

Diving and ranging behaviour of odontocetes: a methodological review and critique

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ABSTRACT

Movements can be analysed in terms of horizontal or vertical dimensions, but cetacean movement is ultimately three-dimensional, and it is the integration of analyses of both horizontal and vertical movements that will provide the most insight about an animal's behaviour. Current field techniques can provide simultaneous information on both diving (vertical movements) and ranging (horizontal movements). We discuss the considerations, techniques and analyses for diving and ranging studies, together with the advantages and disadvantages of each technique. Ranging studies using VHF or satellite-linked radio-transmitters have evolved alongside studies of diving behaviour using time–depth recorders, and problems associated with deployment and attachment techniques apply to both. The diving (and concurrent ranging behaviour) of 13 species of odontocetes has been studied using time–depth recorders or acoustic transponders with VHF-or satellite-transmitters. However, differences in sampling techniques used, and summary statistics presented, have made comparisons difficult. We review these issues and suggest parameters that should be presented in future studies of diving and ranging. In general, studies should be consistent in their presentation of the basic parameters and statistics, and provide enough information for the reader to assess the limitations of the data.

CONTENTS

Introduction	82
Diving methodology	84
Techniques	84
Sampling regime	85
Data retrieval	88
Ranging studies and spatio-temporal scale	89
Deployment and attachment techniques	91
Summarizing diving and ranging between studies	92
Definition of diving behaviour	92
Analysis of ranging data	95
Data resolution	96
Sample size, sampling duration and representativeness	96
Comparative studies	97
Integrating diving and ranging	99
Conclusions	100

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INTRODUCTION

Information on three-dimensional ranging of animals can provide insights into many aspects of their behaviour and ecology, including the mating system, diet, and daily and yearly energy budgets (Harris *et al.*, 1990; Boyd, Lunn & Barton, 1991; de Leeuw, 1996). Cetaceans spend the vast majority of their time beneath the water's surface, where they are invisible to observers, and the lack of ranging information in three dimensions has limited a comprehensive study of their ecology.

The term 'diving' has been used to describe two different aspects of the behaviour of marine mammals. Some authors use 'diving behaviour' to describe the pattern of surfacing (i.e. dive durations without information on dive depths, e.g. Leatherwood & Ljungblad, 1979; Mate *et al.*, 1994, 1995), while others use it to describe subsurface behaviour of marine mammals (i.e. always including information on depths as well as duration of dives, e.g. Martin & Smith, 1992; Westgate *et al.*, 1995). Throughout this review we use the term 'diving' to refer to the subsurface behaviour of marine mammals involving information on the depths of dives. In the past, information on diving behaviour of many cetaceans could only be obtained from incidental reports of whales taking line out when harpooned (e.g. Gray, 1882), from whales entangled in deep sea cables (e.g. Heezen, 1957), or from navy experiments with captured and trained animals (e.g. Ridgway, Scronce & Kanwisher, 1969; Bowers & Henderson, 1972). Knowledge of the diet of a species has also been used to infer dive depth (Fitch & Brownell, 1968; Clarke, 1976; Bernard & Hohn, 1989), but while dietary information can be extremely useful for interpretation of studies of diving, it should not be used in lieu of them. Such techniques alone have provided either snapshots of behaviour or insights into the probable dive depths of some species, but cannot replace detailed description of diving behaviour.

More recently, researchers have been able to follow diving animals using ship-board echosounders or sonar systems, and have managed to track animals through all or part of their dives (Lockyer, 1977; Gordon, 1987; Papastavrou, Smith & Whitehead, 1989; Mano, 1990; Kriete, 1995; Simila, 1997; Hooker & Baird, 1999). This technique is potentially problematic for many odontocetes, because sonar systems may be audible to the study animal, possibly affecting the behaviour observed. In addition, this technique is only feasible for fairly large animals, which show relatively consistent movements. Among odontocetes, sonar-tracking has only been successful with Sperm Whales, *Physeter macrocephalus* (Lockyer, 1977; Papastavrou *et al.*, 1989), Killer Whales, *Orcinus orca* (Simila, 1997), and partially successful with Northern Bottlenose Whales, *Hyperoodon ampullatus* (Hooker & Baird, 1999). With a smaller species, the Bottlenose Dolphin, *Tursiops truncatus*, short sequences of sonar recordings have been used to calculate swim speeds (Ridoux *et al.*, 1997), but no vertical movement information could be recorded using this system.

Studies of ranging behaviour have also been subject to various limitations (Scott *et al.*, 1990). 'Discovery' tags were used during the whaling era to mark individual animals. These were labelled metal cylinders fired into the blubber of large whales (among odontocetes these were primarily Sperm Whales, and occasionally Ziphiids, Killer Whales and Pilot Whales, *Globicephala* spp.) which were later recovered from animals caught in a fishery. However, the potential of these tags to ascertain movements was limited to only the deployment and recovery points, and whales were often tagged and recovered during the same whaling season and on the same whaling grounds (Brown, 1975). Other remotely deployed marking techniques such as spaghetti tags (vinyl covered strands of wire connected to a dart tip) suffered problems due to a high shedding rate (Sergeant & Brodie, 1969; Scott *et al.*, 1990). Paint-marking has also been tested on bow-riding dolphins (Watkins & Schevill, 1976) but marks were only short-term (lasting up to 24 h). Marking of captured animals (freeze-branding, fin

notching, rototags or Petersen-type disk tags) has been fairly successful, but due to the effort involved in capture operations, sample sizes are usually limited, and fairly extensive effort is required to obtain resightings (Evans *et al.*, 1972; Scott *et al.*, 1990). The use of resighting data based on photographs of natural markings bypasses the logistics involved in applying marks, but also requires extensive field effort, and can be biased by a number of factors, including uneven distribution of survey effort or animal distribution, and variable recapture probabilities of individuals (Hammond, Mizroch & Donovan, 1990). Some tracking information has previously been obtained by following cetaceans acoustically using hydrophone arrays, but this is problematic if the animals cease to vocalize at any time (Watkins & Schevill, 1977). While groups of animals can sometimes be followed in this manner (e.g. Whitehead & Gordon, 1986), following one animal is often impossible for periods longer than minutes, unless it is alone or is the only animal vocalizing (Watkins & Schevill, 1977).

