestrial mammals, which has been estimated as 1.7 to 3 times the basal metabolic rate (Wunder 1975, McNab 1980, Peters 1989). Other studies have also yielded similar conclusions on pinnipeds' average daily metabolic rates being similar to those of terrestrial mammals (Kooyman *et al.* 1973, Lavigne *et al.* 1982, Murie 1987).

Metabolic Scope

The minimum estimates of metabolic scopes for the four killer whales studied are lower than those observed in terrestrial mammals which have a typical metabolic scope of 10 (Hemmingsen 1960). Yaka had a respiration rate of up to 180 breaths/h during extremely high activity, and Bain (pers. comm.) observed a minimum breathing rate of 24 breaths/h for Yaka that occurred during what may have been sleep. This is a 7.5 fold increase between the lowest respiration rate observed during continuous rest and the highest sustained breathing rate ever observed in this individual. In addition, the measured oxygen consumption per breath and unit time increased with activity. However, standard metabolic rates may have been overestimated by using the oxygen consumption measured in Activity state 1 and using only respiration rates collected during Activity state 0. Similarly, using oxygen consumption determined during Activity state 3 and respiration rates counted during Activity state 4, may have underestimated maximum metabolic rate if oxygen consumption rates were higher during Activity state 4 than during Activity state 3. While an approximate metabolic scope can be obtained by using the above mentioned

method using both respiration rates and caloric expenditures, ranging from 1.4 to 7.5, maximum exertion was most likely never reached because the whales were not pushed to their maximum limits during and after shows. These metabolic scopes estimated for killer whales are slightly higher than Irving *et al.*'s (1941) and Irving's (1973) estimates that bottlenose dolphins (*Tursiops truncatus*) may not increase their oxygen consumption to more than three or four times their resting rate. Irving *et al.* (1941) and Irving (1973) describe aquatic mammals as having a high metabolic rate compared to other mammals and a modestly expanded metabolic rate for daily activities; he states that marine mammals have little scope for an increase in tidal volume and the degree of oxygen utilization. While metabolic scopes in this study were higher than those reported by Irving *et al.* (1941) and Irving (1973) for bottlenose dolphins, they were lower than those observed in terrestrial mammals. A better understanding of how oxygen uptake rates vary with activity rate as well as pushing the whales to their maximum limit would be needed to accurately determine metabolic scopes.

Difficulties and Reliability

The most questionable factor in the respiration analysis was the determination of tidal volumes. This is because the researcher can not be certain whether the animals exhaled normally. While Hyak, Finna and Yaka adapted well to the breathing apparatus, it was clear that Vigga did not. One important factor in the difference of her data to those of the other whales is that her tidal volumes are low because she did not exhale fully. While no data from Vigga or any of the animals were used where they exhaled again instead of

inhaling after breath collection, it was the strong suspicion of myself, the training staff and other research personnel that Vigga did not exhale fully with the apparatus on her blowhole. As a result, her metabolic rate tested by respiratory analysis may be underestimated by an unknown amount. It is also unknown how uniform tidal volumes are during normal breathing as well as how uniform the extrapolated oxygen uptake rates are because respirations were requested after predetermined apneas.

Some uncertainties existed in the estimated weights of the animals. Weighing the animals on a regular basis at the 2 aquaria where the studies were conducted would add to the knowledge of growth of killer whales in aquaria.

While activity budgets were observed during the study, they change on a daily basis and hence determination of activity budgets would have to be repeated during further studies.

**Chapter 2: FOOD CONSUMPTION AND THE INFLUENCE OF OTHER
FACTORS ON FOOD INTAKE IN CAPTIVE KILLER WHALES, *Orcinus orca***

INTRODUCTION AND OBJECTIVES

Estimates of food intake are fundamental to the study of the ecology of any animal. Direct measurement of food intake by wild cetaceans is difficult because the animals generally feed under water and out of sight. This chapter was designed to compare respiration-based estimates of energy expenditure of captive killer whales (*Orcinus orca*) (Chapter 1) to the food intake by those whales in captivity at the time of the respiration measurements.

In addition, long term food records were evaluated for possible factors affecting food intake. Factors affecting food intake in killer whales and other species may include growth, reproductive status, health, water temperature, ocean of origin and time of year. Caloric intake can be calculated based on the amount and type of food provided. This together with estimates of body size of the animals can be used to develop formulas that can be used to estimate food intake as a function of body size.

Studies on food intake of captive cetaceans have been conducted on several species by analyzing daily food records and relating food intake to growth and estimated weight of the animals. Kastelein and Vaughan (1989) determined the daily food consumption of a captive female Atlantic killer whale by analyzing daily food records and relating food

intake to growth and estimated weight of the animal. This whale consumed 7% of her body weight per day as a 1-year old calf at 315 kg which decreased to 2.1% of her body weight of 1900 kg as a subadult. Two smaller, sub-adult male killer whales (4.67 m long, 1040 kg; and 4.9 m long with a calculated weight of about 1500 kg) consumed 4.3% and 3.9%, respectively, of their body weight on a daily basis (Sergeant 1969).

Captive growing beluga whales (*Delphinapterus leucas*) weighing around 200 kg consumed 4.5% of their body weight per day, which was reduced to 1.2% in adult animals weighing 1400 kg (Kastelein *et al.* 1994).

Adult Commerson's dolphins (*Cephalorynchus commersonii*) weighing between 36 to 43 kg were observed to consume between 9 and 12% of their body weight per day (Kastelein *et al.* 1993). Adult male harbour porpoises (*Phocoena phocoena*) weighing between 32 and 40 kg ate approximately 8% of their body weight per day, while growing animals (16 to 24 kg) consumed 10.4% to 13% of their body weight per day (Andersen 1965, Kastelein *et al.* 1990).

These studies show that small species and young cetaceans typically eat more in relation to their body weight than do large cetaceans. This was confirmed by Sergeant (1969) who reported feeding rates of eight different odontocete species in captivity. He determined that body weight was inversely proportional to food intake as a percentage of body weight.

As indicated by the above studies, body weight is important in determining food intake. Based on empirical data Bigg and Wolman (1975) developed the following equation to estimate body weight of killer whales:

$$[13] M = 0.000208 L^{2.577},$$

where M is body mass in kg and L is total body length in cm.

Mean length at birth for killer whales in British Columbia (based on stranded neonates, n=6) is 244 cm (Bigg 1982). In the North Atlantic, newborns are on the average 213 cm in length (based on whaling records, n=5, Jonsgard and Lyshoel 1970). Growth rates of young killer whales in aquaria average 37-38 cm/y (Bigg 1982, Duffield and Miller 1988). After reaching approximately 488 cm in length, growth rate declines in both sexes, with the females ceasing growth at about 580 to 600 cm body length, while males may grow up to 900 cm in length before growth ceases (Reeves and Mitchell 1987).

Bigg (1982) concluded that data from animals in captivity provided a guide to potential growth rates of wild killer whales, but suggested that captive animals grow faster than their counterparts in the wild. Based on captive growth rates, length at sexual maturity would be reached by 7 y of age, but observed ages of maturity in the wild range from 11 to more than 15 y (Bain pers. comm., Bigg *et al.* 1990, Olesiuk *et al.* 1990). Asper *et al.* (1988) report a length of 400 cm for a 28 month old Atlantic-Pacific hybrid female calf, indicating growth rates in aquaria are enhanced compared to growth rates in the wild where a young killer whale would be approximately 315 cm at that age.

Another factor reported to influence food intake is water temperature. Williams *et al.* (1991) studied the thermal limits of captive bottlenose dolphins by measuring their metabolic rate. The dolphins maintained a stable body temperature in water ranging from 3.6 °C to 17.3 °C, while their metabolic rate was stable between 6 °C and 16 °C. The

thermal neutral zone of killer whales is not known, but the species inhabits the cold waters of the Arctic and Antarctic as well as the warm waters of the equatorial convergence zones (Heyning and Dahlheim in press). Water temperatures between the cold arctic waters and warm equatorial currents range from $-1.3\text{ }^{\circ}\text{C}$ to $27\text{ }^{\circ}\text{C}$ (Sverdrup *et al.* 1946). To maintain a constant body temperature in varying water temperatures, killer whales, and cetaceans in general, have developed many adaptations, such as counter current heat exchange (Bryden 1988), integument modifications (Ridgway 1972), restriction in body surface area, and respiratory modifications (Gaskin 1982). Phenotypic adaptations include variations in blubber thickness and blubber lipid levels (Williams 1991, Worthy 1991). Worthy and Edwards (1990) and Worthy (1991) showed that while cetaceans exhibit seasonal changes in blubber thickness, presumably in response to water temperature changes, there are also data from five species of dolphins to suggest that the lipid content of the blubber layer changes with season, ranging from 30 to 95%. Dramatic regional and seasonal variations in lipid content in bottlenose dolphins was also observed (Worthy 1991). Therefore, both the quantity and quality of the blubber layer can change, and are important for thermoregulation in dolphins.

A seasonal decrease in food intake with increases in water temperatures was observed in captive Commerson's dolphins held at five different aquaria (Kastelein *et al.* 1994). Food intake in captive beluga whales (*Delphinapterus leucas*) is negatively correlated with water temperature, with food intake decreasing approximately 30% during warmer summer months (Kastelein *et al.* 1994). This decrease in food intake corresponds to the same time that wild beluga whales reduce their food consumption due to migration. Perhaps internal

factors rather than lowered heat loss reduce food intake of belugas during this period (Kastelein *et al.* 1994).

Pregnancy and lactation increase food intake in most mammals including captive cetaceans. While food intake increased only slightly during the last month of pregnancy in bottlenose dolphins, increases in food consumption of 129% to 204% were found during lactation (Reddy *et al.* 1991). No increase in food consumption was found during pregnancy in Commerson's dolphins, but food intake in these animals increased by 30% during lactation (Kastelein *et al.* 1994). Food intake in beluga whales increased during lactation by up to 100% (Kastelein *et al.* 1993).

It has been questioned in the past to what degree food intake in captivity reflects food intake in the wild. Aquarium staff today take into consideration the overall appearance and motivation of the animals toward food, and generally feed the animals to satiation.

Studies of terrestrial mammals (Brody 1945, Kleiber 1987) have shown that not all food ingested can be metabolized and used by the animal. To compare energy expenditure to food consumption, food intake needs to be corrected for urinary, fecal and respiratory losses. Net assimilation efficiency (NAE), the ratio of absorption to ingestion (Peters 1983), was reported to range from 67.7% to 74.6% in adult harp seals (*Pagophilus groenlandicus*, Lavigne *et al.* 1982). Worthy (1990) cites studies determining NAE's for different species of pinnipeds ranging from 88% NAE after pollock (*Pollachius virens*) to 97% after herring (*Clupea harengus*) consumption. Assimilation levels for mackerel (*Scomber japonicus*) consumed by Black Sea bottlenose dolphins (*Tursiops truncatus*) were 89% to 90% (Shapunov 1973a and 1973b). A value of 74% for NAE was

suggested for metabolic rates of harbour porpoises, *Phocoena phocoena* (Yasui and Gaskin 1986). Lockyer (1981a, 1981b) estimated this correction factor to be between 70% and 80% for blue (*Balaenoptera musculus*) and sperm (*Physeter catadon*) whales.

In this chapter, the determination on how closely daily energy expenditures estimated by respiration analysis in killer whales (see Chapter 1) match the animals' observed food intake in the aquarium, is described. Such comparisons of measurements of food intake and metabolic rate studies by indirect calorimetry have not been reported before for cetaceans. The food intake data of the same four killer whales studied in Chapter 1 for metabolic rates determined by respiration analysis and two additional individuals were collected.

The objectives were to:

1. determine the quantity of food killer whales were fed in a captive environment;
2. determine any differences in food intake within and among individual whales and identify factors related to food intake;
3. compare food consumption to energy expenditure estimated from respiration analysis (data from Chapter 1); and to
4. estimate net assimilation efficiency.

METHODS

Aquarium personnel at two aquaria have recorded the daily food consumption (species of fish and amount fed) by six killer whales held at two aquaria. Combined, these data amount to a total of 80 whale-years (where data from one whale for 1 year = 1 whale year, Bigg 1982). Each whale's arrival date, size and estimated age at capture and years for which food data were available are summarized in Table 15. In addition, available records of daily water temperatures, reproductive, and health status, together with interviews with the training staffs were used to examine variations in food intake.

While some of the factors such as the amounts of food consumed can be statistically analyzed, others, such as comparisons between aquaria, can only be described because of the small number of independent samples in this study.

Age Estimation

The ages of the individual whales at the time they were captured were estimated as follows:

[14] $\text{age (y)} = [\text{length at collection (cm)} - \text{length at birth (cm)}] / \text{growth rate} + D \text{ (y)}$,
where: length at birth was assumed to be 244 cm for killer whales from British Columbia (Bigg 1982) and 213 cm for whales from Iceland (Jonsgard and Lyshoel 1970, Duffield and Miller 1988). Growth rate is estimated at 37 cm/year up to a length of 488 cm for both Pacific and Atlantic killer whales, and D is the estimated difference in growth of

Table 15. Descriptions of the study animals and availability of food records.

Animal	Sex	Date Collected	Ocean Of Origin	Institution	Length Measured At Capture (cm)	Estimated Year Of Birth	Years At Aquarium	Food Data Available
Skana	F	2/67	Pacific	VA*	439	1961	1967-1980	1967-1969 1971-1980
Hyak	M	4/68	Pacific	VA*	304	1967	1968-1991	1968-1969 1971-1984 1986-1991
Finna	M	11/80	Atlantic	VA*	394	1975	1980-Present	1981-1984 1986-1993
Bjossa	F	11/80	Atlantic	VA*	404	1974	1980-Present	1981-1984 1986-1993
Yaka	F	12/69	Pacific	MWA/USA**	320	1967	1969-Present	1983-1993
Vigga	F	11/80	Atlantic	MWA/USA**	320	1977	1980-Present	1983-1993

*Vancouver Aquarium, Vancouver, B.C.

**Marine World Africa/USA, Vallejo, CA

wild and captive whales (Asper *et al.* 1988). D was set to one year added for all whales coming into captivity after 5 y of estimated age, to correct for the assumed slower growth of the animals in the wild during the first years of rapid growth in killer whales (Bigg 1982, Asper *et al.* 1988).

Weight

The captive animals used for this study had been measured for length (Figure 11) at various time intervals (Table 16). These data were used to calculate weights for the individual animals (Table 16) using Bigg and Wolman's (1975) equation for the relationship between body length and weight. For all weights, except the first one for each animal, 20% extra body weight was used for each whale (see Chapter 1).

Food Data Collection

Aquaria food records date back to 1967 and were collected through 1993. Two individuals (Skana and Hyak) died at the Vancouver Public Aquarium, and for both individuals most food data from the time of their arrival to their deaths were available. The other animals studied were still alive as of 31 December 1993 after which data are not included here.

