DIVING BEHAVIOR OF AIR-BREATHING VERTEBRATES: ALLOMETRY, CLASSIFICATION, AND INTERSPECIFIC COMPARISONS

By

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ABSTRACT

A great deal of knowledge has been acquired concerning the diving behavior of various air-breathing vertebrates, but little has been accomplished to incorporate all of this information into general models that will explain and predict how this group of animals interact with their environment. There are three explanations for this shortcoming: 1) although diving data have been collected on many different species, very few works have attempted to summarize these findings and all of these had a fairly limited range of species, 2) methods for analyzing large data sets of multivariate behavioral observations have not yet been clearly defined, and 3) methods and techniques for analyzing diving behavior are highly variable making interspecific comparisons difficult or impossible. In this thesis, these three problems are addressed.

Maximum dive depth and duration from 129 species of air-breathing vertebrates were examined in relation to body mass. These comparisons showed that there were strong allometric relationships between diving capacity and size and that alcids, penguins, and phocid seals are all exceptional divers relative to their masses while mysticete cetaceans dive to shallower depths and for shorter periods than would be predicted from their size. Cetaceans, as well as some other groups, are probably most greatly affected by their feeding ecology rather than by their physiological limitations.

Next, to address the problem of how to analyze large behavioral data sets, a series of techniques for analyzing these sorts of data were tested and compared. These included k-means and fuzzy c-means clustering techniques from the field of statistics, and Kohonen self-organizing map (SOM) and fuzzy adaptive resonance theory (ART) from the field of artificial neural networks. A series of simulations were performed in order to test the performance of these techniques under various conditions. As well, real data from several species were classified to further assess the suitability of the various techniques. K-means, fuzzy c-means, and SOM all performed equally well on the artificially generated data while fuzzy ART had error rates that were twice as high. When clustering the real data, only k-means classified observations into groups that appeared biologically valid and consequently was determined to be best suited to analyze diving behavior.

Lastly, using quantitative analyses, dive data from 12 species of air-breathing vertebrates were classified, using the same technique and protocol, and interspecific comparisons were made. The behavior was classified into a series of dive shapes (depth versus time: square, V, skewed-right, and skewed-left) with a shape fitting algorithm and possible functions of the dive shapes were proposed. These were pelagic foraging, benthic foraging, exploration, travelling, resting, and food and waste processing. The observed dive patterns varied across species with body size, ecological feeding niche, and conditions of the studies from which the data came. Larger species dived deeper and longer than smaller species, as was expected, although there were a few exceptions. Also, benthic foragers usually had more square dives as well as higher proportions of bottom time during these dives than pelagic foragers. Despite these differences, strong similarities in dive shapes, the abundance of square dives, and the proportion of bottom time during square dives suggest that diving animals exploit the aquatic environment in a similar way.

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Acknowledgements specific to each chapter are given at the end of the chapters.

Thanks **XOQ**.

DEDICATION

To my family and life...

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CHAPTER 1

General Introduction

Many terrestrial vertebrates, including hundreds of species of birds, mammals, and reptiles, have re-invaded aquatic habitats. These animals have a unique and fundamental problem in that, even though much of what they do needs to be done under the water surface (e.g. foraging), they are acutely and constantly dependent on a compound that can only be acquired above the surface, air. This makes for a serious dilemma for these animals, needing to spend as much time as possible under the surface, but being continuously dependent on returning to the surface to replenish their oxygen stores. To solve this problem, temporary, relatively short, excursions below the water surface are taken which are called dives.

The types of dives and overall diving behavior performed by the various diving animals is highly variable and dependent on two main factors: ecology (e.g. location of prey and foraging efficiency) and physiology (e.g. oxygen stores and metabolic rate). In this thesis general trends seen in observed diving behavior are presented, specific methods for analyzing a commonly collected type of dive data are proposed, and a series of analyses are performed on dive data from several species of diving animals. The following paragraphs present 1) a brief history of the study of diving behavior, 2) the methods and devices, as well as means of attachment for the devices, used for recording this behavior, 3) a detailed description of the data provided by time-depth recorders (TDRs), currently the most commonly used device, and lastly, 4) the purpose and objectives of this thesis.

Brief history

Dives and diving behavior have been studied in one form or another, directly or indirectly, for the past 150 years. Although, it is likely that for many hundreds or even thousands of years, people have noticed and observed that aquatic, air-breathing animals were spending time under the water surface. Even the Greek philosopher, Aristotle, realized that dolphins needed to come to the surface to breathe air 2300 years ago (*in lit.*). As time went on, several reports of diving capacity were documented in the late 1800s and the early 1900s (reviewed in Dewar 1924; Irving 1939; Scholander 1940). Many of these were simple observations made using a watch to measure how long animals stayed below the surface, while others were estimates derived from the whaling industry where dive depths and durations were estimated from harpooned whales.

More recently, in the late 1930s and 1940s, experimental studies were conducted that provided many insights into the diving capacities of air-breathing animals and how they are able accomplish these feats (Irving 1939; Scholander 1940). These experiments were generally performed on restrained animals that were forcibly submerged for a period of time. The results were highly artificial, but they did provide some of the first insights into the physiological limits of these animals and how they attain these capacities. Some determinations of maximum diving depths were also accomplished using capillary tubes (see below), although these were also conducted under highly artificial conditions (e.g. attached to a harpooned whale or attached to animals along with a long line and a float: Scholander 1940). Experiments like these were conducted for the next several decades until the focus shifted to trying to determine diving behavior and capacities under more natural conditions.

Some of the first work to be conducted under relatively natural conditions was performed on Weddell seals (Kooyman 1968, 1981). These sorts of studies were accomplished by attaching a device to the animal and releasing it to dive under relatively natural conditions. The conditions were not entirely natural in Kooyman's original work since seals were relocated to isolated breathing holes (holes that were far enough away from any other breathing holes to insure that the seal would return to the same hole) so that devices could be recovered. Capillary tubes were used for this work as well as newly developed time-depth recorders (TDRs). This sort of work has expanded and diversified rapidly over the last 30 years and diving studies have now been done on numerous species under a number of different conditions. Additional devices and methods have also been developed to record additional variables that help in describing and interpreting the diving behavior observed.

Methods and devices

A number of different methods and devices have been used to record diving behavior (Table 1.1). Starting with the most simple and obvious, the duration that an animal stays under the surface can be determined by simply timing how long the animal is not seen (Dewar 1924). The length of time an animal can stay under the surface can also be determined experimentally in the laboratory by forced submersions (Irving 1939; Scholander 1940) and over long distances using radio tags (Wanless et al. 1988). However, none of these methods provide any information about what the animal is doing while it is underwater. The next logical step was to try to determine how deep the animals dive. Depth can be estimated when animals are harpooned by determining the amount of line let out and allowing for the angle of descent (Scholander 1940); from animals caught in traps, nets, or lines (Dewar 1924); from rare direct underwater observations (e.g. submarine: Landis 1965); from animals thought to be diving to the bottom in water of known depth (Dewar 1924); and from trained animals taught to dive to a specific depth (Bower and Henderson 1972). Maximum depth or at least mean depths can also be indirectly inferred from known prey depths (Fitch and Brownell 1968). However, all of these methods only give a very limited number of observations and are subject to considerable risk of error.

Sound produced by animals can also be used to calculate depth by triangulating the location of the sound source (Liechty 1993). However, this method can only be used on animals that produce sound underwater. Active sound or SONAR can be used to track all animals (Watkins et al. 1993), but both methods have difficulty in identifying individuals, let alone whether the signal being received is from the study animal or something else such as a school of fish. Sonic tags and transponders solve this problem (Thompson et al. 1991). A sonic tag, with a pressure transducer that controls the pulse rate, attached to an animal sends information to a hydrophone about a specific individual's general location and depth. Transponders can also be attached to animals and can be interrogated by sound from an external sound source (SONAR). These devices return information about which individual is being observed and at what depth it is located (Watkins et al. 1993). For a sound signal to be received or echoed, however, it must reach the desired object without being blocked and have enough energy to return to the receiver. For example, if a whale with an implanted transponder descends below the vertical migrating layer, it may be difficult to locate because most of the sound will bounce off of the layer and will not reach the whale. Also, if sound does reach the whale, but at an intensity that is too low, the echo produced will attenuate and fail to reach the hydrophone at the surface. All of the above methods utilizing sound have these sorts of limitations.

Other devices have been developed that can be attached to animals and remotely record behavior. Capillary tubes are the simplest form of this sort of device. They are glass or plastic tubes, closed at one end, with an interior dusted with a water-soluble dye (Scholander 1940; Burger and Wilson 1988). As an animal descends, hydrostatic pressure forces water into the tube dissolving the dye. Maximum depth is recorded by a ring left inside the tube at the point of maximum compression. By measuring the distance to the ring and using pre-determined calibrations, depth can be calculated. This device is especially useful because of its simplicity and light weight, but it only records the deepest depth reached by the animal while it wears the device.

The next development in recording devices was the TDR which is still the most common and rigorous device for recording diving behavior. The first TDRs used glass disks and subsequently film that was moved past a light emitting diode (LED) that was coupled to a timing circuit and a pressure transducer (Kooyman 1965; Kooyman et al. 1983a). The LED marked the film at a distance along the film width that was determined by the pressure transducer. Calibration of this distance and the rate at which the film moved allowed depths within a dive to be recorded, as well as when the depths occurred. This information gave the first glimpses of not only how deep animals dived, but what they did while they were diving. As technology advanced, TDRs became microprocessor controlled with increased memory using micro-chips. This has permitted data on diving behavior to be collected over long periods of time (up to eight months continuously on a single individual: Testa 1994). The limiting factors for use of TDRs are memory, power, and recoverability. Therefore, when using a TDR, a sampling time interval must be used that is short enough to record the quickest events, yet long enough such that the memory and power last for the desired period of recording.

Another problem with TDRs, at least originally, was their large size. This is an important problem when studying small marine mammals (e.g. sea otters and small fur seals) and diving birds (e.g. penguins, cormorants, and alcids). This is becoming less of a problem recently because of the miniaturizations of computer hardware that are taking place. In the past, depth histogram recorders (DHRs) were created for use with very small animals to solve the size problem. DHRs are time-depth recorders that count dives within a depth range, instead of recording every depth of every dive (Kooyman et al. 1983a). This saves a considerable amount of memory space and therefore the units can be much smaller. The unit contains a number of counters which increment one count when a dive is made to the specific pressure to which it has been preset. Recently, TDRs and DHRs have been linked to satellites (SLTDRs) and provide not only depth and duration, but also location information (Testa 1994). The frequency of the signal sent from the SLTDR is shifted as the satellite moves toward or away from the source (Doppler shift), allowing location to be determined. Also, some or all of the information recorded by the device is transmitted to the satellite, and remotely reaches the researcher. This means that the animal does not have to be recaptured in order to collect the data.

Knowing an animal's vertical or horizontal location is just part of the information needed to study diving behavior. Stomach contents and scat samples provide insight into what animals are feeding on while diving (Fitch and Brownell 1968), but not what they are doing to get prey items during specific dives. Other devices have been created for this purpose including senors that detect jaw movements (Bornemann et al. 1992) and stomach and esophagus temperature (Ancel et al. 1997) which can used to determine when and potentially how much an animal is feeding. Velocity sensors (Le Boeuf et al. 1992) and triangulation with depth-sonic tags (Kelly and Wartzok 1995) can determine the speed at which an animal is swimming. This sort of information can be used to determine the animal's activity level and provide a more accurate image of the dive profile (3 dimensions versus 1 or 4 dimensions versus 2 when considering time).

In addition to understanding what these animals are doing while below the surface, it is also of considerable interest to understand how they perform the observed behavior. In order to solve various questions in this realm of study, several methods and devices have been developed that measure physiological aspects of diving performance. Measuring intramuscular temperature and heart rate can determine the animal's activity level and potential physiological means by which dive duration can be extended (e.g. lower body temperature and bradycardia: Kooyman et al. 1992b; Ponganis et al. 1993b). Some of these physiological mechanisms can be further assessed by collecting blood during a dive to determine cardiovascular reflexes and blood gas chemistry (Hill 1986; Qvist et al. 1986). By collecting blood before and after a dive, the type of metabolism used (aerobic or anaerobic) can be determined via measurement of plasma lactate concentrations (Kooyman et al. 1980).

Attachment methods

Many different attachment methods have been used to deploy the above mentioned devices. Attachment methodology is an important aspect of the study of diving behavior because it can affect the safety of the animal and the quality of the data obtained. Anytime a device is attached to an animal that is set free, there is a decent chance that it will never be seen again. Also, if the device or attachment methods strongly affect the animal's behavior, the information recorded by the device will not reflect natural activity. Ideally, attachment systems should be temporary and have little or no effect on the animal's behavior. Originally, devices were attached to an ankle strap or a harness which was attached to the animal (Scholander 1940; Kooyman 1968, 1981). The problem with these methods was that if the animal got away, it had to wear the unit for life. Lesions caused by the straps could get infected and lead to death. To solve this problem, harnesses were attached with buckles that rusted easily and therefore would eventually release. Also, straps were attached to seals' backs with hog-rings (Kooyman 1968) which allowed the seal to remove the unit in time. For pinnipeds and seabirds, the current method of choice is to glue the device to the animal's fur or feathers (e.g. Chappell et al. 1993a; Testa 1994; Schreer and Testa 1996). This works well because when the animal molts, the device falls off. For large marine mammals that cannot be captured (i.e. whales) or do not have a thick hair coat (e.g. walruses and whales), other methods of attachment must be used. TDRs have been attached to walrus on the side of their tusks with stainless steel bands (Wiig et al. 1993). TDRs are attached to the dorsal ridge of Beluga whales by attaching a saddle that is held on by nylon pins (Martin and Smith 1992). These pins migrate out of the flesh in a few weeks or months, releasing the unit. Larger whales are very difficult or impossible to handle, so the devices must be attached at a distance. Transponders have been implanted on the dorsal surface of sperms whales (Watkins and Tyack 1991; Watkins et al. 1993) using a shoulder launcher at a distance of up to 50 m. These tags migrate out of the tissue over time.

TDR data

TDR data have been collected on a broad range of animals over the last 15 years. Generally, these devices record an animal's location in the water column at pre-determined time intervals. For many studies these time intervals are set for only one or a few seconds. Therefore, in the case of the one second time interval, 60 observations are recorded every minute, 3600 observations in an hour, and 86,400 observations are recorded in one day. Even at much larger sampling intervals, an enormous number of observations are collected in a very short amount of time. To analyze these data, observations need to be organized into a smaller number of more manageable and understandable groups.

The first step in this process is to organize depth readings into dives, a series of depth readings starting and ending with a depth equal to zero. Dives are a convenient and well-defined unit of behavior in which the animal makes an excursion below the surface. Even once this has been accomplished, there are still an enormous number of dives. Therefore, more organization needs to be performed. One method is to simply identify maximums in the diving behavior recorded. The maximum depth and duration for a series of dives can be determined, but this only utilizes a small fraction of the data (one depth reading and one dive duration for the entire data set). Next, dives can be organized according to the maximum depth and duration for each dive. This method obviously utilizes much more of the data (one depth reading and the dive duration for each dive) than just taking overall maximums. Here, mean maximum depths and durations for all dives can be determined and dives can be organized into different groups based on their maximum depth and duration. However, even with these methods, only one depth reading is used per dive which is still only utilizing a small fraction of the overall data.

To use more of the data, each depth within a dive can be analyzed to generate a dive profile (depth versus time). This technique has only recently been widely utilized and several methods have been used to organize dives into different shapes (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1993, 1995, 1996;

Jonker and Bester 1994; Brillinger et al. 1995; Campagna et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*). These methods have varied considerably, ranging from completely subjective, visual comparisons to automated, shape-fitting algorithms. Differences in individual classification protocols restrict interstudy comparisons. Determining a solution to this problem is a major driving force behind this thesis.

Purpose and objectives

Although a great deal of work has been conducted on the diving behavior of various air-breathing vertebrates, little has been accomplished to incorporate all of this information into general models that will explain and predict how this group of animals interact with their environment. There are three explanations for this shortcoming: 1) although diving data have been collected on many different species, very few works have attempted to summarize these findings and all of these had a fairly limited range of species, 2) methods for analyzing large data sets of multivariate behavioral observations have not yet been clearly defined, and 3) methods and techniques for analyzing diving behavior are highly variable making interspecific comparisons difficult or impossible. In this thesis, these three problems are addressed.

In Chapter 2, diving capacity (maximum depth and duration) is examined in relation to body mass across a wide range of air-breathing vertebrates. Maximum depth and duration were utilized because these data are the most frequently reported and allowed for the broadest interspecific comparison. In Chapter 3, four different algorithms from the fields of statistics and artificial neural networks were tested and compared to determine their suitability for analyzing TDR data. Chapter 4 presents dive analyses on 12 species of diving animals using quantitative techniques. The data from each species were classified according to dive shape and the results were compared within and across species. Possible behavioral functions for the resulting dive types were also proposed.

Table 1.1. Some methods and devices for recording diving behavior.

Method/ Device	Data recorded	Time period	Source[a]
Watch	Duration, surface intervals	hours	Dewar 1924
Water depth	Max. depth	hours	Dewar 1924
Harpoon line	Max. depth	one value	Scholander 1940
Caught, tangled, or hooked on lines, nets, or traps	Max. depth	one value	Dewar 1924
Forced submersion	Duration, heart rate, metabolic rate	hours	Scholander 1940
Swim chamber	Heart rate, metabolic rate, swim speed, duration	hours	Kooyman and Ponganis 1994
Stomach contents, scat samples, or feeding patterns	Max., mean depth	one value	Fitch and Brownell 1968
Directly observed (e.g. submarine)	Max. depth	one value	Landis 1965
Trained	Max., mean depth, duration	one value	Bower and Henderson 1972
Video camera	Body movements, feeding, immediate surroundings	hours	Davis et al. 1993
Passive sound recording (hydrophone)	Depths, duration	hours-days	Liechty 1993
Active sound (SONAR)	Depths, duration	hours-days	Watkins et al. 1993
w/ transponders	identification	hours-days	Watkins et al. 1993
Sonic tags with pressure transducer	Depths, duration	hours-days	Thompson et al. 1991
w/ triangulation	3D location, swim speed	hours-days	Kelly and Wartzok 1995
Capillary tubes	Max. depth	one value	Burger and Wilson 1988
Radio tag	Duration	hours-days	Wanless et al. 1988
Depth-histogram recorder (DHR)	Max. depth	months	Kooyman et al. 1983a
Time-depth recorder (TDR)	Depths, duration	months	Kooyman et al. 1983a
Satellite link (SLTDR)	Location	months	Testa 1994
Velocity sensor	Swimming speed	months	Le Boeuf et al. 1992
External temperature sensor	Water temperature, location	months	Hindell et al. 1991a
Light sensor	Location	months	Hill 1994
Stomach and esophagus temperature sensor	Feeding	days	Ancel et al. 1997
Intramuscular temperature sensor	Muscle temperature, activity	days	Ponganis et al. 1993b
Jaw movement sensor	Feeding	days	Bornemann et al. 1992

Table 1.1 (*continued*).

Method/ Device	Data recorded	Time period	Source[a]
Heart rate tag	Heart rate, metabolic rate, activity	days	Kooyman et al. 1992b
Labeled water	At sea metabolic rate	days-months	Costa and Gentry 1986
Thermodilution	Cardiac output, stroke volume	min.-hours	Kooyman et al. 1992b
Blood extraction, during the dive	Various blood parameters	min.-hours	Hill 1986
Blood extraction, pre- and post-dive	Various blood parameters	min.-hours	Kooyman et al. 1980

[a] Example of a source that utilized or described the method/device.

CHAPTER 2

Allometry of diving capacity in air-breathing vertebrates

Abstract

Maximum diving depths and durations were examined in relation to body mass for birds, marine mammals, and marine turtles. There were strong allometric relationships between these parameters ($\log_{10}$-transformed) among air-breathing vertebrates ($r = 0.71$, $n = 111$ for depth; $r = 0.84$, $n = 121$ for duration), although there was considerable scatter around the regression lines. Many of the smaller taxonomic groups also had strong allometric relationships between diving capacity (maximum depth and duration) and body mass. Notable exceptions were mysticete cetaceans and diving/flying birds, which displayed no relationship between maximum diving depth and body mass, and otariid seals, which showed no relationship between maximum diving depth or duration and body mass. Within diving/flying birds, only alcids had a significant relationship ($r = 0.81$, $n = 9$ for depth). The diving capacities of penguins had the highest correlations to body mass ($r = 0.81$, $n = 11$ for depth; $r = 0.93$, $n = 9$ for duration), followed by odontocete cetaceans ($r = 0.75$, $n = 21$ for depth; $r = 0.84$, $n = 22$ for duration) and phocid seals ($r = 0.70$, $n = 15$ for depth; $r = 0.59$, $n = 16$ for duration). Mysticete cetaceans had a strong relationship between maximum duration and body mass ($r = 0.84$, $n = 9$). Comparisons across the various groups indicated that alcids, penguins, and phocids are all exceptional divers relative to their masses and that mysticete cetaceans dive to shallower depths and for shorter periods than would be predicted from their size. Differences among groups, as well as the lack of relationships within some groups, could often be explained by factors such as the various ecological feeding niches these groups exploit or variations in the methods used to record their behavior.

Introduction

Body size is one of the most important factors influencing how animals interact with their environments and it has been shown to be an excellent predictive tool in ecology (Peters 1983; Schmidt-Nielsen 1984). Many life history traits, as well as morphological and physiological traits of animals, have been compared to body size including metabolic rate (Kleiber 1961), brain size (Stahl 1965; Jerison 1970), and the cost of locomotion (Brett 1965; Tucker 1973; Greenewalt 1975). Diving behavior in air-breathing vertebrates is highly variable and is dependent on many physiological constraints such as metabolic rate (Scholander 1940; Butler and Jones 1982), oxygen stores (Scholander 1940; Butler and Jones 1982; Snyder 1983), and the ability to metabolize anaerobically (Hochachka and Somero 1984). Since many of these factors have been associated with body size, diving behavior should also be related to animal size. This has been shown to be the case in interspecific analyses of diving among alcids and penguins (Piatt and Nettleship 1985; Prince and Harris 1988; Burger 1991) and cormorants (Cooper 1986), and hypothesized or shown in single species by numerous studies (e.g. Irving 1939; Gentry et al. 1986b; Costa 1993; Le Boeuf 1994). Diving air-breathing vertebrates represent an interesting set of organisms for allometric analyses because of their enormous variation in mass, ranging from as small as the 0.09 kg diving petrels, *Pelecanoides georgicus*, (Prince and Jones 1992) to the 145,000 kg blue whale, *Balaenoptera musculus*, (Jefferson et al. 1993) which encompasses more than a million fold difference.

The study of diving behavior has evolved dramatically over the last 30 years. Originally, the study of diving simply involved observing the behavior. In the 1930s several experimental studies were conducted that provided many insights into how air-breathing animals dive (e.g. Irving 1939; Scholander 1940). More recently, with remote sensing and recording methods such as sonar (Thompson et al. 1991; Watkins and Tyack 1991; Watkins et al. 1993, Kelly and Wartzok 1996), capillary tubes (Burger and Wilson 1988), and micro-processor controlled time-depth recorders (TDRs) and satellite-linked time-depth recorders

(SLTDRs) (Kooyman 1981; Kooyman et al. 1983a; Stewart et al. 1989; Wildlife Computers, Woodenville, WA, USA), the study of diving has rapidly expanded and diversified. These newer methods have enabled more accurate and rigorous estimates of diving behavior to be made on a broad array of diving animals. The abundance of recent diving research indicated a need for a current review that could address issues such as the comparative diving behavior of various animals and the limitations of different methods used to collect the data.

This paper reviews available data on observed diving capacity (maximum diving depth and duration) for diving/flying birds (alcids, cormorants, ducks, grebes, loons, and petrels), penguins, cetaceans (odontocetes and mysticetes), pinnipeds (phocids, otariids, and odobenids), sirenians (manatees and dugongs), sea otters, and marine turtles, and compares these values to body mass. Allometric equations were derived for maximum depth and duration versus body mass within and across the major groups mentioned above. The intent of this work was to examine the degree to which diving capacity and body size are related and to explain observed discrepancies from a general pattern. It was expected that the various ecological niches exploited by diving air-breathing vertebrates and the methods used to collect the data would introduce real and artificial variances, respectively. This paper was also intended to be a summary of the available literature and will hopefully serve as a catalyst to direct research toward species where there is little, outdated, or no diving information.

Methods

Data were collected from the literature on body mass (kg), maximum diving depth (m), maximum diving duration (min), and methods used for data collection. Original sources of information were used whenever possible. For mass, mean values were used when they were available, but sometimes midpoints of ranges or maximum values were utilized if these were the only measurements presented. For sexually dimorphic species, the mass of the gender for which diving behavior was recorded was used if this was available. If diving data were reported for both sexes within a species and their masses were considerably different, the two genders were treated as separate observations. Maximum diving depth and duration were utilized because means were often not presented and were more highly dependent on the methods used to collect the data and the location and timing of the study.

Allometric relationships were fitted using linear least squares regression of $\log_{10}$-transformed data for both maximum diving depth and duration against $\log_{10}$-mass (SYSTAT 1992). Equations were first fitted to the entire data set. The data were subsequently split into two major groups, marine mammals and birds, and new equations were derived for these groups. Subsets of the marine mammal data were then analyzed for mysticetes, odontocetes, phocids, and otariids. Birds were first subdivided into penguins and flying birds. Differences within the bird group were then further tested by dividing the flying birds into those groups that had sufficient data to allow comparisons (i.e. alcids, cormorants, and ducks). However, these specific bird groups (except for penguins) were not used within the main comparison of all diving vertebrates because of the data's high variability and small sample sizes. Allometric relationships could not be derived for marine turtles as an independent group because there were too little data on too few species, although this would be warranted taxonomically.

The various equations were compared by testing for homogeneity of slopes and subsequently, if appropriate, by analysis of covariance (ANCOVA: SYSTAT 1992) to test for differences in the adjusted means (specifically differences in the means for a fixed $\log_{10}$ mass: Sokal and Rohlf 1995). Significance was assumed at % = 0.05. It must be stressed that the significance test for a regression line does not determine whether a line can be drawn through the data points, but rather whether the slope of that line is significantly different than 0. Therefore, even non-significant regression lines can be compared (Sokal and Rohlf 1995).

Lastly, hypothetical aerobic dive limits (ADLs), defined as the maximum duration of a breath-hold without any increase in plasma lactate levels above resting during or following a dive (Kooyman 1989), and maximum diving depths were calculated as a function of body mass for phocids, birds, otariids, and cetaceans. Predicted standard metabolic rates (SMR) for birds were calculated using SMR = $13.0M_b^{0.729}$ (Aschoff and Pohl 1970; Kooyman 1989) and for marine mammals (once thought to have higher metabolic rates than terrestrial mammals, but recently found not to be significantly different: Lavigne et al. 1986) using SMR = $10.1M_b^{0.75}$ (Kleiber 1961), where M_b equals body mass (kg) and SMR is in ml of O_2 min^{-1}. SMR was then divided by body mass to scale it to a unit mass. Diving metabolic rates were only available for phocids (e.g. Kooyman et al. 1973; Castellini et al. 1992b), so for the other groups, swimming or at sea metabolic rates were used. Diving metabolic rates were assumed to be approximately 2 x SMR for all groups (Eliassen 1960; Kooyman et al. 1973; Baudinette and Gill 1985; Gentry et al. 1986b; Feldkamp et al. 1989; Kooyman 1989; Kooyman and Ponganis 1990; Burger 1991; Castellini et al. 1992b; Costa 1993; Williams et al. 1993), although a second model for otariids was also derived with a higher diving metabolic rate (5 x SMR) as suggested by Kooyman (1988b) and Costa (1993). Several of the above studies suggested that swimming metabolic rate was 2.5 x SMR; however, in agreement with Feldkamp et al. (1989), it was thought that upon submergence, changes occur (e.g. lower heart rate and decreased peripheral blood flow: Castellini 1991) that lower this value. Oxygen consumption for swimming cetaceans (specifically bottlenose dolphins, *Tursiops truncatus*) was found to be near resting levels; however, the resting levels were found to be 2.5 times predicted SMR (Williams et al. 1993).