The development of miniature instrumentation such as radio transmitters and time–depth recorders (TDRs) has opened up opportunities for following and recording both the diving and the ranging behaviour of aquatic animals (Evans, 1971; Kooyman, Gentry & Urquhart, 1976; Frost, Lowry & Nelson, 1985; Mate, 1989; Scott *et al.*, 1990; Anonymous, 1992b; Martin & Smith, 1992; Stone *et al.*, 1994). However, attachment of these devices to cetaceans is not simple. Unlike land mammals, sea mammals cannot simply be collared. Pinnipeds can be captured fairly easily while hauled out on land, and instruments can be attached with glue and later recovered when the animals return to land to breed or moult (e.g. Le Boeuf *et al.*, 1986). Capture operations for cetaceans, on the other hand, are either fairly complicated or impossible. Consequently, for many species instruments must be remotely deployed. The high epidermal shedding rate and furless skin of cetaceans prohibits simple attachment with glue. Initial attachment of instrumentation to cetaceans involved harness backpacks (Norris, Evans & Ray, 1974), but these were found to cause problems of chaffing and increased drag, and have largely been discontinued for all but short-term deployments. Instead, instruments are now usually either pinned or sutured to the dorsal fin or ridge, or attached via suction-cups (although for male Narwhals, *Monodon monoceros*, the tusk can be used for long-term attachment, Heide-Jorgensen & Dietz, 1995). The relative ease of long-term attachment and recovery of instrumentation on pinnipeds has allowed studies of their diving and ranging behaviour to advance at a much greater rate than those of cetaceans (Butler & Jones, 1997). It has been only recently that researchers have begun to use tags to investigate the diving and ranging behaviour of cetaceans in detail.

Previous comparative reviews of marine mammal movement have focused primarily on diving behaviour, investigating the link between diving and body size across species (Boyd & Croxall, 1996; Schreer, 1997; Schreer & Kovacs, 1997), modelling various aspects of diving behaviour (Kramer, 1988; Houston & Carbone, 1992; Thompson, Hiby & Fedak, 1993; Carbone & Houston, 1996), tests of these models (Boyd, Reid & Bevan, 1995), or reviews of the behavioural and physiological implications of diving (Boyd, 1997; Butler & Jones, 1997; Kooyman & Ponganis, 1998). There have been few comparative reviews of horizontal ranging behaviour among marine mammals. Reviews of other mammal species have investigated the link between home range size, group size and body weight (e.g. primates, Clutton-Brock & Harvey, 1977; carnivores, Gittleman & Harvey, 1982). Technique-orientated reviews have described the various field methods used to study horizontal ranging behaviour in cetaceans (Scott *et al.*, 1990), or compared the analytical techniques used to study home range (Harris *et al.*, 1990). Analysis of three-dimensional home-ranges (e.g. Koepl *et al.*, 1977) appear to be rare. While cetacean movement is three-dimensional, these animals are bound to the water surface by the necessity to breathe, and as such are probably not suited to such three-

dimensional home range analyses. Nevertheless, studies of both diving and ranging complement each other in providing an accurate picture of animal movements.

Among marine mammals, the pattern of diving behaviour appears to be somewhat related to taxonomic groupings (i.e. there are differences between odontocetes, mysticetes, otariids and phocids, Schreer & Kovacs, 1997). For future comparative work on diving and ranging within any taxonomic group, some consistency in presentation of data between species will be required. This paper is the forerunner to such work, and endeavours to point out the current inconsistencies in data collection and presentation for studies of odontocete diving and ranging. The study of odontocete three-dimensional movement is relatively new and can therefore benefit from such a critique. In this review, we discuss the techniques currently available for studying diving and ranging of odontocetes, together with the advantages and disadvantages of each, the results that each technique can provide, and the analytical methods available.

DIVING METHODOLOGY

To date, diving studies (providing information on dive depths) have been reported for 13 species and 19 populations of odontocetes (Table 1), which should provide an ideal basis for interspecific comparisons. However, differences in techniques, sampling regimes, and data retrieval, as well as small sample sizes, present immediate obstacles to such comparisons.

The terminology used to describe different equipment and techniques can be confusing. To minimize this, we use the following.

- TDR: instrument which records depth (and possibly other parameters) with associated information on the time at which depth recordings were taken
- DD-TDR: data downloading TDR (needs to be recovered to download)
- SL-TDR: satellite-linked TDR, transmits (limited) dive data to satellite-receiver
- RL-TDR: VHF radio-linked TDR, transmits (limited) dive data to a VHF receiver
- VHF-TDR: tag containing VHF transmitter and DD-TDR, VHF transmitter is solely for location of TDR.

Techniques

Three methods are currently used to obtain diving behaviour data from tags.

1 Attachment of a time–depth recorder (DD-TDR) which stores the data to be downloaded later to a computer.

These tags record depth information (and often other information such as velocity, temperature and light-levels) at user-defined intervals until the tag is recovered or until its memory is full. The tag must be recovered for the data to be transferred to a computer for analysis. Therefore, either animals must be recaptured, or a buoyancy mechanism and VHF transmitter to locate the tag are required (or, in some cases, tags may be recovered after washing ashore without the need for such a locating transmitter, e.g. Otani *et al.*, 1998).

2 Attachment of a time–depth recorder which transmits the data remotely via (a) VHF signals to a nearby receiver (RL-TDR), or (b) by UHF signals to a satellite (SL-TDR).

Data-transmitting TDRs (either RL-TDR or SL-TDR) require the tag antenna to be above the water surface for transmission. Since cetaceans generally surface for periods of seconds only, this places severe restrictions on the transmission time available. Only limited data collected on-board the TDR (usually a summary or subset) can therefore be transmitted. For VHF radio-transmission, the receiver must be within range to pick up good signals from the tag (commonly 4–10 km; this range depends on the power of the transmitter and height of the transmitting and receiving antennae, among other factors). For UHF radio-transmission,

a receiving satellite must be passing overhead (see Mate, 1989 for details of Argos satellite paths). Furthermore, the reliability of the uplink depends on whether environmental and atmospheric factors degrade the transmitter signal.

3 Attachment of an acoustic transponder tag which can be interrogated sonically, or which transmits continuously while underwater.

Acoustic transponder tags may transmit data continuously at a pulse rate dependent on depth (Goodyear, 1993), or can be interrogated at intervals (Watkins *et al.*, 1993). One problem with acoustic tags is that, generally, the signals can only be received from less than 2 km away (Goodyear, 1993; Watkins *et al.*, 1993). This distance is dependent on the frequency used and the environmental conditions. Lower frequencies can be received at greater distances, but the signals would be more likely to lie within the hearing range of the animal, potentially affecting its behaviour. This is perhaps a greater problem for odontocetes than mysticetes, due to their presumed higher frequency hearing range.