Food records were entered on a daily basis by the training personnel except for Finna and Bjossa during 1991 to 1993, when food data were entered on a weekly basis. Continuous food consumption data were not available for all individuals because of data lost by the aquaria. All available data were used. These data were entered into a

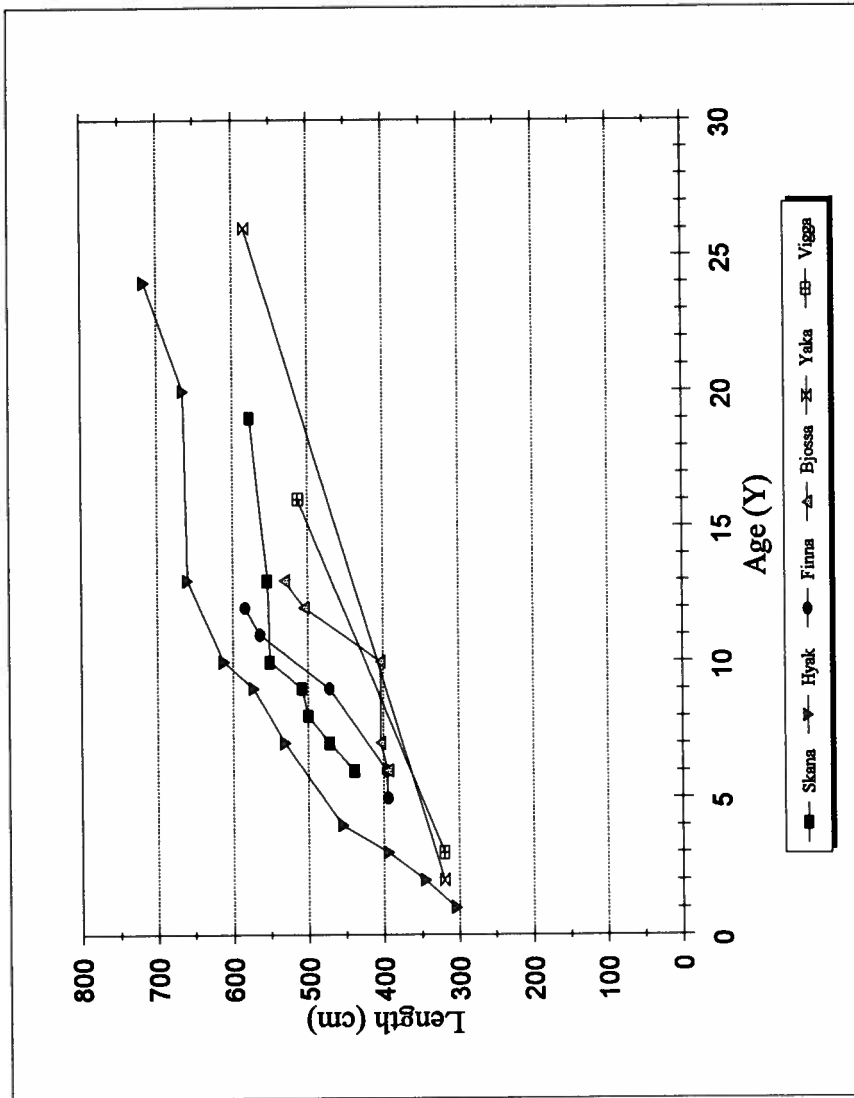


Figure 11. Relationship of body length to age of six killer whales.

Table 16. Estimated weight of six killer whales based on their length.

Animal	Year Of Measurement	Length (cm)	Estimated Weight (Bigg and Wolman 1975) (kg)
Skana	1967	439	1341
	1968	472	1617
	1969	500	1876
	1970	508	1955
	1971	551	2410
	1974	554	2444
	1980	577	2714
Hyak	1968	304	521
	1969	345	721
	1970	394	1015
	1971	455	1471
	1974	531	2191
	1976	572	2654
	1977	612	3159
	1980	660	3837
	1987	665	3913
1991	716	4733	
Finna	1980	394	1015
	1981	396	1029
	1984	472	1617
	1986	564	2559
	1987	584	2800
Bjossa	1980	394	1015
	1981	404	1083
	1984	404	1083
	1986	505	1925
	1987	531	2191
Yaka	1969	320	594
	1993	584	2800
Vigga	1980	320	594
	1993	513	2005

spreadsheet (Quattro Pro), and were separated by species fed and with the corresponding quantities fed. The majority (>60%) of fish fed was herring (*Clupea sp.*) with the remainder consisting of mackarel (*Scomber sp.*), smelt (Osmeridae), capelin (*Mallotus villosus*), salmon (Salmonidae), and cod (*Gadus sp.*). The combination of fish fed changed slightly on a daily basis depending on the availability of fish. Each food species was assigned a caloric value (Perez *et al.* 1990) and all different daily items were summed to estimate the total amount fed in kcal/day.

Yearly food consumption was graphed by age and sex to compare among individuals. Pregnancies were noted in the records and used to examine the effect of reproductive status on food intake.

Urine Collection and Net Assimilation Efficiency

Attempts were made to collect urine from three female killer whales (Yaka and Vigga from Marine World and Bjossa from the Vancouver Public Aquarium). The animals were trained to provide urine samples which were analyzed via the Kjeldahl method (AOAC) to determine urinary nitrogen content (Brody 1945) and correct the total amount of food consumed for the amount of food actually absorbed from the gastrointestinal tract (NAE). However, because it was logistically impossible to collect the total amount of urine and feces excreted throughout the day, these data could not be used to correct for assimilation efficiency. The net assimilation efficiency was estimated as the number of calories burned (Chapter 1) divided by the estimated number of calories consumed by the individual whale during the period of time when the respiration study was conducted.

Growth

The daily growth (kg) was calculated from the estimated weights (Bigg and Wolman 1975) based on length of the animals (Table 16). The energy required for weight gain was calculated based on the combustion of weight gain of 5971 kcal/kg (Blaxter 1989).

STATISTICAL ANALYSES

a) Temporal Variation of Food Consumption

Monthly averages of food consumption were calculated for each whale. A two-way analysis of variance was performed to test the significance of variation in food intake between months and between years. Because pregnancy and lactation can affect food consumption, data for Bjossa were analyzed both as a complete data set and with data from the gestation and lactation period removed to compare her to other females who were not pregnant.

b) Variation in Food Consumption Between Individuals

Intrasex comparisons were made among the whales to determine possible individual differences in food consumption when the animals were compared at the same age. Regression analyses were performed to determine the relationship between the food intake of two different individuals of the same sex at the same age. Paired two-sample t-tests were performed, comparing the annual average of food intake matched for age and to determine if the animals on average consumed the same amount of food at the same age.

Paired tests were used because of the increased power of the test. Due to the small sample size a Mann-Whitney U test was used to determine if differences exist between Yaka and Bjossa.

c) Water Temperature

Linear regressions of daily food intake versus water temperature were calculated for Yaka and Vigga from 1986 to 1993. Water temperature data from the Vancouver Public Aquarium were available only for 1993, hence linear regressions were calculated for Finna and Bjossa for that year only.

d) Reproductive Status

The daily food intake during Bjossa's pregnancies and the peaks of food intake during lactations were compared to the average food consumption for the same months during the years prior to giving birth. These comparisons allowed the examination of changes associated with her reproductive status.

Food Consumption Relative to Body Weight

Average food intake was divided by body weight to estimate food intake in kcal/kg/day. The Nonlin function of Systat was used to calculate the best fit equation of the form:

$$[15] \text{ Food Intake (kcal/day)} = am^b,$$

where a and b are constants and m is body mass in kg (Peters 1983).

Determination of Net Assimilation Efficiency

Data on food consumption were compared to energetic expenditures calculated from respiratory analysis for Hyak, Yaka, Finna and Vigga. Net assimilation efficiencies were calculated independently for each one of the four whales to match food consumption corrected for NAE to the daily energetic expenditure estimated from respiration analysis.

RESULTS

Food Consumption and Individual Variation in Food Intake

Food intake on a yearly basis between the two individual males and the four individual females controlled for age was compared (Figures 12 and 13). Statistical comparisons could not be made between Vigga and Yaka because data were unavailable where ages could be matched (see Figure 13). Regressions and t-tests analyzing variation among individuals in food intake of the two males and among the four females matched by age showed no consistent trends (Table 17). Food consumption as a function of age was highly correlated for the two males. While the correlation of food consumption as a function of age for the two female Pacific whales was weak, the animals also ate very different amounts of food. Although food consumption as a function of age was highly correlated comparing the Icelandic females, Vigga's food intake was consistently greater than Bjossa's. There were low correlations for food intake as a function of age comparing Icelandic versus Pacific whales, even though the amount of food consumed was similar.

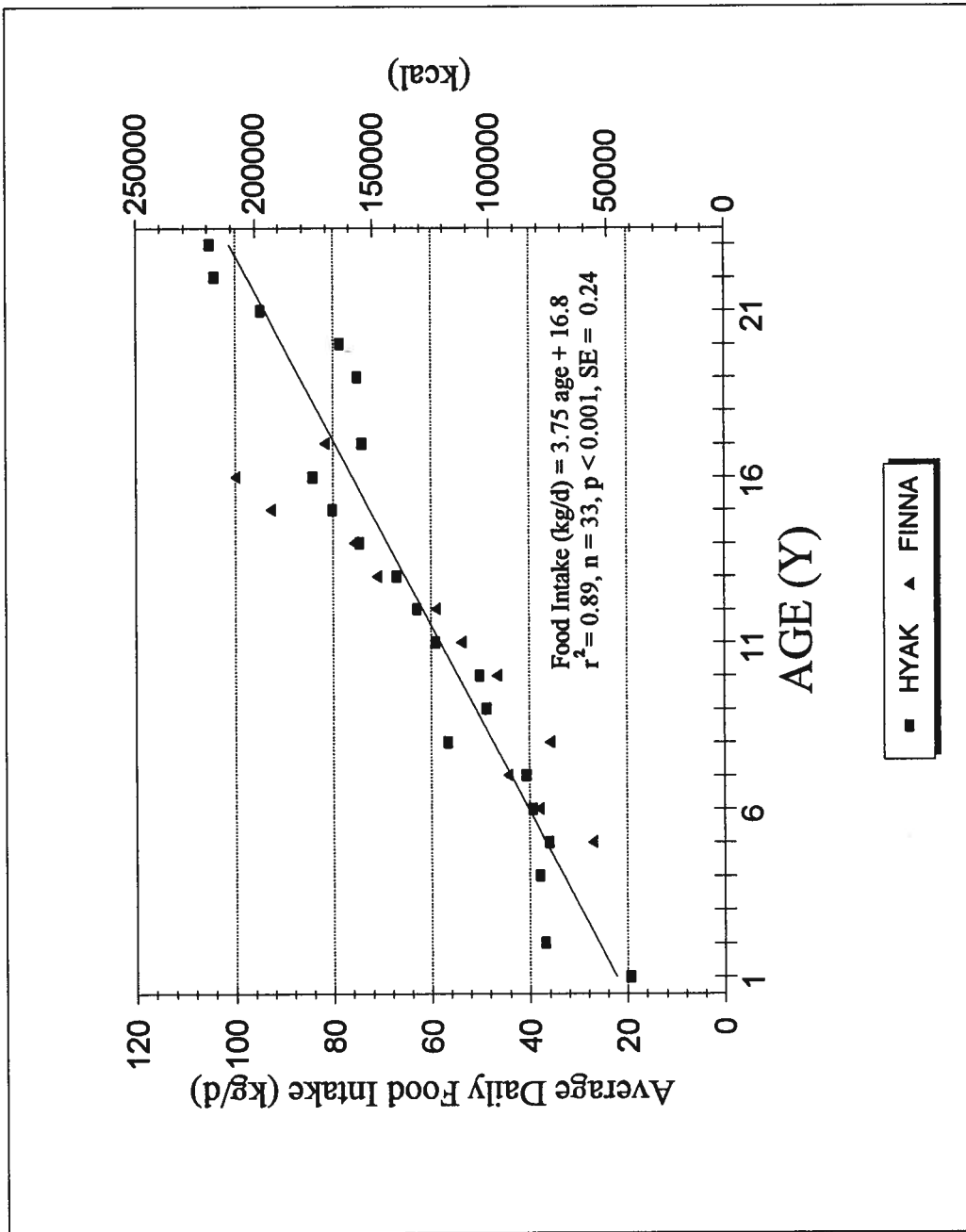


Figure 12. Daily food consumption by male killer whales.

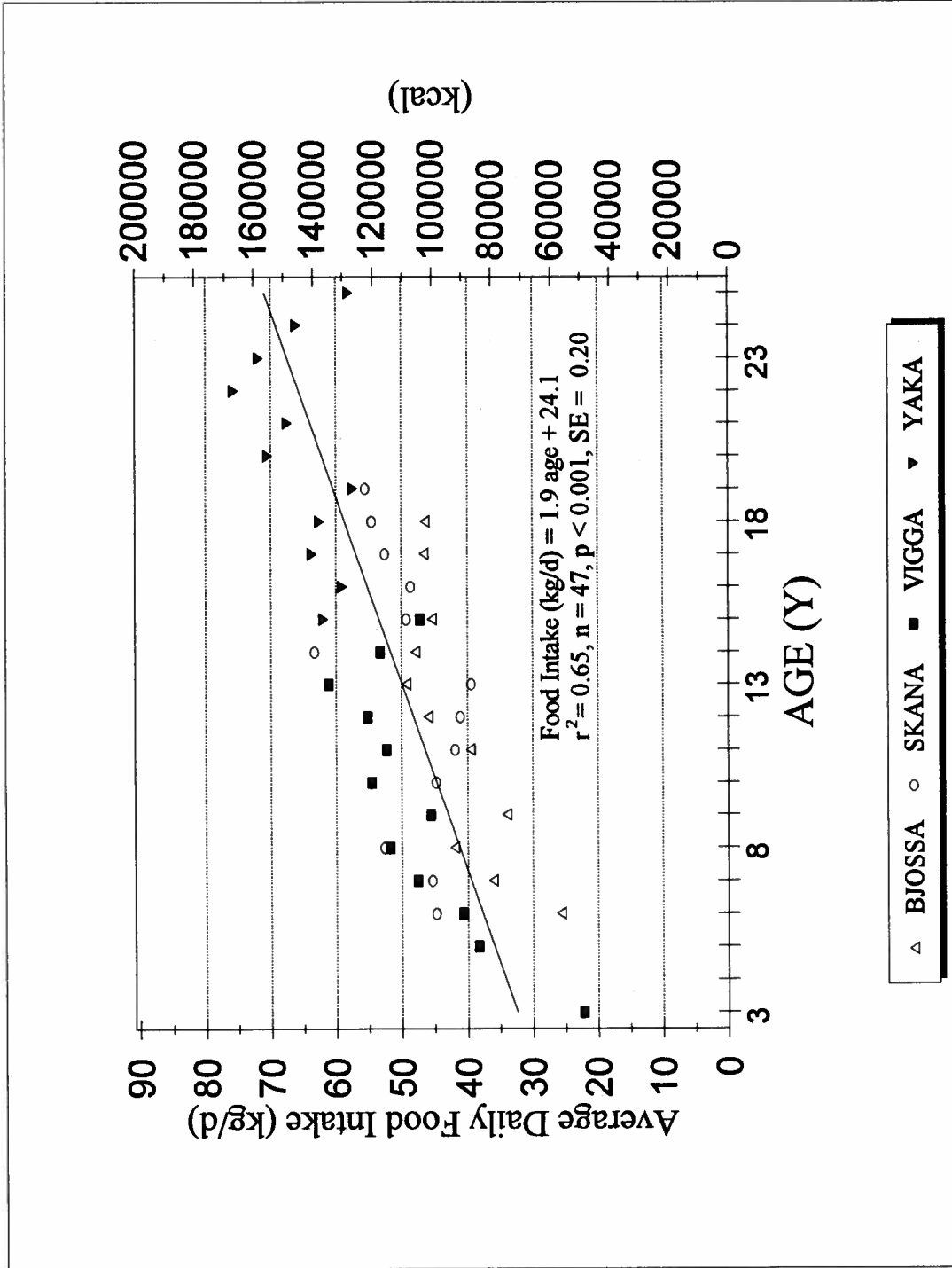


Figure 13. Daily food consumption by female killer whales.

Table 17. Individual variation in food intake among six captive killer whales. Regression analysis showing the relationship between food intake of 2 different individuals matched for sex and age. Paired 2-sample t-test showing whether the annual food intake for 2 whales matched for age and sex are the same.

Animals Compared	# of Years	r ²	Significance	t-value	Significance
Hyak and Finna	12	0.86	p < 0.001	1.87	p > 0.08
Bjossa and Vigga	9	0.73	p < 0.01	2.66	p < 0.02
Skana and Yaka	5	0.05	p > 0.5	3.91	p < 0.01
Skana and Vigga	9	0.1	p > 0.2	0.02	p > 0.98
Skana and Bjossa	11	0.06	p > 0.2	1.98	p > 0.07
Yaka and Bjossa (u)	4	-	-	-	p < 0.05

*all tests = Students t-test, except (u) = Mann-Whitney U test

Factors Related to Variation in Food Intake

a) Temporal Variation of Food Intake within Individuals

Analysis of temporal variations in food consumption (Table 18) shows that food intake of both males differed significantly both by month and by year. For all females except Bjossa, food consumption was not significantly different on a monthly basis. Annual variation was significant for all females.

b) Water Temperature

Daily food intake was compared to water temperature ranging from 7 °C to 23 °C for the two whales at Marine World from 1986 to 1993. The total of 2,724 d for which both food consumption and water temperature data for Yaka were available (Figure 14) and 2,727 d of water temperature and food consumption data for Vigga (Figure 15) were plotted. There was no relationship between food intake and water temperature for either of the two whales ($r^2 = 0.0004$, and $r^2 = 0.00026$, respectively).