ADL (min) was calculated as mass specific oxygen stores (ml O_2 kg^{-1}) ÷ mass specific diving metabolic rate (ml O_2 kg^{-1} min^{-1}). Calculated available oxygen stores (ml O_2 kg^{-1}) for the various groups were 58 for birds (specifically measured for king penguins, *Aptenodytes patagonicus*), 60 for phocids (Weddell seals, *Leptonychotes weddellii*), 40 for otariids (northern fur seals, *Callorhinus ursinus*), and 35 for cetaceans (bottlenose dolphins), taken from Kooyman (1989). The resulting equations were $ADL_{Phocids} = 2.97M_b^{0.25}$, $ADL_{Otariids} = 1.98M_b^{0.25}$, $ADL_{Cetaceans} = 1.73M_b^{0.25}$, $ADL_{Birds} = 2.23M_b^{0.271}$, and $ADL_{Otariids(5xSMR)} = 0.79M_b^{0.25}$.

Maximum diving depths (m) were calculated as 0.5 x (ADL x cruising-swim speed) where cruising-swim speed was assumed to be 1.5 m s^{-1} for all groups (Kooyman 1989). The predicted relationships for ADL and maximum diving depth were compared to observed diving capacities.

Results

The data base compiled for diving air-breathing vertebrates is given in Table 2.1. All available diving data were used to calculate regression equations regardless of the method of collection. The original intent was to use only data collected by TDRs and maximum depth gauges (MDGs), but this would have eliminated more than half of the data, preventing most intergroup comparisons. Also, eliminating the non-TDR/MDG data did not markedly change the correlations or slopes for depth or duration versus mass (Table 2.2), although there was a considerable increase in the Y-intercepts. Maximum depth and duration were significantly correlated with mass for the entire data set of air-breathing vertebrates (Figure 2.1, Table 2.2). Maximum depth and duration were also significantly correlated with mass for many of the smaller taxonomic groups, except for depth in mysticetes, otariids, and flying birds and duration in otariids. Within the bird group, penguins and alcids had significant correlations between maximum depth and mass, and only penguins had a significant correlation between maximum duration and mass (Figure 2.2, Table 2.3).

Figure 2.3 shows the regression lines from observed data, depicted in Figure 2.1, along with the predicted relationships calculated for maximum duration (approximated using ADL) and maximum depth. Phocids had the highest predicted diving capacities relative to mass followed by birds, otariids (2 x SMR), and cetaceans. If 5 x SMR was used for otariids, however, this group would have had the lowest predicted diving capacities. The various predicted lines generally overlapped with the overall vertebrate lines, however, the rates at which predicted diving capacities increased with mass were generally lower than for those calculated using the observed data. The small graph on the bottom right of Figure 2.3 is predicted ADL on a linear scale showing how predicted diving capacity increases at a slower rate with increasing mass. It also shows that the influence of mass on ADL is smaller for animals having higher metabolic rates and lower oxygen stores.

Comparisons among the various groups were compromised by small and unequal sample sizes and the large variability of the observations within groups; however, several significant differences were found. The overall tests indicated that the slopes of the regression lines for depth versus mass were homogeneous while the slopes of the lines for duration versus mass were significantly different ($p = 0.038$, $n = 114$). Subsequent overall comparisons of mass adjusted depths indicated that these values were significantly different across groups ($p < 0.001$, $n = 106$). Individual comparisons demonstrated several significant differences. The regression lines for mysticetes, odontocetes, phocids, and otariids were significantly different across many of these groups. Phocids dived significantly deeper and longer than mysticetes ($p = 0.001$, $n = 21$ for mass adjusted depth; $p = 0.001$, $n = 25$ for mass adjusted duration) and odontocetes ($p = 0.003$, $n = 36$ for mass adjusted depth; $p < 0.001$, $n = 38$ for mass adjusted duration), and significantly longer than otariids ($p = 0.002$, $n = 29$ for mass adjusted duration). Odontocetes dived significantly deeper and longer than mysticetes ($p < 0.001$, $n = 27$ for mass adjusted depth; $p < 0.001$, $n = 31$ for mass adjusted duration), and significantly shorter than otariids ($p = 0.007$, $n = 35$ for mass adjusted duration). Mysticetes had a significantly larger slope for duration versus mass than otariids ($p = 0.041$, $n = 22$). Penguins dived significantly deeper (mass adjusted depth) than mysticetes ($p = 0.028$, $n = 17$), odontocetes ($p = 0.006$, $n = 32$), otariids ($p = 0.018$, $n = 24$), and flying birds ($p = 0.018$, $n = 51$), and nearly significantly deeper than phocids ($p = 0.063$, $n = 26$). Penguins also dived significantly longer (mass adjusted duration) than mysticetes ($p < 0.001$, $n = 18$) and odontocetes ($p = 0.001$, $n = 31$), and had a significantly larger slope for duration versus mass than otariids ($p = 0.003$, $n = 22$) and flying birds ($p = 0.006$, $n = 54$). The flying birds had significantly shorter dives (mass adjusted duration) than phocids ($p = 0.001$, $n = 61$) and otariids ($p = 0.004$, $n = 58$), and a significantly smaller slope for duration versus mass than odontocetes ($p = 0.020$, $n = 67$).

Differences within the bird group were seldom significant, which may be due in part to the small sample sizes. Overall tests indicated that the slopes of all of the regression lines were homogeneous while mass adjusted means were significantly different (both p's < 0.001, $n_{Depth} = 42$, $n_{Duration} = 44$). Individual comparisons demonstrated that alcids dived significantly deeper and longer than cormorants ($p = 0.005$, $n = 16$ for mass adjusted depth; $p = 0.027$, $n = 21$ for mass adjusted duration) and ducks ($p < 0.001$, $n = 24$ for mass adjusted depth; $p = 0.014$, $n = 23$ for mass adjusted duration), and significantly deeper than penguins ($p = 0.005$, $n = 20$ for mass adjusted depth). Neither penguins nor cormorants dived significantly deeper than ducks ($p = 0.050$, $n = 26$ and $p = 0.071$, $n = 22$ for mass adjusted depth, respectively), although the differences were nearly significant.

Comparisons of birds and mammals showed that the slopes of the depth and duration versus mass lines for all marine mammals were significantly smaller than those for birds ($p = 0.002$, $n = 108$ for depth; $p = 0.018$, $n = 118$ for duration). However, when mysticete cetaceans were removed from the relationship, no significant differences were observed.

Discussion

Diving capacity increased with body mass in broad interspecific comparisons as was expected. However, this relationship was not significant for some of the smaller taxonomic groups analyzed. The most obvious limitation to an air-breathing animal's diving capacity is its ability to store oxygen and to effectively utilize this limited oxygen supply (Scholander 1940; Butler and Jones 1982; Kooyman 1989; Schmidt-Nielsen 1990). The maximum duration for which an animal can stay submerged is directly related to oxygen storage, rate of oxygen utilization (i.e. metabolic rate and cost of transport), and its anaerobic capacity. The maximum depth to which an animal can dive is only indirectly related to oxygen because it takes time to dive and consequently the deeper an animal dives the longer it has to stay submerged. Speed of locomotion while diving will of course influence this relationship to some degree, although diving depth and duration have been shown to be strongly inter-correlated (e.g. Gentry et al. 1986b; Castellini et al. 1992a; Croll et al. 1992; Bengtson et al. 1993). Larger animals generally have more blood since blood volume (V_b) increases linearly with body mass (M_b), $V_b = M_b^{1.0}$ (Peters 1983; Schmidt-Nielsen 1984). Consequently, they will be able to store more oxygen, although many diving species have been shown to have elevated total oxygen stores (Butler and Jones 1982; Kooyman 1989). Also, larger animals have a metabolic advantage in that metabolic rate (MR) increases only 0.75 times as fast as body mass, $MR = M_b^{0.75}$ (Kleiber 1961), and therefore larger animals have lower mass specific metabolic rates than their smaller counterparts. A lower metabolic rate requires less energy expenditure and therefore a slower utilization of oxygen stores. Since diving capacity is related to the need for oxygen and larger animals need less oxygen per unit mass, it would be expected that larger animals should be able to dive longer and consequently deeper than smaller animals. This is substantiated in that the ADL increases with mass (Hochachka and Somero 1984; Gentry et al. 1986b; Kooyman 1989; Costa 1993; Figure 2.3 - *this study*).

Another factor that influences an animal's diving performance is its ability to function beyond its ADL (i.e. anaerobically). The difficulty here is to deal with the end products of anaerobic metabolism (e.g. lactic acid). Some animals have a high tolerance for these end products while others are able to recycle or clear the waste products (Hochachka and Somero 1984). It has been shown that an increase in size also increases an animal's ability to function anaerobically and hence, increases potential maximum diving time (Hochachka and Somero 1984; Hudson and Jones 1986). Anaerobic metabolism may be fairly unimportant when considering "normal" or mean diving behavior since it is considerably less efficient than aerobic metabolism (Kooyman et al. 1983b; Kooyman 1989). The lactic acid produced as a result of anaerobic metabolism is cleared very slowly, therefore anaerobic dives require longer surface time than completely aerobic dives. However, this less efficient metabolism becomes quite important when considering potential or maximum capacity.

Finally, a direct limitation to the depth to which an animal can dive is hydrostatic pressure. Complications due to pressure include decompression sickness (the bends), high pressure nervous syndrome (HPNS), mechanical effects of pressure on gas filled spaces, and problems associated with gases at high pressures (e.g. nitrogen narcosis and oxygen toxicity). Several reviews on this subject have been presented so it will only be mentioned briefly here (e.g. Ridgway 1986; Kooyman 1988a, 1989; Castellini 1991). Some animals have an unlimited capacity to tolerate the mechanical distortions caused by compression (Kooyman 1988a). In seals, lung and chest compliance are unlimited (Kooyman 1988a). This eliminates the need for intrathoracic pooling of blood to compensate for changes in volume, as would be the case for humans. Problems with gases (e.g. the bends and nitrogen narcosis) are avoided by a great reduction in gas exchange between the lungs and blood (Kooyman 1988a, 1989). How other problems, such as HPNS, are dealt with remains a mystery (Kooyman 1989; Castellini 1991). Research has revealed that pressure limitations are not a major factor controlling the diving depths attained by some deep diving seals (Castellini 1991) which is indicated by the incredible depths attained by many of these animals. Much of this work has been performed on marine mammals and considerably less is known for birds and reptiles.

Overall

The diving depths and durations attained by diving vertebrates are related to body mass. Fifty per cent of the variability (r^2) observed in depth and 71% of the variation in duration was attributed to mass. However, there was considerable scatter of depth and duration values around the regression lines (Figure 2.1) indicating that factors other than mass also affect the diving capacities of these animals. Diving capacities recorded for cetaceans and flying birds were highly variable. For both cetacean suborders, this may reflect the range of different methods of data collection. Variability among flying birds may represent the inappropriateness of lumping several different bird families into one group, as well as differences in feeding ecology, methods of data collection, and locations of study sites.

Comparisons of diving capacity versus mass for marine mammals and birds indicated that maximum diving depth and duration in birds increased faster with an increase in mass than for marine mammals. However, when the shallow and short diving mysticete cetaceans were excluded from the comparisons, there were no discernable differences in the diving capacities of these two groups relative to mass. This suggests that similar physiological and ecological factors are affecting the diving behavior of these two groups.

The relationships between diving capacity and mass found here were generally in agreement with interspecific comparisons previously conducted. Burger (1991) found a similar relationship in that larger alcids and penguins had deeper maximum diving depths than smaller species. This was not surprising, as that study and this work used much of the same data. The relationship between diving duration and mass for cormorants in Cooper's study (Cooper 1986) was stronger than that found here (for birds diving in water greater than 2 m). However, Cooper had much larger samples sizes, having used values recorded for the same species at different locations as separate observations. Irving (1939) suggested that the exceptional diving capacities of large whales may be due to their large size, but his comparative analysis showed a different result. Unlike the results here, Irving found that breath-hold endurance results acquired experimentally from diving animals ranging in size from 0.6 kg muskrats, *Ondatra zibethicus*, to 100 kg seals demonstrated no relationship between endurance and size. However, Irving's duration values were usually recorded from forced submersions which can often be considerably different from those naturally observed.

Predicted versus observed

The various predicted relationships generally overlapped with the overall observed lines for vertebrates (Figure 2.3); however, the rates at which predicted diving capacity increased with mass were generally lower than for those calculated from the observed data. This may be due to underestimation of many of the flying birds' observed diving capacities, causing the slopes of the overall lines to be steeper. It may also be due to an overestimation of the swimming speeds of smaller divers (e.g. birds). Smaller divers would not be expected to swim as fast as larger ones because drag increases with surface area (L^2), while power increases with muscle volume (L^3). This can be seen in little penguins, *Eudyptula minor*, (Baudinette and Gill 1985) and pochard, *Aythya ferina*, and tufted ducks, *Aythya fuligula*, (Carbone 1995; C. Carbone *personal communication*) which have estimated cruising-swim speeds of 0.7 to 0.8 m s^{-1}. If the smaller divers swim slower, their predicted maximum depths would be shallower and consequently the slope of the predicted relationship would be greater (i.e. more similar to the observed relationship). Lastly, since the predictive models developed here only incorporated aerobic metabolism and not anaerobic metabolism (which is important when considering maximum capacities), the rates of increase may have been underestimated. This is substantiated by the results of Hudson and Jones (1986) and the calculations of Hochachka and Somero (1984) who found that during forced submersions in ducks, the rate of increase in maximum diving time relative to mass is higher when considering anaerobic + aerobic metabolism as compared to just aerobic modes.

Not having incorporated anaerobic metabolism into the predictive models may also explain why many of the observed capacities (at least for duration) were above predicted levels for the corresponding groups. Mysticete cetaceans and flying birds were exceptions, probably as a result of the methods used to record their behavior, the locations of the studies, or the ecological niches occupied by these animals. For depth, observed relationships generally fell close to predicted values. However, had anaerobic metabolism been included in the models, most of the observed values would have fallen below predicted relationships. This would be expected since the observed relationships only represent minimum diving capacities.

Finally, it must be noted that these predictive models are quite crude and rely on many assumptions. If any of the parameters (diving metabolic rate, oxygen stores, or cruising speed) were changed, the relationships would change markedly (e.g. the difference between otariid diving capacity calculated with diving MR equal to 2 or 5xSMR). Many studies have found considerably higher estimates for swimming MRs, ranging from 4 to 10xSMR (e.g. Nagy et al. 1984; Chappell et al. 1993a, b; Costa 1993) and others have estimated much slower cruising-swim speeds, 0.7 to 0.8 m s^{-1} (e.g. Baudinette and Gill 1985; Carbone 1995).

Cetaceans

Cetaceans range dramatically in size from small river dolphins (e.g. Franciscana, *Pontoporia blainvillei*, weighing 34 kg) to the largest animals to have ever lived (i.e. blue whale weighing 145,000 kg and up to 33 m in length) (Jefferson et al. 1993). Mysticetes had the largest mean body mass in this study (55,000 kg), followed by odontocetes (3,200 kg), phocids (610 kg), marine turtles (140 kg), otariids (94 kg), penguins (6.1 kg), and flying birds (1.3 kg). On the basis of body size it would be expected that mysticete and odontocete cetaceans should be able to dive longer and deeper than all other groups because they can store more oxygen and have lower mass specific metabolic rates. Even though the sperm whale, *Physeter catodon*, is one of the longest and deepest divers in this study (138 min and 3000 m: Clarke 1976; Watkins et al. 1985), as well as being one of the largest animals (51,700 kg: Jefferson et al. 1993), both odontocete and mysticete cetaceans were surpassed by the considerably smaller phocids in average diving capacity. Further, the plots of duration and depth versus mass showed that mysticetes always fell below the overall regression lines for both maximum duration and depth. These plots and the regression comparisons also suggest that if penguins were as large as mysticetes or even odontocetes, they would dive much longer and deeper. The plots for predicted diving capacity (Figure 2.3) also support this suggestion. It is interesting to note that an 80 kg human (holding their breath) fits well within the overall regression lines, with a maximum depth of 125 m using a weighted sled (Matthews 1996) and a duration of 13.5 min anchored in a pool after hyperventilating with oxygen (McFarlan and McWhirter 1990). The duration record without supplementary oxygen was 5.5 minutes (Lavigne and Kovacs 1988). However, these amazing feats were accomplished under highly artificial conditions.

There are three possible reasons why cetaceans do not dive as long and as deep as would be expected: 1) this Order may have physiological and morphological limitations relative to some of the other groups, 2) the methods used to measure their diving behavior may underestimate their capacity, or 3) cetaceans may exploit resources that are located at shallower depths than some of the other groups and therefore may not need to dive as deep or for as long. The first point seems unlikely since several cetaceans have exceptional diving capacities (e.g. sperm whales and bottlenose whales, *Hyperoodon sp.*). However, considering total body oxygen stores, cetaceans have considerably less oxygen available per unit mass than either penguins or phocids (Kooyman 1989), which would limit their potential diving capacity (see Figure 2.3 for a schematic representation of this concept).

Some of the cetaceans, specifically the mysticetes, seem to have even more limited diving capacities than would be predicted from oxygen stores. This is perhaps where data collection methods and feeding ecology greatly affect observed diving capacity. Unlike most of the pinniped and penguin diving data, which have been measured with modern depth and duration recorders, much of the cetacean data were inferred from feeding ecology or simply observed directly. Although these methods have provided much insight into the behavior of cetaceans and other groups, they are far less accurate. Depth and duration recorders allow thousands of dives (> 50,000 dives: Hindell et al. 1991b; Schreer and Testa 1995, 1996) for individual species to be recorded over extended periods of time (> 8 months: Testa 1994; Schreer and Testa 1996), while much of the cetacean data were single records or just a few observations collected on one or a few occasions. Also, although probable feeding depths give a potential maximum depth for an animal, these values are probably better estimates of mean diving depth. In many studies using depth recorders, it has been found that a species has preferred depths that are associated with preferred prey, but that the maximum depths reached by the species far exceed these depths (e.g. Hindell et al. 1991b; Prince and Jones

1992; Schreer and Testa 1996). Therefore, many of the values representing cetacean diving capacity are probably underestimates.

The shallow maximum depths and short maximum durations observed among the mysticetes may also be an accurate reflection of their feeding ecology. Many of the largest animals in this study (e.g. blue, bowhead - *Balaena mysticetus*, fin - *Balaenoptera physalus*, and right whales - *Eubalaena sp.*) feed primarily on planktonic or micronektonic crustaceans or small pelagic fish (Gaskin 1982) usually found between 100 and 500 m (Parsons et al. 1984). The relatively shallow depths of the mysticete's prey eliminates their need to dive to great depths. Also, since it takes less time to reach these depths, durations do not need to be as long to forage efficiently (i.e. net energy gain). However, since surfacing takes away from foraging time, diving duration should be maximized for increased efficiency. This may explain why maximum duration is more highly correlated with mass than maximum depth in mysticetes (r = 0.84 versus 0.07). It must be noted that this argument is only valid when dives are shorter than the ADL so as not to cause an increase in plasma lactate concentrations and consequent increase in surface clearance time. To complicate this issue even further, Kramer (1988) and Houston and Carbone (1992) argue that surface time increases with diving time even before reaching the ADL because of diminishing returns in oxygen loading (i.e. it takes longer to load the last few ml of oxygen prior to achieving maximum loading) and that this also influences the duration of dives.

Marked differences in feeding ecology may also explain the differences in observed diving capacity for the two cetacean groups. That is, mysticetes feed on relatively shallow prey while odontocetes feed on prey such as fish and squid which live at greater depths (Gaskin 1982).

Pinnipeds

Diving behavior of pinnipeds as a group could be predicted with reasonable accuracy based on body mass, although there were some differences displayed between Families.

Phocid diving capacity was significantly correlated with mass while otariid diving was not. Additionally, phocid observations generally fell above the overall vertebrate line while otariids generally fell nearer to this line indicating that phocids dive deeper and longer relative to body mass compared to otariids. The mass adjusted mean durations for these two groups also support this conclusion with phocids diving significantly longer. Phocids are generally larger than otariids so it would be expected that they would dive deeper and longer. However, they seem to excel further in diving capacity than expected based solely on this criterion. Phocids have larger blood volumes, higher concentrations of hemoglobin for a given blood volume, and more myoglobin per unit of muscle than otariids which allows them to store more oxygen and hence dive deeper and longer (Snyder 1983; Kooyman 1989; Reed et al. 1994). Phocids also have lower metabolic rates while diving due in part to slower swim speeds (Kooyman 1988b, Costa 1993), which decreases their rate of oxygen consumption. This can be seen in Figure 2.3 with phocids (2 x SMR) having considerably higher predicted diving capacities relative to mass than otariids (5 x SMR).

The comparisons of observed data are preliminary in that the available data does not include large otariids. Most studies of otariid diving behavior have focused on females (e.g. Gentry and Kooyman 1986) which are considerably smaller than males. The inclusion of males may increase the observed similarity between otariids and phocids. This suggestion is substantiated by the depth values from the larger species (e.g. California - *Zalophus californianus californianus*, Hooker's - *Phocarctos hookeri*, and Steller sea lions - *Eumetopias jubatus*), all of which fit well with the lower end of the phocid line.

The otariid duration data are a bit more difficult to interpret. Perhaps their higher swim speeds allow them to reach depths comparable to the smaller phocids, but their physiological limitations (less oxygen and higher metabolic rates) prevent them from staying submerged as long. It has also been suggested that the distribution of prey (Feldkamp et al. 1989) and foraging economics (Gentry et al. 1986b) may be primary factors determining observed diving capacity in otariids. That is, the observed maximums do not reflect true capacity. Their smaller size and physiological limitations relative to phocids, may make it more economical for them to forage on smaller, shallower, and perhaps easier to catch prey while phocids can exploit larger, deeper, and more energy rich prey. This would explain their more limited observed diving capacity relative to phocids, as well as the lack of any relationship between diving capacity and mass.

The walrus, *Odobenus rosmarus*, is a good example of how ecology can strongly affect diving behavior. It is the third largest pinniped in this study, but one of the shallowest and shortest divers. It is thought that walruses may be able to dive to greater depths than the maximums recorded, but have little reason to do so because of the abundance of their benthic prey in shallow waters (Fay and Burns 1988).

Birds

Penguins dive deeper than flying birds (when pooling all flying birds into one group) and their diving duration increases more rapidly with increasing mass as compared to flying birds (i.e. deeper mass adjusted depth and larger slope for duration versus mass). However, the penguin equations were strongly affected by the exceptional depths and durations recorded for emperor, *Aptenodytes forsteri*, and king penguins. Penguin diving capacities had the highest correlations to mass of all the groups examined, indicating that mass is an excellent predictive tool for penguin diving behavior. Some of the differences in diving capacity between penguins and flying birds are likely due to data collection methods. Like the cetacean data, much of the flying bird data were manually observed over short periods of time while most of the penguin data were collected by depth or duration recorders, providing more accurate estimates. Also, lumping all flying birds into one group is perhaps inappropriate and may be a primary reason for the weak and non-significant relationships.

The separate analysis of just the bird data provided more insight into avian diving capacities. Ducks appear to be relatively poor divers, but this may simply be due to the methods of data collection or the shallow inshore water depths of many of the study sites resulting in shorter, shallower dives (e.g. Dewar 1924). Alcids, unlike the other flying bird families, had a strong correlation between maximum depth and mass. The results also indicated that not only do alcids dive deeper and longer than cormorants and ducks, but in agreement with Burger (1991), if they were as big as penguins, they would be able to dive deeper. This is surprising as it would be expected that penguins would be more capable divers than flying birds because of their more highly evolved "aquatic" body morphology and concomitant loss of flight. If the exceptional depths of common and thick-billed murres are excluded, most of the alcid depth values fit well with the extension of the penguin depth line. It has been suggested that large wing-propelled diving/flying birds (i.e. larger alcids) may be approaching the threshold at which a further increase in size would result in a flightless condition (Stonehouse 1975; Piatt and Nettleship 1985). Stonehouse (1975) estimated that wing-propelled diving birds can retain the ability to fly only if they weigh less than 1 kg. Since some alcids may be nearing this condition, it would be expected that their diving capacities would be similar to those of smaller penguins. This can be seen by splitting the birds into predominantly wing-propelled (alcids, penguins, and petrels) and predominantly foot-propelled (ducks, cormorants, grebes, and loons) categories. The values for wing-propelled diving birds are located almost entirely above the overall bird lines for depth and duration versus mass while almost all of the values for foot-propelled birds lie below these lines. This could indicate that wing-propulsion is a more highly evolved or adaptive characteristic for an aquatic life style, although the deep depths achieved by several of the foot-propelled cormorants challenge this conclusion.

Marine turtles

Although there were too few turtle observations to calculate allometric equations, it is obvious that these animals are exceptional divers. Other reptiles or amphibians were not included in this study because many of these animals can reduce their metabolic rates to such low levels that they can stay submerged for days, weeks, and even longer (Butler and Jones

1982). The temperature and oxygen tension of the water also affects the ability of these animals to stay submerged (Butler and Jones 1982). Therefore, mass specific relationships comparable to mammals and birds, which have much higher metabolic rates, even when at rest, would not be expected. Marine turtles were included in this study for the sake of interest and because they have maximum depth and duration values within the ranges of those found for mammals and birds. However, since these animals also have the ability to undergo extended submergences at low temperature (e.g. many weeks for green turtles, *Chelonia mydas*, and loggerhead turtles, *Caretta caretta,* during winter: Butler and Jones 1982), comparisons must be very tentative. Like most marine mammals, marine turtles are able to lower their metabolic rate (within certain organs) when diving (Hochachka and Somero 1984) decreasing oxygen utilization and increasing potential diving duration. In marine mammals this results in hypometabolism in comparison to exercising levels, but still represents metabolic rates above those for resting. However, turtles can lower their overall metabolism below resting levels, in part because of lower body temperatures (Hochachka and Somero 1984; Kooyman 1989). Additionally, marine turtles excel in their ability to metabolize anaerobically (Hochachka and Somero 1984; Kooyman 1989). Marine turtles have large glycogen stores in their tissues as well as having efficient fermentation pathways (Hochachka and Somero 1984) which increases their potential for long duration dives and therefore, deep depths. Along with these adaptations, marine turtles may have an evolutionary advantage for diving in that they have relatively smaller and less complex brains than mammals (Robin 1973). The smaller brain size decreases oxygen utilization, and the lack of complexity may allow marine turtles to tolerate longer periods of anoxia (Robin 1973; Hochachka and Somero 1984). Both of these characteristics would increase potential diving capacity.

Conclusions

Interspecifically, the diving capacities of air-breathing vertebrates were strongly influenced by body mass, although this relationship was not always present when smaller taxonomic groups were analyzed. Differences among groups, as well as the lack of relationships in some groups, could often be explained by factors such as the various ecological niches these groups exploit or the methods used to record their behavior. The addition of data from work currently being conducted and future work on diving behavior of air-breathing vertebrates will undoubtedly improve our understanding of the relationships explored in a preliminary fashion in this paper. Better comparative data bases are likely to provide stronger relationships among some groups of diving vertebrates and provide clearer explanations of observed variance in others. Also, additional data may allow interspecific allometric analyses to be conducted with mean diving values or perhaps dive shapes (e.g. Hindell et al. 1991b; Schreer and Testa 1995, 1996; Chapter 3; Chapter 4) which may better represent the natural diving behavior of air-breathing vertebrates.

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Table 2.1. Diving data and masses for air-breathing vertebrates. Adult body mass, maximum diving depth, maximum diving duration, number of observations, and methods used for data collection.