The major differences in these techniques result from limitations of data sampling and data retrieval. In general, two data-storage/retrieval regimes are used in time–depth recorder studies: storage of the raw depth data, or on-board summarizing or processing of data into a format thought to be representative of each dive. Associated with these are two respective data retrieval methods: recovery of the tag and the stored data, or remote retrieval of data from the tag while still deployed.

Sampling regime

The collection of data at regular intervals over each dive can potentially provide a large amount of data over a short time-span. This method gives the most detailed picture of dive profiles, often providing a second-by-second account of the study animal's depth. This method also allows the user to scan the data for potential errors, which would be impossible to detect if only certain parameters (such as maximum depth) were collected for each dive. For example, if the maximum recorded depth is at the limit of the depth sensor's range, it is impossible to know whether the animal went deeper than this. Viewing the dive profile would help determine whether the animal went beyond the range of the sensor, whereas if only

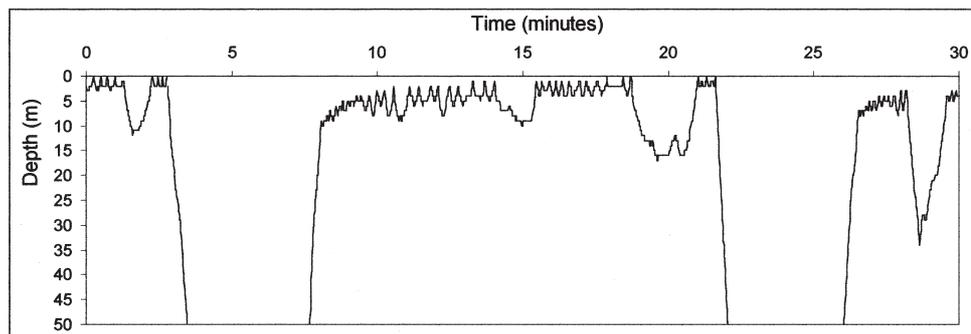


Fig. 1 Dive profile showing temperature-related shifts in depth readings. After ascent from a deep dive the cold temperature, which the tag was exposed to, causes an offset in the depth measurement such that the surface is recorded as 10 m depth. This depth offset gradually returns to zero as the tag warms up over 5 min. This temperature-related shift in depth measurements potentially prohibits accurate assessment of dive durations or amount of time spent at different depths, particularly for tags where dive profiles cannot be observed in detail. Profile from Short-finned Pilot Whale, Hokkaido, Japan, sampling rate 1 second, resolution 1 m; R.W. Baird & M. Amano, unpublished data. Note only the top 50 m of depth readings are shown; this TDR recorded depth to 237 m and the two long dives (~ 4 min) went to over 200 m.

Table 1. Studies of odontocete diving behaviour showing the device used, together with the deployment and attachment methods, number of individuals tagged (*n*) and the sex of these when known. Devices include TDR with attached VHF transmitter (VHF-TDR), satellite-linked TDR (SL-TDR), VHF radio-linked TDR (RL-TDR), and acoustic transmitter. VHF or satellite tracking carried out in conjunction is shown in parentheses

FAMILY/Species	Location	Deploy	Attach	Device	<i>n</i>	Sex	Study
PHOCOENIDAE							
Harbour Porpoise (<i>Phocoena phocoena</i>)	Bay of Fundy, Canada	Incidental catch, herring weir	Pinned to dorsal	VHF-TDR	7	3m 4f	Westgate <i>et al.</i> , 1995 Westgate & Read, 1998
	Hokkaido, Japan	Incidental catch, set net	Pinned to dorsal	TDR	2	2f	Otani <i>et al.</i> , 1998
	San Juan Is., WA, USA	Directed gill-net	Suction-cup	VHF-TDR	1	1f	M.B. Hanson, unpublished
Dall's Porpoise (<i>Phocoenoides dalli</i>)	San Juan Is., WA, USA	Remote by pole or capture by hoop-net	Suction cup or pinned to dorsal	VHF-TDR; VHF-TDR, (satellite, VHF)	1 7	– 2f 5m	Hanson & Baird, 1998 Hanson, Baird & DeLong, 1998; R.W. Baird & M.B. Hanson, unpublished
DELPHINIDAE							
Short-beaked Common Dolphin (<i>Delphinus delphis</i>)	Southern California, USA	Capture by purse seine net	Pinned to dorsal	RL-TDR	3	–	Evans, 1971, 1974
Heaviside's Dolphin (<i>Cephalorhynchus heavisidii</i>)	St. Helena Bay, South Africa	Capture by hoop-net	Pinned to dorsal	SL-TDR (VHF)	3	2m 1f	Sekiguchi <i>et al.</i> , 1998
Pantropical Spotted Dolphin (<i>Stenella attenuata</i>)	E. Tropical Pacific	Capture by purse seine net	Pinned to dorsal	VHF-TDR	11	–	Scott <i>et al.</i> 1993, 1995
	Hawaiian Is., USA	Remote by pole	Suction cup	VHF-TDR	4	–	R.W. Baird, unpublished
Atlantic Spotted Dolphin (<i>Stenella frontalis</i>)	Gulf of Mexico, USA	Rehabilitated	Pinned to dorsal	SL-TDR	1	m	Davis <i>et al.</i> , 1996
Short-finned Pilot Whale (<i>Globicephala macrorhynchus</i>)	Hokkaido, Japan	Remote by crossbow	Suction-cup	VHF-TDR	2	–	Amano & Baird, 1998