However, food intake as a function of water temperature for Finna showed a negative correlation ($r^2=0.34$ and $p<0.001$, Figure 16). Over the range of temperatures observed (7 to 19 °C) this reflects a range of 14.27 kg or $\pm 9.2\%$ of food intake (1.25 kg / °C). A t-test (Zar 1984) was performed to determine that the slope of the regression line was significantly different from 0 ($t = 13.74$, $p < 0.001$). For Bjossa, regression analysis also determined a negative slope ($p<0.001$ and $r^2=0.15$). A range of 3.04 kg or $\pm 3.27\%$ (0.27 kg / °C) of food intake was observed with a change in water temperature. This slope is significantly different from 0 ($t = 7.99$, $p<0.001$), although the magnitude is small (Figure 17).

Table 18. Temporal variation of food consumption by month and year for six captive killer whales. NS = not significant

Whale	Monthly Variation	Yearly Variation
Skana	NS F=0.70 df=11	p<0.001 F=18.46 df=10
Hyak	p<0.001 F=4.99 df=11	p<0.001 F=85.13 df=18
Finna	p<0.001 F=2.73 df=11	p<0.001 F=211.29 df=11
Bjossa	p<0.01 F=2.90 df=11	p<0.01 F=4.69 df=5
Yaka	NS F=0.87 df=11	p<0.001 F=8.84 df=9
Vigga	NS F=0.59 df=11	p<0.001 F=58.0 df=8

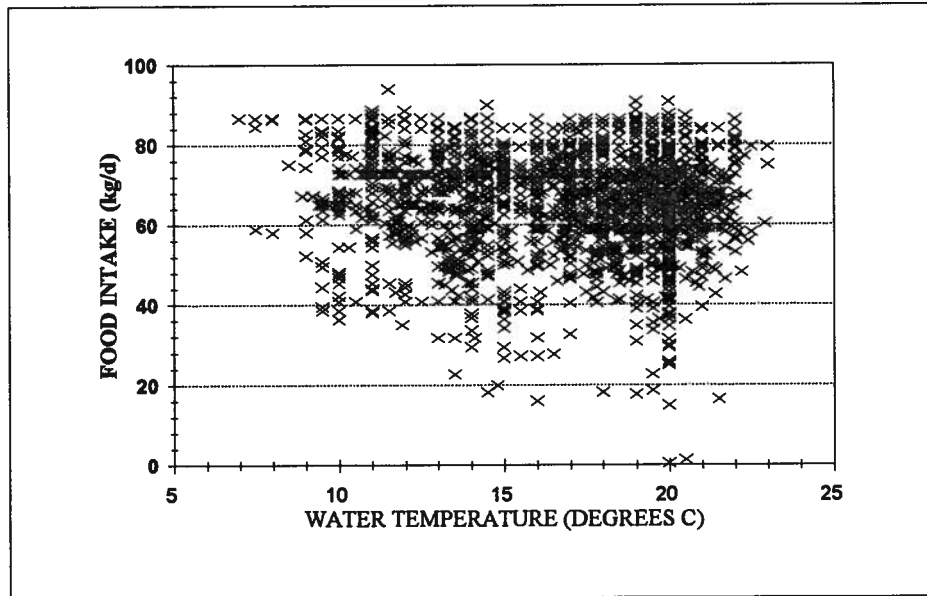


Figure 14. Food intake for Yaka as a function of water temperature.

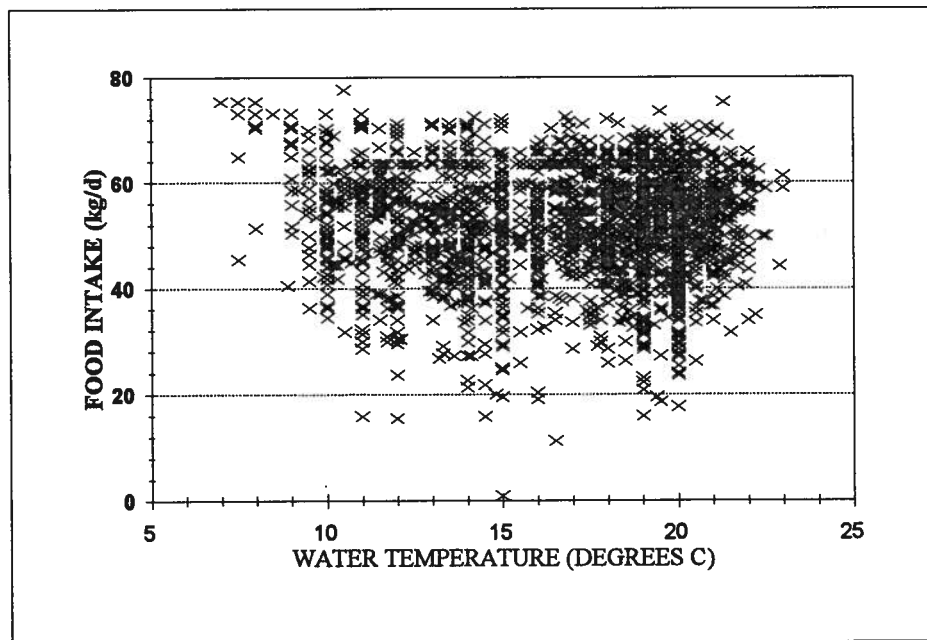


Figure 15. Food intake for Vigga as a function of water temperature.

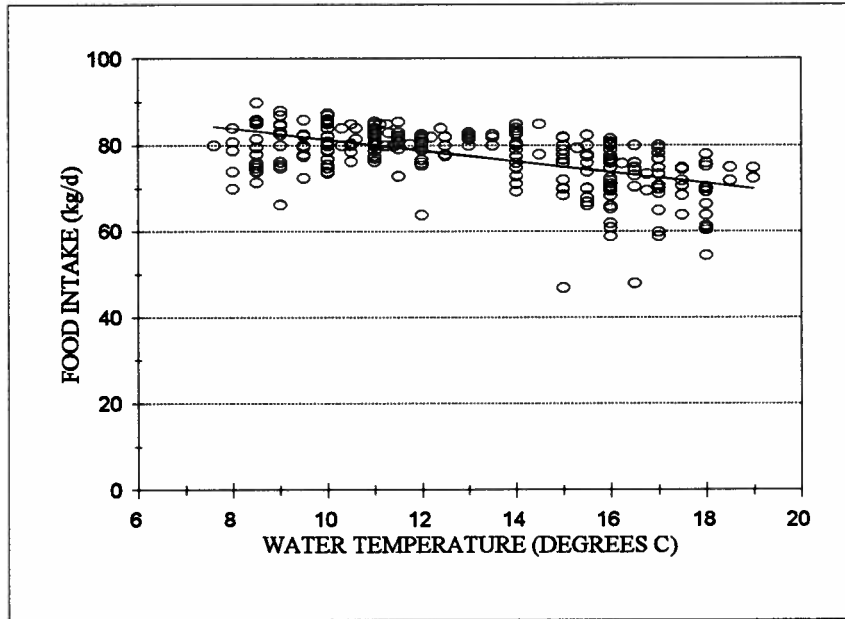


Figure 16. Food intake for Finna as a function of water temperature, 1993.

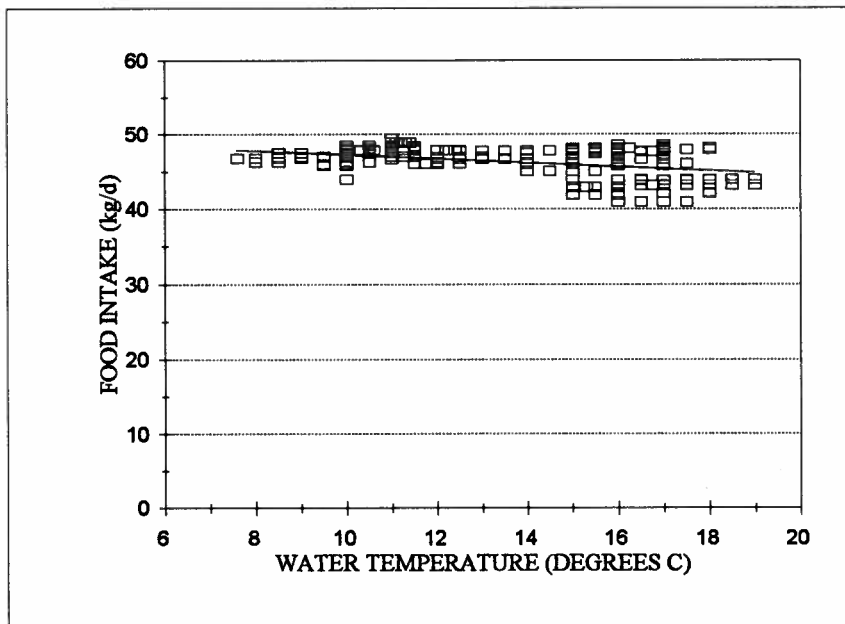


Figure 17. Food intake for Bjossa as a function of water temperature, 1993.

c) Reproductive Status

The yearly food consumption by Bjossa was plotted for the two years (1988 and 1991) in which her calves were born (Figures 18 and 19). While data from the first pregnancy indicate no increase in food consumption before the 1988 calf was born, Bjossa increased her food intake steadily by a total of 25% one month before the second calf was born. After giving birth, Bjossa's food consumption increased by 100% from pre-parturition amounts for the first calf and 60% for the second calf (Figures 18 and 19). In both cases food consumption fell to normal levels within 8 and 16 d, respectively, after the calves stopped nursing.

Growth

Daily growth rates ranged from 0 kg to 1.29 kg which corresponds to a maximum of 7,700 kcal/d used for growth. Calories required for growth were negligible relative to the total food intake (see Figures 12 and 13).

Food Consumption Relative to Body Weight

Food intake as a function of estimated body weight is shown in Figure 20 and is also shown as a fraction of body weight in Figure 21 and yielded the following equation for food intake by killer whales:

$$[16] \text{ Food Intake} = 0.277 M^{0.663} (r^2=0.76, df=78, p<0.001, SE=0.042),$$

where food intake is in kg/d and m = body mass (kg).

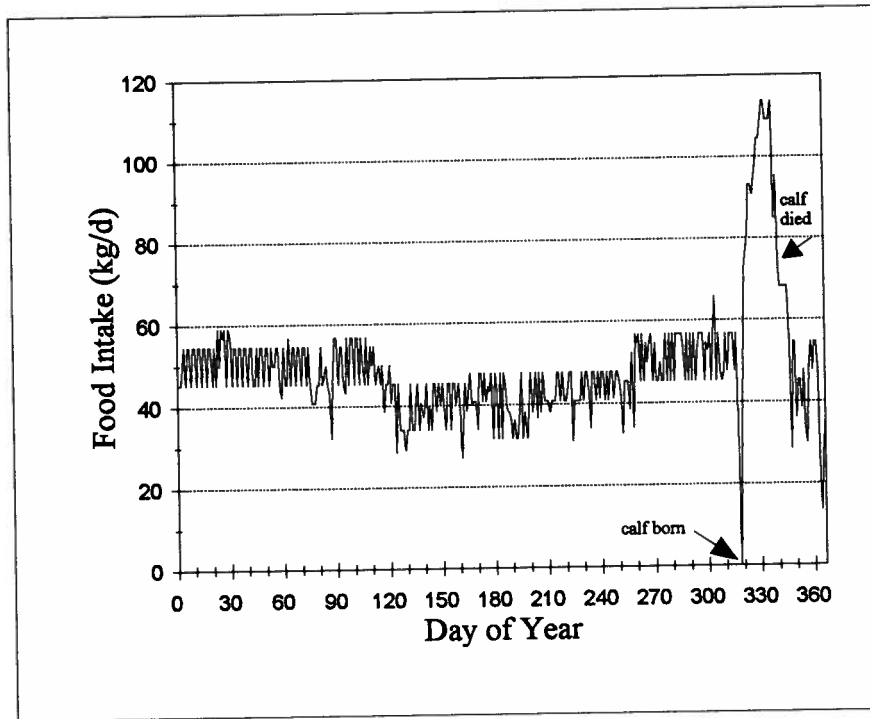


Figure 18. Food intake for Bjossa during pregnancy and lactation, 1988.

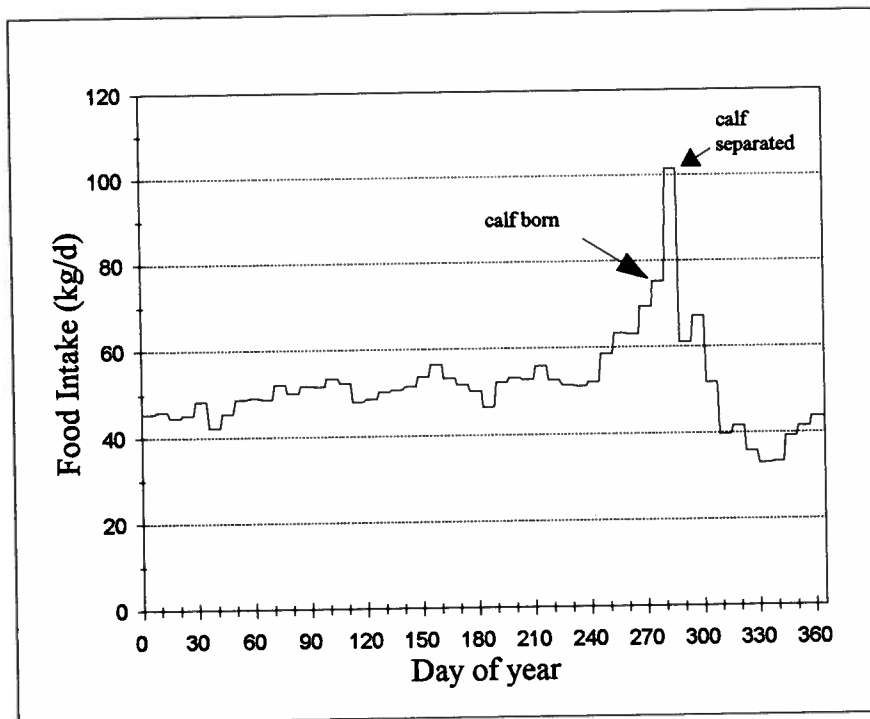


Figure 19. Food intake for Bjossa during pregnancy and lactation, 1991.

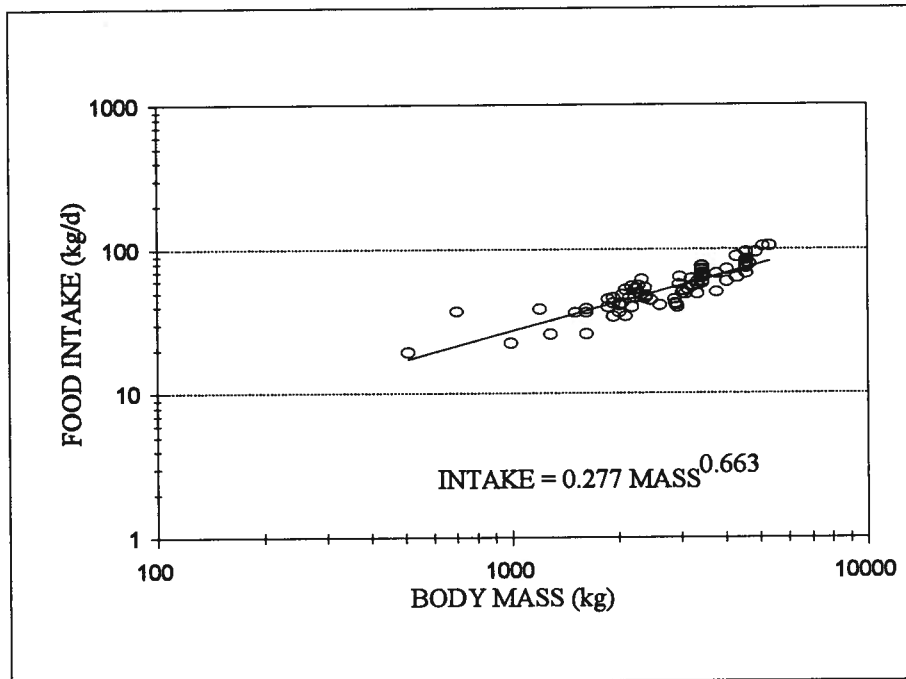


Figure 20. Food intake as a function of estimated body mass in six killer whales.