Common name[a]	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n[b]	Methods[c]	Sources[d]
Whales, Dolphins, and Porpoises	Order **Cetacea**						
Baleen	Suborder **Mysticeti**						
Blue whale	*Balaenoptera musculus*	145000	100	50	-	Feeding; Line	56; 48; 55
Right whale	*Eubalaena sp.*	81600	184	50	-	Sonar; -	56; 44; 107
Bowhead whale	*Balaena mysticetus*	79400	300	80	-	RT; -	56; 68; 55
Fin whale	*Balaenoptera physalus*	68000	500	30	-	Line; -	56; 48; 99
Gray whale	*Eschrichtius robustus*	31800	170	26	-; 11000	TDR; RT	56; 32; 49
Humpback whale	*Megaptera novaeangliae*	31700	148	21	300; 5000	Sonar; Obs.	56; 27
Sei whale	*Balaenoptera borealis*	27200		15	-	Obs.	56; 40
Bryde's whale	*B. edeni*	20400		20	-	Obs.	56; 23
Minke whale	*B. acutorostrata*	12700		17	-	Net	56; 59
Toothed	Suborder **Odontoceti**						
Sperm whale (%)	*Physeter catodon*	51700	3000[e]	138	-	Feeding; Sonar	56; 13; 111
Killer whale (%)	*Orcinus orca*	10000	260	15	100; -	Trained; -	56; 6
Arnoux's beaked whale	*Berardius arnuxii*	7500[f]		70	70	Obs.	56; 53
Bottlenose whale	*Hyperoodon sp.*	4500[f]	1000	120	-	Line; -	56; 4; 55
Cuvier's beaked whale	*Ziphius cavirostris*	3000		30	-	-	56; 51
Pilot whale (%)	*Globicephala sp.*	2000	610	20	300; -	Trained; -	56; 6
False killer whale	*Pseudorca crassidens*	2000	300		-	-	56; 107
Narwhal	*Monodon monoceros*	1600	1000	20	>600	TDR	56; 50
Beluga whale	*Delphinapterus leucas*	1600	1000	25	-	TDR	56; 74
Bottlenose dolphin	*Tursiops truncatus*	650	535	12	-	Trained; Obs.	56; 96; 48
Pygmy sperm whale	*Kogia breviceps*	400		12	-	RT	56; 54
Fraser's dolphin	*Lagenodelphis hosei*	210	500		-	Feeding	56; 97
Dwarf sperm whale	*Kogia simus*	210	300		-	Feeding	56; 34
Dall's porpoise	*Phocoenoides dalli*	200	180		-	Feeding	56; 81
Irrawaddy dolphin	*Orcaella brevirostris*	190		12	-	Obs.	75; 75
Baiji	*Lipotes vexillifer*	180		2	-	Obs.	56; 90
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	180	214	6	100; -	Trained	56; 46; 96
Rough-toothed dolphin	*Steno bredanensis*	150	70	15	-	Line-hp; Obs.	56; 112; 79

Table 2.1 (*continued*).

Common name[a]	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n[b]	Methods[c]	Sources[d]
Atlantic spotted dolphin	*Stenella frontalis*	143	60	5	-	TDR	56; 121
Common dolphin	*Delphinus delphis*	135	258	5	-	TDR	56; 31; 96
Pantropical spotted dolphin	*Stenella attenuata*	120	100	5	-	TDR	56; 102
Southern right whale dolphin	*Lissodelphis peronii*	116	300	7	-	Feeding; Obs.	56; 1; 22
Northern right whale dolphin	*L. borealis*	115	250	6	-	Feeding; Obs.	56; 34; 71
Ganges River dolphin	*Platanista gangetica*	108		3	-	Obs.	56; 95
Spinner dolphin	*Stenella longirostris*	77	250	3	-; 500	Feeding; Obs.	56; 34; 122
Harbor porpoise	*Phocoena phocoena*	60	226	12	8000; -	TDR; Exp.	56; 114; 48
Vaquita	*P. sinus*	35[f]	30		-	Feeding	56; 34
Seals, fur seals, sea lions, and walruses	Suborder **Pinnipedia**						
True seals	Family **Phocidae**						
Southern elephant seal (%)	*Mirounga leonina*	4000	1130	89	25000	TDR	56; 52
Northern elephant seal (%)	*M. angustirostris*	2000	1529	77	35000	TDR	56; 25
Northern elephant seal (&)	*M. angustirostris*	600	1250	62	20000	TDR	56; 72
Southern elephant seal (&)	*M. leonina*	600	1256	120	25000	TDR	56; 52
Weddell seal (&)	*Leptonychotes weddellii*	425	741	82	>20000	TDR	56; 106; 12
Bearded seal (&)	*Erignathus barbatus*	360	250	25	100000	TDR	56; 43
Hooded seal (%)	*Cystophora cristata*	350	1000[g]	52	60000	TDR	56; 35
Bearded seal (%)	*Erignathus barbatus*	260	250	20	100000	TDR	56; 43
Crabeater seal	*Lobodon carcinophagus*	250	528	11	80000; 8000	TDR	56; 87; 2
Grey seal (%)	*Halichoerus grypus*	240	268	23	55000; -	TDR; -	56; 47; 70
Hooded seal (&)	*Cystophora cristata*	220	1000[g]	52	60000	TDR	56; 35
Harp seal (&)	*Phoca groenlandica*	120	370	16	-	TDR; -	56; 86; 70
Spotted seal	*P. largha*	100	100	10	>20000	TDR	56; 37
Harbor seal	*P. vitulina*	100	508[g]	28	500000; -	TDR; Exp.	56; 105; 99
Baikal seal	*P. sibirica*	85		68	-	Exp.	56; 89
Ringed seal	*P. hispida*	80	222[h]	26	10000	Sonic trans.	56; 60
Eared seals	Family **Otariidae**						
Steller sea lion (&)	*Eumetopias jubatus*	270	424	16	100000	TDR	56; 105

Table 2.1 (*continued*).

Common name[a]	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n[b]	Methods[c]	Sources[d]
Hooker's sea lion (&)	*Phocarctos hookeri*	160	474[g]	12	20000; -	TDR	56; 38; 42
South American sea lion (&)	*Otaria byronia*	140	112[h]	6	7000	TDR	56; 113
California sea lion (&)	*Zalophus californianus californianus*	110	482	15	>1500; >1000	TDR; RT	56; 78; 88
Australian sea lion (&)	*Neophoca cinerea*	105	92	6	-	TDR	56; 17
Galapagos sea lion (&)	*Z. californianus wollebaeki*	80	186	6	3000	TDR	56; 66
South African fur seal (&)	*Arctocephalus pusillus*	80	204	8	1000	TDR	56; 63
Northern fur seal (&)	*Callorhinus ursinus*	50	207	8	2000	TDR	56; 41
Guadalupe fur seal (&)	*Arctocephalus townsendi*	50	82	18	>1000	TDR	56; 39
South American fur seal (&)	*A. australis*	45	170	7	1000	TDR	56; 108
New Zealand fur seal (&)	*A. forsteri*	40	238	11	700	TDR	56; 76
Antarctic fur seal (&)	*A. gazella*	35	181	10	60000	TDR	56; 7
Galapagos fur seal (&)	*A. galapagoensis*	30	115	8	3000	TDR	56; 65
Walruses	Family **Odobenidae**						
Walrus (%)	*Odobenus rosmarus*	1900	100[e]	13	-; 1500	Feeding; TDR	56; 33; 116
Sirenians	Order **Sirenia**						
West Indian Manatee	*Trichechus manatus*	1600		16	-	-	56; 55
Dugong	*Dugong dugon*	400		8	-	Obs.	56; 85
Sea otters	Family **Mustelidae**						
Sea otter	*Enhydra lutris*	40	97	4	-	Net; Obs.	56; 83; 61
Marine Turtles	Families **Cheloniidae** and **Dermochelyidae** (Leatherbacks)						
Leatherback	*Dermochelys coriacea*	360	1300	37	5000	TDR	94; 30
Loggerhead	*Caretta caretta*	125	90	99	-	RT	94; 104
Kemp's ridley	*Lepidochelys kempii*	41		167	500	RT	94; 77
Olive ridley[i]	*L. olivacea*	38	290		1	Sub.	62; 69
Birds	Class **Aves**						
Penguins	Family **Spheniscidae**						
Emperor	*Aptenodytes forsteri*	22.0	534	16.0	16000	TDR	8; 65
King	*A. patagonicus*	13.0	304	8.0	>10000	TDR	8; 67

Table 2.1 (*continued*).

Common name[a]	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n[b]	Methods[c]	Sources[d]
Yellow-eyed	*Megadyptes antipodes*	5.5	56		40	MDG	103; 103
Gentoo	*Pygoscelis papua*	5.5	156	4.5	16000	TDR	8; 118
Adélie	*P. adeliae*	5.0	175	4.0	30; 600	MDG; TDR	8; 115; 82
Macaroni	*Eudyptes chrysolophus*	4.6	115	6.3	5000	TDR	8; 21
Humboldt	*Spheniscus humboldti*	4.2	80	2.7[j]	-; 18	MDG; Obs.	8; 120; 29
Magellanic	*S. magellanicus*	3.5	90		60	MDG	8; 101
Chinstrap	*Pygoscelis antarctica*	3.5	121	3.0	12000	TDR	8; 3
Jackass	*Spheniscus demersus*	3.2	130	4.0	15; 50	MDG; Obs.	8; 119
Galapagos	*S. mendiculus*	2.0[f]		1.3	-	Obs.	24; 5
Little	*Eudyptula minor*	1.2	69		30	MDG	8; 80
Loons	Family **Gaviidae**						
White-billed	*Gavia adamsii*	5.2	27	1.5	-	Net; Obs.	24; 26; 98
Common	*G. immer*	3.6	61	2.0	-	Net; Obs.	24; 100; 26
Black-throated	*G. arctica*	2.4	6[e]	2.0	35; -	Obs.	24; 26; 18
Red-throated	*G. stellata*	1.7	9[e]	1.5	200; -	Obs.	24; 26
Cormorants	Family **Phalacrocoracidae**						
White-breasted	*Phalacrocorax carbo lucidus*	2.9		0.9	50	Obs.	16; 16
Japanese	*P. capillatus*	2.8	45	2.4	10000	TDR	110; 110
Great	*P. carbo*	2.3	37	1.2	-; 460	Net; Obs.	24; 26
Blue-eyed	*P. atriceps*	2.2	125	5.2	-; 700	MDG; TDR	8; 8; 20
Pelagic	*P. pelagicus*	2.0		1.0	40	Obs.	24; 28
Shag	*P. aristotelis*	2.0	80	1.7	-; 150	Net; Obs.	24; 45; 73
Bank	*P. neglectus*	1.8	70	1.1	2; 160	MDG; Obs.	24; 8; 15
Guanay	*P. bougainvillii*	1.7[f]		1.3[j]	16	Obs.	24; 29
Red-legged	*P. gaimardi*	1.3		1.0[j]	70	Obs.	16; 29
Cape	*P. capensis*	1.2	92		7	MDG	24; 8
Crowned	*P. coronatus*	0.8	11	1.0	2; 140	MDG; Obs.	24; 8; 117
Pygmy	*P. pygmaeus*	0.7		0.7	8	Obs.	24; 18
Reed	*P. africanus*	0.6		0.7	30	Obs.	16; 16
Ducks	Family **Anatidae**						
Common eider	*Somateria mollissima*	2.1	55	0.8	-; 300	Net; Obs.	24; 26
King eider	*S. spectabilis*	1.8	45[e]	1.4	-; 8	Feeding; Obs.	24; 26; 18
Goosander	*Mergus merganser*	1.5	4	2.0	100; -	Obs.	24; 26
Velvet scoter	*Melanitta fusca*	1.5	30[e]	3.0	-	Obs.	24; 26
Tufted	*Aythya fuligula*	1.2	11	1.0	-	Net; Obs.	24; 84; 26
Canvasback	*A. valisineria*	1.2	10[e]		-	Obs.	24; 26

Table 2.1 (*continued*).

Common name[a]	Scientific name	Mass (kg)	Depth (m)	Duration (min)	n[b]	Methods[c]	Sources[d]
Scaup	*A. marila*	1.1	6	1.0	150; -	Obs.	24; 26
Red-breasted merganser	*Mergus serrator*	1.1	9[e]	2.0	8; -	Obs.	24; 28; 26
Common scoter	*Melanitta nigra*	1.0	30[e]	0.8	-	Obs.	24; 18; 26
Pochard	*Aythya ferina*	1.0	6[h]	1.0	100; -	Obs.	24; 11; 26
Surf scoter	*Melanitta perspicillata*	1.0	12[e]	1.1	-; 20	Obs.	24; 26; 28
Common goldeneye	*Bucephala clangula*	0.9	9	1.0	-	Obs.	24; 84; 26
White-headed	*Oxyura leucocephala*	0.7	2[e]	0.7	>50	Obs.	24; 18
Smew	*Mergus albellus*	0.7	4[e]	0.8	60; -	Obs.	24; 18
Long-tailed	*Clangula hyemalis*	0.7	61	1.2	-	Net; Obs.	24; 100; 26
Grebes	Family **Podicipedidae**						
Red-necked	*Podiceps grisegena holboellii*	1.0		1.0	-	Obs.	18
Great crested	*P. cristatus*	1.0	30	0.9	160; -	Net; Obs.	24; 18
Western	*Aechmophorus occidentalis*	0.9		1.2	70	Obs.	24; 36
Horned	*Podiceps auritus*	0.4	4	1.2	150; -	Obs.	24; 26; 18
Black-necked	*P. nigricollis*	0.3	6[e]	0.8	-	Obs.	24; 18
Little	*Tachybaptus ruficollis*	0.2	2	0.4	100	Obs.	24; 26
Alcids	Family **Alcidae**						
Common murre	*Uria aalge*	0.9	180	3.4	12000; 250	Net; RT	8; 91; 109
Thick-billed murre	*U. lomvia*	0.9	210	3.7	60; 1000	MDG; TDR	8; 19
Razorbill	*Alca torda*	0.7	140	0.9	1; 450	Sub.; Obs.	8; 58; 26
Rhinoceros auklet	*Cerorhinca monocerata*	0.5	65	1.1	15; 3	MDG; Exp.	8; 8; 14
Atlantic puffin	*Fratercula arctica*	0.5	68	1.9	10; 450	MDG; RT	8; 10; 109
Pigeon guillemot	*Cepphus columba*	0.5	30	1.1	2; 4	MDG; Exp.	8; 8; 14
Black guillemot	*C. grylle*	0.4	50	1.3	40; -	Net; Obs.	8; 91; 26
Cassin's auklet	*Ptychoramphus aleuticus*	0.2	43	2.0	20; 10	MDG; Obs.	57; 9; 26
Dovekie	*Alle alle*	0.2	35	1.1	-	-	8; 92; 26
Diving-Petrels	Family **Pelecanoididae**						
South Georgia	*Pelecanoides georgicus*	0.1	49		6	MDG	24; 93

[a] Gender indicated in parentheses where appropriate.

[b] Approximate number of observations, usually dives (depth and duration, respectively). A dash represents that the number of observations was not reported or that depth was estimated from feeding. For MDGs, each observation represents many dives. A single value is listed if n was equal for both depth and duration, or if only one parameter was reported.

Table 2.1 (*continued*).

[c] Methods for measuring depth and duration are listed, respectively. If the methods for measuring depth and duration are the same, only one method is listed. Exp., forced dives, usually restrained in various types of tanks used for diving or simulating diving; Feeding, estimated from known prey depths; Line, estimated from amount of rope let out, allowing for angle of descent; Line-hp, line with hydrophone attached; MDG, maximum depth gauge (e.g. capillary tubes); Net, caught or tangled in net, trap, or on hook; Obs., direct observations (e.g. timed with watch); RT,
radio tag; Sonar, echo sounding; Sonic trans., sonic transmitter; Sub., observed from submarine; TDR, time-depth recorder or satellite-linked time-depth recorder; Trained, trained free-swimming dives; -, not reported.

[d] Sources for mass followed by diving capacity are listed. If sources for depth and duration are different, sources for mass, then depth, then duration are listed. 1) Baker 1981; 2) Bengtson and Stewart 1992; 3)Bengtson et al. 1993; 4) Benjaminsen and Christensen 1979; 5) Boersma 1976; 6) Bower and Henderson 1972; 7) Boyd and Croxall 1992; 8) Burger 1991; 9) Burger and Powell 1990; 10) Burger and Simpson 1986; 11) Carbone et al. 1996; 12) Castellini et al. 1992a; 13) Clarke 1976; 14) Cody 1973; 15) Cooper 1985; 16) Cooper 1986; 17) Costa et al. 1989; 18) Cramp and Simmons 1977; 19) Croll et al. 1992; 20) Croxall et al. 1991; 21) Croxall et al. 1993; 22) Cruickshank and Brown 1981; 23) Cummings 1985; 24) del Hoyo et al. 1992; 25) DeLong and Stewart 1991; 26) Dewar 1924; 27) Dolphin 1988; 28) Dow 1964; 29) Duffy 1983; 30) Eckert et al. 1989; 31) Evans 1971; 32) Evans 1974; 33) Fay and Burns 1988; 34) Fitch and Brownell 1968; 35) Folkow and Blix 1995; 36) Forbes and Sealy 1988; 37) Frost et al. 1993; 38) Gales and Mattlin 1995; 39) Gallo-Reynoso et al. 1995; 40) Gambell 1985; 41) Gentry et al. 1986a; 42) Gentry et al. 1987; 43) I. Gjertz *personal communication*; 44) Goodyear 1995; 45) Guyot 1988; 46) Hall 1970; 47) Hammill et al. 1993; 48) Harrison and Kooyman 1971; 49) Harvey and Mate 1984; 50) Heide-Jørgensen and Dietz 1995; 51) Heyning 1989; 52) Hindell et al. 1991b; 53) Hobson and Martin 1996; 54) Hohn et al. 1995; 55) Irving 1939; 56) Jefferson et al. 1993; 57) Johnsgard 1987; 58) Jury 1986; 59) Katona et al. 1993; 60) Kelly and Wartzok 1996; 61) Kenyon 1981; 62) Kooyman 1989; 63) Kooyman and Gentry 1986; 64) Kooyman and Kooyman 1995; 65) Kooyman and Trillmich 1986a; 66) Kooyman and Trillmich 1986b; 67) Kooyman et al. 1992a; 68) Krutzikowsky and Mate 1995; 69) Landis 1965; 70) Lavigne and Kovacs 1988; 71) Leatherwood and Walker 1979; 72) Le Boeuf et al. 1989; 73) Lumsden and Haddow 1946; 74) A.R. Martin *personal communication*; 75) Marsh et al. 1989; 76) Mattlin 1993; 77) Medonca and Pritchard 1986; 78) Melin et al. 1993; 79) Miyazaki and Perrin 1994; 80) Montague 1985; 81) Morejohn 1979; 82) Naito et al. 1990; 83) Newby 1975; 84) Nilsson 1972; 85) Nishiwaki and Marsh 1985; 86) E.S. Nordøy *personal communication*; 87) Nordøy et al. 1995; 88) Orr and Aurioles-Gamboa 1995; 89) Pastukhov 1969; 90) Peixun 1989; 91) Piatt and Nettleship 1985; 92) Prince and Harris 1988; 93) Prince and Jones 1992; 94) Pritchard 1979; 95) Reeves and Brownell 1989; 96) Ridgway 1986; 97) Robinson and Craddock 1983; 98) Sage 1971; 99) Scholander 1940; 100) Schorger 1947; 101) Scolaro and Suburo 1991; 102) Scott et al. 1993; 103) Seddon and van Heezik 1990; 104) Soma 1985; 105) U. Swain *personal communication*; 106) Testa 1994; 107) Tinker 1988; 108) Trillmich et al. 1986; 109) Wanless et al. 1988; 110) Watanuki et al. 1996; 111) Watkins et al. 1985; 112) Watkins et al. 1987; 113) Werner and Campagna 1993; 114) Westgate et al. 1995; 115) Whitehead 1989; 116) Wiig et al. 1993; 117) Williams and Cooper 1983; 118) Williams et al. 1992; 119) Wilson 1985; 120) Wilson and Wilson 1990; 121) Worthy and Davis 1995; 122) Würsig et al. 1994.

[e] Water depth where diving occurred. Animal assumed to have be diving to the bottom.

[f] Mass estimated from the length.

[g] Depth limited by the depth range of the pressure sensor.

[h] Depth limited by water depth.

[i] Incorrectly identified and reported as a green turtle in Landis (1965) according to Eckert et al. (1986).

[j] Estimated from mean + 2 x SD.

Table 2.2. Allometric relationships between $\log_{10}$ diving capacity (maximum depth, in m, and duration, in min) and $\log_{10}$ body mass (M_b, in kg) for various groups of air-breathing vertebrates.

Group	n[a]	Regression equation[b]	r[c]	r^2	p
All	111	Max depth = 36.31 $M_b^{0.33}$	0.71	0.50	<0.001
	121	Max duration = 1.62 $M_b^{0.37}$	0.84	0.71	<0.001
All (TDR or MDG)	57	Max depth = 68.23 $M_b^{0.30}$	0.74	0.55	<0.001
	39	Max duration = 2.34 $M_b^{0.37}$	0.75	0.56	<0.001
Marine mammals	57	Max depth = 131.83 $M_b^{0.13}$	0.32	0.10	0.016
	64	Max duration = 3.63 $M_b^{0.24}$	0.56	0.31	<0.001
Marine mammals without mysticetes	51	Max depth = 34.67 $M_b^{0.39}$	0.65	0.42	<0.001
	55	Max duration = 1.78 $M_b^{0.39}$	0.61	0.37	<0.001
Birds	51	Max depth = 28.84 $M_b^{0.60}$	0.48	0.23	<0.001
	54	Max duration = 1.35 $M_b^{0.50}$	0.69	0.48	<0.001
Pinnipeds	29	Max depth = 33.88 $M_b^{0.43}$	0.60	0.36	0.001
	30	Max duration = 1.70 $M_b^{0.48}$	0.63	0.40	<0.001
Cetaceans	27	Max depth = 120.23 $M_b^{0.11}$	0.31	0.10	0.114
	31	Max duration = 1.38 $M_b^{0.32}$	0.78	0.61	<0.001
Odontocetes	21	Max depth = 22.91 $M_b^{0.42}$	0.75	0.56	<0.001
	22	Max duration = 0.51 $M_b^{0.51}$	0.84	0.71	<0.001
Mysticetes	6	Max depth = 89.13 $M_b^{0.07}$	0.07	0.01	0.895
	9	Max duration = 0.04 $M_b^{0.61}$	0.84	0.71	0.004
Phocids	15	Max depth = 25.70 $M_b^{0.52}$	0.70	0.49	0.004
	16	Max duration = 3.39 $M_b^{0.42}$	0.59	0.35	0.015
Otariids	13	Max depth = 27.23 $M_b^{0..46}$	0.51	0.26	0.073
	13	Max duration = 6.22 $M_b^{0.10}$	0.17	0.03	0.59
Penguins	11	Max depth = 42.66 $M_b^{0.71}$	0.81	0.66	0.003
	9	Max duration = 0.98 $M_b^{0.90}$	0.93	0.86	<0.001
Flying birds	40	Max depth = 23.99 $M_b^{0.21}$	0.14	0.02	0.394
	45	Max duration = 1.26 $M_b^{0.22}$	0.34	0.12	0.023

[a] n = number of maximum depth or duration observations.

[b] Y-intercepts for diving capacity were calculated for a mass of 1 since $\log_{10}$ of 1 = 0.

[c] r = Pearson correlation coefficient.

Table 2.3. Allometric relationships between $\log_{10}$ diving capacity (maximum depth, in m, and duration, in min) and $\log_{10}$ body mass (M_b, in kg) for various Families of diving birds.

Group	n[a]	Regression equation[b]	r[c]	r^2	p
All	51	Max depth = $28.84\ M_b^{0.60}$	0.48	0.23	<0.001
	54	Max duration = $1.35\ M_b^{0.50}$	0.69	0.48	<0.001
Penguins	11	Max depth = $42.66\ M_b^{0.71}$	0.81	0.66	0.003
	9	Max duration = $0.98\ M_b^{0.90}$	0.93	0.86	<0.001
Alcids	9	Max depth = $158.49\ M_b^{1.04}$	0.81	0.66	0.008
	9	Max duration = $2.14\ M_b^{0.37}$	0.40	0.16	0.283
Cormorants	7	Max depth = $30.90\ M_b^{0.99}$	0.53	0.28	0.223
	12	Max duration = $0.98\ M_b^{0.59}$	0.56	0.31	0.059
Ducks	15	Max depth = $10.72\ M_b^{1.41}$	0.45	0.20	0.093
	14	Max duration = $1.10\ M_b^{0.51}$	0.41	0.17	0.143

[a] n = number of maximum depth or duration observations.

[b] Y-intercepts for diving capacity were calculated for a mass of 1 since $\log_{10}$ of 1 = 0.

[c] r = Pearson correlation coefficient.

Figure 2.1. Relationships between $\log_{10}$ diving capacity (maximum depth and duration) and $\log_{10}$ body mass for mysticete cetaceans, odontocete cetaceans, flying birds, penguins, otariid seals, and phocid seals (solid lines denote significant results and broken lines denote nonsignificant results). The thickest lines represent the relationships for the entire data set. These lines include values for sea otters, walruses, sirenians, and marine turtles in addition to the taxonomic groups listed above. e, otariid; f, flying bird; m, mysticete; mu, sea otter; o, odontocete; p, penguin; s, phocid; si, sirenian; t, turtle; w, walrus.

Figure 2.2. Relationships between $\log_{10}$ diving capacity (maximum depth and duration) and $\log_{10}$ body mass for alcids, cormorants, ducks, and penguins (solid lines denote significant results and broken lines denote nonsignificant results). The thickest lines represent the relationships for the entire bird data set. These lines include values for grebes, loons, and petrels in addition to the taxonomic groups listed above. a, alcid; c, cormorant; d, duck; g, grebe; L, loon; p, penguin; pet, petrel.

Figure 2.3. Relationships between $\log_{10}$ predicted diving capacity (maximum depth and duration) and $\log_{10}$ body mass for birds, phocids, otariids, and cetaceans overlaid upon the regression lines calculated for observed data from Figure 2.1 (solid lines denote significant results and broken lines denote nonsignificant results). Predicted maximum diving duration was approximated by the calculated ADL. The lines with symbols represent predicted diving capacities. Diving metabolic rates were assumed to be 2 x SMR for all groups. The large dotted lines represent a second set of predicted diving capacities for otariids using diving metabolic rates equal to 5 x SMR. The small graph at the bottom right shows the various predicted lines on a linear scale.

CHAPTER 3

Classification of dive profiles: a comparison of statistical clustering techniques and unsupervised artificial neural networks

Abstract

Recent advances in technology for sampling diving behavior of animals have enabled enormous data sets to be collected on a variety of diving animals. Methods used to analyze these data vary considerably across studies, complicating interspecific comparisons. The primary problem is that methods for analyzing large, multivariate dive-data sets have not been clearly defined. This study examines and tests various algorithms for analyzing multivariate observations and assesses their suitability for classifying diving data. These include k-means and fuzzy c-means clustering techniques from the field of statistics, and Kohonen self-organizing map (SOM) and fuzzy adaptive resonance theory (ART) from the field of artificial neural networks. A Monte Carlo simulation was performed on artificially generated data, with known solutions, to test clustering performance under various conditions (i.e. well defined or overlapping groups, varying numbers of attributes, varying numbers of groups, and auto-correlated attributes). As well, performance was tested on real data sets from Adélie penguins (*Pygoscelis adeliae*), southern elephant seals (*Mirounga leonina*), and Weddell seals (*Leptonychotes weddellii*). K-means, fuzzy c-means, and SOM all performed equally well on the artificially generated data while fuzzy ART had error rates that were twice as high. All techniques showed decreasing performance with increasing overlap among groups and increasing numbers of groups, but increasing performance with increasing numbers of attributes. Fuzzy ART was the most sensitive to the varying simulation parameters. When clustering real data, both c-means and SOM classified observations into clusters that were closer together (relative to k-means) and hence had less distinct boundaries separating the clusters. K-means performed as well as c-means and SOM, but its classification of real data was more logical when compared to the actual dive profiles. K-means is also readily available on most statistical software packages. Considering all of these factors, k-means clustering appears to be the best method among

those examined for grouping multivariate diving data.