FAMILY/Species	Location	Deploy	Attach	Device	<i>n</i>	Sex	Study
Long-finned Pilot Whale (<i>Globicephala melas</i>)	Ligurian Sea, Mediterranean	Remote by pole	Suction-cup	VHF-TDR	5	–	R.W. Baird, unpublished
Killer Whale (<i>Orcinus orca</i>)	Residents: Haro Strait, WA, BC; SE Alaska	Remote by crossbow or pole	Suction-cup	VHF-TDR	34	17m 13f	Baird, 1994; Baird, Dill & Hanson, 1998, R.W. Baird, unpublished
	Transients: WA, BC; SE Alaska	Remote by crossbow or pole	Suction-cup	VHF-TDR	6	4f	Baird, 1994; Baird, Dill & Hanson, 1998, R.W. Baird, unpublished
MONODONTIDAE							
Beluga (<i>Delphinapterus leucas</i>)	Cunningham Inlet, NWT Canada	Capture by hoop-net	Pinned to dorsal ridge	SL-TDR	13	2m 11f	Martin & Smith, 1992; Martin, Smith & Cox, 1993; Smith & Martin, 1994; Martin, Smith & Cox, 1998
	Eastern Devon Is., NWT Canada	Capture by hoop-net in shallows	Pinned to dorsal ridge	SL-TDR	6	2m 4f	Heide-Jorgensen, Richard & Rosing-Asvid, 1998; Richard, Heide-Jorgensen & St. Aubin, 1998
Narwhal (<i>Monodon monoceros</i>)	Baffin Island, NWT, Canada	Driven into nets in shallows	Pinned to dorsal ridge	SL-TDR	3	3f	Martin, Kingsley & Ramsay 1994
	Melville Bay, north-west Greenland	Driven into nets	Tusk mounted/pinned to dorsal ridge	SL-TDR	9	5m 4f	Heide-Jorgensen & Dietz 1995
ZIPHIIDAE							
Northern Bottlenose Whale (<i>Hyperoodon ampullatus</i>)	The Gully, E. Canada	Remote by crossbow	Suction-cup	VHF-TDR	2	–	Hooker & Baird, 1999
PHYSETERIDAE							
Sperm Whale (<i>Physeter macrocephalus</i>)	Caribbean Is.	Remote by crossbow or gun	Dart	Acoustic	2	2m	Watkins <i>et al.</i> , 1993

**Not represented: Kogiidae, Platanistidae, Iniidae, Pontoporiidae.

maximum depth is recorded the means to check this is lost and must be inferred from the distribution of depth values (Heide-Jorgensen & Dietz, 1995). Furthermore, it is only possible to correct for temperature-related depth shifts when the entire dive profile can be viewed (e.g. see Fig. 1). Viewing such a profile, it is apparent that the surface is recorded at increased depth immediately after ascent from a deep dive (into much cooler waters) and then gradually shifts back to 0 metres over a period of time spent in warmer surface waters.

The collection of summary statistics for each dive, in contrast, provides a much coarser resolution of data over the same time period. There is some debate as to the best method to summarize dives such that the least amount of information is lost (Anonymous, 1992a). Currently, summary statistics are often generated as frequency distributions of dives within certain depth and duration ranges. For example, summary statistics recorded for satellite-tagged Narwhals included: maximum depth during 24 h, number of dives deeper than a pre-defined value in various depth categories in four 6-hour sampling periods, and frequency of dives in six duration categories for each 6-hour period (from Heide-Jorgensen & Dietz, 1995). However, without prior information on a species' diving behaviour, the definition of these ranges may not be optimal. For investigations of the diving behaviour of new species or populations it would appear to be valuable initially to sample depth values (and other parameters) at frequent intervals, to ascertain some of the basic dive characteristics from which to define an optimal sampling regime for use in longer-term studies.

Histogram summary statistics are useful for asking specific behavioural questions in terms of broad categorization of results (e.g. are there differences in summary dive parameters between the four 6-hour time periods?). One recent study showed broad-scale similarity between biological data recorded using histogram summary statistics and those obtained from downloading raw dive data (Burns & Castellini, 1998). However, summary statistics provide no information on the behaviour of the animal during these dives, or on the animal's descent and ascent rates, as can be gained from the dive profile. Because dive information is obtained within broad user-defined limits, researchers are unable to look at dive shapes (Schreer & Testa, 1995), or to investigate dive features such as the correlation of dive depth and duration. Furthermore, short-term changes in diving behaviour (e.g. crepuscular activity) would easily be overlooked using long periods over which summary data are calculated.

Data retrieval

Tag recovery (and downloading of archived data) provides the potential to store only a fixed amount of data (usually governed by the finite memory capability but potentially also the limited battery life of the tag). This finite capacity leads to a trade-off between sampling rate and total sampling time, at least for long duration attachments (Boyd, 1993). There are also problems in comparisons between studies using different sampling rates, as this can affect the resolution of dive shape obtained (Schreer, 1997), and can also provide quite varying results for parameters such as time spent at the surface and the number of shallow dives. A higher sampling rate will always provide the most detailed data, and will be of most value for fine-scale analysis of feeding ecology, but will result in a shorter data collection time-span. For description of diving behaviour, at minimum a sampling rate should be used which provides a good representation of dive shape.

Using satellite-linked data retrieval, it is only possible to send small amounts of data at each uplink. The number of uplinks will be affected by the number of satellite passes and the behaviour of the study animal. The number of satellite passes is latitude-dependent, with at least three satellite passes at the equator and up to 27–30 at high latitudes, from between two and three satellites per day (Mate, 1989; A.R. Martin, pers. comm.). Species which surface

for short periods, or which show very little of their back (or tagged surface) above the water will have fewer viable uplinks. Martin, Smith & Cox (1993) describe the problems found in using this method to study Beluga Whales:

‘The constraint on the amount of data that can be sent and received within the ARGOS system proved to be a considerable limitation in this project and will inevitably be so in any study of marine mammals using ARGOS. A maximum of 256 bits of data can be sent in a transmission, and the probability of any such transmission coinciding with a satellite pass, and therefore potentially being received by the satellite (termed an ‘uplink’), is small. Even then, many uplinks are corrupted, often by the animal submerging during the propagation of the signal itself.’

The major advantages of this method are the world-wide coverage, rendering ship-tracking unnecessary, and the potential for longer sampling time (up to months), allowing a great deal of information to be gained from one study animal. However, increased sampling time is not equivalent to increased sample size, which is based principally on the number of animals sampled (Machlis, Dodd & Fentress, 1985). Increased sampling time is likely to increase the probability of detecting the extremes within the data, such as the maximum depth or the maximum dive time (Link & Sauer, 1996), and to detect long-term periodic variation. However, mean or modal values are better indicators of routine dive depths or durations than are maximum values, and are of more value in comparisons between different studies. The other major advantages of the data-transmission method are that the tags do not have to be recovered in order to access the data, and simultaneous monitoring of more than one animal is far simpler than when each animal needs to be tracked acoustically or by VHF. However, the increased cost of this method may necessitate a small sample size.

In general, recovered TDRs tend to use regular and frequent sampling and are often deployed for only short intervals and so are not limited in terms of data storage or retrieval. As these tags are retrieved they may also be deployed multiple times on several individuals. Satellite-linked TDRs are used to collect longer-term but limited data, so researchers can either collect summary statistics on all dives, or more complete information on a selected sample of dives prior to the uplink (e.g. Martin & Smith, 1992; Martin *et al.*, 1993). These tags are generally not recoverable and therefore cannot be reused.