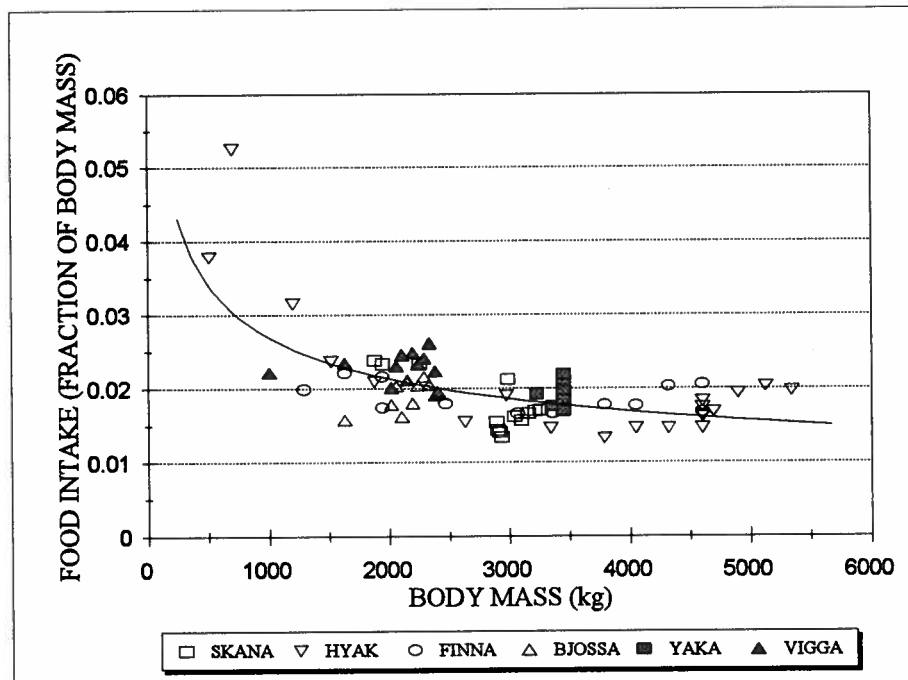


Figure 21. Food intake as a fraction of estimated body mass in six killer whales.

Statistics on the log-transformed data showed that the slope of the line was significantly different from 0 ($p < 0.001$).

Food intake by males declined from 5.3% to 1.3% of their estimated body weight per day as the animals were growing from a 1-year old to adulthood, and females' food consumption declined from 2.6% to 1.3% of their estimated body weight while growing from 3-year old juveniles to adults (Figure 21).

Net Assimilation Efficiency and Daily Caloric Consumption vs. Daily Caloric Expenditure

Net assimilation efficiencies calculated for food intake for each whale were matched to the energy expenditure measurement by respiration analysis as closely as possible. For three out of the four whales (Hyak, Finna and Yaka), the net assimilation efficiency ranged from 0.80 - 0.83 (Table 19). Vigga's NAE was estimated at 0.46 (Table 19). This stands in contrast to the other whale's and reports of NAE's for other marine mammals cited in the literature which report that NAE's for fish eating marine mammals is consistently high (>67%). The mean NAE for all four killer whales was calculated at 0.73.

Table 19. Comparison between daily energetic expenditure measured by respiration analysis and food intake in four captive killer whales. Food intake was corrected individually for net assimilation efficiency (NAE) to match the estimated energy expenditures based on respiration analysis.

	Estimated Energy Expenditure based on Respiration Analysis	Food Intake	NAE Required to Match Food Intake to Estimated Energy Expenditure from Respiration Analysis
	kcal/day	kcal/day	
Hyak	141,600	170,000	0.83
Finna	88,301	110,000	0.80
Yaka	107,669	130,000	0.83
Vigga	50,891	110,000	0.46

DISCUSSION

Food Intake and Individual Variation in Food Consumption

Not surprisingly, food intake varied among individuals and within an individual at a given age. The sample of four females and two males is too small to statistically determine whether variation of food consumption was affected by factors such as sex, aquarium, or ocean of origin, or simply reflected individual differences. Although animals in both aquaria were fed to satiation, individual differences appear to be a factor in food intake. It will be necessary to include and perform analyses of more food records of killer whales and more institutions holding killer whales before the effects of individual variation and institutions on food consumption can be ascertained. It did appear that all animals showed a significant difference in year to year variation in food intake. This is to be expected because the animals were growing during much of the period over which the data were recorded. While the food species fed in the aquaria is similar to those found to be consumed by wild killer whales in the Atlantic with the majority of food being herring (Christensen 1984), the prey items for wild Pacific killer whales consists mainly of salmon with a smaller percentage of other fish species during spring, summer and fall, and a variety of fish species during the remainder of the year (G. Ellis, pers. comm.). For that reason, caloric values of fish fed to the whales should be determined rather than just reporting the amount of food (kg) consumed by the whales.

The best fit for food intake rate as a function of body weight for the six different killer whales:

$$[17] \text{ Food Intake} = 0.277 \text{ Mass}^{0.663},$$

is similar to Innes *et al.*'s (1987) equation

$$[18] \text{ Food Intake} = 0.258 \text{ Mass}^{0.69},$$

describing the feeding rates of a variety of immature and mature cetaceans.

Body weight is correlated with food consumption. This inverse relationship between feeding rate per unit body weight and body weight is what is expected from what has been shown in terrestrial mammals and by the relationship between basal metabolic rate and body weight (Brody 1945, Schmidt-Nielsen 1990).

Water Temperature

There was no correlation between water temperatures and food intake for the two female killer whales at Marine World. Although there was a negative correlation between these two factors for two whales from the Vancouver Public Aquarium, the magnitude was small. This difference could be due to several factors:

- a. The temperatures experienced in the two aquaria are well within the range of

temperatures experienced by the species in the wild and the water temperatures were likely within the thermal neutral zone of killer whales. No or very little changes in food intake were observed.

- b. Changes in activity levels or in body weight may cancel out changes in heat loss. The two killer whales at Marine World have a heavier performance schedule with more shows during the summer, so increases in food intake required for higher activity levels may cancel out the effect of increased water temperature on food consumption.
- c. Trainers at the two aquaria have different criteria for feeding the whales. It is only in the last 5 y that feeding to satiation was really practiced consistently at the Vancouver Aquarium (Jeremy Fitz-Gibbon, pers. comm.).

Reproductive Status

No marked increase in food intake occurred during Bjossa's first pregnancy, it only occurred during the last month of her second pregnancy. An increase in food consumption late in pregnancy has been reported in captive Commerson's dolphins and beluga whales (Kastelein *et.al.* 1993, 1994), bottlenose dolphins (Reddy *et.al.* 1991) and a small increase in food consumption has been theorized for sperm whales (*Physeter catadon*) during the latter part of pregnancy (Lockyer 1981b).

Bjossa's food consumption increased by 100% after the birth of each calf. This increase in daily food intake has been recorded for other cetaceans held in aquaria, such as bottlenose dolphins (Reddy *et al.* 1991) and beluga whales (Kastelein *et.al.* 1994) as well as in pinnipeds (Perez and Mooney 1986). These data support Kastelein *et al's*.

(1994) theory that gestation does not impose a marked energy load until the last stages of pregnancy, while a large energy demand is seen during the first part of lactation. Bjossa's food intake decreased to normal levels within 8-16 d after she stopped nursing.

Comparison between Caloric Intake and Caloric Expenditure and Net Assimilation

Efficiency

The results of the comparisons between caloric intake and caloric expenditure for the whales were very similar to each other for 3 out of the 4 whales (Hyak, Yaka and Finna). Their individually calculated net assimilation efficiencies (80% - 83%) only vary by 3%. These NAE's fall well within the reported range of NAE's for fish-eating marine mammals (NAE between 0.67 to 0.93, Shapunov 1973, Lockyer 1981a, 1981b, Lavigne 1982, Worthy 1990). Vigga's NAE is considerably lower than those of the other three whales. Her NAE (0.46) is also well below NAE's reported in the literature for fish eating mammals (> 0.67). The reason for her low NAE is that her caloric expenditure is much lower than her food consumption, possibly due to her dislike for the funnel (see Chapter 1).

This comparison between determining energy expenditures of three killer whales by respiration analysis and verifying the data by looking at food intake indicates that respiration analysis is a consistent method and valuable tool for estimating metabolic rates of most, but not all, captive killer whales.

**Chapter 3: COST OF TRANSPORT, DRAG AND REALIZED METABOLIC RATE
ESTIMATES IN FREE-RANGING KILLER WHALES, *Orcinus orca*.**

INTRODUCTION AND OBJECTIVES

An individual's energetic demands depend on its minimal metabolic rate [which can be thought of as the energy to maintain necessary life functions as defined by Brody (1945) and Kleiber (1987)], plus energy associated with locomotion, thermoregulation, and production energy necessary for growth and reproduction (Wunder 1975, Gaskin 1982, Lavigne *et al.* 1982, Peters 1989). The animal's minimal metabolic rate, the basal, or standard, metabolic rate, can be estimated fairly accurately for generalist species not adapted for specialized conditions requiring elevated or reduced metabolism. Regression equations established by many (Brody 1945, Hemmingsen 1960, Kleiber 1987, Peters 1989; see also Chapter 1) are generally used to relate the metabolic rate to the animal's body weight. Realized metabolic rates, or the average daily metabolic rates, are determined in large part using data on animal activity (Peters 1989). The focus of this paper will be on the locomotion component of realized metabolic rate in killer whales (*Orcinus orca*), which can be a significant fraction of the total energy used by an animal (Prange and Schmidt-Nielsen 1970, Gaskin 1982, Peters 1989).

A common method to determine the energy necessary for locomotion is to measure the cost of transport (COT; the amount of energy necessary to move a unit of mass a given distance) of an animal at different velocities including its minimum cost of transport

(Schmidt-Nielsen 1972, Tucker 1975) and its maximum range speed (Williams *et al.* 1993). For captive terrestrial mammals, COT is determined by measuring oxygen consumption and body temperatures while at rest and while running on a treadmill at various speeds (Taylor *et al.* 1970). The amount of energy expended above the energy that the animal uses for its basal or standard metabolic rate represents the increase in the metabolic rate due to locomotion.

Since it is difficult to measure COT on free-ranging animals directly, an indirect method of calculating energetic cost in the case of swimming in cetaceans has been developed. Swimming velocities and respirations are measured per unit time on free-ranging marine mammals, and tidal volumes and oxygen consumption are measured on captive animals or obtained from respiratory allometric estimates (Gaskin 1982).

Measuring COT indirectly has been applied to several species of marine mammals. The swimming metabolism of harbour seals (*Phoca vitulina*) was studied by placing the animals into a flow channel and having the seals swim at different velocities by adjusting the flow velocity of the water (Davis *et al.* 1985). Oxygen consumption and carbon dioxide production were measured to determine the cost of transport at different swimming velocities. Standard metabolic rates were defined by having the seals rest in still water. Hydrodynamic characteristics and swimming performance were also measured in harbour seals and demonstrated the importance of streamlining in this species to decrease their cost of transport during swimming (Williams and Kooyman 1985). Cost of transport by swimming sea otters (*Enhydra lutris*) was determined by measuring oxygen consumption and carbon dioxide production in captive individuals and analyzing

swimming modes and preferred velocities from videotapes of otters swimming in pools (Williams 1989).

Other techniques for estimating the cost of locomotion in marine mammals have been based on measures of actual weight loss in large cetaceans. Energy expenditures in migrating mysticetes were estimated from body weight difference due to the combustion of fat before and after the migration (Rice and Wolman 1971). Weight loss was then calculated as a function of oxidation of fat, equated to energy requirements and the animals' cost of transport was estimated. Similarly, COT in fin whales (*Balaenoptera physalus*) was inferred by measuring the difference in the amount of whale oil before and after migration (Kawamura 1975). Kawamura (1975) extrapolated COT for the whales from results of the cost of locomotion in salmon and based his calculations on having the animal experience laminar flow of water around its body.

The cost of transport in migrating gray whales (*Eschrichtius robustus*) was estimated by measuring swimming velocities and breathing rates. These data were combined with extrapolations of tidal volumes and oxygen consumption measured on unrestrained wild calves and a captive gray whale calf to estimate the minimum COT (Sumich 1983).

An estimate of COT and realized metabolic rate can also be obtained from theoretical calculations on hydrodynamics in cetaceans. A simple calculation permitting an approximate assessment of streamlining is the fineness ratio (FR) which describes the relationship between body length and its maximum thickness. This dimensionless number indicates to what degree a body approaches the optimal hydrodynamic shape (Gaskin 1982). A fineness ratio of 4.5 is optimal for creating minimal drag for a given body

volume (Webb 1975, Feldkamp 1987). Cetaceans have developed several adaptations to minimize drag (drag is the pressure times the area, and the drag on an object is the net pressure across its projected area times that area [Vogel 1988]) and to delay turbulent flow until a higher swimming velocity. These adaptations include streamlining with the elimination of unnecessary protruding parts that would offer resistance to the water (such as external ear pinnae, protruding mammary glands or reproductive organs, and hair) and a powerful tail to propel the animals through the water (Gaskin 1982, Evans 1987, Bryden 1988). Despite these adaptations, even a streamlined cetacean has to overcome drag. Water provides resistance against movement and drag develops at the skin surface as the animal moves through the water.

Gray (1936) described experiments with a rigid dolphin model. These experiments indicated that the power required to overcome the drag the animals experienced during swimming was greater than the maximum power available from the locomotor muscles (Gray's paradox). According to physical calculations, the animals would have to experience mostly laminar flow around the body to be able to sustain the observed swimming velocities. While rigid bodies towed at velocities measured in swimming cetaceans showed that the drag at those speeds was mainly turbulent, comparisons between rigid bodies and cetaceans lead to uncertainties about the mix of laminar and turbulent flow, and, as a result of this uncertainty, frictional drag is unknown. This also leads to uncertainty of the pressure drag because the separation of the boundary layer is unknown. Surface drag also needs to be considered in the drag calculations, but because the amount of time cetaceans spend at the water surface is negligible, this number is

generally ignored. Muscle efficiency is also an uncertainty since either the muscles work much more efficiently than proposed or the animals encounter mainly laminar flow around the body.

While Purves (1963) explained how laminar flow is predicted to occur over the body at low swimming speeds, it is still not understood how cetaceans deal with the turbulent flow that is expected to occur at higher swimming velocities. To determine at what velocity an animal experiences turbulent flow, as opposed to laminar flow, a dimensionless number, the Reynolds number (calculated by multiplying body length of the animal by its velocity and dividing this product by the viscosity of water) has been developed (Alexander 1982, 1983, Vogel 1988). While drag is directly proportional to speed at low Reynolds numbers, it is approximately proportional to the square of velocity at high Reynolds numbers (i.e. Stokes' law). Webb (1975) reports that in stable conditions, water flow over streamlined bodies becomes turbulent at Reynolds numbers greater than about 5×10^6 .

Theoretical calculations of energy expenditure based on drag in cetaceans have been presented and many theoretical models have been developed to calculate drag at different swimming velocities in cetaceans (Parry 1949, Lang 1961, 1965, Au and Weihs 1980, Lockyer 1981a, 1981b, Blake 1983). However, much uncertainty still exists because cetacean hydrodynamics are not well understood.

To try to resolve some of these uncertainties, COT was estimated both theoretically and from direct measurements in killer whales, *Orcinus orca*. Information on swimming velocities and breathing rates, together with measurements of oxygen consumption and standard metabolic rates conducted on captive killer whales (Chapter 1), can yield an

estimate of COT and realized metabolic rates. However, for estimates of drag on killer whales, measurements of the body and its appendages are necessary. The body can then be modelled as a cylinder with four appendages, the two pectoral fins, a dorsal fin and flukes, to use in calculations for drag estimates at different swimming velocities.

Empirical data on killer whale's COT during travelling were collected to compare killer whale energy expenditures during travelling to theoretical data based on hydrodynamic models.

In general, swimming killer whales take three to five short dives of 10 to 35 sec in duration followed by a longer dive which can range from 1 to 10 min or more (Norris and Prescott 1961, Lenfant *et al.* 1968, Leatherwood *et al.* 1982, Baird 1994). Adult male killer whales have been observed to dive for up to 30 min (Bain pers. comm.). This breathing pattern lends itself to studying the animals by theodolite tracking. This technique (see Davis *et al.* 1981 for a discussion of theodolite surveying methodology) has been a useful method in determining general movement patterns of cetaceans and killer whales in localized areas (Kruse 1991, Wuersig *et al.* 1991) as well as for determining swimming velocities and respiration rates of the animals. It is also possible to track whales by boat and measure the animals' locations using a loran C device each time they surface. Tracking whales by this procedure has the advantage that the length of the track can be increased relative to a theodolite, being limited only by bad weather and darkness.