Introduction

The recent widespread use of telemetric devices (e.g. time-depth recorders (TDRs), satellite-linked time-depth recorders, heart rate monitors, and global positioning collars) has provided new insight into the physiology, behavior, and ecology of many organisms (e.g. Le Boeuf 1988, 1992; Hindell et al. 1991b; Boyd and Croxall 1992; Priede 1983; Rodgers and Anson 1994; Testa 1994; Kooyman and Kooyman 1995; Schreer and Testa 1996). However, methods for analyzing the enormous data sets recorded by these devices have not yet been clearly defined. A good starting point for these types of analyses is to reduce the dimensionality of the data by organizing the observations into more manageable and understandable groups. This can be accomplished via supervised or unsupervised learning methods, using either traditional statistical techniques or analytical tools from the recently expanding discipline of artificial neural networks (ANNs).

Several sources have provided reviews on ANNs (e.g. Rogers 1991; Lau 1992; Vemuri 1992; Gallant 1993; Ripley 1993, 1994; Cheng and Titterington 1994; Elmasry 1994; Sarle 1994). Briefly, ANNs typically consist of a set of interconnected computational units that attempt to mimic biological systems. They use large numbers of individually functioning neurons (simple computing elements) to collectively perform tasks that exceed the abilities of even the fastest computers. Unlike the serial or Von Neumann computer, ANNs process information in a parallel manner and can learn through training.

In supervised learning, the preferred output (e.g. the number and types of groups) is known for the data and a mathematical model must be trained in order to group new unclassified observations. For this type of learning to occur, the data structure must be well understood and many preconceptions must be applied to new data. Examples of supervised ANNs are back-propagation (Rumelhart and McClelland 1986) and counter-propagation (Hecht-Nielsen 1987). Regression, analysis of variance, and discriminant function analysis (Dillon and Goldstein 1984; Sokal and Rohlf 1995) are examples of statistical techniques that employ supervised learning. However, often little is known about the structure of the data and consequently, projecting preconceived ideas onto the data introduces subjective bias.

In unsupervised learning, the classification is unknown and the data must be clustered into similarity groupings. The structure of the data is analyzed and data are grouped such that observations within a group are more similar to each other than they are to observations in other groups. There are several types of ANNs useful for clustering. Two of these are self-organizing maps (SOM: Kohonen 1982, 1989, 1990) and adaptive resonance theory (ART: Grossberg 1976; Carpenter and Grossberg 1987a, b, 1988; Carpenter et al. 1991). Statistical analogies are principal component analysis (Pearson 1901; Hotelling 1933), k-means clustering (MacQueen 1967), and fuzzy c-means clustering (Dunn 1973; Bezdek 1981, 1987). For recent reviews of these statistical procedures see Dillon and Goldstein (1984), Jain and Dubes (1988), Afifi and Clarke (1990), and Everitt (1993).

Until recently, statistical techniques would have been the obvious choice for analyzing dive data, but with the recent advances in the area of ANNs, additional techniques are now available. Many of these newer techniques have not been well tested or compared to the older, more traditional statistical methods. As well, many of the ANN techniques remain unknown to much of the scientific community. ANNs classify observations in a manner that is fundamentally different from statistical techniques. Instead of studying the structure of all of the data simultaneously, each observation is considered in turn and parameters are adjusted if the observation is misclassified (Fukunaga and Young 1991). Some comparisons between these two different approaches have been made (Balakrishnan et al. 1994; Sarle 1994), but new algorithms also need to be tested for characteristics such as complexity, convergence, performance, robustness, and stability (Bezdek 1991).

This work is part of a larger, quantitative study of the diving behavior of air-breathing vertebrates. Since most recent analyses of diving behavior have utilized data collected via TDRs (Chapter 2), it was necessary to determine possible methods for analyzing data from these instruments. These devices are attached to an animal and record their depth in the water column (via a pressure sensor) at pre-determined time intervals. A typical data record (i.e. all data collected on a single individual) consists of a series of depth values that can be partitioned into dives. These dives, which are a series of depths over time starting and ending with depth equal to zero, can be perceived as two dimensional shapes, depth versus time. Since TDRs can record millions of observations, representing tens of thousands of dives on a single individual, analytical methods are needed to objectively and automatically categorize the data into meaningful, behavioral groupings.

Most studies of diving behavior, utilizing TDRs, have primarily grouped dives subjectively according to perceived similarities in maximum depth and duration (e.g. Kooyman 1968; Croxall et al. 1991; Goebel et al. 1991; Wanless et al. 1992; Williams et al. 1992; Chappell et al. 1993a). It is perhaps inappropriate to solely include maximum depth and duration into classification analyses because both of these variables may display strong diel variation (e.g. Bengtson and Stewart 1992; Castellini et al. 1992a; Boyd et al. 1994; Schreer and Testa 1996) that can obscure the determination of behavioral groupings. Also, using only the maximum depth and duration of a dive excludes most of the observations collected (i.e. the rest of the depth readings). Therefore, to solve these two shortcomings, several studies have utilized the two dimensional shape of the dive, the dive profile, to classify diving behavior (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1993, 1995, 1996; Jonker and Bester 1994; Brillinger et al. 1995; Campagna et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*, Chapter 4). Many of these works, however, have relied solely or primarily on subjective comparisons of the dive profiles. This introduces human bias and prevents interstudy comparisons due to individual classification protocols. A few studies have attempted quantitative classification of diving patterns (Hindell et al. 1991b; Schreer and Testa 1993, 1995, 1996; Boyd et al. 1994; Brillinger et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*, Chapter 4). However, the individual classification protocols for these analyses have also varied considerably (e.g. principal component analysis, cluster analysis (various algorithms), shape fitting algorithms, as well as combinations, some of which included maximum depth and duration) and their performances have usually not been tested.

In this paper, the capabilities of several statistical techniques (k-means and fuzzy c-means clustering) and ANNs (Kohonen self-organizing map (SOM) and adaptive resonance theory (ART)) capable of unsupervised learning are compared. First, performance of the techniques was assessed by determining the number of misclassified points when clustering artificially generated data with independent variables and with known cluster solutions. Next, the performance of the techniques was tested on data artificially generated to simulate characteristics of diving data (i.e. specific dive shapes with auto-correlated depths). Lastly, a series of subsampled real diving data from three species of air-breathing vertebrates were clustered to further test the performance of the various techniques and to assess their suitability for analyzing real data.

Methods

The algorithms

A common statistical clustering technique, k-means, a non-disjoint statistical clustering technique related to k-means, fuzzy c-means, and two types of unsupervised neural networks, SOM and ART, were chosen for study and comparison. K-means, SOM, and ART were chosen because of their availability in numerous software packages (e.g. SAS, SPSS, SYSTAT, NeuralWorks Professional II Plus) and because of their abundant use. Fuzzy c-means was chosen because it has characteristics (fuzzy clustering and cluster memberships, see below) that are potentially useful for clustering the relatively continuous data observed for diving behavior.

K-means - K-means is a non-hierarchical clustering procedure that uses Euclidean distances to divide observations into disjoint clusters. Observations are assigned to the cluster which has the closest center. The k-means algorithm was performed using PROC

FASTCLUS in SAS (SAS Institute Inc. 1990). Initial cluster seeds are the first n observations, where n equals the number of clusters. Using the MAXITER option in FASTCLUS, cluster seeds are replaced by cluster means following each iteration. This is continued until the changes in cluster seeds become small or zero. The number of clusters desired is set prior to the analysis.

C-means - In fuzzy c-means, data are partitioned so that each observation is assigned a degree of membership to each cluster rather than assigning it to only one cluster as is the case for "hard" clustering (e.g. k-means). The fuzzy c-means algorithm was performed using a modified FORTRAN program created by Kamel and Selim (1994). This program also uses Euclidean distances between observations to divide data into clusters. However, these clusters are not disjoint since an observation can belong to more than one cluster. In fact, after each iteration, cluster seeds are not replaced by the means of the observations in that group, but instead are replaced by the means of all of the observations, with each observation being weighted by its membership to that cluster. Initial cluster seeds are randomly selected from the data and the number of clusters desired is set prior to the analysis. Cluster membership (M), as outlined by Kamel and Selim (1994), is calculated by

$$M_{ij} = 1/\sum_{l=1}^{c} (d_{ij}/d_{il})^{2/(m-1)},$$

for $d_{il} > 0$, œ i,j, where c = the number of clusters, m is the fuzziness parameter ($m > 1$), and d_{ij} is the Euclidean distance between the ith observation vector and the jth cluster center vector. If $d_{il} = 0$ then $M_{il} = 1$ and $M_{ij} = 0$ for j ... l.

Artificial neural networks are typically organized into layers (Figure 3.1). At the bottom, there is an input layer that contains nodes through which data are input. The top is an output layer that generates the output interpreted by the user. Between these two layers, there can be one or more layers called hidden layers. The output of each layer is input into the next layer until the signal finally reaches the output layer which then generates the observable output. For our purposes, each input node represents a variable and each node in the output layer represents a cluster. Artificial neural networks cluster observations in two main stages, a *training* or *learning* stage and a *recall* stage (NeuralWare Inc. 1991). In the first stage, a learning rule is used to *train* the network for a specific data set. Following this training stage, the second or *recall* stage actually classifies the observations.

SOM - Kohonen SOM is a topology-preserving map motivated by the structure of the mammalian brain where sensory inputs are mapped into a number of "sheets" of cells (Kohonen 1982, 1989, 1990; Gallant 1993). Topology is preserved in that similar sensory inputs (i.e. stimulation of two parts of the body that are near each other) will cause groups of brain cells near each other to fire. In the ANN situation, similar inputs lead to output nodes being activated that are close together. In Figure 3.1 for example, a data set with ten variables is input into the network. Then nodes of the hidden layer compete to produce an output (one of five clusters), and the output layer indicates which node has won. The winner is determined by having the minimum Euclidean distance between the vector of the hidden node (a cluster center) and the input vector (an observation). The hidden nodes are organized so that nodes representing similar cluster vectors will be near each other. This is in contrast to statistical clustering where clusters are ordered randomly or ART where clusters are ordered relative to the order of the input vectors. To accomplish this topology preserving property, a "conscience" mechanism is used to prevent a particular output node from representing the entire data set (DeSieno 1988; Balakrishnan et al. 1994). This mechanism ensures that, along with the winning node, some of the nodes nearest to this winning node also update their weights. For these networks, one node on either side of the winning node was also updated.

The networks were created within the NeuralWorks Professional II/Plus package, Version 5.2 (NeuralWare Inc., Pittsburgh, PA, USA). Networks were created so that the number of nodes in the input layer was equal to the number of variables in the data set, and the number of nodes in the hidden layer and output layer was equal to the number of clusters.

The data were randomized before training and networks were trained for 30 iterations as recommended by NeuralWorks.

ART - There are two main groupings of ART for non-hierarchical clustering: ART1 for binary input patterns (Carpenter and Grossberg 1987a) and ART2 for analog or continuous input patterns (Carpenter and Grossberg 1987b). In this study, a version of ART, called fuzzy ART, was used. This algorithm incorporates computations from fuzzy set theory into the ART1 neural network, allowing analog input patterns to be analyzed (Carpenter et al. 1991). In ART the number of clusters is not set, but rather clusters are created as needed. Clusters are then modified only if the cluster center is sufficiently close to the training observation, otherwise a new cluster is formed. A parameter called vigilance controls cluster granularity. Vigilance basically represents the maximal allowable size (in the multidimensional space) of the cluster. A high vigilance tolerates only slight mismatches between the cluster center and the input observation causing large numbers of clusters to be found. The converse is true for low vigilance. Figure 3.2 is a schematic of the general ART architecture. A multivariate observation (F_0) is input into the network and fed into the F_1 layer where a normalization occurs. The vector from F_1 is fed to the F_2 layer where the nodes compete to produce an output. The winner is determined by having the minimum Euclidean distance between the vector of the F_2 node and the vector of the F_1 layer. The vector from the winning node is then compared to the input observation to see if it is sufficiently close as determined by the vigilance. If the difference is greater than that set by the vigilance, the winner is turned off and a new node (cluster center) is created. If the difference is less, the vector of the winning node is updated appropriately. The last step is for all the nodes to be re-enabled to allow the next input to be processed.

The networks were created within the NeuralWorks Professional II/Plus package, Version 5.2 (NeuralWare Inc., Pittsburgh, PA, USA) by modifying a fuzzy ARTMAP network. The output nodes were deleted so that the network could function without supervision and the activity (i.e. the memberships to the various clusters) of the F_2 nodes was monitored through the committed node instrument (see fuzzy ARTMAP, NeuralWorks Professional II Plus, Version 5.2). Two types of fuzzy ART networks were created, one for the artificially generated data with known cluster solutions and a second type for clustering real dive data. The first type of network was created so that the number of nodes in the input layer (F_0) was equal to the number of variables in the data, and the number of F_2 nodes was set equal to the number of clusters desired. Since ART finds clusters as needed, the vigilance parameter was raised until the desired number of clusters was found (i.e. each F_2 node was activated). Once this level of vigilance was determined, the vigilance level was raised by 0.01 increments for a total of 10 separate runs for each data set. The output from all of these runs was then analyzed and the output with the fewest misclassifications was selected to represent the performance for that particular data set. For clustering of the real data, for which cluster solutions were unknown, a second type of network was created with the number of F_2 nodes set to be > 10. Vigilance was lowered until only 2 clusters were found and was then raised by 0.01 increments until 3 clusters were found. This was continued until 9 output data sets were generated with 2-10 clusters. The networks were trained for 30 iterations.

Data generation

Three types of data were used to test the performance and applicability of the various algorithms. First, data sets with known cluster solutions were artificially generated with 100 observations per data set and an equal number of observations per cluster group. Normally distributed data were generated with each variable being independent (Introduction to Clustering Procedures, SAS Institute Inc. 1990). Various data sets were generated with varying numbers of clusters (2, 3, 4, and 5), varying numbers of independent variables or attributes (4, 6, 8, and 10), and varying amounts of cluster overlap (low, medium, and high). A total of 144 data sets (3 data sets per level) were created.

The second type of data consisted of 5 shapes (described by 10 depths) commonly observed as dive profiles for the species included in this study. These data were artificially generated as multivariate normal with auto-correlated depths similar to that observed from real data. Using k-means clustering (PROC FASTCLUS, SAS Institute Inc. 1990), cluster solutions (cluster means and correlation structures) were determined for dive data from Weddell seals (*Leptonychotes weddellii*) (data from Testa 1994; Schreer and Testa 1995, 1996). Five distinct cluster means (i.e. shapes) were observed: 1) soft-square, 2) "V", 3) skewed-right, 4) skewed-left, and 5) hard-square (e.g. cluster level 5 in Figure 3.3). Next, a covariance structure was determined for each dive shape so that the auto-correlation between the 10 depths could be calculated. Three data sets, with 1000 observations each, were generated for the simulations. Numbers of observations per cluster group were approximated from the natural cluster solutions: 37 % soft-square, 20 % "V", 13 % skewed-right, 13 % skewed-left, and 17 % hard-square.

The third and last type of data consisted of a series of subsamples from real diving data (depth versus time) from Adélie penguins (*Pygoscelis adeliae*) (data from Chappell et al. 1993a), southern elephant seals (*Mirounga leonina*) (data from Hindell et al. 1991b), and Weddell seals (data from Testa 1994; Schreer and Testa 1995, 1996). Three data sets, each containing a subsample of 3,000 dives, were taken from the dive data recorded for each of the different species. Before sampling the data, some short, shallow dives were excluded from the data sets. Any dive with a maximum depth less than or equal to 2 times the depth resolution of the TDR was excluded due to erroneous drift of the zero depth in the TDR and possible effects of wave action. Also, since this work involves the determination and comparison of dive shape, only dives with at least 5 depth readings were analyzed. This was decided upon since fewer than 5 depth readings for even simple geometric shapes resulted in considerable degradation of the shape pattern.

Depth values for each dive were interpolated so that the dive was represented by 100 depths, allowing corresponding depths among all dives to be compared (Schreer and Testa 1995). Dives were then standardized such that the maximum depth of each dive was equal to

1, and the rest of the depths scaled less than 1. The means for every 10 depths, for a total of 10 means, were calculated for data reduction and to smooth the dive profiles. Ten standardized depths for each dive enabled all dives to be compared regardless of their maximum depth or duration, allowing comparison of the dive shapes.

Analysis

Much of this work followed Balakrishnan et al. (1994) in which k-means clustering was compared to several types of Kohonen ANNs (e.g. SOM) using artificially generated data. Here, the comparisons were expanded to include other types of unsupervised learning (fuzzy c-means and fuzzy ART) and these techniques were also applied to real data. Using data from the two types of artificially generated data sets, the performance of the four algorithms was compared in terms of the number of observations misclassified. For the first type of artificially generated data, square-root transformed misclassification rates were analyzed using a factorial analysis of variance to determine the effect of the simulation parameters on the clustering results.

Lastly, using real observations from the animals mentioned above, the data were grouped by the various techniques, compared across techniques, and compared to the original categorizations suggested by the authors who originally collected and classified the data. Our original intention was to determine the number of groups (clusters) within a data set by comparing R^2 values and Pseudo F statistics (Calinski and Harabasz 1974; Milligan and Cooper 1985; Proc CLUSTER and Proc FASTCLUS, SAS Institute Inc. 1990) over the number of clusters following Schreer and Testa (1995) (e.g. upper right graph in Figure 3.3). The formulas, as outlined by Proc CLUSTER and Proc FASTCLUS (SAS Institute Inc. 1990), are as follows:

$$R^2 = 1 - \frac{\sum_{j=1}^{c} \sum_{i \in c_j} d_{ij}^2}{\sum_{i=1}^{n} d_i^2}$$

and

$$Pseudo\ F = \frac{R^2/(c-1)}{(1-R^2)/(n-c)},$$

where n is the number of observations, c is the number of clusters, d_{ij} is the Euclidean distance between the ith observation vector and the jth cluster center vector, and d_i is the Euclidean distance between the ith observation vector and the overall sample mean vector. However, this technique was found to be unstable for the fairly continuous data observed for the diving behavior used in this study. When clustering subsamples of various data sets, different numbers of clusters were suggested by the R^2 values and Pseudo F statistics for different subsamples. These indicators, however, are good starting points when grouping data because if very strong cluster boundaries exist, a good indication of the correct number of groups can be determined. This was not the case here, so an *ad hoc* method for determining a suitable number of clusters for a data set was also used (Figure 3.3). Each data set was clustered into 2 through 10 groups and the cluster means were plotted. The number of suitable clusters was determined as the level of clustering after which all additional clustering 1) generated no additional, novel clusters, but instead, divided pre-existing clusters into a continuum of slightly different groups (e.g. several skewed shapes with different amounts of skewness) or 2) created unstable clusters (i.e. cluster means that occur at one level, but either change drastically or do not occur at subsequent levels). This procedure was performed on three subsamples of a particular data set to insure that the results were consistent.

Clustering results were then compared to actual dive profiles to assess the validity of the various clustering solutions. Differences among clustering results were compared by calculating the mean Euclidean distance between each cluster center and its nearest cluster neighbor for each data set. This procedure was conducted on analyses set to produce five clusters to allow direct comparisons.

Results

Artificial data

The performance of the various algorithms were very similar except for Fuzzy ART which always performed considerably worse than the other methods (Table 3.1). The main effects were significant across all techniques as shown in Table 3.2. An increase in the number of clusters caused a small but significant increase in the misclassification for all techniques except for Fuzzy ART in which the increase in misclassification was considerably higher. An increase in cluster overlap also caused an increase in misclassification across all techniques with Fuzzy ART again being the most sensitive. An increase in the number of variables caused the misclassification error to decrease in all techniques. There were also a few significant interactions, although these were all relatively weak.

The analysis using five dive shapes with auto-correlated depths produced similar results to those presented above, with all algorithms performing similarly except for fuzzy ART which, again, performed considerably worse. The mean misclassification rate was 12 % for k-means and fuzzy c-means, 11 % for SOM, and 24 % for fuzzy ART. For k-means, fuzzy c-means, and SOM, most of the misclassification occurred when soft-square shapes were classified as hard-square shapes (6-18 % of the soft-square dives were misclassified, accounting for 23-49 % of the total misclassification) and when "V" shapes were misclassified as soft-square shapes (5-17 % of the "V" shapes were misclassified, accounting for 9-24 % of the total misclassification). Fuzzy ART had higher misclassification rates across the groups and in two instances, misclassified almost the entire group. Seventy-one percent of the hard-square shapes were misclassified as soft-square, accounting for 47 % of the total misclassification in one data set. Another data set had 80 % of the "V" shapes misclassified as soft-square, accounting for 64 % of the total misclassification.

Real data

Dives shapes and their relative proportions determined for Weddell seals, southern elephant seals, and Adélie penguins by the various algorithms are shown in Table 3.3, 3.4, and 3.5. Weddell seals had five distinct dive types as compared to four for both southern elephant seals and Adélie penguins. Fuzzy c-means and SOM had the least variability in proportions across the various dive shapes (coefficient of variation (CV) averaged over the three subsamples and the three species was 30 % for c-means and 29 % for SOM) and had results which were very similar to each other. These two algorithms were also the most consistent across the three subsamples within a species. That is, the mean dive shapes and frequencies for the 2 through 10 cluster groupings were very similar across the samples (a, b, and c). Relative to c-means and SOM, k-means had more variability in dive shape frequencies (CV = 65 %) while fuzzy ART had the most variability (CV = 136 %) with some groups including as much as 86 % or as little as 1 % of the data. For both the Weddell seal and Adélie penguin data, fuzzy ART often did not discriminate between two groupings found by all of the other algorithms (e.g. no separation of "V" and soft-square dive shapes).

Comparisons of the clustering results to actual dive profiles indicated that dives within the different groups determined by fuzzy c-means and SOM were more difficult to discriminate from each other than those determined by k-means. That is, some dives within one group had shapes that appeared to be more suited to a different group. Dives within the different groups determined by k-means were considerably easier to discriminate from each other while dives within the fuzzy ART groupings were either easy or difficult to discriminate depending on the group. This was seen quantitatively by the degree of separation between the various cluster means among techniques (performed on analyses producing five clusters). Except for fuzzy ART, k-means had the largest mean distances (MD, averaged for the three subsamples) between cluster centers and their nearest cluster neighbors ($MD_{Weddell} = 0.564$, $MD_{Elephant} = 0.384$, $MD_{Adélie} = 0.353$). Mean distances for c-means ($MD_{Weddell} = 0.533$, $MD_{Elephant} = 0.304$, $MD_{Adélie} = 0.312$) and SOM ($MD_{Weddell} = 0.532$, $MD_{Elephant} = 0.338$, $MD_{Adélie} = 0.323$) were smaller. Fuzzy ART had mean distances that were considerably larger than those found for the other techniques ($MD_{Weddell} = 0.703$, $MD_{Elephant} = 0.577$, $MD_{Adélie} = 0.548$). However, these mean distances were highly variable, indicating that while certain cluster means were far from their neighbors, others were very close.

Discussion

This work tested and compared several possible methods for analyzing the enormous data sets recorded by modern telemetric devices. All of the methods improve the level of objectivity compared to manual grouping of the behaviors. As well, the methods expedite analyses due to their relatively automated nature. However, there were considerable differences across the methods in misclassification performance with the artificially generated data, and across the similarity groupings determined for the real data, that indicated the benefits of certain algorithms for these sorts of analyses.

Comparisons across algorithms

All of the algorithms had low misclassification rates when grouping the artificially generated data, except for fuzzy ART which had error rates that were twice as high as the other methods. The performance of the various methods was more variable when grouping the real data. This part of the comparison was considerably more subjective since there were no "correct" solutions and the performance was generally determined by how well the cluster means represented the dive shapes within a group and whether there were any obvious biological explanations for the groupings. The following four subsections will present a discussion of the results from each of the four algorithms and will be ordered from "worst" to "best" in performance/suitability.

ART - Fuzzy ART had many interesting qualities, but its performance was the poorest of all the algorithms examined. The various ART algorithms are said to be "stable" for a specific data set in that the final clusters will not change with additional iterations (Carpenter and Grossberg 1987a; Gallant 1993). However, the order in which the training data are input into the network may influence the final cluster means and frequencies (Gallant 1993; M. Gjaja *personal communication*; *personal observation*). In the networks used here, the training data were randomized before each iteration. Therefore, each time the same data set was input into the network, the order of the data was different. However, even though ART was "stable" within a single training session, it was unstable across sessions. That is, if the same data sample was clustered by ART three separate times (including a retraining of the network), the cluster solutions would be different each time (e.g. different cluster means, frequencies, or number of clusters: *unpublished data*). Regardless of how many iterations of the data were used to train the network, ART was not stable across separate sessions indicating that the order of the training data was affecting the results. In contrast, SOM, as well as k- and c-means always produced the same results each time the same data set was analyzed.

Another characteristic of ART is of considerable interest and is another potential cause of its poorer performance. Of all the algorithms examined here, ART is the closest to being truly unsupervised. With the other algorithms, the number of clusters desired must be provided beforehand. Only a vigilance level needs to be provided for ART. The network then clusters the data into logical groupings according to the maximum allowable size (in space) of the clusters as set by the vigilance. If a new observation is too different from pre-existing clusters, as determined by vigilance, a new cluster is created. However, this characteristic which Carpenter and Grossberg (1987a) suggest solves the *stability-plasticity dilemma* (i.e. lets the network adapt, but prevents new inputs from destroying past training), allows the system to be *too* plastic for some applications. That is, depending on the vigilance level and the order of the input data, not only will solutions with different numbers of clusters be found, but even solutions with the same number of clusters may have different clusters sizes (i.e. the number of observations within the clusters) and means. This plasticity may prevent ART from having performance equal to the other algorithms, but it does show potential for its use in truly unsupervised situations like remote applications (e.g. classifications on-board a telemetric device).

SOM - SOM had excellent performance, equal to the statistical methods. In fact, SOM had nearly identical performance rates to k- and c-means when clustering the artificially generated data, and had similar results to c-means when clustering real data. This is in contrast to the results of Balakrishnan et al. (1994) where SOM performed considerably worse than k-means. SOMs poorer performance in the work of Balakrishnan et al. (1994) was probably due to the larger number of nodes in their hidden layers which allowed more topology-preserving properties, but poorer performance. In the SOM networks used here, there were fewer nodes in the hidden layers. If each node has no other neighbors, then the topology-preserving properties are lost and SOM is very similar to k-means (Gallant 1993). Since the SOM networks used here had so few nodes in the hidden layer, they probably functioned similar to k-means. This is substantiated by their similar performances. The conscience mechanism which allowed the few nodes surrounding the winning node to be updated, as well as the winning node, may have made SOM function in a fashion more similar to c-means. This is substantiated by the similar results produced by these two algorithms when clustering the real data. SOMs characteristic of updating cluster centers near the winning center enables it to cluster data in a fuzzy sense, like c-means. In fact, the performance of these two algorithms was so similar that they were generally considered to be tied for their overall performance/suitability. C-means was ranked slightly higher because of its additional characteristic of assigning a membership coefficient to each observation. The fuzzy updating of both SOM and c-means is most likely useful when considering outliers, but may have the negative side effect of producing clusters that are too similar to each other.

This point will be expanded on in the discussion below on c-means.