The choice of technique to be used for each potential study will be based on a variety of considerations, e.g. the species, habitat, available funding, boats, experience of researchers, questions to be asked, etc. Associated considerations include the ranging information that can be obtained simultaneously and the deployment and attachment techniques needed. Each study should be assessed in its own right based on the pros and cons of different techniques and a decision made as to the methodology to be used.

RANGING STUDIES AND SPATIO-TEMPORAL SCALE

For the purposes of this paper, a comprehensive review of ranging behaviour is not practical, and a good review of the topic is available in Scott *et al.* (1990). Our aim instead is to discuss the study of ranging in conjunction with the study of diving behaviour. The same radio-tracking mechanisms used for telemetry of dive-data or for recovering dive-recording tags are used to follow (VHF radio-telemetry) or remotely track (satellite-linked radio-telemetry) animals. We will compare these with the other commonly used field technique – photographic re-identification of individuals. The major problem involved in studies of ranging is scale (i.e. the spatial and temporal resolution at which behaviour is measured). An animal’s behaviour may appear very different if viewed over a scale of seconds compared to

one of years, or over a range of a few metres compared to one of thousands of kilometres. To understand behaviour, observation should take place at a similar scale to the behaviour being studied (Levin, 1992; McConnell & Fedak, 1998). Studies using photo-identification are opportunistic in space and time. A more detailed view of a particular animal's behaviour is obtained by focal following of one individual or group (see review of methodology in Mann, 1999). Photo-identification, VHF radio-tracking and satellite-linked radio-tracking all operate over different scales, with potential implications for interpretation or comparison of results (Table 2). However, not all techniques are equally applicable to all species for reasons discussed below.

For cetaceans, which are relatively slow-moving and are found in small groups, photo-identification of natural or man-made marks may be used to identify individual animals, and to provide movement information when an individual is re-sighted in different locations. (This technique is more difficult for offshore cetaceans both due to increased cost and logistically, e.g. for oceanic dolphins found in groups of several hundred.) As many odontocetes cannot be followed easily between surfacings, photo-identification can provide only a series of snapshots of animal positions. In addition, these locations are highly dependent on boat position, and unless coverage is equal in space and time, will not accurately represent the animal's ranging behaviour (Kenney & Winn, 1987; Whitehead, Christal & Tyack, 2000). While snapshots of movements within a certain study area over a long time-scale may be obtained, the possibility of the study animals making long-distance movements to unsampled areas cannot be refuted (e.g. the short-term movements of Right Whales, *Eubalaena glacialis*, out of areas in which they are usually encountered, Mate, Nieu Kirk & Kraus, 1997).

For some populations, animals can be followed in real time on the basis of their marks (e.g. Killer Whales, Baird & Dill, 1995; some Bottlenose Dolphin populations, Mann &

Table 2. Measurement of ranging behaviour

Type of tag	Temporal scale (study duration)	Sampling rate	Accuracy	Disadvantages	Advantages
Photography of natural marks	Months – decades	Highly variable (hours – years)	~ 100 m (using GPS or LORAN)	Biased by distribution of effort in space and time; often spatially limited to nearshore areas	Inexpensive for inshore species; large sample sizes; simultaneous behavioural data can be collected
VHF tags	Up to months	Each surfacing or every few surfacings	~ 100 m – 1 km (dependent on tracking distance)	Small sample sizes; tracking may be difficult in some areas, e.g. offshore; moderate cost	Simultaneous behavioural data can be collected
Satellite tags	Up to months	Approx 1–3 times per day, dependent on satellite coverage	~1–10 km + (measure of accuracy available with each satellite pass)	High cost; small sample sizes	Does not require field effort post-deployment; global coverage

Smuts, 1998). However, for species that have unreliable markings or that make long, unpredictable dives, radio-telemetry provides a means for tracking animals. VHF radio-tracking can potentially give the most detailed information about animal movement at small spatial and temporal scales, allowing researchers to track animal location during every surfacing bout, either visually or by using a ground-truthed signal strength and bearing from a known position. From this, it is possible to calculate rates of movement for each surfacing, or over short time periods of hours to a few days (for methods see White & Garrott, 1990; Turchin, 1998). However, this type of radio-tracking is often logistically constrained over larger scales, due to boat size or fuel limitations, or, in the case of shore-based studies, when animals swim out of receiver range.

Satellite-linked radio-tracking usually provides a less-detailed but longer-term and larger scale picture of animal movements. Coverage of Argos satellites varies depending on geographical area, with more frequent satellite passes (and thus more potential locations) in higher latitudes (Mate, 1989). This technique is more suitable for monitoring long-distance movements, providing on average one or two reliable locations per day from dorsal ridge- or dorsal fin- attached transmitters (Dietz & Heide-Jorgensen, 1995; Davis *et al.*, 1996). The accuracy of these positions can be quite variable however (Burns & Castellini, 1998). The Argos manufacturers are attempting to introduce various improvements for their next generation of equipment (Taillade, 1998). These include improving satellite coverage, increasing data volume transmission capability, improving satellite receiver sensitivity to reduce platform power requirements or enhance transmission performance, and to allow control of platforms remotely by two-way communication with the transmitter through the satellite receiver (Taillade, 1998).

DEPLOYMENT AND ATTACHMENT TECHNIQUES

The major problem with using TDRs or radio-transmitters on odontocetes has been tag attachment. There are two major deployment techniques: capturing the study animal and attaching the tag, or remotely deploying the tag (Table 1). Associated with these are two attachment techniques: penetrating – pinning through the dorsal fin or using a barb/hook attachment to the blubber; or non-penetrating – using suction-cup attachment to the skin surface (Table 1).

Capturing odontocetes is only feasible for smaller to midsize species (Asper, 1975; Walker, 1975). Methods of capture include hoop-netting smaller species (e.g. Dall's Porpoise, *Phocoenoides dalli*, and Heaviside's Dolphin, *Cephalorhynchus heavisidii*), purse-seine netting and drive captures for midsize species (e.g. Belugas, *Delphinapterus leucas*, and Narwhals). The expense and logistical difficulty of such operations encourage the use of penetrating tags since these usually have longer-term attachments than suction-cup tags. Furthermore, long-term attachment is needed to ensure that 'normal behaviour' can be recorded after the potential initial shock of their brief capture. Some odontocetes have been tagged after incidental capture in herring weirs or other fisheries (Westgate *et al.*, 1995; Read & Westgate, 1997; Otani *et al.*, 1998). While this is feasible for coastal fisheries, the logistics of getting researchers to incidentally caught (but living) animals offshore may be problematic (Otani *et al.*, 1998).