In this chapter realized metabolic rates of wild killer whales are estimated using two approaches:

- a) determining the cost of transport (COT) of different age and sex classes of wild killer whales by measuring swimming speeds, respiration rates and diving depths, and
- b) computing theoretical drag values for different sized killer whales at different swimming velocities, and estimating the power required to overcome it.

METHODS

Energy required for costs of transport and realized metabolic rates were estimated by measuring swimming velocities and respiration rates of free-ranging killer whales.

Oxygen consumption rates measured in captive killer whales at the respiration rates determined in free-ranging animals were used to estimate how much energy the animals in the wild require to swim (see Chapter 1). Drag was estimated from morphometric data of different age and sex classes of killer whales and the data were analyzed for drag using already existing equations (Hoerner 1965, Blake 1983).

Costs of transport, drag, and Reynolds numbers were calculated to determine the most efficient swimming velocity. Tracks were only recorded when the whales were travelling. Travelling was operationally defined as members of the pod swimming in the same direction (on the same course) at approximately the same swimming velocity, and no interactive behaviour or feeding was observed (Ford 1994).

Swimming Speeds, Respiration Rates and Diving Depths

a) Theodolite Study:

The summer study area for free-ranging southern resident killer whales was eastern Haro Strait on the west side of San Juan Island, Washington, USA. Between July and September 1986 and May and September 1987 killer whales were observed at a site approximately 2 nautical miles south of the Limekiln Lighthouse (48° 30'N, 123° 10'W). Data were collected between sunrise and sunset from a vantage point 74.5 m above mean low low water (MLLW). This site provided an expansive view over Haro Strait as far as Victoria, ranging from South Bank (48° 29'N, 123° 05'W) south of the observation site to Bay (48° 30'N, 123° 29'W) north of the site. Tracked whales travelled along the west side of San Juan Island and were usually within 2 km of the coastline. The animals were easily observed and identified at a distance of 2 km and distinctive individuals up to a distance of 4 km. When a pod of whales was sighted, an individual animal which was either in the lead, on the periphery, or at the rear of the group, was chosen as a focal animal to avoid confusion with others. Individual killer whales were identified by saddle patches and nicks and scratches on their dorsal fins and saddle patch area (Sugarman and Shepard 1984, Bigg *et al.* 1987). Identification of an individual killer whale was established by two observers.

The theodolite was used to establish the vertical angle between the observation site and the whale's position during an exhalation. For each subsequent surfacing and respiration, new vertical angles and the horizontal angles between surfacings were measured (Figure 22).

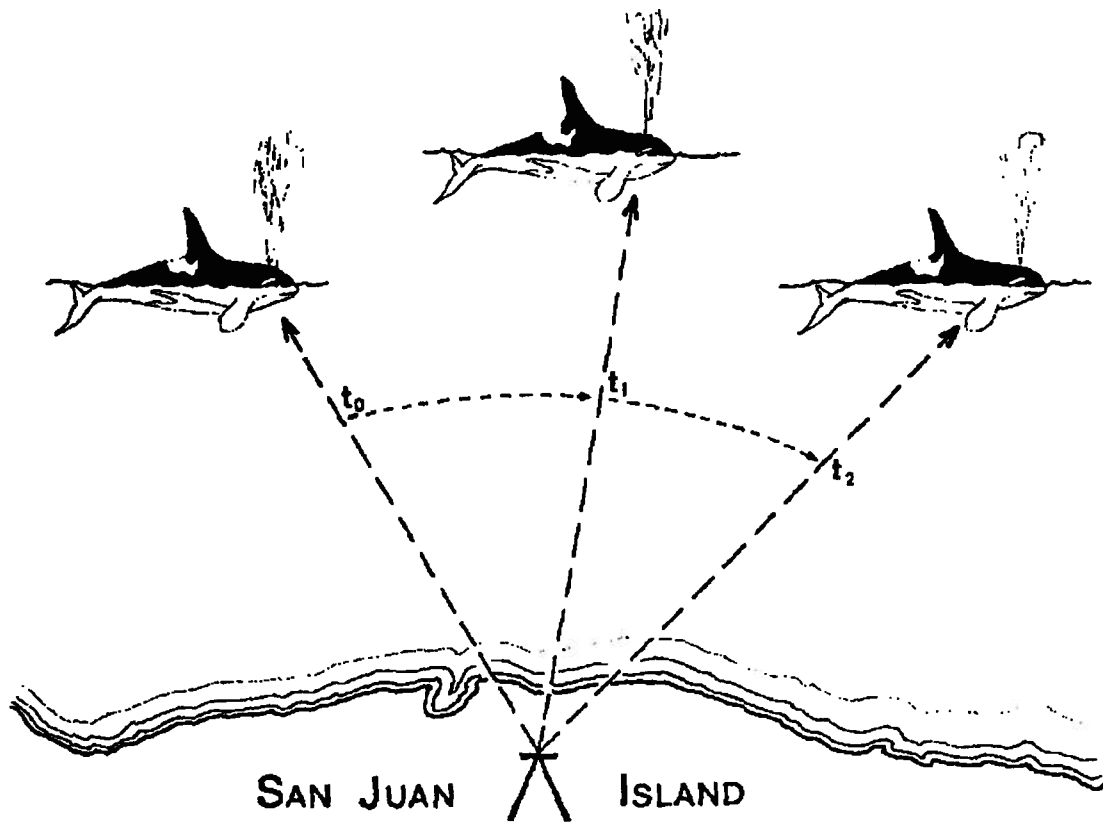


Figure 22. Theodolite tracking of killer whales.

Observations of killer whales and measurements of diving distances were made using a Sokkisha Electronic Digital Theodolite DT 20E, with a 160 mm telescope length and a magnification of 30x. The accuracy was within 20 s of arc. Individual animals and their behaviours were observed through the 30x spotting scope of the theodolite by the principal investigator and with 8x40 Leitz binoculars by an assistant.

One observer (with binoculars) called out each time the whale came to the surface, while the other observer measured the whale's position at each surfacing and recorded it with a Sony portable tape recorder. This procedure was continued until the whale disappeared from view or could no longer be positively identified.

Several criteria were established to avoid incorrect measurements. Observations were rejected if any of the following occurred:

1. there was any uncertainty about the whale's identity during sampling,
2. breaking waves were such that they could be mistaken for a spout (i.e., whale at the surface),
3. behaviours such as play, chasing fish or feeding took place, or
4. the individual whale suddenly changed direction and/or changed position within the pod.

During dives it was assumed that the whale swam in a straight line between surfacing points. After each observation session, the recorded data were transcribed onto data sheets, along with tide and current conditions at that time.

b) Southern and Northern Boat Studies:

During the summer of 1988, observations of swimming killer whales and their respiration rates were made from a 6.2 m Thunderbird Cathedral Hull open boat. The observation area ranged from Iceberg Point on Lopez Island (48° 24'N, 122° 58'W) to Point Roberts (48° 55'W, 123° 00'W).

From late April to mid June 1989, data were collected using the northern resident killer whale population at the central coast of British Columbia. The area in which the animals were observed ranged from Addenbrook Island (51° 36'N, 127° 53'W) to Bella Bella (52° 10'N, 128° 06'W), and NE as far as Nascall Island in Dean Channel (52° 40'N, 127° 15'W) and SE as far as South Bentinck Arm (51° 15'N, 126° 56'W).

While the driver of the boat and one other observer called out surfacings and respirations, a third researcher noted the longitudes and latitudes at a distance of approximately 100 m from the focal whale using the loran. Locations of whales when they surfaced to breathe were made with a Micrologic ML-8000 loran C. The same four criteria mentioned above for minimizing invalid measurements were also applied to data collection here.

Diving depths were recorded after the loran tracking was finished and whenever it was possible to have the whale swim under the boat. This sometimes required the boat operator to move in front of the whale and to wait for the animal to swim beneath the boat. A Humminbird 400 D depth sounder was used to determine the depths at which individual whales swam below the boat. The driver of the boat navigated directly above a diving whale so that the animal was visible on the depth sounder's screen. Due to the

large size of killer whales, it was unlikely to confuse whales with fish or other objects.

To ensure correct identification of the focal animal while measuring diving depths, an animal was chosen only if it was swimming by itself and at a distance of at least 200 m from any other whale.

Analysis

a) Track Distance Calculations

To determine the distance the animals travelled between respirations, several variables need to be known: the height of the theodolite station and the vertical and horizontal angles of the location where the focal animal surfaced to breathe. The height of the theodolite above the sea surface was determined with a Topcon GTS-3B infrared laser electronic distance measurement total station theodolite and was corrected for tides from predictive tide tables (Tide Tables, U.S. Dept. of Commerce, NOAA, 1986 and 1987).

The distance between the theodolite station and the whale was calculated using the exact height of the theodolite and the vertical angles measured by the theodolite. After the vertical angles were converted from degrees, minutes and seconds to fractions of degrees, the tangents of these angles were multiplied by the height of the theodolite to determine the distance of the animal tracked from the theodolite. The horizontal angle measured between two vertical angles determined the distance the animal had swum between two respirations (see Figure 22). Again, minutes and seconds of the angle were converted to fractions of degrees, and the cosine of the horizontal angle was computed to determine the distance between the two vertical angles to calculate the distance of two surfacings to the

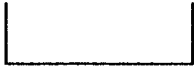


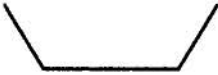


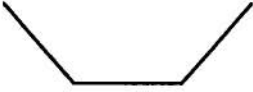
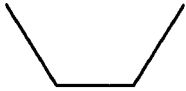
shore. The successive positions were added to determine the distance over which the animal was tracked along the water surface.

Another spreadsheet was developed to convert the longitudinal and latitudinal data and observation times into swimming distances and velocities. Differences between two consecutive latitudes and longitudes were determined. Longitudinal differences in minutes between the whale's surfacing were multiplied by 1852, the number of meters in a nautical mile. Longitudinal differences in minutes between surfacings were multiplied by 1150, the number of meters in a minute of longitude at the latitude where the observations were recorded. The Pythagorean theorem was applied to calculate distances swum between respirations. As with the theodolite data, the successive positions were added to calculate the distance the animals had swum along the water surface.

b) Dive Models

Eight theoretical dive models were developed to correct for distance travelled vertically (Figure 23). Models 1 to 4 did not have a fixed dive angle but suggested that the whales dive to a determined depth, while models 5 to 8 have a fixed or no angle for descent and ascent. Each whale track was tested with each dive model to determine which model produced the least variance in swimming velocity. A mean and variance was calculated for swimming velocity and measured between each surfacing. Variances produced by the different dive models were compared and the dive model producing the least variance was identified as the best fitting model.

Dive Models

Dive Model Name	Drawing	Formula	
		(Female)	(Male)
Box		$D + 2 * 18$	$D + 2 * 25$
V-Shape		$2 * \sqrt{\left(\frac{D}{2}\right)^2 + 18^2}$	$2 * \sqrt{\left(\frac{D}{2}\right)^2 + 25^2}$
1/3		$\frac{D}{3} + 2 * \sqrt{\left(\frac{D}{3}\right)^2 + 18^2}$	$\frac{D}{3} + 2 * \sqrt{\left(\frac{D}{3}\right)^2 + 25^2}$
1/4		$\frac{D}{4} + 2 * \sqrt{\left(\frac{D}{4}\right)^2 + 18^2}$	$\frac{D}{2} + 2 * \sqrt{\left(\frac{D}{4}\right)^2 + 25^2}$
0		D	D
30		$D + 2 * (2 - \sqrt{3}) * 18$	$D + 2 * (2 - \sqrt{3}) * 25$
45		$D + 2 * (\sqrt{2} - 1) * 18$	$D + 2 * (\sqrt{2} - 1) * 25$
60		$D + 2 * \frac{18}{\sqrt{3}}$	$D + 2 * \frac{25}{\sqrt{3}}$

Where D = surface distance measured by theodolite or loran in meters
 (18 and 25 represent estimated dive depths in meters for females and males, respectively)

Figure 23. Potential dive profiles.

c) Swimming Velocities

Swimming velocity, using the dive model which fit best, was determined from the equation:

$$[19] \text{ Velocity} = (\text{Distance from the V-shaped model})/\text{Time},$$

where: Velocity = m/sec; Distance = meters; and Time = the total time elapsed (s) during the observation.

The number of respirations the animal took were counted from beginning to end of each track. Theodolite tracks were analyzed for bias in respiration rates due to time constraints during theodolite tracking. A regression equation of breathing rates as a function of swimming velocities was calculated. Regression lines were then calculated between the residuals and sample size both in duration of the track and in number of breaths. If the slope of the line is different than zero, it indicates the breathing rate is a biased estimate of metabolic rate.

Observations were separated into mean swimming velocities and mean breathing rates for each age and sex category during summer and spring.

Breathing rates were graphed as a function of swimming velocities for the different age and sex classes for the different seasons.

To determine whether it was appropriate to pool data of theodolite and loran tracks, t-tests were used to compare slopes and intercepts of the regression lines for breathing rates as a function of swimming velocity between seasons (Zar 1984). Respiratory intervals

were determined for each age and sex class for summer and spring seasons by comparing dive durations in summer and spring with a t-test.

d) Cost of Transport

Cost of transport (COT) was approximated for each age and sex class of swimming killer whales using the following equation (Schmidt-Nielsen 1972, Tucker 1975, Sumich 1983):

$$[20] \text{COT}_b = [\text{RR} * (1000\text{m}/\text{km}) / (60/\text{min})] / \text{velocity},$$

where: COT_b = breaths/km; RR = respiration rate in breaths/minute; and velocity = swimming speed in m/sec.

Metabolic rates were estimated by combining respiration rates measured in wild killer whales with oxygen consumption per breath determined in captive killer whales (see Chapter 1). To correct swimming velocities for the correct activity state, the following speeds were assumed to fit the different activity states:

- a. 0 m/sec to 0.5 m/sec = Activity state 1;
- b. 0.51 m/sec to 2.0 m/sec = Activity state 2;
- c. 2.1 m/sec to maximum velocity measured = Activity state 3.

For males, a mean oxygen extraction was calculated between Activity states 1 and 3 to correct for the missing Activity state 2. Oxygen consumption was then transformed into kcal/breath (see methods Chapter 1) and into kcal/kg/d, using mean body weights

calculated by Bigg and Wolman (1975) for the wild orcas: 5,000 kg for males (731.5 cm long), 2,800 kg for females (584 cm long), and 618 kg for the young juveniles (325 cm long).

Metabolic rates were determined using respiration rates from wild killer whales based on activity budgets (Ford 1984, Osborne 1986, Nichol 1990), and oxygen consumption according to activity states from Chapter 1. The following equation was used:

$$[21] \text{ MR} = \# \text{ of breaths taken/day} * (\text{kcal/breath}) / \text{M},$$

where MR = metabolic rate (kcal/kg/day) and M is body mass in kg.

Individual data points were entered into the Nonlin function in Systat and the best fitting equation was determined using the form:

$$[22] \text{ MR} = a * \text{Vel}^{2.5},$$

where MR = metabolic rate (kcal/kg/day); a = a constant; and Vel = swimming velocity in m/sec.

Metabolic rate was converted to COT using the following conversion:

$$[23] \text{ COT}_e = (\text{metabolic rate} / \text{velocity}) * (1000\text{m} / \text{km}) * (1\text{day} / 86400 \text{ s}),$$

where COT_e = measured in kcal/kg/km; MR = kcal/kg/s (determined as in equation [21]); and velocity = m/sec.

A curve was fitted rather than a straight line because the power required to overcome drag increases with swimming velocity to the power of 2.5 to 2.8, depending on whether the flows are laminar or turbulent (Blake 1983).