C-means - Fuzzy c-means clustering had very good performance that was similar to that of k-means and SOM. Its performance when clustering the artificially generated data and its clustering solutions for the real data were very similar to k-means which was expected since they are closely related. However, its even stronger similarity to SOM was surprising. It suggests that a SOM network with few nodes in the hidden layer and a conscience mechanism functions much the same as c-means. Originally, it was thought that c-means would have the best performance and would be the best suited for grouping the dive data. Since every observation belongs to every cluster, outliers would have less of an effect on the cluster centers because their impact would be spread out over all of the clusters. Also, this fuzzy quality allowed each observation to be evaluated on how well it fits within a cluster. That is, observations with high cluster memberships could be considered to be good representatives of that particular group while observations with low cluster memberships in two or more clusters could be considered to be hybrids (having characteristics of more than one group). It was hoped that this characteristic would be useful for the relatively continuous data recorded for diving behavior. Observations with high cluster memberships would be used as representatives of a dive type and subsequently compared using additional variables like maximum depth, duration, time, and location. The hybrids could either be excluded from the subsequent analyses or combined into one or more hybrid groups. This would create larger boundaries between the dive types and potentially provide a more useful picture for discriminating different diving behaviors. However, the fuzzy classification used by both c-means and SOM (i.e. updating neighboring cluster centers in addition to the winning cluster center) decreases the separation between each cluster which creates less distinct boundaries between these clusters. Therefore, there was considerably more overlap across clusters, and physical and biological distinctions between dive shapes from different groups were more difficult to determine. This could also be seen in that the variability in group sizes (numbers per group) was relatively small, suggesting that cluster coverage was equally spread over the data space.

K-means - K-means clustering performed as well as c-means and SOM, but its classification of the real data was more logical (i.e. dive shapes within a group generally had characteristics that made it obvious why it was classified in that group and not another). K-means' ability to classify observations into more distinct groups than the other methods suggests that it is the most suited for analyzing the relatively continuous data recorded for behavioral observations. The characteristic of fuzzy c-means that allows hybrids and cluster representatives (high cluster membership) to be identified can also be duplicated by k-means. By monitoring the Euclidean distance between an observation and its cluster center, hybrids could be identified as those observations with two or more distances that are nearly equal between two or more clusters. Cluster representatives and outliers could be identified as observations that are very near to or far from their corresponding cluster center, respectively. These qualities suggest that, of all the algorithms examined here, k-means has the most promise as a tool for analyzing behavioral observations.

Classification of real diving data

These analyses suggested that five distinct dive shapes represent the diving behavior of Weddell seals while only four were indicated for both southern elephant seals and Adélie penguins. The shapes were similar across species with two square dive types (soft and hard), a "V" shaped dive type, and two skewed dive types. Only Weddell seals had both skewed-right and skewed-left dive types while southern elephant seals had only the skewed-left and Adélie penguins had only the skewed-right. Possible functions for these various dive shapes are: 1) foraging for hard- and soft-square shaped dives (Le Boeuf et al. 1988; Hindell et al. 1991b; Chappell et al. 1993a; Schreer and Testa 1996), 2) predator avoidance (Hindell et al. 1991b) or exploration/search (Hindell et al. 1991b; Chappell et al. 1993a; Schreer and Testa 1996) for "V" shaped dives, 3) sleeping/resting/processing (Hindell et al. 1991b; Le Boeuf et al. 1992), exploration (Schreer and Testa 1996), foraging (Chappell et al. 1993a), or bathymetrically constrained (i.e. following the bottom down: Schreer and Testa 1996) for skewed-left shaped dives, and 4) foraging (Chappell et al. 1993a), exploration, bathymetrically constrained (i.e. following the bottom up), or processing (Schreer and Testa 1996) for skewed-right shaped dives. A dive shape found by previous studies on southern elephant seals and Adélie penguins, but not found here was parabolic shaped dives. It has been suggested that this type of dive may represent travelling (Hindell et al. 1991b; Chappell et al. 1993a). However, the difference between "V" and parabolic shaped dives is small. Also, two types of square dives reported previously for Weddell and elephant seals were also not discriminated here because only shapes were compared regardless of actual depth or duration. These were very long and deep flat bottomed dives thought to represent benthic foraging in Weddell and elephant seals (Hindell et al. 1991b; Le Boeuf et al. 1992; Schreer and Testa 1996) and very long and shallow dives thought to represent travelling in Weddell seals (Schreer and Testa 1996).

The dive shapes found here for Adélie penguins, elephant seals, and Weddell seals were generally similar to the types reported previously (Hindell et al. 1991b; Chappell et al. 1993a; Schreer and Testa 1995, 1996). However, Chappell et al. (1993a) reported only three primary types of dives (shallow-parabolic, shallow-square, and deep-square) for Adélie penguins and these were primarily discriminated subjectively using maximum depth. Chappell et al. (1993a) did allude to three variants of these primary patterns (V, and two types of foraging dives that could be interpreted as skewed-right and skewed-left) indicating more similarity with the results found here. Southern elephant seal dive shapes have been classified by several authors (Hindell et al. 1991b; Jonker and Bester 1994; Campagna et al. 1995) and the results are generally similar to those found here. Exceptions were a flat bottomed square dive type (Hindell et al. 1991b; Campagna et al. 1995) (see above), a parabolic dive type (Hindell et al. 1991b) (see above), and a skewed-right dive type (Jonker and Bester 1994), although this last type of dive was only suggested by one study and its occurrence was relatively rare. The dive types originally reported by Schreer and Testa (1995) for Weddell seals were very similar to those found here. Although, this was not surprising since Schreer and Testa (1995) used a k-means clustering algorithm to group their observations and much of the same data are used here. For both southern elephant seals and Adélie penguins, more subjective analyses were conducted using dive shape, maximum depth, and duration, although Hindell et al. (1991b) did find two preliminary groups using principal component analysis. Most of the differences between the results found here and those reported previously were due to additional information being used for the classification (maximum depth and duration) and subjective bias.

Conclusions

All of the algorithms examined show potential for classifying multivariate observations into more understandable groups. K-means, fuzzy c-means, and SOM all had low misclassification rates when classifying artificially generated data while fuzzy ART had error rates that were twice as high. Therefore, basing a comparison of these algorithms on just the results from the classification of artificially generated data indicates that all the methods, excluding fuzzy ART, should perform equally well for classifying observations. When the performance of the methods was tested using real diving data, however, both c-means and SOM classified observations in a way that created clusters that were closer together (relative to k-means) and hence had poorer boundaries separating the clusters. K-means performed as well as c-means and SOM, but its classification of the real data was more logical when comparing the results to actual dive profiles. K-means is also readily available on most statistical software packages. Considering all of these factors for the algorithms examined in this study, k-means clustering appears to be the most suited for grouping multivariate diving data.

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Table 3.1. Mean misclassification rate (%) of observations by the various simulation parameters.

Variable	Level	k-Means	c-Means	SOM	Fuzzy ART
Overall		4.49	4.26	4.64	9.27
Number of clusters	2	2.64	2.69	2.64	3.86
	3	4.36	4.42	4.81	8.56
	4	5.39	5.22	5.36	11.75
	5	5.58	4.69	5.75	12.92
Number of variables	4	8.97	8.53	9.25	14.31
	6	4.61	4.56	5.01	10.17
	8	2.92	2.56	2.61	7.31
	10	1.47	1.39	1.69	5.31
Overlap	Low	1.04	0.98	1.06	2.04
	Medium	3.56	3.54	3.83	8.36
	High	8.88	8.25	9.02	17.42

Table 3.2. Significance levels (F-ratios and (p-values)) by the various simulation parameters for the square-root of misclassification rate.

Variable	Hard k-means	Fuzzy c-means	Kohonen SOM	Fuzzy ART
Number of clusters	14.24 (0.00)	14.22 (0.00)	14.08 (0.00)	103.21 (0.00)
Number of variables	88.95 (0.00)	108.33 (0.00)	81.47 (0.00)	120.90 (0.00)
Overlap	197.95 (0.00)	241.10 (0.00)	187.15 (0.00)	589.76 (0.00)
Number of clusters x Number of variables	1.58 (0.13)	1.70 (0.10)	1.30 (0.25)	1.15 (0.33)
Number of clusters x Overlap	2.37 (0.04)	1.82 (0.10)	1.51 (0.18)	12.32 (0.00)
Number of variables x Overlap	1.30 (0.27)	2.02 (0.07)	1.22 (0.31)	2.68 (0.02)
Number of clusters x Number of variables x Overlap	0.98 (0.49)	0.83 (0.66)	0.74 (0.76)	2.95 (0.00)

Table 3.3. Proportions of representative dive shapes determined by the various algorithms for Weddell seal diving behavior[a].

Clustering method		Dive shape					
							other
k-means	a[b]	37	25	17	9	12	0
	b	34	21	15	11	19	0
	c	42	26	22	10	0	0
	mean	38	24	18	10	10 (16)[c]	0
c-means	a	31	20	15	12	22	0
	b	30	20	15	12	23	0
	c	25	19	12	11	18	15
	mean	28	20	14	12	21	5 (15)
SOM	a	31	20	15	13	21	0
	b	28	18	12	10	20	12
	c	28	20	18	14	20	0
	mean	29	19	15	13	20	4 (12)
Fuzzy ART	a	36	28	3	4	27	2
	b	67	<[d]	6	3	20	4
	c	70	<[d]	8	8	4	10
	mean	58	9 (28)	6	5	17	5

[a] Data from Testa (1994) and Schreer and Testa (1995, 1996).

[b] a, b, and c are three subsamples.

[c] Numbers in parentheses are means excluding dive types with 0 % of the data.

[d] Dives of this type clustered into the soft-square group.

Table 3.4. Proportions of representative dive shapes determined by the various algorithms for southern elephant seal diving behavior[a].

		Dive shape				
Clustering Method						other
k-means	a[b]	35	44[c]	13	8	
	b	37	41	13	9	
	c	40[c]	48[c]	6	6	
	mean	37	44	11	8	
c-means	a	35	27	22	16	
	b	35	31	19	15	
	c	32	39[c]	17	12	
	mean	34	32	19	15	
SOM	a	33	27	20	20	
	b	32	37[c]	16	15	
	c	31	38[c]	16	15	
	mean	32	34	17	17	
Fuzzy ART	a	72	3	23	1	1
	b	55	3	28	13	1
	c	73	2	22	2	1
	mean	67	3	24	5	1

[a] Data from Hindell et al. (1991b).

[b] a, b, and c are three subsamples.

[c] Two similar groups combined. A novel cluster mean occurred at a level after which a pre-existing cluster mean had already begun to be partitioned into a continuum of similar groups. Therefore, data within groups in the continuum were combined.

Table 3.5. Proportions of representative dive shapes determined by the various algorithms for Adélie penguin diving behavior[a].

Clustering Method		Dive shape				
						other
k-means	a[b]	41	13	43	3	
	b	42	17	37	4	
	c	35	23	21	15	6
	mean	39	18	34	7	2 (6)[c]
c-means	a	34	20	23	23	
	b	28	24	24	24	
	c	30	26	20	24	
	mean	31	23	22	24	
SOM	a	26	18	21	16	19
	b	27	26	24	23	
	c	28	26	20	26	
	mean	27	23	22	22	6 (19)
Fuzzy ART	a	86	<[d]	10	1	3
	b	86	7	<[d]	3	4
	c	53	10	6	30	1
	mean	75	6 (9)	5 (8)	11	3

[a] Data from Chappell et al. (1993a).

[b] a, b, and c are three subsamples.

[c] Numbers in parentheses are means excluding dive types with 0 % of the data.

[d] Dives of this type clustered into the soft-square group.

Figure 3.1. General schematic of an artificial neural network and the Kohonen self-organizing map (SOM) used for this work.

Figure 3.2. General schematic of an adaptive resonance (ART) network and the network used for this work.

Figure 3.3. Example of the *ad hoc* procedure for determining a suitable number of clusters for a data set. Each row of shapes is the cluster solution for that particular number of clusters. In this example, the data were a subset of Weddell seal dives (data from Testa 1994; Schreer and Testa 1995, 1996). The cluster solutions, which were calculated using k-means clustering, indicated that 5 clusters was a suitable number for the data set. The graph on the upper right shows R^2 and Pseudo F Statistic values which also suggest that 5 clusters is a suitable number. Sq, square; S-R, skewed-right; S-L, skewed left.

CHAPTER 4

Comparative diving patterns of pinnipeds and seabirds

Abstract

More than 230,000 dives from 12 species were analyzed and approximately 150,000 of these dives were classified according to dive shape. The species included one cormorant, 3 penguins, 2 eared seals, 5 true seals, and a walrus. Dive profiles (scaled to equivalent depth and duration) could generally be characterized as one of four shapes: square, V, skewed-right, or skewed-left. Comparative analyses across these dive types and the different species, revealed that square dives were always, and by far, the most abundant dive type, usually followed by V dives, and then the skewed dives. The proportion of time the animals spent at the bottom of square dives was also quite uniform across species (~50%) indicating that similar foraging patterns were being used, at least relative to the shapes of dives. Observed differences across species revealed that, as expected, larger divers generally dived deeper and longer than smaller ones, although fur seals and the walrus were exceptions with more limited diving capacities than expected based on body size. Also, smaller divers had a tighter coupling between dive depth and duration than larger ones. Surprisingly, however, few other dive variables (e.g. the rate at which dive duration increases with depth, the proportion of square dives, and the proportion of bottom time during square dives) were affected by body size, but instead physical (water depth) and ecological (type of prey) constraints played major roles. Analyses using estimated ADL indicated that better estimates of ADL are needed. However, even using crude estimators, comparisons of ADL across dive types indicated that square dives most often exceeded the estimated ADL. This is expected since square dives likely represent foraging and divers would be expected to push their limits most during this activity. Functional analyses of the determined dive types were in general agreement with those from previous work indicating that the various dive types have foraging (benthic and pelagic), travelling, exploring, resting, and processing functions. However, for most species, skewed dives were rare and are likely to be of little importance to these animals' diving regimes. Overall similarities in the dive patterns of the various species suggest that these

animals exploit the aquatic environment in a similar way.

Introduction

Most studies of diving behavior, utilizing time-depth recorders (TDRs), have primarily grouped dives subjectively according to perceived similarities in maximum depth and duration (e.g. Kooyman 1968; Croxall et al. 1991; Goebel et al. 1991; Wanless et al. 1992; Williams et al. 1992; Chappell et al. 1993a). It is perhaps inappropriate to include solely maximum depth and duration into classification analyses because both of these variables may display strong diel variation (e.g. Bengtson and Stewart 1992; Castellini et al. 1992a; Boyd et al. 1994; Schreer and Testa 1996) that can obscure the determination of behavioral groupings. For example, an animal may perform similar behaviors at different times of day (e.g. foraging). If its prey vertically migrate, the animal under study will forage at different depths throughout the day depending on the location of its prey. Therefore, even though the shape of a dive (depth versus time) may remain similar (due to optimizing time at the prey patch) and indicate comparable behavior, depth and duration could vary drastically.

Recently, several studies have included dive shape as a means of grouping diving behavior (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1993, 1995, 1996; Jonker and Bester 1994; Brillinger et al. 1995; Campagna et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*; Chapter 3). Many of these works have relied solely or primarily on subjective comparisons of dive profiles. This introduces human bias and prevents interstudy comparisons due to individual classification protocols. A few studies have attempted quantitative classification of diving patterns (Hindell et al. 1991b; Schreer and Testa 1993, 1995, 1996; Boyd et al. 1994; Brillinger et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*; Chapter 3), although the individual classification protocols for these analyses have also varied considerably (e.g. principal component analysis, cluster analysis (various algorithms), shape fitting algorithms, as well as combinations, some of which included maximum depth and duration). In short, the methods for classifying diving patterns have varied considerably making interspecific comparisons difficult.

This work involves classifying diving data from 12 different species of diving air-breathing vertebrates (i.e. pinnipeds and seabirds), comparing the results across species, and proposing behavioral functions for the dive types observed. The same methods are used on all species to allow more direct comparisons. It is hoped that observing patterns among many species will result in a better understanding of the functions of various dive types. As well, differences and similarities within and across species will shed more light on how these animals exploit the marine environment.

Methods

Previously acquired TDR data sets were compiled for this study (Table 4.1). These included 12 different species: blue-eyed shags (*Phalacrocorax atriceps*), Adélie penguins (*Pygoscelis adeliae*), royal penguins (*Eudyptes schlegeli*), gentoo penguins (*Pygoscelis papua*), Galapagos fur seals (*Arctocephalus galapagoensis*), Antarctic fur seals (*Arctocephalus gazella*), harp seals (*Phoca groenlandica*), grey seals (*Halichoerus grypus*), hooded seals (*Cystophora cristata*), Weddell seals (*Leptonychotes weddellii*), southern elephant seals (*Mirounga leonina*), and walrus (*Odobenus rosmarus*). Table 4.1 can be consulted for direction to specific methods of device attachment and deployment.

A dive was defined as a series of depths over time starting and ending with depth equal to zero. Due to erroneous drift of the zero depth in TDRs and possible effects of wave action, a depth of 2 times the resolution of the TDR was considered to be representative of the surface. Only dives with a maximum depth greater than this depth were analyzed. Also, since this work involves the determination of a dive shape (depth versus time), only dives with at least 5 depth readings were analyzed for shape because fewer readings result in considerable degradation of the precision of even simple geometric shapes (*unpublished data*).

Classification

Dives from each species were classified following Schreer and Testa (1995, 1996) and Chapter 3. Briefly, depth values for each dive were interpolated so that each dive was represented by 100 depths. Each dive was then scaled to equivalent depth and duration and smoothed by taking the mean of every ten depths. K-means clustering (Proc FASTCLUS, SAS Institute Inc. 1990) was used to find groups or types of dives. To determine a suitable number of clusters for each data set, R^2 and Pseudo F Statistic values versus the number of clusters were plotted and visually inspected for any inflections that might indicate an appropriate stopping point from further clustering (Calinski and Harabasz 1974; Milligan and Cooper 1985; Proc CLUSTER and Proc FASTCLUS, SAS Institute Inc. 1990; Schreer and Testa 1995; Chapter 3). However, as indicated in Chapter 3, this method was somewhat unstable across subsamples. Therefore, a more robust, *ad hoc* procedure developed in Chapter 3 was also used. For this procedure, the mean dive shapes for 2-10 clusters were plotted and visually inspected. A suitable number of clusters was determined as the point at which any additional clustering only created redundant or unstable dive types (i.e. two or more groups with similar shapes, or groups that occur at one clustering level, but not at subsequent levels).

Having performed these analyses on all 12 species, similarities in the dive patterns were found across the species that indicated the need for a unified method for classifying and comparing dive profiles. Additional variables (e.g. swim velocity, stomach temperature, jaw movements, and heart rate), that have only recently begun to be measured, may allow dive patterns within and across species to be better discriminated with clustering techniques. However, with only depth and time being measured, as is the case for the data presented in this study, dives will generally fall into one of four shapes (*Square*, *V*, *Skewed-Right*, and *Skewed-Left*) and cluster analyses of dive data across species will generally show similar patterns. Therefore, to allow more direct comparisons across species, a method first presented by Schreer and Testa (1996) and further developed here was used. This method compares each dive to four simple geometric shapes (*Square*, *V*, *Skewed-Right* and *Skewed-*

Left) that have been adjusted to reflect realistic dive profiles (Figure 4.1 and see Schreer and Testa 1996). For example, a "square like" shape with bottom time equal to half of the dive duration was used as opposed to a truly square shape that would have an animal diving from the surface to the maximum depth of the dive in 0 time.

Using this procedure, in addition to fuzzy clustering theory developed by Bezdek (1981), summarized in Kamel and Selim (1994), and explored as a dive analysis tool in Chapter 3, a new shape fitting protocol was developed. Dive profiles, scaled to equivalent depth, were compared to the four shapes as in Schreer and Testa (1996). For each dive, four shapes were generated with the number of depth values equal to that of the dive. The similarity of each shape to the dive was determined by calculating the Euclidean distance between the dive and the generated shape. Then to determine which shape was most similar to the dive, a group membership (*M*), as outlined in Kamel and Selim (1994) and described in Chapter 3, was calculated by

$$M_{ij} = 1/\sum_{l=1}^{c}(d_{ij}/d_{il})^{2/(m-1)},$$

for $d_{il} > 0$, œ i, j, where $c = 4$ (the number geometric shapes), m is the fuzziness parameter ($m > 1$), and d_{ij} is the Euclidean distance between the ith dive pattern vector and the jth geometric shape vector. If $d_{il} = 0$ then $M_{il} = 1$ and $M_{ij} = 0$ for j ... l. This results in four "probabilities" (one for the similarity of the dive profile to each shape) that sum to one.

Dives from each individual within each species were classified with this method and were subsequently pooled for each species. It has been shown that the diving behavior among individuals within a species can have considerable variation (Hindell et al. 1991b; Testa 1994, Burns et al. *in press*). However, within this work, small numbers of individuals and the lack of additional distinguishing parameters (e.g. physiological measures such as hematocrit, hemoglobin concentration, plasma lactate concentration, etc.: Burns et al. *in press*) made any explanation of individual variability difficult. Therefore, data from individuals within a species were pooled. The only exception was that southern elephant seals were split into male and female samples because of their exceptional sexual, size dimorphism.

After preliminary classifications of data from different species, it was realized that the sampling interval for which the data were recorded would affect the results. This type of problem for interspecific comparisons of dive patterns was first discussed by Boyd (1993). He found that as the sampling interval increased (using data resampled at different sampling intervals from the same original data set), mean maximum depth, duration, and post-dive surface interval also increased, while the number of dives detected decreased. Here, a similar trend was found when resampling two data sets (Adélie penguins and Galapagos fur seals: Table 4.2). Sampling interval was also found to affect a dive shape and hence the proportion of dives classified within each shape category. As the sampling interval increased, the proportion of *Square* dives decreased while the proportion of *V*, *Skewed-Right*, and *Skewed-Left* dives increased (Table 4.2). The reduction in the number of depth readings per dive (increased sampling interval) would miss true inflection points at the bottom of *Square* dives making them appear more triangular shaped. Hence, less *Square* dives and more *V*, *Skewed-Right*, and *Skewed-Left* dives would be detected. To correct for these differences, a similar sampling interval was used for each data set. More importantly, a similar number of observations per the patterns to be analyzed (i.e. a dive) was used. Since the shape of the dive profile was the pattern being analyzed, each data set was resampled so that, on average, dives within each species had a similar number of depth readings per dive.

Dive comparisons

Once all dives were classified into the four dive shapes, dive variables generated here and by pre-packaged dive analysis software (Table 4.3) were compared within and across species. The original intent was to compare proportions of dive types with Chi-square tests and differences in mean dive variables with 2-way factorial ANOVA (shape by species).

However, due to the large sample sizes, these tests nearly always found significant differences (even when differences were considerably smaller than what would have been considered biologically significant) while any non-significant differences were more due to small sample sizes than actual similarities among groups. Therefore, differences in these patterns were visually analyzed. Additional comparisons were performed on just *Square* dives using bottom time (BT), BT ÷ duration (%BT), wiggle count (WC), WC ÷ BT, average wiggle distance (AVWD), AVWD ÷ depth, and the standard deviation (STD) and coefficient of variation (CV: 100 x STD ÷ mean) for the depth readings during BT. Diel patterns within dive types were also visually analyzed and compared within and across species. For all of these analyses, only dive types with >30 observations per group were used. The only exception to this was for hooded seals, which had dive types represented by less than 30 dives, but still a relatively large proportion of all their dives (due to the small number of hooded seal dives in the total sample).

Prior to these analyses, group memberships were used to determine which dives had shapes that were intermediate to two or more geometric shapes. This was done since *hybrids* would likely display characteristics of more than one dive type and would blur differences between the types. The elimination of hybrids was accomplished by comparing the first and second highest group memberships for each dive. If the highest group membership was not at least 25% higher than the second highest group membership, the dive was considered to be hybrid and not used in the comparative analyses of dive shape.

Hierarchical classifications

Several dive variables were also used to determine if any further divisions were warranted within a dive type, in addition to being used for comparisons. Variables were decided upon that could potentially divide dives of similar shape into groups representing dive functions suggested previously in the literature. For example, it has been suggested that *Square* dives represent pelagic and benthic foraging (e.g. Hindell et al. 1991b; Le Boeuf et al. 1988, 1992; Schreer and Testa 1996). Therefore, several variables that describe the variability in depth during the BT were analyzed with histograms to determine if any multimodality existed. The presence of strong multimodality would suggest that more than one type of behavior was occurring. A possible difference in the variability of depth values during BT could indicate pelagic or benthic foraging (high variability: pelagic, low variability: benthic). Variables used for this stage of the analysis were maximum depth ÷ duration (Q), average rate of depth change (R), BT, %BT, post-dive surface interval (SI), SI ÷ duration, WC, WC ÷ BT, AVWD, AVWD ÷ depth, STD, and CV (Table 4.3). STD and CV were used in addition to the variables provided by the pre-packaged software because they were thought to reflect the appearance of the dive pattern during bottom time more accurately. For example, a square shaped dive with a somewhat U shaped bottom may not have any wiggles, but would be unlikely to represent benthic foraging. CV was subsequently excluded from these analyses since it detected mainly differences in maximum depth.

Aerobic dive limit

Dive durations within each dive type were compared to the estimated aerobic dive limit (ADL), defined as the maximum duration of a breath-hold without any increase in plasma lactate levels above resting during or following a dive (Kooyman et al. 1980; 1983b; Kooyman 1989), for that species. There has been considerable speculation regarding the calculation of ADL and direct post-dive lactate levels have only been collected on one species, Weddell seals (Kooyman et al. 1980, 1983b). In this species, it has been shown that ADL can be accurately estimated from calculations of total body oxygen stores (TBO_2) and the diving metabolic rate (DMR) (Kooyman et al. 1980, 1983b). This technique has been used by many researchers to estimate ADL for a wide variety of species without further calibration (e.g. Gentry et al. 1986b; Feldkamp et al. 1989; Hindell et al. 1992; Chappell et al. 1993a, Wiig et al. 1993; Boyd and Croxall 1996; Chapter 2). In addition to this shortcoming, the variables needed to calculate ADL are rarely directly measured, being estimated instead. TBO_2s have been measured for a few species (Kooyman 1989), but are usually only estimated when calculating ADL. As is the case for ADL, DMRs have only been directly measured on Weddell seals, and they have been found to vary with dive type and duration (Kooyman et al. 1973, 1980, 1983b; Castellini et al. 1992b; Ponganis et al. 1993a). Metabolic rates during a dive have never been measured under natural conditions (Boyd 1997). DMR is of considerable concern since these values have varied considerably in the literature (e.g. 2 to 10 x standard metabolic rate (SMR): Kooyman et al. 1973; Nagy et al. 1984; Kooyman and Ponganis 1990; Burger 1991; Castellini et al. 1992b; Chappell et al. 1993a, b; Costa 1993) and have a direct effect on the estimate of ADL. For example, if a DMR of 4 x SMR is used instead of 2 x SMR, the estimated ADL is halved.

Because of these many complications, ADLs were calculated from the generalized equations derived in Chapter 2, where DMR was assumed to be 2 x SMR for all phocids and seabirds, and 2 or 5 x SMR for otariids and the walrus. Two times SMR was used to estimate DMR, even though several researchers have suggested that swimming MR is considerably higher (Nagy et al. 1984; Chappell et al. 1993a, b; Costa 1993, Boyd and Croxall 1996), because, in agreement with Feldkamp et al. (1989), it was thought that upon submergence, changes occur (e.g. lower heart rate and decreased peripheral blood flow: Castellini 1991) that lower this value. Five times SMR was also used for otariids since there is strong evidence that otariids have DMRs that are considerably higher than phocids (Kooyman 1988b; Costa 1993; Boyd et al. 1995). These equations are undoubtedly overly simple, but they are an attempt to allow for more meaningful interspecific comparisons.

Functional analyses

Using the above analyses (i.e. interspecific similarities and differences) and comparing these results to previous studies on pinnipeds and seabirds, possible functions were proposed for the various dive types. In addition to this, life history information (mass, reproductive status, etc.) for the various species and conditions and locations of the studies were also used to propose possible functions of the dive types and to compare diving patterns across species.

Results

The species included in this study varied considerably in mass (2 to 2000 kg) and life stage (lactating females, gestating females, reproducing males, etc.: Table 4.4). As well, recording protocols and length of coverage varied considerably across species (Figure 4.2, Table 4.5). Analyzing the depth records for the 12 species resulted in 230,992 dives, of which 169,771 had 5 or more depth readings. When several of the data sets were resampled at larger sampling intervals this number decreased to 148,247 . Excluding hybrids from the resampled data reduced the number of dives to 135,072. This was approximately 91% of the data classified according to dive shape.