Tags may be remotely deployed by crossbow or long pole (Baird, 1994, 1998; Stone *et al.*, 1994; Schneider *et al.*, 1998) or by shotgun (Watkins *et al.*, 1993). Pole deployment is relatively simple for large, slow-surfacing or bowriding species (Stone *et al.*, 1994; Giard & Michaud, 1997; Hanson & Baird 1998), but is problematic for odontocete species which do not normally bowride, such as Killer Whales or Northern Bottlenose Whales. Crossbow-deployed tags are usually more successfully applied using penetrating barb attachments than

using suction-cup attachments, as the latter have a high chance of bouncing off. However, remote deployment of penetrating tags is unsuitable for many small odontocetes, due to relatively thin blubber layers and thus the increased chance of harming the animal (see diagram in Goodyear, 1993). For larger odontocetes, whose capture is not feasible, remotely deployed suction-cup tags are therefore gaining popularity, despite deployment difficulties. Typically these remain attached for hours (a mean of 9.75 h for 41 deployments on Killer Whales; R.W. Baird unpublished data), although such attachments have held for up to 38 h on a Harbour Porpoise (M.B. Hanson unpublished data), and up to 3 days on a Fin Whale (Giard & Michaud, 1997; Baird, 1998). A suction-cup system has recently been designed to be used on captured small cetaceans, and involves a moulded dorsal-fin design using multiple small suction cups and velcro straps (Shippee *et al.*, 1995).

The behavioural impact of different attachment and deployment methods has been noted for many studies and generally appears to be low-level, although at times strong reactions have been observed. Capture of free-ranging dolphins has been conducted successfully for a large number of species and does not appear to cause excessive stress to the study animals (Table 1 and references therein). Capture and attachment of tags by pinning through the dorsal fin was found to cause slight short-term reaction limited to the first few minutes after tag attachment, but no long-term reaction for Boto, *Inia geoffrensis*, over periods of years during and after tag attachment (Martin & da Silva, 1998). Penetrating tags deployed by shotgun were found to cause little response from Sperm Whales (Watkins *et al.*, 1993). Slight short-term reactions in the first few minutes after tag attachment were also observed for suction-cup attachment by pole or crossbow (Stone *et al.*, 1994; Hanson & Baird, 1998; Hooker & Baird, 1999). However, Bottlenose Dolphins off New Zealand were found to show strong reactions to suction-cup attachment (Schneider *et al.*, 1998). The magnitude of reaction therefore appears to vary more for different species or populations than for different techniques.

SUMMARISING DIVING AND RANGING BETWEEN STUDIES

To date, TDR studies have been 'published' (in theses or peer-reviewed literature) on the diving behaviour of nine odontocete species (Table 1), almost all of which have also used either satellite or VHF radio-tracking simultaneously with collection of dive data. We discuss some of the inconsistencies in data collection, analysis, and presentation among these. Suggestions for future studies are made to minimize these differences, making comparisons between studies both more appropriate and more feasible.

Definition of diving behaviour

Two issues affect how diving behaviour is analysed and interpreted by researchers. First is the question of function. The nature of cetacean adaptation is that almost all behaviour (including travelling behaviour) is subsurface. 'Diving' behaviour therefore often encompasses several behavioural functions, yet a single 'mean dive depth' is often presented. Second is the question of the minimum depth necessary to constitute a dive. Diving and subsurface behaviour are generally thought to be synonymous, but depth sensor resolution, zero-offset drift and wave action all influence the level of uncertainty about whether an animal was in fact at the surface or underwater.

Many authors define a dive as deeper than twice the value of error or resolution of the depth sensor (this appears to have originated from the design of analysis programs by the TDR manufacturer Wildlife Computers, Redmond, WA, rather than from any rigorous

definition). TDRs were first developed for use on seals which often stay continuously at the surface of the water between dives, and for which such a cut-off dependent on sensor-resolution is useful. In contrast, the deep, foraging dives of cetaceans are usually followed by a surfacing bout of shallower dives, the purpose of which may be to travel or replenish oxygen stores. Inclusion of these surfacing bouts can potentially cloud the analysis of 'diving' behaviour, since several dive classes, including a large number of short shallow dives, are combined in analyses. The use of this 2× resolution value provides a cut-off point for what is underwater and what is at the surface, but usually includes a large proportion of these short, shallow dives and is therefore likely to affect interpretation of results substantially. To infer 'foraging' behaviour from all dives greater than this value (which are likely to incorporate both foraging and respiratory bout dives) is therefore a misrepresentation. Furthermore, it is apparent that use of tags with different depth resolution would give very different estimates of measures such as 'time spent at surface' or 'mean depth of dives' using this criterion. Likewise, the size of the study species will probably influence the depth of surfacing bouts. A Harbour Porpoise may remain above 2 m during surfacing bouts, whereas a Killer Whale or Bottlenose Whale is likely to submerge deeper than this solely due to its body size.

There has been a good deal of interest in how to classify dives (Anonymous, 1992a; Schreer & Testa, 1995; Schreer, 1997; Lesage, Hammill & Kovacs, 1999). While these studies have usually been concerned with delineating more categories than deep vs. surface, the issue is still to find an objective criterion for differentiating between dive types, in this case shallow, short dives during respiration bouts, and longer, deeper dives which serve other functions (e.g. foraging).

Various methods have been used in both cetacean and pinniped studies to discriminate surface from deeper dives objectively. An example dataset of 24 h of diving data (recorded at 1 s intervals to 1 m resolution using a Wildlife Computers Mk 6 TDR, Table 3) from a southern 'resident' Killer Whale in Haro Strait, WA (Baird, Dill & Hanson, 1998) is used to demonstrate differences between these methods (Fig. 2):

1 Elimination of any dives less than twice the depth sensor resolution from analysis and presentation (Fig. 2a). This criterion often appears to be used by default. Satellite-linked TDRs, for which post-hoc investigation of dives is limited, require the use of a simple definition of this type (e.g. Heide-Jorgensen & Dietz, 1995; Davis *et al.*, 1996). This cut-off has also been used for TDR studies (although the presence of a variety of dive types may be noted, e.g. Baird, 1994; Westgate *et al.*, 1995).