Morphometrics

a) Fineness Ratio

Morphometric measurements of stranded or collected animals provided by Dale Rice and Al Wolman (National Marine Mammal Laboratory, Seattle, WA) were used to calculate the fineness ratio of individual animals and assess streamlining; consequently, the coefficient of frictional drag is estimated from the fineness ratio for determining the drag the animal is experiencing (Hoerner 1965). The fineness ratio was calculated following Webb (1975) and Feldkamp (1987):

$$[24] \text{ FR} = \text{body length}/\text{maximum body diameter},$$

where: FR is a dimensionless number and body length and diameter are measured in cm.

b) Reynolds Number

Reynolds numbers were calculated for differently sized animals swimming at different swimming velocities (Blake 1983, Alexander 1983, Vogel 1988) to predict turbulence effects. The following equation was used:

$$[25] \text{ Re} = LU/v,$$

where: Re is a dimensionless number, L = body length (m); U = swimming velocity (m/sec); and v = the kinematic viscosity of water in m²/s.

c) Drag

Drag was estimated following Blake (1983). The power needed to overcome drag is estimated as:

$$[26] \frac{1}{2}\rho S_w U^3 (kC_D)\delta,$$

where ρ = the viscosity of sea water; S_w = the wetted surface area of the animal in m²;

U = the velocity at which the animal is swimming in m/s; k = the excess drag due to changes in body shape during swimming motions (dimensionless); C_D = the coefficient of drag (dimensionless); and δ = the excess drag due to swimming near the surface (dimensionless).

The kinematic viscosity of sea water at 10°C is $1.30777 \times 10^{-6} \text{ m}^2 \text{ sec}^{-1}$ (Dorsey 1940). Morphometric data on stranded animals were used to estimate the wetted surface area of the animal. The area of the cylindrical body was calculated as length * girth. The area of the dorsal fin was calculated as two triangles (base * height), and the area of the flukes was calculated as the span of the flukes * the width of the flukes. The surface area of the pectoral fins were calculated as the length of the fin * the width of the fin * 2. K is likely to have a value in the range of 1 to 4 (Blake 1983). δ was ignored because the

whales were assumed to spend a negligible time near the surface, and C_D for an animal with a fineness ratio of 5 is about 1.2 times C_f , which is the coefficient of frictional drag (Hoerner 1965). C_f scales with Reynolds number^{-0.5} for laminar flow, and with Reynolds number^{-0.2} for turbulent drag (Blake 1983). Metabolic rates at different swimming speeds were compared to the power needed to overcome drag.

The proportion of laminar and turbulent flow was estimated as follows:

1. the COT curve was fitted to the metabolic rate as a function of velocity data.
2. drag was calculated for 100% laminar or 100% turbulent flow and the best fit of partial laminar and turbulent flow was determined.

The modelled COT based on estimated drag, postural cost, muscle efficiency and drag augmentation factor was predicted as:

$$[27] \quad COT_{drag\ model} = (1-t) \left(\frac{P_{smr} + \frac{D_l}{cm\mu}}{v} \right) + t \left(\frac{P_{smr} + \frac{D_t}{cm\mu}}{v} \right)$$

where: $COT_{drag\ model}$ = kcal/kg/km, t = the fraction of turbulent flow, $1-t$ = the fraction of laminar flow, P_{smr} = "postural cost" specific metabolic rate (kcal/kg/sec), which is the energy required for swimming at a velocity of 0 m/s, D_l = the power to overcome drag due to laminar flow (J/sec), D_t = the power to overcome drag due to turbulent flow (J/sec), c = the conversion from J to kcal (4.187J = 1kcal, Perez *et al.* 1990), m = mass in kg, μ = the efficiency of conversion of metabolic to movement energy, and v = swimming velocity in m/s.

RESULTS

Observations

Of a total of 157 observations of both theodolite and loran tracking, 82 were considered acceptable. This constituted a total time of 42.27 hours and covered 238.23 km of tracking.

Diving Depths and Dive Models

The mean diving depths measured with the depth sounder were 25 m for males, and 18 m for females and juveniles. (Males: $\bar{x} = 25$ m, $n = 6$, range = 21 to 27 m, SE = 0.93; females: $\bar{x} = 18$ m, $n = 4$, range = 15 to 20 m, SE = 1.18; juveniles: $\bar{x} = 18$, $n = 3$, range = 18 to 19 m, SE = 0.33).

The model which fit the measured data most consistently for the measured distance over which the whales were tracked was the V-shaped model, described as:

$$[28] \quad 2 * \sqrt{[(\text{Distance}^2/2) + \text{depth}^2]},$$

where: Distance is in m and depth is in m.

The seven models were compared for the 82 valid tracks. The V-shaped model produced the least variance in 64 (78%) of the 82 tracks and was used in further analysis to calculate the distance the whales travelled between surfacings.

Bias

A bias towards overestimation of respiration rates existed for short theodolite tracks (Figure 24) as indicated by the negative slope of the regression lines. To eliminate this, all tracks less than 10 min in length were shown in Figure 25 but not used for further calculations because it was believed that they did not accurately reflect respiration rates. In addition, because tracks started and ended with surfacings which did not always pick up an integral number of respiratory cycles, too many surfacings were measured over the distance travelled in some cases. To correct for this overestimation of respirations, the initial breaths and corresponding times were eliminated so that all tracks began with a long respiratory interval and ended with a breath, except for tracks where respiratory intervals were uniform. This method reduced the bias, and the bias was negligible after 10 min of theodolite tracking. Respiration rates as a function of swimming velocity for juveniles were graphed (Figure 25c). Because metabolic rates determined from respiration studies (see Chapter 1) were not available, further analysis of data from juveniles was precluded.

Breathing Rates and Swimming Velocities

Simple linear regressions were fitted to the data of breathing rates of adult males, adult females and juveniles during summer and spring as a function of swimming velocities (Figure 25, Table 20 and 21). Data for males in summer and spring were pooled after determining that the slopes and intercepts of the individual seasonal regression lines did not differ statistically (slopes: $t=0.46$, $p>0.5$; intercepts: $t=0.89$, $p>0.2$). The pooled

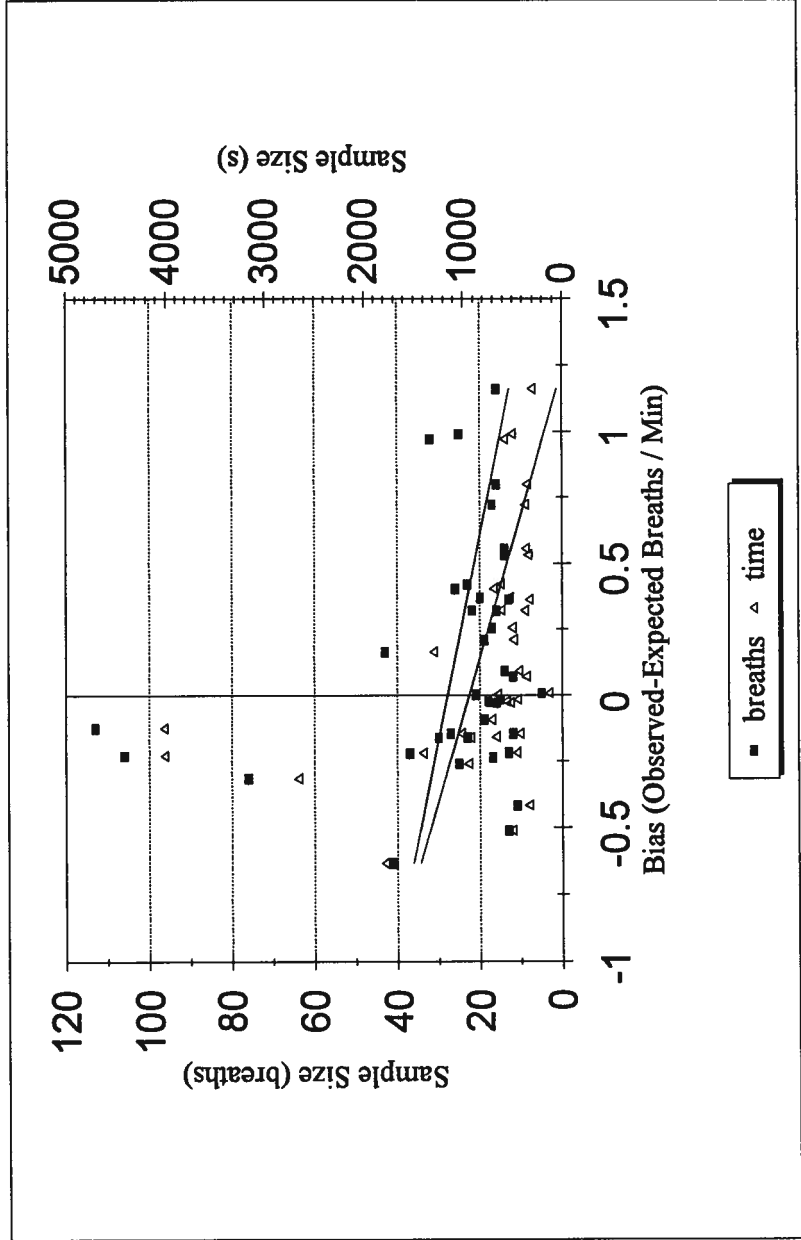


Figure 24. Relation of bias in breathing rate to sample size for females.

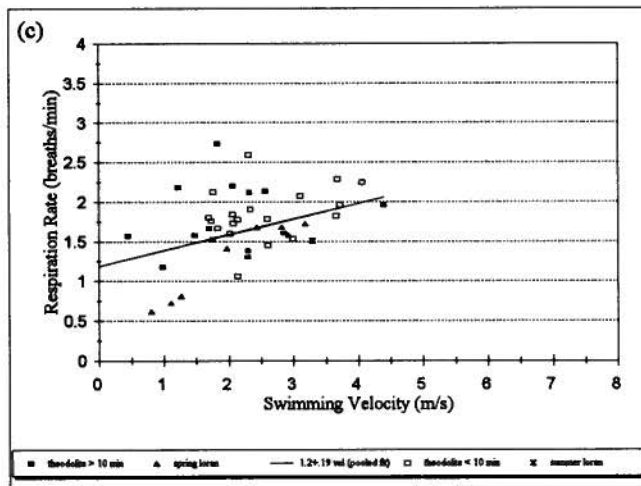
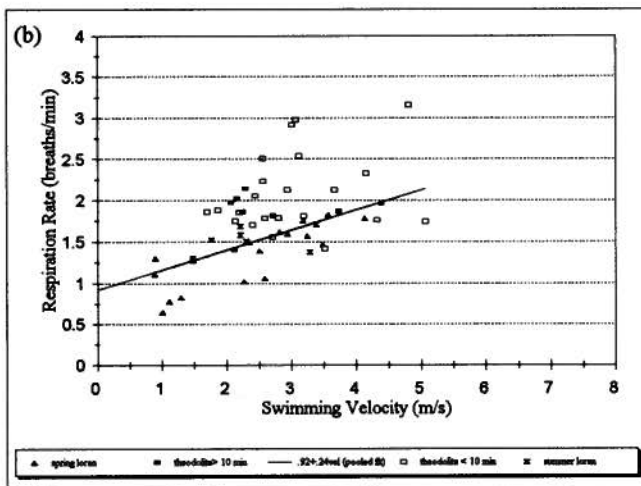
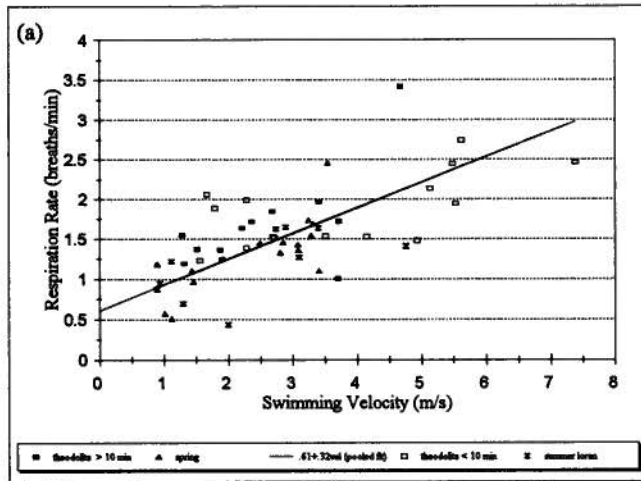


Figure 25. Respiration rates as a function of swimming velocity in killer whales.
 (a) males, (b) females, (c) calves and juveniles.

Table 20. Swimming velocities and breathing rates in free-ranging killer whales during the summer and spring.

	Summer			Spring				
	Mean	Range	Standard Deviation	Number of Observations	Mean	Range	Standard Deviation	Number of Observations
Mean Velocity (m/s)								
males	2.41	0.9 - 4.7	1.16	22	2.47	0.9 - 3.6	0.98	15
females	2.40	1.5 - 4.4	0.81	16	2.39	0.9 - 4.1	1.06	16
juveniles	2.16	0.5 - 4.4	0.96	15	2.06	0.8 - 3.2	0.91	8
Mean Breathing Rate (breaths/min)								
males	1.58	0.9 - 3.4	0.58	22	1.33	0.5 - 2.5	0.47	15
females	1.72	1.4 - 2.1	0.28	16	1.33	0.7 - 1.8	0.38	16
juveniles	1.79	1.2 - 2.7	0.43	15	1.28	0.6 - 1.7	0.48	8

Table 21. Regression equations and statistics for the relationship between respiration rates (RR in breaths/min) and swimming velocities (m/s) in male, female and juvenile killer whales.

Sex	Equation	Number of Observations	r²	Significance Level	SE of y Intercept	SE of x Coefficient
Males	RR = 0.61 + 0.32Vel	37	0.41	p < 0.001	0.42	0.06
Females	RR = 0.92 + 0.24Vel	32	0.36	p < 0.001	0.30	0.06
Juveniles	RR = 1.19 + 0.20Vel	23	0.14	p < 0.1	0.47	0.11

regression analysis for adult males showed a significant correlation between breathing rate and velocity ($r^2=0.41$, $N=37$, $df=35$, $p<0.001$). For adult females, the summer and spring data were pooled as well; while the slopes were not statistically different from each other, the intercepts were significantly different (slope: $t=1.66$, $p>0.1$; intercept: $t=3.77$, $p<0.001$). Although the summer data were corrected for bias, the differences may be due to sampling technique. Despite the differences, data were pooled and the pooled regression line showed significant correlation ($r^2=0.36$, $N=32$, $df=30$, $p < 0.001$). While the slopes of the regression lines between respiration rates and swimming velocities for males and females did not differ ($df = 2$, $df = 88$, $F = 0.74$, $p > 0.5$), the intercepts were significantly different ($df = 9$, $df = 90$, $F = 134.5$, $p < 0.001$). Interseasonal comparisons between juveniles are significantly different from each other.

Metabolic Rates

Metabolic rates during travel at different swimming velocities for males (Figure 26a) were calculated as:

$$[29] \text{ MR (kcal/kg/d) } = 29.317 + 1.109 V^{2.5},$$

where V is the swimming velocity in m/sec.