Dive comparisons

Square dives were invariably, and markedly, the most abundant dive type (Figure 4.3A, for specific values see Table 4.6). *V* dives were usually the next most abundant, followed by the skewed dives, although this trend was not always consistent for all of the species. Proportions of dive types did not appear to be influenced by body size, but rather by water depth and preferred prey. That is, limited water depth and possible benthic foraging increased the proportion of *Square* dives (e.g. blue-eyed shags, grey seals, and walruses: also see Table 4.4). The proportion of dive types changed when data from several of the species were resampled at larger sampling intervals (Figure 4.3A versus B, for specific values see Table 4.6). This confirms that a similar number of readings per dive is needed for interspecific comparisons.

Mean maximum dive depth and duration generally increased with body mass within pinnipeds and seabirds (Figure 4.3C and D, for specific values see Table 4.4 and 4.6). The trend for both groups combined was very weak for maximum depth, but could still be seen for duration. The walrus was an exception with very shallow, short dives for its mass. The type of behavior thought to be performed and the water depth also seemed to be of considerable importance in affecting mean maximum depth and duration (also see Table 4.4). Maximum depth and duration patterns across dive types indicated that *V* shaped dives were usually the deepest, *Skewed-Left* dives were the shallowest, and both of these types of dive were relatively short. The rate at which duration changed with depth (slope, Figure 4.4A) did not appear to be affected by body size, but divers that were limited by water depth or those that dived to the bottom (benthic foragers) (i.e. blue-eyed shags, walrus, and harp, grey, and hooded seals) increased dive duration more rapidly with an increase in maximum depth than did the other species. The amount of variability in duration due to changes in maximum depth (r^2, Figure 4.4B) was affected by body size and decreased with increasing body size in a fairly regular pattern for all dives combined. This pattern was also seen for *Square* dives, but was weaker or not apparent for the other dive types (probably due to small sample sizes). Comparing R across species revealed a weak trend towards higher rates for smaller divers (Figure 4.4C).

SI generally increased with increasing body size similar to duration, although when SI was scaled to equivalent duration (SI ÷ duration), it generally decreased with increasing size (Figure 4.5A and B). This trend, however, was not apparent for all dive types and no obvious trend was observed across dive types. Increasing dive duration generally did not affect SI for most species (Figure 4.5C and D), although a weak pattern could be seen across species indicating that smaller divers increased SI more rapidly with increasing duration than larger ones. Also, blue-eyed shags and Antarctic fur seals showed a relatively rapid increase in SI with increasing duration, although only blue-eyed shags had a strong relationship between these variables. Similar trends were also seen when SI and duration were plotted along with a LOWESS smoother (SYSTAT 1992). All species generally showed a weak increase in SI with increasing duration (Figure 4.6), although there was considerable scatter around the curves. As indicated by the linear regression results above, blue-eyed shags and

Antarctic fur seals showed the strongest increases, although Weddell seals also showed a fairly strong increase. Several of the species had inflections at certain durations, although except for blue-eyed shags, these were quite weak.

The amount of BT for *Square* dives generally increased with mass in a similar pattern to duration. However, when BT was scaled to equivalent duration, it was surprisingly similar across species (41 to 74 %, 41 to 53 % when excluding the 4 highest values), but was higher for benthic foragers (blue-eyed shags, grey seals, and walrus: Figure 4.7A and B, also see Table 4.4). Comparison of dive variables describing the bottom of *Square* dives indicated no obvious trends except for STD, which generally increased with mass, considering seabirds and pinnipeds separately, similar to maximum depth (Figure 4.7: C, D, and E).

Diel patterns

All species exhibited some sort of diel pattern, although these patterns varied considerably across species (Figure 4.8A and B). Patterns within a species were generally consistent across dive types, although there were several exceptions. All species dived more at certain times of the day, but there were no consistent trends across all species. Some subgroups, however, showed some similar patterns with all seabirds diving almost exclusively during the day and both fur seals diving almost entirely at night. Species thought to be pelagic foragers generally dived deeper and longer during the day (i.e. Weddell seals, female southern elephant seals, and royal, Adélie, and gentoo penguins), while benthic foragers (obligate or facultative: i.e. blue-eyed shags, male southern elephant seals, walrus, and grey seals) or species performing behaviors other than foraging (i.e. grey, harp, and hooded seals) generally had no or weak diel patterns in maximum depth and duration (see also Table 4.4). These patterns were difficult to interpret for the fur seals since they dived almost exclusively at night. However, Antarctic fur seals showed a tendency towards deeper, longer dives during the day, dawn, and dusk while Galapagos fur seals tended to increase dive depth and duration as they increased dive frequency during the night. It needs to be noted that some of these interpretations are very limited due to small number of dives during certain times of day for several species.

Hierarchical classifications

Five of the species had sufficient multimodality in one or more dive variables to warrant subdivisions of dive types (Figure 4.9). Walrus *Square* dives were divided into three groups based on R (<0.6m s^{-1}, ≥0.6 but <1.0m s^{-1}, and ≥1.0m s^{-1}). Male southern elephant seal *Square* dives and Antarctic fur seal *V* dives were each divided into two groups based on R (elephant seal: <1 m s^{-1} and ≥1 m s^{-1}, Antarctic fur seal: <0.8 and ≥0.8 m s^{-1}). Harp seal *Square* and *V* dives were each divided into two groups based on R (*Square*: <0.5 and ≥0.5 m s^{-1}, *V*: <0.48 and ≥0.48 m s^{-1}). Weddell seal *Square* dives were dived into two groups based on Q (<4 and ≥4).

Relevant dive variables for the hierarchical groups indicated some differences between dive types (Table 4.7). Dives with high values for R (Antarctic fur seals, harp seals, walrus, and male southern elephant seals) were deeper, longer (except for male southern elephant seals), and had longer BTs and %BTs than dives with low values for R. These dives also had more wiggles (WC) (except for the walrus) and greater variability in depth during BT (STD). Dives with high values for Q (Weddell seals) were deeper and longer than dives with low values for Q, had more and larger wiggles, had more variability in depth during BT, but had similar %BTs.

Diel patterns for these dive type subdivisions showed a general trend towards deeper and longer dives for higher values of R and Q (Figure 4.8A and B). For male southern elephant seals and harp seals, less diel variation in maximum depth was observed for higher values of R. For Weddell seals, less diel variation in maximum depth was observed for lower values of Q. Diel patterns for the two groups of *V* dives for Antarctic fur seals are not shown because there were too few dives to show patterns adequately for maximum depth and duration.

Aerobic dive limit

Estimated ADLs for the various species are presented in Table 4.8. Using these estimates, seabirds and fur seals (ADL estimated with DMR = 2 x SMR) rarely exceeded their ADL while some phocids exceeded their ADL for a majority of their dives. Also, among all of the large data sets (i.e. Adélie penguins, Galapagos fur seals, Weddell seals, and female and male southern elephant seals), only phocids had large proportions of dives that exceeded their estimated ADL. When DMR = 5 x SMR was used to calculate ADL for the two fur seals and the walrus, a majority of the dives exceeded the estimated ADL for both Galapagos fur seals and the walrus, but Antarctic fur seal dives still rarely exceeded their estimated ADL. Within the dive types, *Square* dives generally had the largest proportion of dives greater than their estimated ADL. However, for two of the seabirds (royal and gentoo penguins) and for Antarctic fur seals (DMR = 5 x SMR), *V* dives had the highest proportions of dives that exceeded the estimated ADLs.

Discussion

There were several strong similarities in diving patterns across very different species indicating the use of similar behavioral patterns. Dive profiles (scaled to equivalent depth and duration) could generally be characterized as one of four shapes: *Square*, *V*, *Skewed-Right*, and *Skewed-Left*. In addition, *Square* dives were always, and by far, the most abundant dive type. *V* dives were usually the next most abundant dive type followed by the skewed dives.

Dive type functions

Discussing general trends in dive type functions across species is very difficult because functions of dive types may not be consistent from one species to another. In any regard, most probable functions of the dive types will be proposed and possible variants will be noted.

Square dives - Almost all of the studies that have grouped diving behavior according to shape have suggested that some of the profiles had some sort of square shape (e.g. Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Boyd and Croxall 1992; Chappell et al. 1993a; Jonker and Bester 1994; Campagna et al. 1995; Schreer and Testa 1995, 1996; Burns et al. *in press*; Chapter 3). *Square* dives have been suggested to represent foraging since they are very abundant, occur in bouts or series, generally have a uniform depth within a bout, and often exhibit diel variation in maximum depth (Le Boeuf et al. 1988; 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Chappell et al. 1993a; Jonker and Bester 1994; Campagna et al. 1995; Schreer and Testa 1996). Also, the mere shape of a *Square* dive suggests that it may have a foraging function since the animal is maximizing the proportion of the time spent at a particular depth (i.e. the bottom of the dive where the prey may reside) and is descending rapidly and directly to this depth. *Square* dives for the species observed here were always, and by far, the most abundant dive type, often occurred in bouts (*personal observation*), had uniform depths within a bout (*personal observation*), and exhibited diel variation in maximum depth (within several of the species: royal penguins, Galapagos fur seals, Antarctic fur seals, southern elephant seals, and Weddell seals) which substantiates a foraging function. Diel patterns may not have been observed for *Square* dives in the other species because 1) the sample sizes were too small (blue-eyed shags and hooded seals), 2) these dives may have represented a myriad of functions for species that were not primarily foraging (grey, harp, and hooded seals), or 3) the species primarily feed on benthic prey and therefore would not exhibit diel variation in maximum depth since their prey do not vertically migrate (blue-eyed shags, grey seals, walrus, *Square* dives with R>1 for male southern elephant seals: see below).

Other functions suggested for *Square* dives are specifically benthic or pelagic foraging (Le Boeuf et al. 1988; 1992, Hindell et al. 1991b; Schreer and Testa 1996), exploring, or travelling (Kooyman 1968; Schreer and Testa 1996). Dives thought to be benthic usually have fewer wiggles than pelagic dives and exhibit weaker or no diel variation in maximum depth. This would be expected since benthic prey have a much more limited vertical range. Walrus, grey seals, and blue-eyed shags are all thought to be benthic foragers (Fay and Burns 1988; Croxall et al. 1991; del Hoyo et al. 1992; Jefferson et al. 1993; Wiig et al. 1993; Bevan et al. 1997) and all of these species had very few and small wiggles and no diel pattern towards deeper dives during the day. Male southern elephant seals have also been thought to perform some benthic foraging. *Square* dives for this species had fewer and smaller wiggles than their female counterparts. As well, when male southern elephant seal *Square* dives were subdivided based on R, dives with higher values for R had less diel variation in maximum depth, which could indicate that these were benthic dives. *Square* dives for the other species probably represented pelagic foraging with higher numbers of wiggles and stronger diel variation in maximum depth.

Square dives thought to have an exploratory or travelling function have been proposed for Weddell seals (Kooyman 1968; Schreer and Testa 1996) and were also seen in this study for this species. These were dives that had long durations relative to maximum depth (rectangular: *Square* dives with $Q < 4$). Schreer and Testa (1996) proposed that these dives would be useful for travelling since the seal spent a large amount of time below the surface (reducing drag: Williams and Kooyman 1985) and travelling potentially in a horizontal direction (although a horizontal line within a profile of depth versus time indicates only that the animal is not moving up or down for a period of time and not necessarily that it is moving horizontally). These dives had little or no diel variation in maximum depth (compared to deeper *Square* dives) suggesting that foraging is not likely (Schreer and Testa 1996). However, shallow-benthic foraging can not be ruled out.

V dives - Most studies of dive profiles have also indicated that some of the dives had a *V* or spiked shape (e.g. Hindell et al. 1991b; Bengtson and Stewart 1992; Jonker and Bester 1994; Campagna et al. 1995; Schreer and Testa 1995, 1996; Burns et al. *in press*; Chapter 3).

These dives have been thought to represent predator avoidance (Hindell et al. 1991b), travel (Hindell et al. 1991b; Le Boeuf et al. 1992; Campagna et al. 1995), or exploration (Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1996). In any event, the animal dives deep below the surface, following a direct path, to avoid predators, to search for a prey patch, or to get a better acoustical or visual image of its surroundings. The relative deepness of the *V* dives found for most species in this work is consistent with these suggestions. Also, the relatively short durations for these dives is consistent with maximizing depth while staying within duration limits (preventing extended periods of surface time while exploring).

However, the *V* dives for several species may also have a foraging function which has been suggested by Boyd and Croxall (1992) and Burns et al. (*in press*). The relatively large proportion of *V* dives performed by some of the species (royal and gentoo penguins) and strong diel variation in maximum depth and duration (stronger than that for *Square* dives: Adélie, royal, and gentoo penguins) supports this conclusion. All of these species are relatively small and would be more duration limited than the larger species. Therefore, when performing foraging dives to relatively deep depths, bottom time may have to be sacrificed in order to remain within aerobic limits causing these dive to have more of a V shape. Weddell seals and female southern elephant seals also showed strong diel variation in maximum depth and duration for *V* dives, but unlike Adélie and royal penguins which had longer mean durations for *V* dives relative to *Square* dives, their *V* shaped dives had relatively shorter durations which suggests a more exploratory function.

Skewed-Right dives - *Skewed-Right* dives have been suggested as a dive type in far fewer studies than *Square* or *V* dives (Kooyman and Gentry 1986; Chappell et al. 1993a; Jonker and Bester 1994; Schreer and Testa 1995; 1996; Burns et al. *in press*; Chapter 3) and not surprisingly were nearly absent for several of the species here (blue-eyed shags, gentoo penguins, grey seals, and walrus: <2% of all dives). These dives have been suggested to have an exploratory function (Kooyman and Gentry 1986; Jonker and Bester 1994), a travelling function (Jonker and Bester 1994), a processing function (Schreer and Testa 1996), a foraging function where prey were pursued vertically as well as horizontally (Chappell et al. 1993a), or they may simply be a result of the animal following the bottom back to a haul-out site (Schreer and Testa 1996). In any event, these dives are relatively rare and they exceed 10% of all dives in only three species (harp, hooded, and Weddell seals). This suggests that *Skewed-Right* dives may not be a terribly important component of most of the species diving regimes and are simply hybrid dives (e.g. an aborted *Square* foraging dive that has become an exploratory dive) or random dives with no specific function. Harp and hooded seals were in relatively shallow water for all of their dives reported in this study, so a bathymetric limitation seems plausible for this dive type for these animals. Dive records for Weddell seals lasted more than 6 months, covering by far the longest portion of an animal's annual cycle in this study, so it is possible that a dive type observed for Weddell seals would not be observed in other species because of the limited duration of their dive records. For Weddell seals, it has been suggested that these dives, which were most common farthest from the initial haul-out sites (Schreer and Testa 1996), may allow the seal to process food when hauling out is unlikely.

Skewed-Left dives - *Skewed-Left* dives are also fairly rare in studies of dive shape (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Jonker and Bester 1994; Schreer and Testa 1995, 1996; Burns et al. *in press*; Chapter 3) and, similar to *Skewed-Right* dives, are nearly absent for many of the species examined here (blue-eyed shags, Adélie penguins (consistent with cluster analyses from Chapter 3), royal penguins, gentoo penguins, Antarctic fur seals, grey seals, walrus, and male southern elephant seals: <2% of all dives). The rarity of this dive type suggests that it may be fairly unimportant to most species (as for *Skewed-Right* dives). However, these dives have been suggested to have a seemingly important function for northern and southern elephant seals, despite their low proportions. Several studies have suggested that these dives represent resting, sleeping, or processing of food or anaerobic metabolites underwater (Hindell et al. 1991b, Le Boeuf et al. 1992). It is thought that the period of slow descent represents when a seal stops swimming and slowly sinks. This suggestion has been substantiated by swim velocity profiles which have shown very slow velocities during part of the descent phase of these dives (Le Boeuf et al. 1992; Hindell and Burton 1993). It seems plausible that these dives do in fact represent resting in elephant seals since this species dives nearly continuously for several months (Le Boeuf et al. 1988, 1989, Hindell et al. 1991b). For the other species, however, this function seems unlikely. Many of the species (blue-eyed shags, Adélie penguins, royal penguins, gentoo penguins, Galapagos fur seals, Antarctic fur seals) generally dived continuously for less than 24 h and therefore could either rest at the surface or when hauled out.

An additional explanation, as for *Skewed-Right* dives, is simple bathymetric limitation (Schreer and Testa 1996). The two species with the highest proportions of these dives (harp and hooded seals) spent all of their recorded time in shallow waters and therefore may have been following the bottom down.

Comparisons across species

Comparing the diving patterns among species must be tentative in this study because of differences in sampling regimes, life stage, number of individuals and dives, and length of coverage. Differences in sampling intervals could be adjusted for by resampling. However, differences in life stage, number of individuals (1 to 36), total number of dives (366 to 83,404), and length of coverage (2 to 195 days) remain. These sorts of problems exist for all interspecific, interstudy comparisons and, short of collecting equal amounts of data under similar conditions for all species (usually logistically and financially impossible), must simply be considered and addressed when making comparisons.

Diving capacity - The body size of the species had an impact on diving patterns as expected. This has also been shown for larger interspecific comparisons using maximum depth and duration (Piatt and Nettleship 1985; Cooper 1986; Prince and Harris 1988; Burger 1991; Boyd and Croxall 1996; Chapter 2). Larger animals would be expected to be able to dive longer and hence deeper since they can store more oxygen (more blood) and use this oxygen more slowly (lower mass specific metabolic rate) (see Chapter 2 for a discussion of these concepts). Within the two main groups, seabirds and pinnipeds, this relationship is fairly clear with larger seabirds and pinnipeds diving deeper and longer than smaller ones. This trend can also be seen over all 13 groups, but the relationship is considerably weaker. Fur seals, which are considerably larger than penguins, do not dive deeper or longer than the larger penguins. This was also observed for maximum depth and duration in Chapter 2. Otariids, which often prey on food items that are similar to those of penguins, such as krill and cephalopods, may not need to dive deeper or longer than penguins since their prey occur at similar depths. In contrast, if otariids do have higher DMRs and less TBO_2s than phocids and seabirds, their shorter and shallower diving patterns may be due to physiological limitations. This can be seen in Table 4.8 with fur seals having only slightly longer ADLs than penguins when DMR = 2 x SMR, and the lowest ADLs of all species when DMR = 5 x SMR. Other species that would be expected to dive deeper and longer based on their body size are walrus and grey, harp, and hooded seals. In the case of the seals, these animals are all known to dive considerably deeper than the dives analyzed here (Lavigne and Kovacs 1988; Hammill et al. 1993; Folkow and Blix 1995; E.S. Nordøy *personal communication*) and their performances reported in this study are almost certainly due to limited water depth. The limited observed diving ability of the walrus is likely to be real and may be due to physiological limits if their DMR is 5 x SMR, resulting in an ADL of only 4.9 min. However, it would be unexpected for a benthic forager that feeds on non-motile prey to have such high DMRs. A more plausible explanation is that they may be able to dive to greater depths and for longer durations than have been recorded, but have little reason to do so because of the abundance of their benthic prey in shallow waters (Fay and Burns 1988).

Dive shape - The proportion of dives within each dive type across species were surprisingly similar, with *Square* dives being always, and by far, the most abundant, *V* dives being the next most abundant dive type, and the skewed dives being the least abundant. Even more surprising was that the %BTs among *Square* dives was extremely consistent across species. The only explanations for the differences observed in proportions and %BTs of *Square* dives was the type of foraging performed, water depth, and life stage (e.g. the main activity during the recording periods). The species with the three highest proportions and %BTs of *Square* dives (blue-eyed shags, grey seals, and walrus) were all benthic foragers. Also, male southern elephant seals, which are also thought to perform some benthic foraging, had the fourth highest proportion of *Square* dives. Additionally, when *Square* dives for male southern elephant seals were split using R, dives with higher values (suspected to be benthic dives because of the lack of diel variation in maximum depth) had higher %BTs. This suggests that when an animal is able to dive to the bottom depth, which is considerably shallower than its physiological depth limit (due to limited travel time to and from the bottom depth, and not a direct limit due to hydrostatic pressure), it can spend more time at the bottom of the dive (i.e. higher %BTs). These higher values would make dive profiles appear more "square" and hence more *Square* dives would be detected. Also, since these animals are diving to non-moving benthic sites, less time would be needed for exploratory dives (i.e. searching for prey sites). This is substantiated by very low numbers of *V* shaped dives for the four above mentioned species.

Contrary to the high proportions mentioned above, hooded seals had the fewest *Square* dives and the smallest %BTs among all dives combined. This was the one species that was suspected not to forage during the measurement period (Kovacs et al. 1996), which would be consistent with the low proportion of *Square* dives and %BTs. Weddell seals also had low proportions of *Square* dives and %BTs, but were observed for more than 6 months during the overwinter, gestation period, which would indicate that foraging must have been of primary importance. However, the length of these records may explain the lower proportions observed. Since the long recording periods sampled so much of these animals' behavior, it is possible that behavior recorded for Weddell seals was simply missed for other species due to their relatively short lengths of coverage. Also, unlike the penguins and fur seals that forage for only hours or days at a time, the Weddell seal spends months in the open ocean and therefore may need more time for exploring (i.e. more *V* dives), resting, or other non-foraging activities.

Depth versus duration - The rate at which duration changes with depth (slope) did not appear to be affected by body size, but divers that were limited by water depth or dived to the bottom (i.e. blue-eyed shags, walrus, and harp, grey, and hooded seals) increased dive duration more rapidly with an increase in maximum depth than did the other species. The amount of variability in duration due to changes in maximum depth (r^2) was affected by body size and decreased with increasing body size in a fairly regular pattern for all dives. This pattern was also seen for *Square* dives, but was weaker or not apparent for the other dive types, probably due to small sample sizes. Boyd and Arnbom (1991) have shown that for southern elephant seals, dive duration increases rapidly with increasing depth to a point when the rate of increase becomes much slower. If this applies to all divers, those that are limited by depth (i.e. benthic foragers and those in relatively shallow water) would only be using the first part of the curve where duration increases rapidly with increasing depth (i.e. large slopes for duration versus depth). Divers that are diving to all depths within their abilities (i.e. pelagic foragers) would follow the entire curve shown in Boyd and Arnbom (1991) and therefore would, on average, increase duration more slowly with depth (smaller slopes).

Depth and duration are more tightly coupled in smaller divers because these animals may be more duration and velocity limited than larger ones. Figure 4.4C shows that smaller divers have equal or greater Rs than larger ones. However, smaller divers would not be expected to swim as fast as larger ones because drag increases with surface area (L^2), while power increases with muscle volume (L^3). Also, smaller divers have less oxygen stores and higher mass specific metabolic rates so they cannot stay submerged as long. Considering these two factors, duration and depth should be more tightly coupled for smaller divers. Larger divers have more time during the dive cycle (longer durations) to make adjustments in swimming velocity (specifically, the rate of depth change) to increase or decrease the resulting maximum depth. Also, since these species have the potential to swim faster because of larger muscle volume to surface area ratios, and swim at equal or slower rates than smaller species, larger divers have more potential for making adjustments in swim velocity to change resulting maximum depths. The duration limitation of smaller divers is not corroborated by estimates of ADL in this study (see below), where smaller divers exceeded their ADL less often than larger divers. However, if the slopes of SI versus duration (Figure 4.5C) and previous work on ADL (Boyd and Croxall 1996) are considered (showing a weak trend toward a more rapid increase in SI with increasing duration for smaller divers and suggesting that smaller seabirds exceed their estimated ADL more often than larger pinnipeds, respectively) a stronger duration limit is indicated for smaller divers.

ADL - Comparison of ADLs and the proportion of the diving behavior that exceed these values must be tentative because, as mentioned in the methods section, many assumptions and estimates need to be made in order to calculate ADL. From the calculations performed here, the four largest divers (Weddell seals, female southern elephant seals, walrus (DMR = 5 x SMR), and male southern elephant seals) made the highest proportion of dives that exceeded their estimated ADLs. The trend for the smaller species was less clear, but most rarely exceeded their estimated ADL. This difference in the proportion of dives that exceed the estimated ADL made by small and large divers may be real or may simply indicate that the simplified models used here do not accurately estimate ADL, that calculated ADLs do not accurately reflect actual observed ADLs, or that there is no one specific ADL for a diving animal, but instead a varying limit that changes with dive type and duration.

It is likely that the results found here are due to several of these factors. Other work on this topic has shown the opposite trend to that found here, with seabirds exceeding their estimated ADLs more often than the larger pinnipeds (Boyd and Croxall 1996). However, Boyd and Croxall use a DMR of 4 x SMR in their calculations of ADL. Also, closer examination of their work shows that the largest divers, and only phocid species examined (female southern elephant seals), exceeded their estimated ADL for more than 90% of their dives while the one otariid species studied (male and female Antarctic fur seals) almost never exceeded their estimated ADL. Both of these results are similar to what was found here and the varying conclusions may merely reflect differences in the animals studied. Also, there is evidence that estimated ADLs often do not reflect the actual ADL (Burns and Castellini 1996; Boyd 1997) which may indicate that it is inappropriate to make these sorts of comparisons. If the results here for Weddell seals are compared to the only study that has measured the actual ADL in an adult (Kooyman et al. 1980), the estimates made here grossly underestimate ADL (13 versus 20 to 25 min). The methods of Boyd and Croxall (1996) would have underestimated the ADL of Weddell seals by an even larger margin. It is likely that there is no one method for estimating ADL and its components, TBO_2 and DMR. Moreover, it is probably time to measure TBO_2, DMR, and ADL directly in more species so that better models can be developed.

The estimates produced in this study likely overestimate ADL for smaller divers and underestimate ADL for larger dives. These errors are probably mainly due to errors in the estimates for DMR. If the ADL results produced here are compared to SI versus duration (Figure 4.5C and Figure 4.6) to determine if a behavioral ADL exists (Burns and Castellini 1996), it indicates that these estimated ADLs are not reflected behaviorally. Looking at the relationships between SI and duration indicates that for all species, except perhaps blue-eyed shags and Antarctic fur seals, the duration of the dive had little or no effect on the subsequent SI. This lack of relationship has been observed by others (Boyd and Croxall 1996; Boyd 1997) and suggests that most species rarely exceed their actual ADL. When looking at SI versus duration smoothed with the LOWESS method (Figure 4.6), several species exhibit an increase in SI with an increase in dive duration. However, except for blue-eyed shags, Antarctic fur seals, and perhaps Weddell seals, the increase is very small and inflections are very weak. It is clear that different methods for estimating ADL can drastically influence conclusions drawn from the results and that one must be very tentative when making conclusions based on uncorroborated ADL measurements.

The trend across dive types may still be useful, however, since the differences are relative and should be consistent within a species. The finding that *Square* dives most often exceed the estimated ADL is probably realistic. *Square* dives are likely to represent foraging and a diver would be expected to maximize the length of these dives even at a cost. Also, consistent with the suggestion that some of the smaller divers may also forage when performing *V* dives and that foraging dives may appear more V shaped when pushing duration limits, gentoo penguins and Antarctic fur seals exceed their estimated ADLs most often when performing these dives.