2 Subjective grouping of 'diving' behaviour according to certain dive characteristics (Hindell, Slip & Burton, 1991; Martin & Smith, 1992; Le Boeuf *et al.* 1993; van Dam & Diez, 1996). A result of this is that criteria such as 'foraging dives are considered to be those of more than 1 min at maximum depth' are applied (e.g. Hindell *et al.*, 1991) (Fig. 2b). Martin & Smith (1992) use a similar subjective definition and present information for flat-bottomed dives deeper than 150 m. However, this weights dive statistics toward deeper and longer dives, whereas studies including 'respiration' dives are weighted toward shallow, short dives.

3 Use of multivariate statistical analyses such as cluster analysis or artificial neural networks to identify groupings within the data (Schreer & Testa, 1995; Schreer, 1997) (Fig. 2c). Considerable care must be taken as to how many groupings there are within the data, however.

4 Investigating the multimodal nature of a three-dimensional plot of depth and duration can be used to discriminate shallow, short-duration dives from longer, deeper dives (Boveng, Walker & Bengtson, 1996) (Fig. 2d). Independent histograms of either duration or depth can be used, but tend not to represent the data as clearly.

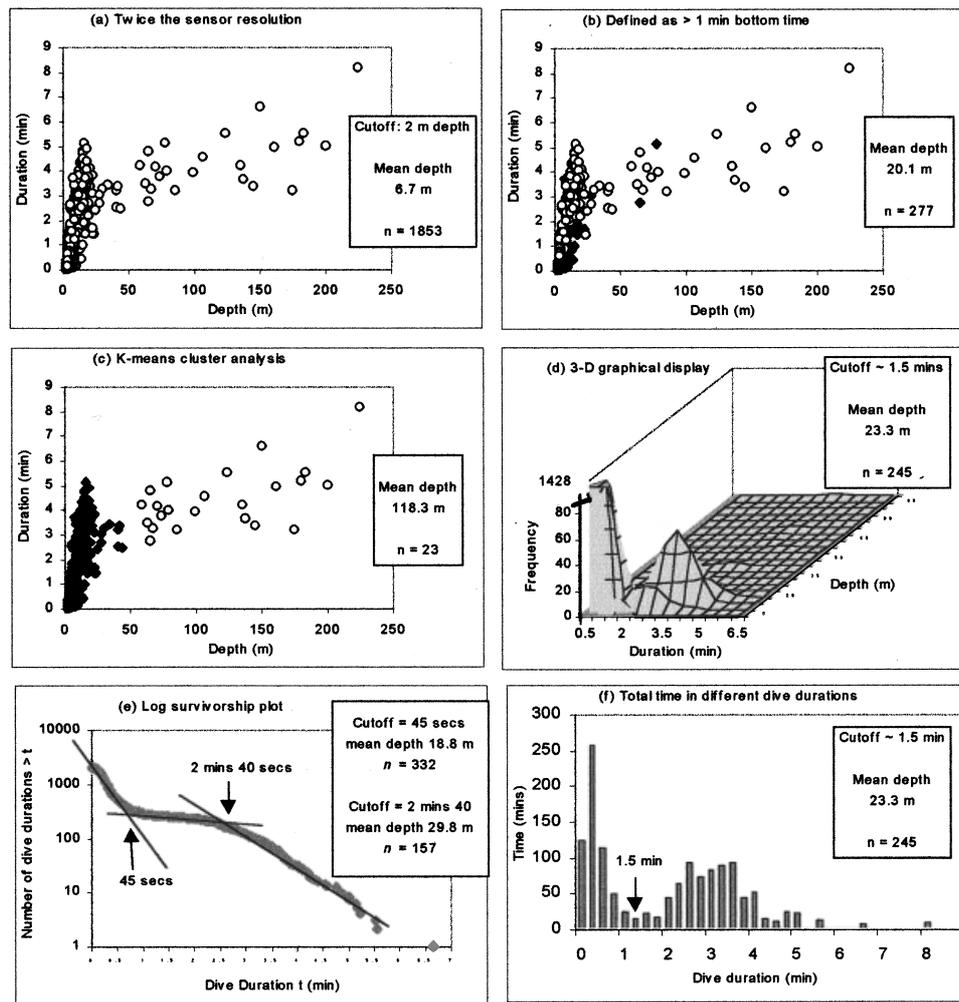


Fig. 2. Examples of different methods used to categorize dives, illustrated using data from a single southern 'resident' Killer Whale, Haro Strait, WA (R.W. Baird, unpublished data): (a) using twice the data resolution; (b) using a subjective definition such as more than 1 min at maximum depth; (c) using cluster analysis; (d) using a three-dimensional frequency histogram of depth and duration; (e) using a log-survivorship plot of dive durations; (f) using the bimodality of a plot of cumulative time spent in dives of different durations. Values given in boxes represent mean dive depth of 'long, deep' dives, and give the number of such dives recorded with each technique. For (a), (b) and (c), open circles show dives of the definition given.

Table 3. Time at surface showing differences in definition of surface, based on same data as used in Fig. 2, from a single southern resident Killer Whale, British Columbia (R.W. Baird, unpublished data)

Depth interval (m)	Percentage time at each depth layer	Cumulative percentage time between surface and layer
0-2	12.8	12.8
2-4	30.8	43.6
4-6	9.4	53.0
6-8	7.1	60.0
8-10	12.7	72.7

5 Use of a log-survivorship plot of dive or surface durations (Fagen & Young, 1978; Gentry & Kooyman, 1986; Beavers & Cassano, 1996) (Fig. 2e). This technique is used for identifying bouts of behaviour, and can therefore be used to separate bouts of respiration dives from deeper dives. A break or inflection in the slope of the log survivor function represents a change in probability of the event, signalling the presence of bouts within the data.

6 Investigating the cumulative time spent in dives of different durations and using the bimodality of this to distinguish between long and short dives (Hooker & Baird, 1999) (Fig. 2f). This technique weights the duration of dives according to the time involved in such dives, presenting a perspective on the investment rather than solely the number of dives in duration categories.