For females (Figure 26a), this equates to:

$$[30] \text{ MR (kcal/kg/d) } = 32.285 + 1.256 V^{2.5}.$$

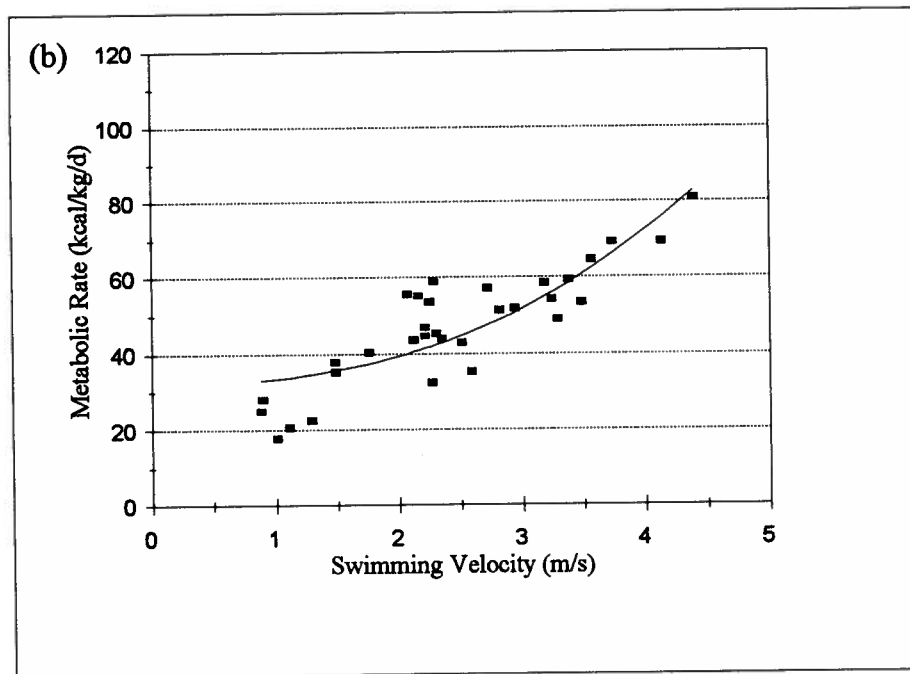
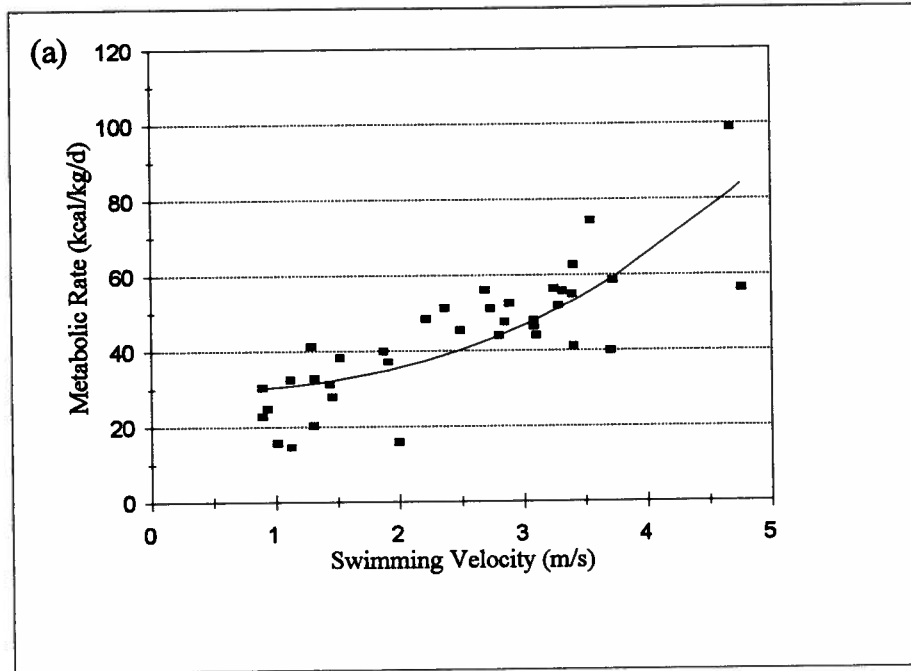


Figure 26. Metabolic rate as a function of swimming velocity in killer whales. (a) males, (b) females.

While the slopes of the two regressions of log-transformed data were not statistically different ($t = 0.67$, $df = 65$, $p > 0.5$, the intercepts were significantly different ($t = 15.7$, $df = 66$, $p < 0.001$). No further calculations could be conducted with data from juveniles because metabolic rates could not be determined by respiration analysis in captivity.

Cost of Transport

The minimum COT at which the male killer whales took the least breaths/km was at a measured velocity of 3.1 m/s (Figure 27a) and corresponds to 0.18 kcal/kg/km. For adult females, the lowest COT was measured at 3.1 m/s (Figure 27b) with an energetic output of 0.2 kcal/kg/km.

Morphometrics

a) Fineness Ratio

Fineness ratios were calculated for each individual animal for which data on length and girth were available (Table 22). The values of fineness ratio ranged from 4.51 to 5.87, with a mean of 4.96. The position of the maximum diameter along the body was estimated from 13 animals, and ranged from 30-43% behind the snout with a mean of 36%. The surface areas of the different appendages are also presented (Table 22). From these data, the surface area was calculated to be 23.07 m² for an adult male killer whale at 7.4 m and a calculated weight of 5153 kg (Bigg and Wolman 1975), 13.17 m² for a female measuring 5.79 m (2738 kg), and 3.86 m² for a juvenile at an approximate age of 2 years (3.19 m; 589 kg).

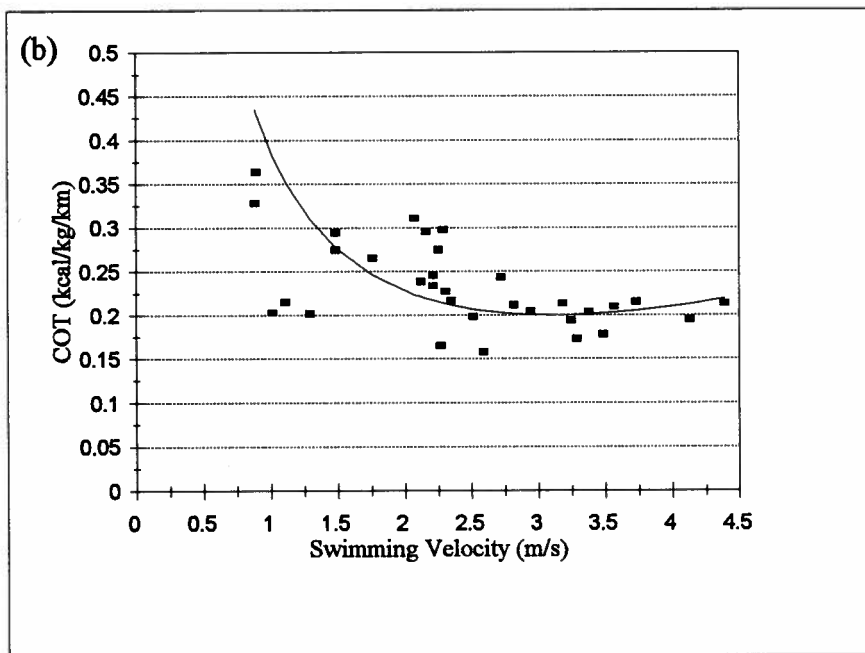
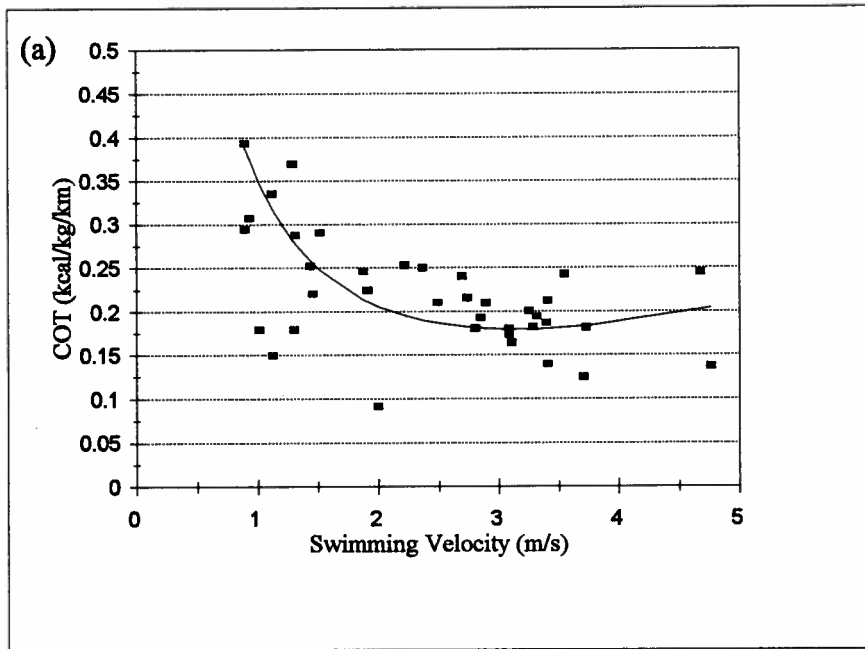


Figure 27. Cost of transport of male (a) and female (b) killer whales as a function of swimming velocity.

Table 22. Body measurements of stranded killer whales.

Animal	Sex	Length (m)	Girth (m)	Base of Dorsal Fin (m)	Height of Dorsal Fin (m)	Span of Flukes (m)	Width of Flukes (m)
1965-4	M	7.4	4.88	1.18	1.3	2.3	0.61
Namu	M	6.56	3.85	0.9	1.2	2.05	0.47
1970-101	M	3.19	2.12	0.39	0.43	0.77	0.18
1972-3	M	2.99	2.07	0.43	0.34	0.76	0.25
1963-832	M	7.24	4.84	0.92	1.45	2.55	0.75
US-60-1	M	5.18	2.77	0.56	0.63	1.38	0.39
US-61-1K	M	7.6	4.69	1.17	1.66	2.73	0.62
3204	M	6.3	3.9	0.9	0.98	2.1	0.5
3264	M	3.85	2.6	0.66	0.48	1.06	0.29
3266	M	6.98	4.52	1.17	1.37	2.36	0.62
1962-605	M	6.86	4.78	1.07	1.52	2.44	0.71
1964-986	F	5.65	3.44	0.68	0.6	1.48	0.4
3265	F	5.79	3.68	1.07	0.71	1.58	0.49
3774	F	4.92	2.93	0.72	0.63	1.38	0.36

Length of Pect. Fins (m)	Width of Pect. Fins (m)	Weight (kg)	Body Area (m ²)	Dorsal Fin Area (m ²)	Fluke Area (m ²)	Pectoral Fin Area (m ²)	Total Appendages (m ²)
1.33	0.78	5153	18.06	1.53	1.40	2.07	5.01
1.37	0.75	3778	12.63	1.08	0.96	2.06	4.10
0.39	0.22	589	3.38	0.17	0.14	0.17	0.48
0.43	0.23	499	3.09	0.15	0.19	0.20	0.53
1.6	1.04	4871	17.52	1.33	1.91	3.33	6.57
0.75	0.42	2055	7.17	0.35	0.54	0.63	1.52
2.05	1.22	5520	17.82	1.94	1.69	5.00	8.64
1.1	0.63	3404	12.29	0.88	1.05	1.39	3.32
0.61	0.3	957	5.01	0.32	0.31	0.37	0.99
1.6	0.9	4433	15.77	1.60	1.46	2.88	5.95
1.52	1.02	4239	16.40	1.63	1.73	3.10	6.46
0.79	0.41	2571	9.72	0.41	0.59	0.65	1.65
0.96	0.51	2738	10.65	0.76	0.77	0.98	2.51
0.74	0.35	1800	7.21	0.45	0.50	0.52	1.47

Surface Area (m ²)	Log Weight (kg)	Log Area (m ²)	Surface Volume (m ³)	Appendage Surface Volume (m ³)	Body Surface Volume (m ³)	Fineness Ratio
23.07	3.71	1.26	4.48	0.97	3.50	4.76
16.73	3.58	1.10	4.43	1.08	3.34	5.35
3.86	2.77	0.53	6.55	0.81	5.74	4.73
3.63	2.70	0.49	7.28	1.07	6.21	4.54
24.10	3.69	1.24	4.95	1.35	3.60	4.70
8.70	3.31	0.86	4.23	0.74	3.49	5.87
26.46	3.74	1.25	4.79	1.56	3.23	5.09
15.60	3.53	1.09	4.58	0.97	3.61	5.07
6.00	2.98	0.70	6.27	1.03	5.23	4.65
21.72	3.65	1.20	4.90	1.34	3.56	4.85
22.86	3.63	1.21	5.39	1.52	3.87	4.51
11.37	3.41	0.99	4.42	0.64	3.78	5.16
13.17	3.44	1.03	4.81	0.92	3.89	4.94
8.68	3.26	0.86	4.82	0.82	4.00	5.28

b) Reynolds Number

Reynolds numbers ranged for males from $5 \cdot 10^6$ at a swimming speed of 0.43 m/sec to $5 \cdot 10^7$ at 4.76 m/sec. For females, Reynolds numbers ranged from $3.9 \cdot 10^6$ at 0.88 m/sec to $1.9 \cdot 10^7$ at 4.39 m/sec, and for juveniles, the range was from $1 \cdot 10^6$ at 0.45 m/sec to $1 \cdot 10^7$ at 4.39 m/sec.

c) Drag

Assuming that 30% of the energy consumed by muscles is used to overcome drag [which lies within the range of general assumptions and Blake (1983) assumed 25% for dolphins], and $k=2$ (the excess drag due to changes in body shape), then 88% of the flow was laminar, and 12% turbulent for males (Figure 28a). For females, 89% of the flow was laminar and 11% turbulent using the same assumptions (Figure 28b).

DISCUSSION

Dive Models

The V-shaped dive model provided the best fit in 78% of all tracks tested and was therefore used to complete distance calculations for all tracks. Similar dive types in killer whales were recognized by Baird (1994) using a recoverable, suction-cup attached time-depth recorder (TDR) VHF radio-tag. Baird (1994) reported that the proportion of the different dive types varied with dive duration, dive depths and behaviour of the animals, but that the majority of the whales' time was spent at depths less than 20 m from the

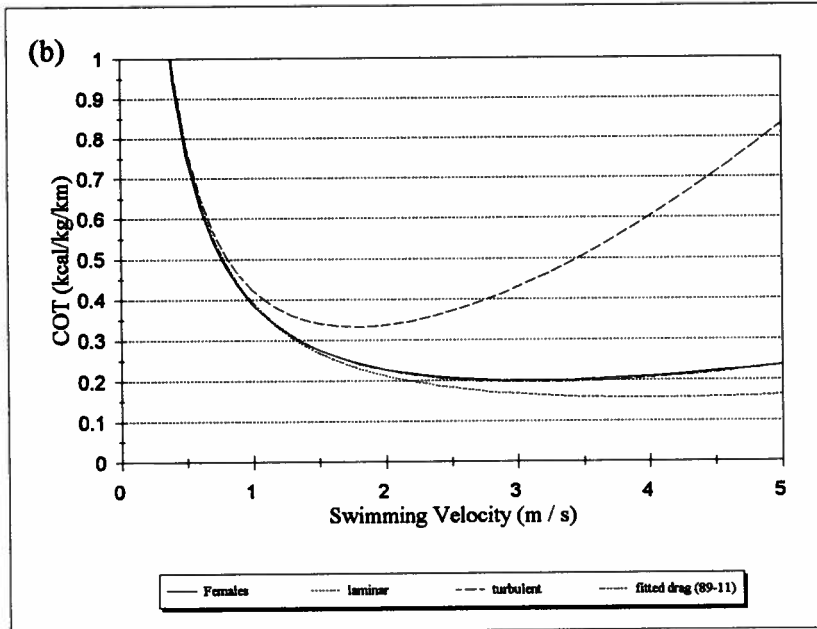
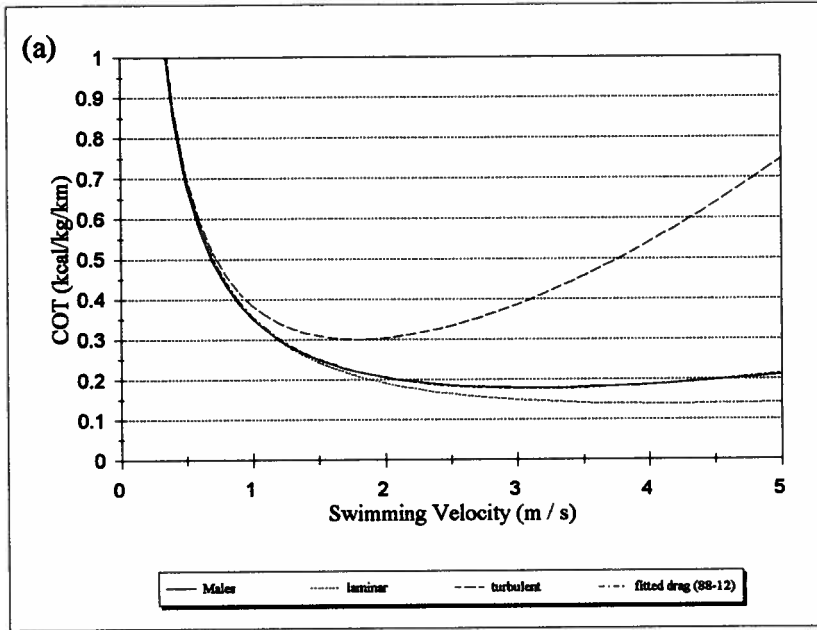


Figure 28. Comparison of COT based on respiration as a function of swimming velocity and fitted drag models for killer whales. (a) males, (b) females.

surface. The small number of measured diving depths in my study on travelling killer whales suggests that killer whales do not dive to deep depths during travelling. Baird (1994) for killer whales, and Le Boeuf *et al.* (1993) for pinnipeds, suggested that longer dive durations and deeper diving depths may be associated with prey searching behaviour. Because swimming velocities and diving depths were only measured during travelling behaviour, no deep diving depths were measured in this study as have been reported for killer whales (Heezen and Johnson 1969, Bowers and Henderson 1972).