Comparisons with previous work

For all of the species studied here, except royal penguins, previous work had been conducted on either the same data sets used here or different data. Many of these works involved some sort of dive classification using maximum depth, duration, or the shape of the dive profile (Table 4.9). Dives from royal penguins, Galapagos fur seals, grey seals, hooded seals, and walrus have not been previously classified (Kooyman and Trillmich 1986a; Fay and Burns 1988; Wiig et al. 1993; Lydersen et al. 1994; Folkow and Blix 1995). Dives from most of the other species (blue-eyed shags, Adélie penguins, gentoo penguins, Antarctic fur seals, and harp seals) were classified using primarily maximum depth and duration and do not allow for reasonable comparisons with this work (Croxall et al. 1991; Boyd and Croxall 1992; Wanless et al. 1992; Williams et al. 1992; Chappell et. al. 1993a; Boyd et al. 1994; Lydersen and Kovacs 1996; Bevan et al. 1997). However, some of these works did address dive shape at least peripherally. Chappell et al. (1993a) found dives with all of the same basic shapes defined here for Adelie penguins, but considered both skewed dive shapes to be a type of foraging where prey were pursued vertically as well as horizontally. There is no concrete evidence to contradict this here, but the lack of diel variation in maximum depth for both skewed dive shapes suggests that they may not have a foraging function (although Adelie penguin *Square* dives also showed very little diel variation in maximum depth). For Antarctic fur seals, in contrast to the 81 % *Square* dives found here, Boyd and Croxall (1992) found that most Antarctic fur seal dives had a V shape while *Square* dives were rare. This is surprising since even visual inspection of Antarctic fur seal dive profiles in this study indicate that most dives have a square shape. However, the work done by Boyd and Croxall (1992) and that conducted here utilized different data sets and therefore these conflicting determinations may be real.

For only two of the species studied here (Weddell seals and southern elephant seals), had previous work been conducted to classify dive patterns using the shape of the dive profile (Hindell et al. 1991b; Jonker and Bester 1994; Campagna et al. 1995; Schreer and Testa 1995, 1996; Burns et al. *in press*). However, work conducted on northern elephant seals (Le Boeuf et al. 1988, 1992) and crabeater seals (Bengtson and Stewart 1992) should also be mentioned as some of the first studies to use dive profiles as a classification criteria. Weddell seal diving patterns were originally classified using only the maximum depth and duration of the dive (Kooyman 1968), but more recently were classified into 6 dive types using dive shape (Schreer and Testa 1995, 1996). The similarity in the results found here and those reported by Schreer and Testa (1995, 1996) are not surprising since most of the same data were used and a modified version of the shape fitting algorithm presented in Schreer and Testa (1996) was used to classify dives here. However, there were some differences. Schreer and Testa (1996) found all of the same dive types as those determined here, but also found a third type of *Square* dive that was suggested to represent benthic foraging (i.e. few wiggles during bottom time and weak diel variation in maximum depth). However, even in their work, this dive type could not be distinguished using quantitative methods and was only indicated as a dive type through subjective visual analyses. Also, this dive type was rare, accounting for only 1.8 % of all the dives.

The results found here and those reported previously for southern elephant seals were also quite similar, due in part to using some of the same data (specifically for Hindell et al. 1991b). Three of the dive types presented here (*Square*, *V*, and *Skewed-Left*), four when the *Square* dives were split into two groups (potentially pelagic and benthic) based on R for males, have been reported previously in all studies of both southern and northern elephant seals (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Jonker and Bester 1994; Campagna et al. 1995). Even *Skewed-Right* dives have been previously reported by one study on female southern elephant seals (Jonker and Bester 1994). An additional dive type previously reported, but not explicitly presented here, very shallow and short dives, probably represent many of the same dives that were excluded from the shape analyses because of too few observations per dive. A difference between this work and some of the previous work on elephant seals was that a specific benthic foraging dive type could not be discriminated for females and the separation of male *Square* dives into pelagic and benthic dives was done on the basis of R, not the number or size of wiggles during bottom time. The lack of a benthic *Square* dive for females may be realistic since other work has also found that this sort of dive was not present in female records (Hindell et al. 1991b; Jonker and Bester 1994) or it was very rare (Campagna et al. 1995). As for the subdivision of *Square* dives made by males, there was no evidence found here to separate these dives based on the number and size of wiggles (*unpublished data*), although the separation based on R may have resulted in a similar subdivision. In general, previous classifications of elephant seal data (primarily subjective, but representing the largest body of literature on shape classification for a single genus of two closely related species) have strong similarities to the quantitative classifications performed here. This is encouraging and suggests that these sorts of quantitative classifications are dividing the data into potentially biologically meaningful groupings.

Utility of quantitative shape analysis

It has been shown here and by many other works (e.g. Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1996) that dives classified on the basis of shape may represent meaningful behavioral groupings. However, this type of classification may not be applicable to all species. Three species in this study (blue-eyed shags, grey seals, and walrus) basically had only one dive type that represented more than 97 % of all their dives. For these species it was useful to learn that almost all of their dives had a square shape, although this was probably already known by simply looking at the dive profiles. Therefore, either these species only perform one type of diving behavior or other criteria are needed for dive classification. It should be noted, however, that in all three species, a small number of dives (<2000), from few individuals (<6), over a short time range (<14 days), were recorded which undoubtedly presents a limited view of their overall diving patterns and abilities.

Another limitation of the shape classification is that it only uses two variables, depth and time. Dive types and functions are inferred from two dimensional patterns when the actual three dimensional activity during these dives is unknown. In general, shape classification is the logical next step, after simply looking for patterns in depth and duration, for grouping dive patterns measured as time versus depth. These sorts of analyses have given us a glimpse of not only how deep and long animals dive, but what they do during the dives. Additional variables (e.g. velocity, stomach temperature, and jaw movements) will give more information about what an animal is doing while diving and will undoubtedly help in determining more representative dive types and more accurate functions for these types. However, the quantitative techniques presented here should also be useful for analytical interpretations of these additional data.

Conclusions

There were several strong similarities in diving patterns across different species indicating the utility of a unified classification approach and that these species appear to utilize similar behavioral patterns. Dive profiles (scaled to equivalent depth and duration) could generally be characterized as one of four shapes: *Square*, *V*, *Skewed-Right*, and *Skewed-Left*. Variation in diving patterns across species could be attributed to four main factors: 1) body size, 2) water depth, 3) foraging ecology, and 4) life stage. As expected, larger divers dived deeper and longer than smaller ones, although foraging ecology and water depth also had a large impact. Surprisingly, body size had no discernable effect on other diving patterns (e.g. proportions of dive types, the proportion of a dive that was considered bottom time, and the rate at which duration increased with depth) which were mainly affected by foraging ecology and water depth. Two strong similarities across species were that *Square* dives were always, and by far, the most abundant dive types and that approximately 50% of the duration of these dives was spent near the maximum depth (although small differences in these two factors could be attributed to foraging ecology and water depth). Functional analyses indicated similar functions for dive types to those previously reported. However, as in most previous work, behavioral determinations of dive types were highly speculative and indirectly inferred. Additional information such as velocity, stomach temperature, and heart rate will permit more credible assessments of dive functions as well as more meaningful groupings of observed dive patterns.

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Table 4.1. Sources of raw TDR dive data.

Species[a]	Source	Resulting or relevant publications
Blue-eyed shag	I.L. Boyd	Bevan et al. 1997
Adélie penguin	M.A. Chappell	Chappell et al. 1993a, b
Royal penguin[b]	M.A. Hindell	Hindell et al. 1996
Gentoo penguin[b]	I.L. Boyd	-
Galapagos fur seal	M. Horning	Horning 1992, Horning and Trillmich 1997
Antarctic fur seal[b]	I.L. Boyd	Boyd and Croxall 1992; Boyd et al. 1994
Harp seal	C. Lydersen and K.M. Kovacs	Lydersen and Kovacs 1993, 1996
Grey seal	C. Lydersen and K.M. Kovacs	Lydersen et al. 1994
Hooded seal	K.M. Kovacs and C. Lydersen	Kovacs et al. 1996
Weddell seal	J.W. Testa and J.F. Schreer	Testa 1994; Schreer and Testa 1995, 1996
Walrus	Ø. Wiig	Wiig et al. 1993
Southern elephant seal	M.A. Hindell	Hindell et al. 1991a, b; 1992

[a] Scientific names: Adélie penguin (*Pygoscelis adeliae*), Antarctic fur seal (*Arctocephalus gazella*), Galapagos fur seal (*Arctocephalus galapagoensis*), gentoo penguin (*Pygoscelis papua*), grey seal (*Halichoerus grypus*), harp seal (*Phoca groenlandica*), hooded seal (*Cystophora cristata*), royal penguin (*Eudyptes schlegeli*), blue-eyed shag (*Phalacrocorax atriceps*), southern elephant seal (*Mirounga leonina*), walrus (*Odobenus rosmarus*), and Weddell seal (*Leptonychotes weddellii*).

[b] Data not previously published.

Table 4.2. Dive statistics (mean±s.d.: maximum depth (m) and duration (min)) and proportions of dive types for records from Adélie penguins and Galapagos fur seals resampled at different sampling intervals. Int., sampling interval (sec).

Int.	All dives			Dives $ 5 obs.			Square			V			Skewed-Right			Skewed-Left		
	n	Depth	Dur	n	Depth	Dur	n (%)	Depth	Dur	n (%)	Depth	Dur	n (%)	Depth	Dur	n (%)	Depth	Dur
Adélie Penguin																		
1	2571	23.1	0.95	2348	24.3	1.03	1706	19.7	0.92	555	39.0	1.41	68	20.3	0.95	19	23.2	0.99
		±29.8	±0.55		±15.6	±0.50	(72.7)	±13.7	±0.48	(23.6)	±12.7	±0.38	(2.9)	±7.6	±0.29	(0.8)	±9.5	±0.23
2	2512	22.9	0.99	2282	24.8	1.08	1613	20.1	0.96	584	38.5	1.41	63	19.3	0.93	21	22.2	0.99
		±15.9	±0.54		±15.5	±0.48	(70.7)	±13.6	±0.46	(25.6)	±12.8	±0.38	(2.8)	±7.6	±0.29	(0.9)	±9.6	±0.23
3	2463	23.8	1.02	2202	25.5	1.13	1470	20.5	1.01	646	37.6	1.41	66	19.1	0.96	18	20.6	0.96
		±30.2	±0.53		±15.2	±0.46	(66.8)	±13.3	±0.44	(29.3)	±13.1	±0.39	(3.0)	±7.3	±0.30	(0.8)	±9.1	±0.26
4	2440	23.4	1.05	2149	25.9	1.16	1370	20.9	1.05	681	36.9	1.41	74	19.4	0.97	24	20.2	0.97
		±15.7	±0.52		±15.1	±0.45	(63.8)	±13.3	±0.43	(31.7)	±13.2	±0.39	(3.4)	±8.0	±0.29	(1.1)	±10.3	±0.24
5	2406	23.6	1.08	2060	26.7	1.21	1219	21.5	1.10	739	36.2	1.42	76	19.8	1.04	25	21.5	1.05
		±15.7	±0.51		±14.8	±0.43	(59.2)	±13.0	±0.41	(35.9)	±13.5	±0.40	(3.7)	±6.9	±0.26	(1.2)	±10.6	±0.31
10	2354	23.6	1.18	1650	30.3	1.43	629	25.3	1.35	912	34.8	1.52	78	22.3	1.24	28	23.3	1.22
		±15.4	±0.50		±13.5	±0.37	(38.1)	±12.7	±0.37	(55.3)	±12.9	±0.36	(4.7)	±7.5	±0.24	(1.7)	±7.4	±0.26
Galapagos Fur seal																		
5	10469	22.5	1.15	7052	30.5	1.58	4996	29.7	1.69	1089	39.1	1.42	333	26.8	1.40	629	23.6	1.16
		±26.7	±0.86		±19.6	±0.73	(70.8)	±18.4	±0.74	(15.4)	±23.9	±0.69	(4.7)	±16.9	±0.59	(8.9)	±16.9	±0.55
10	9361	24.0	1.36	5626	34.9	1.93	3799	33.3	2.02	1088	45.1	1.80	306	28.9	1.72	430	27.7	1.56
		±24.0	±0.84		±18.7	±0.60	(67.5)	±17.0	±0.61	(19.3)	±21.6	±0.55	(5.4)	±16.5	±0.49	(7.6)	±17.3	±0.46
15	8465	25.4	1.57	4722	37.8	2.19	3083	35.0	2.25	1011	49.8	2.12	289	30.1	2.01	334	34.2	1.97
		±20.0	±0.81		±18.1	±0.51	(65.3)	±15.8	±0.53	(21.4)	±20.0	±0.46	(6.1)	±16.5	±0.46	(7.1)	±17.4	±0.44
20	7741	26.8	1.78	3733	41.0	2.49	2246	37.6	2.54	925	53.2	2.43	251	32.9	2.40	306	35.3	2.40
		±24.5	±0.81		±17.7	±0.47	(60.2)	±14.4	±0.48	(24.8)	±19.2	±0.40	(6.7)	±16.8	±0.46	(8.2)	±17.7	±0.51
25	7126	27.6	1.98	2619	43.1	2.89	1496	39.3	2.89	668	56.4	2.77	211	36.3	3.00	239	36.2	3.06
		±19.7	±0.87		±18.4	±0.58	(57.1)	±14.5	±0.50	(25.5)	±19.4	±0.44	(8.1)	±19.1	±0.81	(9.1)	±17.9	±0.97
30	6587	28.4	2.20	1615	42.1	3.45	837	39.0	3.37	385	57.7	3.25	184	33.0	3.71	204	33.7	3.89
		±19.7	±0.99		±19.9	±0.97	(51.8)	±15.8	±0.71	(23.8)	±20.7	±0.70	(11.4)	±19.8	±1.26	(12.6)	±17.7	±1.63

Table 4.3. Dive variables used for comparisons across species and to determine dive-type subdivisions.

Dive variable	Definition	Source
Maximum depth (m)	The maximum depth reading during the dive	-
Duration (min)	The duration between the first and last reading of the dive, plus one sampling interval	-
Q (m min^{-1})	Maximum depth ÷ duration	Schreer and Testa 1995
Slope	The rate at which one variable changes with another	-
r^2	The amount of variability in one variable accounted for by another (i.e. how tightly the two variables are coupled)	-
Bottom time (BT, in min) and BT ÷ duration (%BT)	The time interval between the first and last depths equal to or greater than 80% of the dive's maximum depth	Dive Analysis[a]
Wiggle count (WC) and WC ÷ BT (per min)	The number of ascent-to-descent occurrences that occur during bottom time and differ by more than 2 times the resolution of the TDR	Dive Analysis[a]
Average wiggle distance (AVWD, in m) and AVWD ÷ Depth	The average depth difference between the deepest and shallowest points of a wiggle	Dive Analysis[a]
Average descent rate (m s^{-1})	The rate of travel between the start of the dive and the beginning of bottom time	Dive Analysis[a]
Average ascent rate (m s^{-1})	The rate of travel between the end of bottom time and the end of the dive	Dive Analysis[a]
Average rate of depth change (R, in m s^{-1})	The average rate of depth change: (descent rate + ascent rate) ÷ 2	This study
Post-dive surface interval (SI, in min) and SI ÷ duration	The time between the end of a dive and the beginning of the subsequent dive	-
STD (m)	The standard deviation or variability of depth readings during BT	This study
CV	The coefficient of variation: 100 x (STD ÷ mean)	This study

[a] Dive Analysis manual (Version 4.0) and program (Version 4.08), Wildlife Computers, Woodinville, WA, USA.

Table 4.4. Life history information on the various species relevant to the interpretation of their diving records in this study.

Species (Gender)	Mass (kg)		Primary prey	Distribution	Relevant details	Source
	Lit.	This study (mean±s.d.)				
Blue-eyed shag (%,&)	2	2.42 ±0.23	Benthic fish	Southern S. America	Foot-propelled pursuit-diver	Burger 1991; del Hoyo et al. 1992; Bevan et al. 1997
Adélie penguin (%,&)	5	3.8 ±0.3	Krill	Circumpolar (S)	At-sea periods lasting up to 26 h. Ten min to 5 h to begin foraging. Not limited by water depth.	Burger 1991; Chappell et al. 1993a
Royal penguin (?)	5.3[a]	5.3[b]	Krill and amphipods	Macquarie Is. (S. of New Zealand)	Sometimes considered a subspecies of Macaroni penguin. Offshore pelagic feeder.	del Hoyo et al. 1992
Gentoo penguin (?)	5.5	5.5[b]	Krill and fish	Subantarctic	At-sea periods last ~14 h. Inshore feeder that may forage for benthic prey.	Burger 1991; Williams et al. 1992; Robinson and Hindell 1996
Galapagos fur seal (&)	30	29.0 ±3.2	Cephalopods and fish	Galapagos Is.	Continuous swimming and diving while at sea for ~16 h (7.6-27). Diving bouts start and end ~2 h before and after being ashore. ~19 km (4.7-65) to foraging areas. Depart just before dark and return soon after daylight.	Kooyman and Trillmich 1986a; Jefferson et al. 1993
Antarctic fur seal (&)	35	34.4 ±2.9	Krill and fish	Antarctic convergence	Lactating females taking foraging trips of approximately 3-5 days.	Jefferson et al. 1993; Boyd and Croxall 1992; I.L. Boyd *personal communication*
Harp seal (&)	120	138.2 ±6.7	Pelagic fish and crustaceans, bottom fish	Arctic and N. Atlantic Ocean	Pupping in drifting pack-ice. Record from within 12 day lactation period (day 1-day 11). Mean at-sea period is 3.9 h. Water depth of ~63 m, but to at least 106 m (deepest dive).	Jefferson et al. 1993; Lydersen and Kovacs 1993, 1996

Table 4.4 (*continued*).

Species (Gender)	Mass (kg)		Primary prey	Distribution	Relevant details	Source
	Lit.	This study (mean±s.d.)				
Grey Seal (&)	240	201.6 ±29.9	Benthic fish and invertebrates, pelagic fish	Subarctic temperate in N. Atlantic	Lactating, ice-breeding females. No correlation between female mass loss and pup mass gain, therefore females are likely to be feeding. 44.8-99.6% of time hauled-out. Max depth of water was 19 m. Often benthic feeders. Spent 73% of the time in water at the surface. Nurse every 2-3 h.	Jefferson et al. 1993; Lydersen et al. 1994
Hooded seal (%)	350	353.5 ±51.6	Cephalopods and fish	Arctic and N. Atlantic Ocean	During breeding season spending ~85% of their time hauled out. Dived for a few hours at a time (otherwise spending days at a time on the ice surface). Most lost weight. Shallow water depth (50-70 m). Seals that spent more time in the water lost more weight than those spending shorter amounts of time. Therefore, unlikely that they were feeding, but instead performing energy expensive activity.	Jefferson et al. 1993; Kovacs et al. 1996
Weddell seal (&)	425	339.2 ±42.8[a]	Fish	Circumpolar (S)	Gestating females diving within pack-ice. Movements of up to 1500 km (in total).	Jefferson et al. 1993; Testa 1994
Southern elephant seal (&)	600	394.0 ±65.1	Cephalopods and fish	Circumpolar (S)	Most seals used foraging grounds more than 1000 km from the Is. and took 2-4 weeks to get there. Most females thought to perform only pelagic dives.	Hindell et al. 1991b; Jefferson et al. 1993;
Walrus (%)	1900	1500	Benthic invertebrates	Circumpolar (N)	Water depth of less than 100 m, 30 m in vicinity of the tagging site.	Jefferson et al. 1993; Fay and Burns 1988; Gjertz and Wiig 1992; Wiig et al. 1993

Southern elephant seal (%)	4000	2272.5 ±909.0[a]	Cephalopods and fish	Circumpolar (S)	Same as female southern elephant seals except that males thought to perform both pelagic and benthic dives.	Hindell et al. 1991b; Jefferson et al. 1993;

[a] Mass estimated from interspecific length versus mass regression.

[b] Mass taken from the published literature.

Table 4.5. Recording and processing information for each species. Species with a second set of results from data sampled at a slower sampling interval were resampled so that the number of observations per dive was approximately equal for all species.

Species	Individuals
Blue-eyed shag	
Adélie penguin	
Royal penguin	
Gentoo penguin	
Galapagos fur seal	
Antarctic fur seal	
Harp seal	
Grey seal	
Hooded seal	
Weddell seal	
Southern elephant seal &	
Walrus	
Southern elephant seal %	

Table 4.6. Dive statistics (mean±s.d.): maximum depth (m) and duration (min). All dives $5 depth readings per dive. *Hybrid* dives are excluded for shape classification. Species with a second set of results from data sampled at a slower sampling interval were resampled so that the number of observations per dive was approximately equal for all species. Obs. per dive, average number of observations per dive.

Species	Obs. per dive	All			n, minus hybrids	Square			V		
		n	Max. depth	Duration		n (%)	Max. depth	Duration	n (%)	Max. depth	Duration
Blue-eyed shag	74	588	18.6±18.8	1.24±0.88	574	564 (98.3)	18.9±19.1	1.26±0.89	3 (0.5)	10.7±1.5	0.68±0.41
	16	489	21.7±19.4	1.55±0.80	477	469 (98.4)	22.0±19.6	1.57±0.80	3 (0.6)	15.0±4.4	0.90±0.20
Adélie penguin	60; 12	22897	19.2±13.2	0.99±0.39	20283	16001 (78.9)	15.6±10.1	0.90±0.36	3250 (16.0)	34.4±16.3	1.28±0.40
	12	22267	19.6±13.2	1.02±0.37	19567	14908 (76.2)	15.6±9.9	0.94±0.34	3615 (18.5)	34.0±16.1	1.29±0.40
Royal penguin	59	3185	44.6±29.7	1.98±0.83	2785	2151 (77.2)	35.4±24.4	1.83±0.85	493 (17.7)	80.5±25.5	2.54±0.55
	14	2826	49.0±28.2	2.31±0.67	2473	1580 (63.9)	37.9±21.9	2.17±0.67	774 (31.3)	72.8±26.9	2.61±0.58
Gentoo penguin	65	742	68.3±49.5	2.16±1.13	700	574 (82.0)	59.9±42.8	1.97±1.06	108 (15.4)	122.3±50.9	3.29±0.74
	17	553	89.2±38.0	2.87±0.66	482	326 (67.6)	81.2±25.8	2.74±0.49	148 (30.7)	113.0±49.6	3.28±0.79
Galapagos fur seal	22	52149	33.1±20.2	1.81±0.86	45266	33048 (73.0)	33.3±19.3	1.96±0.86	6516 (14.4)	39.4±24.1	1.51±0.80
	13	44333	36.7±19.4	2.12±0.74	36155	27642 (72.0)	36.0±18.0	2.25±0.75	6209 (16.2)	46.1±22.0	1.94±0.66
Antarctic fur seal	14	4455	27.4±21.0	1.24±0.45	3853	3124 (81.1)	26.1±16.6	1.25±0.42	458 (11.9)	48.6±34.2	1.43±1.34
Harp seal	28	6835	42.4±26.8	4.64±2.40	5926	3997 (67.4)	51.7±24.4	5.60±2.27	621 (10.5)	33.0±25.4	2.78±1.52
	17	4998	49.0±25.0	5.60±2.04	4389	2964 (67.5)	57.1±20.7	6.43±1.75	477 (10.9)	46.2±25.7	3.87±1.32
Grey seal	17	1091	9.7±3.5	2.82±1.27	1058	1030 (97.3)	9.7±3.4	2.89±1.26	3 (0.3)	13.3±2.1	1.17±0.29
Hooded seal	25	193	33.3±18.6	4.14±3.73	160	79 (49.4)	33.5±19.9	4.56±3.34	36 (22.5)	29.0±16.8	2.00±0.98
	16	140	39.2±17.4	5.47±3.89	115	52 (45.2)	40.7±18.0	6.10±3.29	19 (16.5)	37.7±18.3	3.30±2.31
Weddell seal	15	40166	198.7±121.9	15.75±6.06	33127	16761 (50.6)	207.5±117.9	16.43±6.03	6912 (20.9)	251.7±140.0	14.22±5.51
Southern elephant seal &	43	21893	448.9±185.2	21.43±5.22	19769	15808 (80.0)	414.0±153.9	21.74±4.99	2932 (14.8)	639.9±210.5	20.41±5.20
	15	21752	442.4±181.7	21.92±4.93	19134	13880 (72.6)	399.2±150.1	22.43±4.73	4268 (22.3)	579.4±204.8	20.67±4.85
Walrus	38	1386	23.5±12.9	6.31±1.82	1363	1324 (97.1)	23.4±12.5	6.43±1.75	9 (0.7)	32.3±20.2	3.80±1.83
	14	1342	23.9±12.4	6.82±1.61	1325	1289 (97.3)	23.9±12.3	6.90±1.58	9 (0.7)	34.8±17.3	4.78±1.18
Southern elephant seal %	52	14190	433.8±122.1	25.79±6.85	13318	11893 (89.3)	442.5±108.8	26.37±6.11	856 (6.4)	400.2±166.1	20.84±7.47
	18	14023	436.2±116.7	26.42±6.42	12917	10985 (85.1)	444.3±101.5	27.11±5.82	1298 (10.0)	405.0±144.6	22.20±6.06

Table 4.6 (*continued*).

Species	Obs. per dive	Skewed-Right			Skewed-Left		
		n (%)	Max. depth	Duration	n (%)	Max. depth	Duration
Blue-eyed shag	74	5 (0.9)	13.6±10.0	0.89±0.52	2 (0.3)	9.0±4.2	0.82±0.19
	16	2 (0.4)	24.0±9.9	1.50±0.42	3 (0.6)	7.7±0.6	0.67±0.06
Adélie penguin	60; 12	796 (3.9)	18.7±8.4	1.01±0.32	236 (1.2)	18.7±10.0	1.01±0.34
	12	811 (4.1)	18.5±8.1	1.02±0.31	233 (1.2)	18.6±10.2	1.01±0.35
Royal penguin	59	107 (3.8)	39.8±17.4	1.89±0.63	34 (1.2)	25.5±12.8	1.78±0.54
	14	92 (3.7)	40.3±17.4	2.09±0.63	27 (1.1)	22.8±9.9	1.87±0.47
Gentoo penguin	65	12 (1.7)	24.8±19.3	1.43±0.83	6 (0.9)	18.3±18.5	1.13±0.85
	17	7 (1.5)	18.9±16.6	1.50±0.37	1 (0.2)	47	3
Galapagos fur seal	22	2418 (5.3)	28.4±18.9	1.55±0.81	3284 (7.3)	25.0±16.5	1.33±0.71
	13	2005 (5.2)	30.9±18.4	1.88±0.71	2537 (6.6)	28.2±16.6	1.70±0.62
Antarctic fur seal	14	197 (5.1)	14.4±7.0	1.01±0.34	74 (1.9)	16.2±11.4	0.94±0.35
Harp seal	28	750 (12.7)	33.8±24.9	3.83±2.00	558 (9.4)	22.1±18.6	3.02±1.69
	17	600 (13.7)	39.6±25.6	4.88±1.74	348 (7.9)	26.1±21.3	3.98±1.83
Grey seal	17	19 (1.8)	11.6±3.7	1.54±0.68	6 (0.6)	12.8±1.8	1.89±1.47
Hooded seal	25	16 (10.0)	45.0±16.8	5.33±3.98	29 (18.1)	33.8±18.1	2.83±2.09
	16	14 (12.2)	48.1±15.0	6.24±3.82	30 (26.1)	36.3±16.9	4.29±3.03
Weddell seal	15	6358 (19.2)	179.5±99.3	16.82±6.10	3096 (9.3)	128.2±90.9	13.44±6.18
Southern elephant seal &	43	460 (2.3)	495.4±201.2	21.5±6.59	569 (2.9)	337.3±136.2	19.99±6.08
	15	464 (2.4)	477.4±204.7	21.58±6.70	522 (2.7)	337.8±131.7	21.32±5.87
Walrus	38	21 (1.5)	21.2±6.3	4.23±1.60	9 (0.7)	30.7±37.0	3.06±1.35
	14	20 (1.5)	21.0±11.4	5.15±1.00	7 (0.5)	21.1±8.7	4.29±0.49
Southern elephant seal %	52	354 (2.7)	385.1±187.6	27.2±10.4	215 (1.6)	345.7±163.7	20.73±9.25
	18	403 (3.1)	404.5±160.7	29.14±9.21	231 (1.8)	356.0±145.2	22.52±8.98

Table 4.7. Dive statistics (mean±s.d.) for dive types resulting from a hierarchical classification. R, average rate of depth change ($m\ s^{-1}$); Q, maximum depth ÷ duration ($m\ min^{-1}$); BT, bottom time; %BT, bottom time ÷ duration; WC, wiggle count; AVWD, average wiggle distance; STD, standard deviation of the mean BT depth.