Diving to deep depths during travelling would increase the total distance the animal has swum during the time it was tracked. Determining diving profiles and direction and determining depths with recently developed sonar equipment will better determine diving depths during travelling by cetaceans in future studies.

Bias

Due to a bias in respiration rates as a function of swimming velocities during short theodolite tracks, all tracks less than 10 min in duration were discarded and all others were corrected to begin with a long dive interval. While difficulties and errors associated with incorrect measurements and inaccuracy in theodolite tracking have been reviewed (Wuergsig *et al.* 1991), the recognition of bias due to short tracks has not been previously reported. For future studies, it can be recommend using only tracks longer than 10 to 15 min in length to ensure a representative sample of breathing rates as a function of swimming velocity.

Respiration Rates, Swimming Velocities and Metabolic Rates

Measured maximum swimming velocities were slower (7.4 m/s) than the reported maximum speeds measured in killer whales in the open sea over short distances of about 15.4 m/s (Lang 1966).

A linear relationship between respiration rates and swimming velocities was found for all age and sex classes of killer whales, while the relationship of metabolic rate as a function of increasing swimming velocity was curvilinear. This suggests that respiration rates and metabolic rates are not related linearly to each other, hence by just collecting respiration rates in marine mammals, energy demands cannot be deduced directly from respiration rates. Curvilinear relationships between metabolic rates and increases in swimming velocity have also been determined in other swimming animals, such as in fish (Brett 1964), turtles (Prange 1976), ducks (Prange and Schmidt-Nielsen 1970), mink (Williams 1983), sea otters (Williams and Kooyman 1985), and seals (Davies *et al.* 1985). For terrestrial mammals and birds running on a treadmill, metabolic rate increases linearly with speed (Taylor *et al.* 1970, Taylor *et al.* 1982, Schmidt-Nielsen 1990).

Cost of Transport

The male and female killer whales in this study reached their lowest cost of transport between 0.18 kcal/kg/km and 0.2 kcal/kg/km at a velocity of 3.1 m/s. These results fit in very well with data reported in the literature: gray whales' (*Eschrichtius robustus*), weighing 15 t, minimum cost of transport is 0.1 kcal/kg/km at 2.0 to 2.2 m/s (Sumich 1983, 1986); bottlenose dolphins (*Tursiops truncatus*) weighing only 145 kg, reached a

minimum COT with 0.31 kcal/kg/km at 2.1 m/sec (Williams *et al.* 1992). Comparing the energy for COT in cetaceans to that of theoretical fish of similar sizes, cetaceans require more energy than fish. Male killer whales used 2.9 times the predicted value of energy expenditure of a 5,000 kg fish, while females were very close to the value of males with 2.8 times the predicted energy used by a fish of 3,000 kg (Brett 1964). Sumich (1983, 1986) calculated gray whales' COT as 2.6 times that of a fish of comparable size; bottlenose dolphins' COT is 2.1 that predicted for a fish of the same size (Williams 1992). In harbour (*Phocoena vitulina*) and harp seals (*Pagophilus groenlandicus*) (Craig and Pasche 1980, Lavigne *et al.* 1982, Davis *et al.* 1985), the cost of transport was 3-4 times higher for yearling and adult animals than for salmon extrapolated to the same size as the pinnipeds. However, when comparing marine mammals' COT to that of other aquatic and semi-aquatic animals such as mink (Williams 1983), sea otters (Williams 1989) and ducks (Prange and Schmidt-Nielsen 1970), cetaceans and pinnipeds have considerably lower COT's. Humans are extremely inefficient swimmers: their COT is 8-12 times that predicted for dolphins (Williams 1992). It is interesting to note that the average swimming velocities observed during summer in killer whales in both the southern and northern residents (2 m/s) (this Chapter, Kruse 1991) is lower than their energetically optimal swimming speed of 3 m/s, at which the animals' COT is lowest. While the difference in caloric expenditure of swimming between 2 and 3 m/s is only 0.05 kcal/kg/km for male and female killer whales, the slightly lower than optimal velocity may be related to the behaviour in which the animals are engaged. During late spring and summer, salmon swim in large schools through Haro and Johnstone Strait (Heimlich-

Boran 1986, 1988, Nichol 1990) and northern and southern resident killer whales follow these salmon stocks (Felleman *et al.* 1988). Similar differences in swimming velocity have been reported for seals (Thompson *et al.* 1993).

Fineness Ratio, Reynolds Numbers and Drag

The fineness ratio is representative of the quality of body streamlining, and, therefore, of the efficiency of streamlining in reducing drag among solid bodies (Williams and Kooyman 1985). The values for the fineness ratio calculated for the killer whales for which morphometric data were available indicated that killer whales have fineness ratios (4.51 to 5.87 with a mean of 4.96) close to the optimum of 4.5, indicating a body shape which produces a minimum drag for a maximum body volume (Webb 1975, Feldkamp 1987). In comparison, fineness ratios ranged from 3.8 to 5.5 for a variety of cetaceans and large fishes (Hertel 1966) and from 5.5 to 7.0 in fishes which swim in the subcarangiform mode (Webb 1975).

Reynolds numbers were calculated for all velocities. For velocities greater than 1 m/s turbulent flow is predicted ($Re > 5 \times 10^6$, Webb 1975) for males and females, while juveniles started to encounter turbulent flow at a swimming velocity of 1.4 m/s.

Drag in marine mammals is poorly understood and empirical data have only been collected on carcasses (Williams and Kooyman 1985), and data have been approximated theoretically. Drag was estimated for adult male and female killer whales, however, several unknown variables had to be assumed as mentioned in the methods of this chapter. Drag estimates are based on three unknown and only assumed factors: k , the excess drag

due to changes in body shape during the swimming motion, which ranges between 1 and 4 where it has been measured. Blake (1983) assumed $k=4$ for a hypothetical dolphin calculation. The efficiency of the muscle for marine mammals is unknown; Blake assumed this to be on the order of 25%. Last, the amount of laminar and turbulent flow is not known; while the adult killer whales in this study had Reynolds numbers indicating turbulent flow across the body, the Reynolds numbers for juveniles at swimming velocities less than 1.4 m/s were low enough to suggest laminar flow. Based on theoretical calculations, the adult males and females should encounter turbulent flow over the majority of their body area if swimming faster than 1 m/s. When the drag curve was fitted to the COT curve for the different sex classes, however, this was not observed: the majority of flow was laminar (89% for males and 88% for females). While the maximum diameter along the animal's body is located 36% of the body length behind the rostrum and this position is far enough back to ensure laminar flow over the forward portion of the animal and reduce drag (Hoerner 1958), the fitted laminar flow of 88% in males and 89% in females (Figure 28) is still 52% and 53% higher than expected for male and female killer whales respectively. In harbour seals, the drag coefficient was determined to be less than that found on humans, cars, submarines and torpedo shapes (Williams and Kooyman 1985). This suggests that the water flow around the body of seals is relatively smooth which can also be observed when seals are seen swimming through bioluminescent plankton (Williams and Kooyman 1985). The same has been observed for Dall's porpoises (pers. obs.) and dolphins (Stevens 1950, Hill 1950).

Estimated Daily Caloric Expenditure

Energetic expenditures can be estimated by approximating daily behaviour budgets with activity states studied in Chapter 1. On average, free-ranging killer whales spend 71% of their time travelling and foraging, 13% resting, and 15% socializing, including rubbing, during the summer months (Ford 1984, Osborne 1986, Nichol 1990, Ford *et al.* 1994). The travel/forage behaviour was approximated with Activity states 2 to 3, rest and rubbing behaviour with Activity state 1, and social behaviour was approximated with Activity state 3. Using an intermediate value between Activity states 2 and 3 for the travel/forage category, the best estimate for caloric requirements is 184,900 kcal/d for adult males and 136,500 kcal/d for adult females. Using these estimates, and approximating the travel/forage mode with Activity state 2 or Activity state 3, the estimate for male killer whales ranges from 150,700 kcal/d to 225,730 kcal/d, while female killer whales require from 108,420 kcal/d to 164,400 kcal on a daily basis.

Chapter 4: SUMMARY AND CONCLUSIONS

This chapter summarizes the different components of the energy budget of killer whales in captivity and in the wild and identifies research topics that require further consideration and experimentation. Energy utilization, including faeces, apparent digestible, metabolizable, maintenance and production energy, has been examined for many different species of wild and domestic animals (Brody 1945, Harris 1966, Kleiber 1975). For cetaceans, some of the components of the bioenergetic model have been examined (Lockyer 1981a, 1981b, Lavigne *et al.* 1982, Innes *et al.* 1987), but to date it has not been possible to quantify all of the different components for a single cetacean species through actual measurements. The problems of conducting experimental work with cetaceans have been raised in the previous chapters. Nevertheless an attempt to quantify the energy budget of the killer whale, *Orcinus orca*, has been made. It should be remembered that the variables measured may be altered somewhat by the conditions of captivity but corrections for this were attempted where necessary. At the same time data collection directly from killer whales in the wild also posed considerable problems in obtaining a representative sample of the wild population. These problems are not unique to this study and have been discussed by others (Caughley 1966, Brodie 1975, Lockyer 1981a, 1981b, Lavigne *et al.* 1982, Innes *et al.* 1987).

While variations exist and the problems pointed out should not be overlooked, they should not deter scientists from studying cetaceans and other marine mammals from a more holistic point of view than has been done in the past.

It has been suggested by many (Kanwisher and Sundnes 1965, Irving 1972, Slijper 1979, Kasting *et al.* 1989) that the standard metabolic rates of marine mammals and cetaceans, and killer whales in particular, are higher than those of terrestrial mammals. However, measurements of oxygen consumption by unrestrained captive male and female killer whales indicate the SMR is between 1.2 and 1.3 times that of Kleiber's (1975) prediction of basal metabolic rates, hence comparable to terrestrial carnivores of the same size (McNab 1982). Others (Oritsland and Ronald 1975, Gallivan 1977, Parson 1977) have found that basal metabolism in confined pinnipeds is near, and even below, Kleiber's (1975) equation for mammals.

While the killer whales' tidal volumes at rest are between 2.65 and 4.18 times higher than those of terrestrial mammals, the vital capacities of these animals are between 68 and 94% that of terrestrial mammals of comparable size (Stahl 1967) and fall within values suggested for cetaceans (Dolphin 1987). Oxygen measurements at different activity rates showed that killer whales take up O₂ at higher rates at higher activities; the minimum estimate of metabolic scope of orcas of about 6 is between 30 and 50% smaller than that observed in most terrestrial mammals. However, these metabolic scopes are most likely underestimated because the whales were not pushed to their maximum limits of exertion.

The quantity of food ingested per meal, the frequency of feeding, the amount of different food items consumed and the caloric equivalents of these food items can be obtained from food records for captive animals. While food items of wild killer whales are well known and have been reviewed (Rice 1968, Castello 1977, Slijper 1979, Heyning 1988, Thomas and Felleman 1988, Wenzel and Sears 1988, Hoyt 1990), the amounts of

food consumed by wild animals have not been determined. As expected, husbandry records from captive orcas indicate that food intake increases with increasing body mass, but decreases on a per body weight scale (Food Intake = $0.277 M^{0.663}$, where M = body mass in kg).

More information about the regulation of food intake from the animal's point of view is gained from examining seasonal variation in food intake together with effects of water temperature. Very little or no (<1.3% / °C) variation was found for captive killer whales, suggesting that normal activity produces sufficient heat to maintain body temperature in water ranging from 7° to 23°C.

During the female killer whales' approximately 17 months of gestation (Walker *et al.* 1988), food consumption varied < 25% from food intake prior to pregnancy, whereas the energetic cost during lactation was twice that of previous non-pregnant levels. While pregnancy is not expensive energetically, lactation is very costly.

By comparing the food consumed to the energy expended determined by respiration analysis, the mean net assimilation efficiency (NAE) of captive killer whales was calculated to be 0.73, a high food utilization compared to terrestrial mammals but similar to NAE's reported for other marine mammals [0.67- 0.97 (Shapunov 1972a, 1972b, Lavigne *et al.* 1981, Yasui and Gaskin 1986, Worthy 1990)].

The diurnal activity patterns of killer whales are well documented in captivity (Bain 1986, Ray *et al.* 1986) and also in the wild during day time activities (Ford 1984, Osborne 1986, Nichol 1990). By assigning caloric expenditures to the different activities and summing those over a 24 h period, estimated caloric expenditures indicate that killer

whales' energetic necessities closely fit findings for other cetaceans (Innes *et al.* 1987) as well as those for terrestrial mammals of similar size.

By studying free-ranging killer whales to estimate energetic expenditures during swimming, observations longer than 10 min and preferably 15 min in duration were necessary to obtain unbiased theodolite data on respiration rates as a function of swimming velocity. While the relationship of respiration rates as a function of swimming speed was linear for all age and sex classes, they were different for each gender and age category. Metabolic rates and cost of transport (COT) as functions of swimming velocity as well as the optimal COT were shown to be curvilinear in shape as found for other aquatic animals. Maximum range velocities occurred at a velocity of 3 m/s for adult males and females. To swim efficiently and to reduce drag, it was shown that killer whales have an almost ideal fineness ratio of 4.51 to 5.87 (mean = 4.96). Drag was higher than predicted for a rigid body but lower than expected for a flexible body. Flow was interpreted to be much higher in laminar content than expected from theoretical assumptions reported in the literature. Values were inferred for a number of parameters that still need to be determined individually. Certain adaptations such as streamlining and a fusiform body shape as well as the reduction of hair on the body surface aid in increasing laminar flow occurring over the body. However, more adaptations, which at this point are not understood, are necessary to swim as efficiently as cetaceans and other marine mammals do.

Captive studies together with observations of wild animals can yield valuable information on how much energy animals must expend for standard metabolic rates and

daily activities. They also provide insights into how efficiently an animal uses the energy it has available for locomotion. Estimating realized metabolic rates from the activities of free-ranging killer whales, combined with oxygen consumption information from captive orcas, showed that realized metabolic rates of wild killer whales are 25-33% higher than estimates for the two captive adult animals. This discrepancy might be accounted for by the differences in activity levels and reproductive status between captive and wild animals. Much more research, using new technologies for wild whales and trained whales in captivity, can be conducted to increase the knowledge we have at this time. Laminar flow around a cetaceans' body can be determined with animals in captivity, using recently developed equipment. By visualizing water flow around a killer whale's body, the calculated estimate of the proportion of laminar and turbulent flow could be verified.

More data during very slow (<1.5 m/s) and fast (>4 m/s) swimming should be collected to determine whether some of the data points occurring at low and high swimming velocities as seen in the COT curves of male and female killer whales possibly correspond to the different gaits as seen in moving horses (Schmidt-Nielsen 1990). Respiration collections could be obtained from trained juvenile killer whales in other aquaria. Combining those respiration data with respiration rates correlated with different swimming velocities measured in wild juvenile animals, COT's can be determined for all age classes of killer whales. Following this, the sharing of the cost of locomotion, by which female killer whales assist young whales in locomotion by swimming in the echelon position (Waite 1988), can be quantified energetically and hydrodynamically. Fadely *et al.* (1990) developed a new technique to determine net assimilation efficiencies from the collection

of partial fecal samples. Samples of killer whale feces can be collected in aquaria to analyze for NAE and to compare those findings to the calculated NAE determined here.

By knowing the quantity of food required by different age and sex classes of killer whales, and by knowing how many killer whales frequent areas of valuable fish sources, such as with the blackcod (*Anoplopoma fimbria*) industry in Alaska (Matkin 1988) and different salmon species (*Oncorhynchus sp.*) in British Columbia and Washington waters, the impact of depredation on these fish species by killer whales can be estimated.

While it is extremely difficult, if not currently impossible to conduct many aspects of physiological and behavioural studies on wild cetaceans, imaginative ways of combining studies of captive cetaceans with research conducted on free-ranging whales and dolphins can help shed light on some aspects of the life of marine mammals. Many more intriguing questions about cetaceans are unsolved. While it is not possible to answer all of these questions, undoubtedly many more will be solved with improving technology and new ways of thinking about scientific research.

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