Species	Dive type	Criteria	n	%	Max. Depth (m)	Duration (min)	BT (min)	%BT	WC	AVWD (m)	STD (m)
Antarctic fur seal	V	R<0.8	110	24	13.6±5.35	0.92±0.30	-	-	-	-	-
		R$0.8	348	76	59.7±31.9	1.59±0.59	-	-	-	-	-
Harp seal	Square	R<0.5	425	14	13.7±13.3	3.91±1.84	1.84±1.54	45.3±22.1	0.19±0.44	0.63±1.62	2.18±1.44
		R$0.5	2539	86	64.3±10.2	6.85±1.32	4.47±1.38	64.0±10.7	0.23±0.58	1.68±4.48	6.21±4.19
	V	R<0.48	222	47	24.8±18.3	3.76±1.55	-	-	-	-	-
		R$0.48	255	53	64.9±14.1	3.97±1.07	-	-	-	-	-
Weddell seal	Square	Q<4	1947	12	24.8±19.2	11.00±6.15	6.16±5.31	51.7±24.6	0.23±0.63	1.45±3.86	5.13±3.18
		Q$4	14814	88	231.5±103.5	17.14±5.64	8.99±3.90	51.4±11.1	0.95±0.90	17.87±20.48	26.77±18.05
Walrus	Square	R<0.6	519	41	19.7±7.2	6.39±1.52	4.43±1.63	67.2±14.4	0.02±0.13	0.06±0.45	2.05±2.05
		0.6#R<1.0	494	38	24.3±11.4	7.17±1.52	5.57±1.35	77.4±5.7	0.01±0.08	0.01±0.19	3.53±2.64
		R$1.0	276	21	31.2±17.1	7.39±1.54	6.02±1.35	81.5±5.4	0.00±0.06	0.01±0.18	6.19±3.03
Southern elephant seal %	Square	R<1.0	3250	30	368.5±104.1	28.51±7.12	13.23±5.28	45.3±10.2	0.42±0.71	9.22±20.92	32.50±20.64
		R$1.0	7735	70	476.2±81.4	26.52±5.05	15.25±4.59	56.7±8.6	0.74±0.86	6.66±12.11	46.59±30.64

Table 4.8. Estimated aerobic dive limits (ADLs) and the proportion of dives that exceed these values. Sq, *Square*; SR, *Skewed-Right*; SL, *Skewed-left*.

Species	Mass (kg)		ADL (min)[c,d,e]	%>ADL					
	Lit.[a]	This study[b] (mean±s.d.)		All	All $ 5 obs.	Sq	V	SR	SL
Blue-eyed shag	2.2	2.42±0.23	2.8	5.1	6.1	6.4	0.0	0.0	0.0
Adélie penguin	5.0	3.8±0.3	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Royal penguin	5.3[f]	5.3[g]	3.5	0.4	0.4	0.1	1.2	0.0	0.0
Gentoo Penguin	5.5	5.5[g]	3.5	8.0	11.0	1.2	36.5	0.0	0.0
Galapagos fur seal	30	29.0±3.2	4.6 *1.8*[h]	0.2 *38.6*	0.3 *66.3*	0.4 *73.4*	0.1 *57.3*	0.3 *50.2*	0.1 *38.9*
Antarctic fur seal	35	34.4±2.9	4.8 *1.9*	0.0 *5.1*	0.0 *7.7*	0.0 *6.7*	0.0 *20.5*	0.0 *1.0*	0.0 *1.4*
Harp seal	120	138.2±6.7	10.2	0.3	0.5	0.5	0.0	0.0	0.6
Grey Seal	240	201.6±29.9	11.2	0.0	0.0	0.0	0.0	0.0	0.0
Hooded seal	350	353.5±51.6	12.9	2.6	5.7	5.8	0.0	7.1	3.3
Weddell seal	425	339.2±42.8	12.7	50.0	68.7	74.3	59.0	74.7	47.4
Southern elephant seal (&)	600	394.0±65.1	13.2	97.1	97.8	99.0	95.4	94.8	95.6
Walrus	1900	1500	12.3[i] *4.9*	0.2 *82.3*	0.2 *90.8*	0.2 *92.6*	0.0 *44.4*	0.0 *60.0*	0.0 *14.3*
Southern elephant seal (%)	4000	2272.5±909.0	20.5	85.5	86.9	92.4	60.9	82.9	57.6

[a] Sources for mass: Burger 1991, del Hoyo et al. 1992, and Jefferson et al. 1993.

[b] Mass used to calculate ADL.

[c] Diving metabolic rate (DMR) (ml O_2 min^{-1}) is assumed to be 2 x standard metabolic rate (SMR) for all species except for the two fur seals where DMR is assumed to be either 2 or 5 x SMR. SMR for the seabirds was calculated using SMR = $13.0M_b^{0.729}$ (Aschoff and Pohl 1970; Kooyman 1989) and for marine mammals using SMR = $10.1M_b^{0.75}$ (Kleiber 1961), where M_b equals body mass (kg) and SMR is in ml of O_2 min^{-1}. SMR and DMR were divided my mass to scale them to a unit mass (ml O_2 min^{-1} kg^{-1}).

[d] Calculated available mass specific O_2 stores (ml O_2 kg^{-1}) for the various groups was 58 for birds, 60 for phocids, and 40 for otariids (Kooyman 1989).

[e] ADL (min) = mass specific O_2 stores ÷ mass specific DMR with these resulting equations: $ADL_{Phocids} = 2.97M_b^{0.25}$, $ADL_{Otariids(2xSMR)} = 1.98M_b^{0.25}$, $ADL_{Otariids(5xSMR)} = 0.79M_b^{0.25}$, and $ADL_{Birds} = 2.23M_b^{0.271}$.

[f] Mass estimated from interspecific length versus mass regression.

[g] Masses taken from lit.

[h] Numbers in italics are for DMR = 5 x SMR.

[i] The walrus ADL was calculated using the otariid equations.

Table 4.9. Previous dive classifications. Dives from royal penguins, Galapagos fur seals, grey seals, hooded seals, and walrus have not been previously classified.

Species	Classification criteria	Sources
Blue-eyed shag	1) short and shallow (# 2 min. and < 20 m) 2) long and deep (>2 min and > 35 m)	Croxall et al. 1991; Wanless et al. 1992; Bevan et al. 1997
Adélie penguin	1) short (<0.33 min or no abrupt inflections in descent and ascent rate) 2) long and deep ($20 m, $1 min, or abrupt inflections in descent and ascent rate): 2a) mean depth 13-15 m, 2b) mean depth 34-46 m $2_{\text{Variations}}$) Square, V, skewed-right, and skewed-left shapes.	Chappell et al. 1993a
Gentoo Penguin	1) shallow (<21 m) 2) deep (>30)	Williams et al. 1992
Antarctic fur seal	Dive classification 1) V shaped 2) square shaped *Bout classification* 1) short (17 min) 2) long (80 min) 3) shallow (12 min, near surface) 4) deep (19 min, 40-50 m)	Boyd and Croxall 1992; Boyd et al. 1994
Harp seal	1) shallow, short (means of 5 m and 0.5 min) 2) intermediate (means of 49 m and 4.6 min) 3) deep, long (means of 63 m and 7.2 min)	Lydersen and Kovacs 1996
Weddell seal	*Original classification* (1968) 1) short, shallow (<100 m and 5 min) 2) long (<200 m and >20 min) 3) deep (>200 m and 8-15 min) *Shape classification* (1995, 1996) 1) square shaped 1a) many wiggles during bottom time 1b) no or few wiggles during bottom time 1c) rectangular (long and shallow) 2) V shaped 3) skewed-right shaped 4) skewed-left shaped	Kooyman 1968; Schreer and Testa 1995; 1996
Southern elephant seal (&)	1) square 1a) many wiggles during bottom time 1b) no or few wiggles during bottom time (rare) 2) parabolic shaped, V shaped 3) skewed-right shaped 4) skewed-left shaped 5) short, shallow (<1.5 min) 6) hybrids	Hindell et al. 1991b; Jonker and Bester 1994; Campagna et al. 1995. Also see Le Boeuf et al. 1988, 1992 for similar classification of the closely related northern elephant seal (*Mirounga angustirostris*)
Southern elephant seal (%)	similar to females except that 1b (square dives with no or few wiggles during bottom time) were much more common	Hindell et al. 1991b

Figure 4.1. Shapes used for the classification protocol.

Figure 4.2. Annual coverage for the various species.

Figure 4.3. Dive type proportions, mean maximum depth, and mean duration. A) Proportion (%) of dive types using resampled data, B) Proportion (%) of dive types using the original sampling intervals (see text), C) Mean maximum depth (m), D) Mean duration (min). Species are organized from smallest (left) to largest (right). Shag, blue-eyed shag; GFS, Galapagos fur seal; AFS, Antarctic fur seal; SES-F, female southern elephant seal; SES-M, male southern elephant seal.

Figure 4.4. Maximum depth versus duration and mean rate of depth change. A) Slope and B) r^2 for maximum depth versus duration, C) Mean rate of depth change (R in m). Species are organized from smallest (left) to largest (right). Shag, blue-eyed shag; GFS, Galapagos fur seal; AFS, Antarctic fur seal; SES-F, female southern elephant seal; SES-M, male southern elephant seal.

Figure 4.5. Post-dive surface interval and post-dive surface interval versus duration. A) Mean post-dive surface interval (min), B) Mean post-dive surface interval ÷ duration, C) Slope and D) r^2 for post-dive surface interval versus duration. Species are organized from smallest (left) to largest (right). Shag, blue-eyed shag; GFS, Galapagos fur seal; AFS, Antarctic fur seal; SES-F, female southern elephant seal; SES-M, male southern elephant seal.

Figure 4.6. Post-dive surface interval versus dive duration smoothed by the LOWESS method. For Adélie penguins, Galapagos fur seals, Weddell seals, and female and male southern elephant seals, a subsample of approximately 5500 dives was used.

Figure 4.7. Statistics for the bottom time of *Square* dives. Mean A) Bottom time (BT in min), B) Bottom time ÷ duration (%BT), C) Wiggle count (WC) and WC ÷ BT, D) Average wiggle distance (AVWD in m) and AVWD ÷ maximum depth, E) Standard deviation (STD in m) and coefficient of variation (CV) for depth during BT. Species are organized from smallest (left) to largest (right). Shag, blue-eyed shag; GFS, Galapagos fur seal; AFS, Antarctic fur seal; SES-F, female southern elephant seal; SES-M, male southern elephant seal.

Figure 4.8A. Diel variation in percent dive frequency, standardized maximum depth (mean± s.e.), and standardized duration (mean± s.e.) for blue-eyed shag, grey seal, hooded seal, Galapagos fur seal, Antarctic fur seal, gentoo penguin, walrus, and harp seal. Patterns are shown for each dive type (*Square*, *V*, *Skewed-Right*, and *Skewed-Left*) and for any additional dive types that resulted from the hierarchical classifications. Dive types with too few observations to show patterns adequately or with very similar patterns to previously displayed types are not shown. Maximum depth and duration were standardized for each species with the mean equal to 0.5 and one standard deviation equal to 0.25. R, average rate of depth change (m s^{-1}).

Figure 4.8B. Diel variation in percent dive frequency, standardized maximum depth (mean± s.e.), and standardized duration (mean± s.e.) for female and male southern elephant seal, royal penguin, Weddell seal, and Adélie penguin. Patterns are shown for each dive type (*Square*, *V*, *Skewed-Right*, and *Skewed-Left*) and for any additional dive types resulting from the hierarchical classifications. Dive types with too few observations to show patterns adequately or with very similar patterns to previously displayed types are not shown. Maximum depth and duration were standardized for each species with the mean equal to 0.5 and one standard deviation equal to 0.25. R, average rate of depth change ($m\ s^{-1}$); Q, maximum depth ÷ duration ($m\ min^{-1}$).

Figure 4.9. Frequency histograms for dive variables that indicated additional dive divisions within several species. R, average rate of depth change (m s^{-1}); Q, maximum depth ÷ duration (m min^{-1}).

CHAPTER 5

General Conclusions

In this thesis, general patterns in the reported diving capacities of nearly all groups of air-breathing vertebrates were examined, various algorithms for analyzing and classifying time-depth recorder (TDR) data were presented, tested, and compared, and diving behavior from 12 species of pinnipeds and seabirds were classified and compared.

In the most general sense, this work has shown that body size has a considerable effect on an animal's diving behavior, although foraging ecology and factors surrounding the collection of the data are also of considerable importance. Interspecifically, the maximum depths and durations attained by air-breathing vertebrates increase with increasing body mass, although this relationship was not always present when smaller taxonomic groups were analyzed (Chapter 2). This has been shown previously for various seabirds (alcids, cormorants, and penguins: Piatt and Nettleship 1985; Cooper 1986; Prince and Harris 1988; Burger 1991), although this work and the concurrent work done by Boyd and Croxall (1996) were the first to quantify this relationship for pinnipeds. This work was also the first to show this relationship for cetaceans, to include reported values for nearly all diving animals, and to compare these relationships across all major taxa of diving animals.

In these comparisons it was shown that most of the smaller taxonomic groups also had strong allometric relationships between diving capacity (maximum depth and duration) and body mass. Notable exceptions were mysticete cetaceans and diving/flying birds, which displayed no relationship between maximum diving depth and body mass, and otariid seals, which had no relationship between maximum diving depth or duration and body mass. Within diving/flying birds, only alcids had a significant relationship (for depth). The diving capacities of penguins had the highest correlations to body mass, followed by odontocete cetaceans and phocid seals. Mysticete cetaceans had a strong relationship between only maximum duration and body mass. Comparisons across the various groups indicated that alcids, penguins, and phocids are all exceptional divers relative to their masses and that mysticete cetaceans dive to shallower depths and for shorter periods than would be predicted from their size. Also, in agreement with Burger (1991), alcids dive deeper than penguins relative to their size, and in agreement with Boyd and Croxall (1996), seabirds generally have greater mass specific diving capacities than pinnipeds. Lastly, at the end of Chapter 2, it was suggested that using mean values and dive shape would be useful for comparing diving patterns across species because they may better reflect natural diving behavior as opposed to the rarely performed maximums.

Calculating mean values for diving behavior is a relatively easy process, but organizing diving behavior into different groups is a far more difficult problem. Most studies that have attempted to organize diving behavior have primarily grouped dives subjectively according to perceived similarities in maximum depth and duration (e.g. Kooyman 1968; Croxall et al. 1991; Goebel et al. 1991; Wanless et al. 1992; Williams et al. 1992; Chappell et al. 1993a). It is perhaps inappropriate to include solely maximum depth and duration into classification analyses because both of these variables may display strong diel variation (e.g. Bengtson and Stewart 1992; Castellini et al. 1992a; Boyd et al. 1994; Schreer and Testa 1996) that can obscure the determination of behavioral groupings. For example, an animal may perform similar behaviors at different times of day (e.g. foraging). However, if its prey vertically migrate, the animal under study will forage at different depths throughout the day depending on the location of its prey. Therefore, even though the shape of a dive (depth versus time) may remain similar (due to optimizing time at the prey patch) and indicate comparable behavior, depth and duration could vary drastically.

Recently, several studies have included dive shape as a means of grouping diving behavior (Le Boeuf et al. 1988, 1992; Hindell et al. 1991b; Bengtson and Stewart 1992; Schreer and Testa 1993, 1995, 1996; Jonker and Bester 1994; Brillinger et al. 1995; Campagna et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in* *press*). Many of these works relied solely or primarily on subjective comparisons of dive profiles. This introduces human bias and prevents cross-study comparisons due to individual classification protocols. A few studies have attempted quantitative classification of diving patterns (Hindell et al. 1991b; Schreer and Testa 1993, 1995, 1996; Boyd et al. 1994; Brillinger et al. 1995; Schreer et al. 1995; Brillinger and Stewart 1997; Burns et al. *in press*), although the individual classification protocols for these analyses have also varied considerably. In short, the methods for classifying diving patterns have varied considerably, obscuring interspecific comparisons.

Therefore, to determine a suitable method for classifying dive profiles that could be applied to all sorts of diving behavior, four techniques for grouping multivariate observations were tested and compared (Chapter 3). These included k-means and fuzzy c-means clustering techniques from the field of statistics, and Kohonen self-organizing map (SOM) and fuzzy adaptive resonance theory (ART) from the field of artificial neural networks. A Monte Carlo simulation was performed on artificially generated data, with known solutions, to test clustering performance under various conditions (i.e. well defined or overlapping groups, varying numbers of attributes, varying numbers of groups, and auto-correlated attributes). As well, performance was tested on real data sets from Adélie penguins (*Pygoscelis adeliae*), southern elephant seals (*Mirounga leonina*), and Weddell seals (*Leptonychotes weddellii*). K-means, fuzzy c-means, and SOM all performed equally well on the artificially generated data while fuzzy ART had error rates that were twice as high. All techniques showed decreasing performance with increasing overlap among groups and increasing numbers of groups, but increasing performance with increasing numbers of attributes. Fuzzy ART was the most sensitive to the varying simulation parameters. When clustering real data, both c-means and SOM classified observations into clusters that were closer together (relative to k-means) and hence had less distinct boundaries separating the clusters. K-means performed as well as c-means and SOM, but its classification of real data was more logical when compared to the actual dive profiles. K-means is also readily available on most statistical software packages. Considering all of these factors, k-means clustering appears to be the best method, among those examined, for grouping multivariate diving data. As a side note, however, several of the other methods showed much promise for certain situations. For example, group memberships obtained when using fuzzy c-means would be useful for identifying hybrids (an observation with characteristics of more than one group). Also, even though fuzzy ART had the poorest performance of all methods examined, its characteristic of being able to group observations in an almost entirely unsupervised way (e.g. without having to input the number of groups beforehand) shows much potential for remote applications (e.g. "on board" processing). Therefore, improvements in all of these methods (specifically the neural network methods which are currently evolving rapidly) should be monitored for their applicability for analyzing behavioral data.

Now that a suitable technique for organizing diving behavior had been found, this technique was then applied to dive data from several different species (Chapter 4). The species included one cormorant, 3 penguins, 2 otariids (eared seals), 5 phocids (true seals), and a walrus. However, after classifying dive data from the different species, dive shapes observed were so similar that it seemed appropriate to use a more unified and simple approach. Therefore, dives were compared to simple geometric shapes and classified as the type of shape to which it was most similar. This method was relatively generic, automated, and allowed more direct comparisons across species. More than 230,000 dives from 12 species were analyzed and approximately 150,000 were classified according to dive shape. Dive profiles (scaled to equivalent depth and duration) could generally be characterized as one of four shapes: square, V, skewed-right, and skewed-left. Comparative analyses across these dive types and the different species, revealed that square dives were always, and by far, the most abundant dive type, usually followed by V dives, and then the skewed dives. Also, the proportion of time the animals spent at the bottom of square dives was quite uniform across species (~50%) indicating that similar foraging strategies were being used, at least relative to the shapes of dives. Observed differences across species revealed that, as expected, larger animals generally dived deeper and longer than smaller ones, although fur seals and the walrus were exceptions with more limited diving capacities than expected based on their body size. Also, smaller divers had a tighter coupling between dive depth and duration than larger ones. Surprisingly, few other dive variables (e.g. the rate at which dive duration increases with depth, the proportion of square dives, and the proportion of bottom time during square dives) were affected by body size. It appears, instead, that physical (water depth) and ecological (type of prey) constraints were prevalent in the observed patterns.

Analyses using estimated ADL indicated that this was not a good estimate of actual ADL. However, comparisons of ADL across dive types, which may still be valid since the differences are relative and should be consistent within a species, indicated that square dives most often exceeded the estimated ADL. This was to be expected because square dives likely represent foraging and diving animals may push their limits most during these types of dives. Lastly, functional analyses of the determined dive types were in general agreement with those from previous work indicating that the various dive types have foraging (benthic and pelagic), travelling, exploration, resting, and processing functions. However, for most species, skewed dives were exceptionally rare and are likely to be of little importance to many of the animals' diving regimes.

Having summarized the major findings from this thesis, some limitations must be pointed out. Comparisons of maximum depth and duration are useful for large interspecific comparisons, however, mean or normal values can be considerably different (Hindell et al. 1991b; Prince and Jones 1992; Schreer and Testa 1996). Therefore, even though maximum values may shed light on differences between groups of divers, mean values may be more useful in representing natural behavior. In addition, many of the values reported on diving behavior were acquired under highly artificial conditions, were a result of very small sample sizes, or were indirectly inferred. At this time, there are too few studies that do not have one or more of these shortcomings and therefore it would be impossible to perform broad interspecific comparisons utilizing only the more rigorous data. However, as more studies are conducted, and more data are collected, these limitations will be eliminated, allowing more rigorous interspecific comparisons.

These same sorts of limitations also affected the classification, comparative, and functional analyses. Depth and time are just two variables that can be measured on diving behavior. Much of our understanding of the diving behavior of animals has been acquired with these variables. However, when considering the shape of a dive or the physical location of an animal throughout a dive, the image can present a misleading picture. Lines within a dive profile can be misinterpreted as movement when in fact they simply represent an animal's vertical position over time. For example, a flat bottomed dive may look like the animal descended to the maximum depth of the dive, moved horizontally, and then returned to the surface. In actuality, the animal may have remained in one location at the bottom of the dive. To get a more accurate image of the animal's position and movement during a dive, information on the horizontal position is also needed (i.e. a 3D image or 4D when including time). This sort of data has been collected for ringed seals, *Phoca hispida*, although no reports have been made on how these dive profiles differ from traditional two-dimensional (depth versus time) profiles (Kelly and Wartzok 1995, 1996). Another way to determine the actual activity during a dive is to record swim velocity in addition to depth and time. This sort of data has been collected on several species recently (e.g. Castellini et al. 1992b; Le Boeuf 1992; Hindell and Burton 1993), and has helped in interpreting the functions of dives types determined using just depth and time. Velocity has been used to substantiate that skewed-left shaped dives in elephant seals may have a sleeping or resting function because the seals stop swimming and sink for part of the descent phase of the dive (Le Boeuf 1992; Hindell and Burton 1993). This information, as well as three-dimensional location, would also be useful to determine if dives thought to represent travelling actually had considerable horizontal movement.

In addition to these physical variables, physiological measurements are also needed to better organize dives into different behavioral groupings. For example, dives that have been suggested to represent foraging could be validated if the animal was known to be opening it's mouth during these dives (Bornemann et al. 1992) or if stomach temperature had dropped due to an influx of cold water and prey (Ancel et al. 1997). However, unsuccessful foraging attempts where the animal was unable to catch prey could not be distinguished with these data. Parameters such as heart rate, cardiac output, metabolic rate, and body temperature (Kooyman et al. 1992b; Ponganis et al. 1993b; Kooyman and Ponganis 1994) would allow an animal's activity level during a dive to be determined and would be useful in classifying dives. However, many of these variables cannot yet be measured on free-diving animals and to date, no work has been done to use any of these additional variables to classify dives.

The analyses performed in this thesis have constituted several steps towards a better understanding of the way in which air-breathing vertebrates exploit their aquatic habitat. Examination of diving capacity has shown that larger animals can generally dive deeper and longer than smaller ones, but that ecological niches or preferences are also of considerable importance. Comparison of possible classification procedures and classification results have indicated that a statistical technique, the k-means clustering algorithm, is a good method for grouping observations and that strong similarities in the types of dive profiles exists across species. Further comparisons of dive shape patterns across species have shown additional similarities in the proportions of the dive types and the proportion of bottom time within the square, potentially foraging, dive type. Differences observed in these patterns were usually due to foraging ecology and water depth. Additional variables and information collected on diving animals will corroborate or refute some of these conclusions, but hopefully, in concert with the work done here, will improve our understanding of how this diverse group of air-breathing animals exploit the aquatic environment.

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BIOGRAPHICAL INFORMATION

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Citizenship	USA and Permanent Resident of Canada (1996)
Education	Ph.D. in Biology, 1997, University of Waterloo, Ontario, Canada - Defense, 3 September, 1997 M.S. in Marine Biology, 1994, University of Alaska Fairbanks, Alaska, USA - Defense, 13 April 1994 B.S. (Magna Cum Laude) in Biology, 1991, State University of New York at Stony Brook, New York, USA Secondary, 1987, Niskayuna High School, New York, USA

Research Experience

Post Doctoral, Waterloo Biotelemetry Institute, Department of Biology, University of Waterloo, Ontario, Canada (1997-). Examination of the effects of physical and chemical stressors on the physiology of Salmonid fish. Experimental analysis using Doppler flow probes to directly measure cardiac output. Experience with surgical procedures for attaching probes and with Blazka swim speed chambers for determining swim performance and pressure effects. Field work with Atlantic Salmon (*Salmo salar*) [Grand Falls - Windsor, Newfoundland, Canada].

Ph.D., Department of Biology, University of Waterloo, Ontario, Canada (1994-1997). Study of the diving behavior of air-breathing vertebrates. Field work with grey (*Halichoerus grypus*) [Amet Island, Nova Scotia, Canada], harp (*Phoca groenlandica*) [Magdalen Islands, Québec, Canada], and harbor (*Phoca vitulina*) seals [Mont Joli, Québec, Canada] involving behavioral studies, attachment and retrieval of time-depth recorders (TDRs) and satellite-linked time-depth recorders (SLTDRs), and biological sampling (blubber biopsies, incisor extraction, and blood, milk, hair, vibrissae, and urine samples). Use of several statistical packages (SAS, SYSTAT, Resampling Stats, and personal program codes), programming languages (C++, Fortran, Basic, and Pascal), and neural network simulators (NeuralWorks Professional II/Plus, Stuttgart Neural Network Simulator, and personal program codes).

M.S., Institute of Marine Science, University of Alaska Fairbanks, Alaska, USA (1991-1994).

Study of the diving behavior and population dynamics of the Weddell seal (*Leptonychotes weddellii*). Field work in the Antarctic [McMurdo Station] involving tagging and surveying, as well as retrieval of SLTDRs. Use of several multivariate statistical techniques through packages including SAS, SPSS, and SYSTAT.

B.S., State University of New York at Stony Brook, New York, USA (1988-1991). Examination of ecological parameters (critical thermal minimums and maximums, fecundity, consumption rate, and growth rate using otolith analysis) of the Atlantic silverside (*Menidia menidia*) and general field surveys [Great South Bay and Long Island Sound, Long Island, New York, USA].

Teaching Experience

Instructor, Department of Biology, University of Waterloo, Ontario, Canada (1997-). Lecture and Laboratory course: Behavioural Ecology.

Teaching Assistant, Department of Biology, University of Waterloo, Ontario, Canada (1994-1997). Laboratory courses: Behavioural Ecology, Comparative Animal Physiology, and Introductory Vertebrate Zoology. Lecture courses: Evolution, Ecology, and Introductory Biology. Field courses: Biology of Marine Mammals and Experimental Studies in Marine Biology.

Teaching Assistant, State University of New York at Stony Brook, New York (1990). Lecture course: Cybernetics.

Academic Awards

- Nominated for the W.B. Pearson Medal in recognition of creative research as presented in the Ph.D. thesis (1997)
- University of Waterloo Graduate Scholarship (1994, 1996 - 1997)
- Ontario Graduate Scholarship (1995 - 1996)
- University of Waterloo travel grant (1995)
- University of Waterloo International Student Fee Waiver (1994 - 1996)
- University of Alaska travel grant (1993)
- Phi Beta Kappa National Honor Society (1991)
- Golden Key National Honor Society (1991)
- Sigma Beta Honor Society, SUNY Stony Brook (1990)
- Dean's list, SUNY Stony Brook (1987 - 1991)

Professional Affiliation

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Publications and Presentations

Schreer, J.F. 1997. Diving behavior of air-breathing vertebrates: allometry, classification, and interspecific comparisons. Ph.D. Thesis. Department of Biology, University of Waterloo, Waterloo, Ontario, Canada.

Schreer, J.F., Kovacs, K.M., and O'Hara Hines, R.J. 1997. Comparative diving patterns of pinnipeds and seabirds. *In Prep*.

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