These techniques range from completely subjective (No. 2) to almost completely objective (Nos 5 and 6) means to identify dive type. Different techniques will be optimal for different datasets. Among published odontocete diving studies there are very few explanations or definitions for the delineation of foraging dives. For the dataset shown (Fig. 2), it is interesting to note that four of the six methods give relatively similar mean dive depths for 'long' dives (and relatively similar sample sizes), while the other two methods produce widely divergent results. Data based on twice the resolution of the depth sensor (Fig. 2a) do not appear to be sufficient when sensor resolution is relatively precise, as many short, shallow dives are lumped into the 'long, deep' dive category. At the other extreme, standardized cluster analysis into two clusters appears to group many intermediate depth and duration dives with surfacing dives, and so includes only very long and very deep dives in the 'long, deep' dive category (see Schreer (1997) for more detailed discussion of statistical clustering techniques). The log-survivorship function shows quite clearly that there appear to be at least three behavioural types (Fig. 2e), the first of which, the 45-second cut-off, is likely to define surfacing bouts. The other techniques were relatively straightforward and give quite similar results. It is clear from these example data using different definitions that interpretation of results should be conducted with great care.

Our primary recommendation is the explicit categorization of dives by statistical or graphical investigation of dive type. At minimum, odontocete dives should be separated into those involved in respiratory bouts and those more likely to represent foraging behaviour.

Analysis of ranging data

There does not appear to be any standard method for display of ranging data. The three-dimensional nature of cetacean ranging data (point locations, x and y , at sequential time, t) renders visual analysis difficult since this is usually done in two dimensions. Data are therefore generally either displayed statically in time, in terms of a spatial representation of (x , y)-locations (e.g. Read & Westgate, 1997; Mate *et al.*, 1995), or features of movement, such as distance travelled between fixes, are plotted against time (White & Garrott, 1990). Mammalian movement has generally been analysed spatially by investigating plots of movements and describing home range, following the definition given by Burt (1943) as 'that area traversed by the individual in its normal activities of food gathering, mating, and caring for the young'. An alternative method of displaying movement data has been proposed by Turchin (1998) following the theoretical framework of random movement (diffusion) models. Plots of net displacement (or net displacement squared) for increasing time intervals can be used to illustrate both rate of movement and range displacement (see Turchin, 1998 for details). This method of analysis may apply well to odontocete movement and appears likely to prove valuable in future.

Data resolution

Sampling rate for detailed TDR records varies both within and between studies. Westgate *et al.* (1995) use a sampling rate of 1–3 s for research on Harbour Porpoises. While this variation in rate does not have a large effect on the recorded depths and durations of deep dives, it may cause some error in accuracy. Otani *et al.* (1998) use a sampling rate of 10 s for the same species and it can be seen that the distribution of dive durations they recorded is quite different to that observed by Westgate *et al.* Many of the short surface respiration dives appear not to have been recorded using a 10-s sampling rate (see Otani *et al.*, 1998). Schreer (1997) showed that sampling rate can also affect dive shapes. The sampling interval should be small enough both to allow resolution of the dive profile and to identify all surface intervals accurately (see Boyd, 1993 for more detailed discussion of this problem). A 10-s sampling rate for Narwhals, which have a mean dive duration of 5 min (Heide-Jorgensen & Dietz, 1995), is likely to produce far more accurate results than a 10-s sampling rate for Harbour Porpoise, which have a mean dive duration of 1 min (Otani *et al.*, 1998).

The resolution of ranging data also affects the resultant data. Animal movements are continuous, but records of ranging data are typically collected by noting position at regular or irregular time intervals. A good review of the effects of oversampling and undersampling of movements is available in Turchin (1998). Oversampling is rarely a problem in marine mammal studies, due to the logistics of gaining position data on animals over short time intervals. The straight-line distance assumed between locations is an underestimate of the continuous distance the animal travelled, and the longer the intervals between recorded locations, the more biased the estimates of distances travelled and the speeds will be. Dietz & Heide-Jorgensen (1995) noted such an effect for calculations of the speed at which Narwhals travelled and stated that speeds were underestimated if calculated over intervals longer than 0.5–5 h. The most detailed (but usually somewhat impractical) measurement of movement is to record the velocity of the animal and view this in conjunction with the dive profile. Over longer time intervals, position fixes can provide longer-term ranging information; for example, core-areas and long-term ranges.

The primary inconsistency in presentation of ranging statistics by different authors is to present a single rate of travel (calculated based on the sampling interval – per minute/hour/day). However, if animals are not travelling in straight lines, the sampling interval will have a large effect on this estimated rate of travel. In some studies estimates of rate of travel are presented for two different time intervals (e.g. rate of movement per hour and rate of movement per day) where one is merely a multiple of the other (e.g. Davis *et al.*, 1996). For the majority of temperate latitude satellite-tracking data, locations tend to be sampled approximately once or twice a day and so the rate of travel is better presented as average daily movement than as hourly movement. One solution to this is to present these data graphically, showing how displacement varies with time interval (see methodology suggested above). In this manner displacement over various time intervals, ranging from the sampling interval up to the study duration, can be displayed.

The sampling interval from which diving and ranging data are calculated should be explicitly stated in all studies. Sampling interval is crucial both for interpretation of results and for comparison between studies.

Sample size, sampling duration and representativeness

A further obstacle in the comparison presented here, which applies to both the diving and ranging studies, is the difference caused by sample size and ‘quality’ of study animals. Some

of the studies noted in Table 1 include a number of individuals sampled for periods up to months (Heide-Jorgensen & Dietz, 1995; Westgate *et al.*, 1995; Read & Westgate, 1997), while others are of a single rehabilitated study animal (Davis *et al.*, 1996) or animals sampled for only short periods, i.e. 1–30 h (Baird *et al.*, 1998). Whether studies of rehabilitated animals are representative of the behaviour of free-ranging wild animals may be questionable. However, it is possible that attachment of any tag, regardless of the condition of the study animal, may cause behavioural modification (e.g. Schneider *et al.*, 1998).

Sample size and duration of sampling affect the maximum values of data parameters, e.g. the maximum dive depth ever recorded, or maximum speed ever recorded, more so than they affect mean or modal dive depth or duration (see Link & Sauer, 1996). While these parameters can provide an indication of the potential of a species, their strong dependence on sample size prohibits fine-scale interspecific and interpopulation comparisons of diving behaviour for datasets of widely differing sample sizes.

Differences in diving or ranging summary measures with increasing duration and sample size have not been investigated. The number of samples required to obtain a reliable mean foraging depth could be investigated visually by plotting the mean depth for increasing number of dives or number of individuals (bootstrap or jackknife analyses; Krebs, 1989). A similar method is used to test the number of fixes required to obtain an accurate measure of home range size (Voigt & Tinline, 1980).

Comparative studies

In addition to the general problems described above, resulting from differing methodologies and definitions, there are differences between studies in the data presented. We will summarize the parameters commonly used and note some of the differences in calculation and presentation of these values by different authors.

The terminology used for dive parameters can be confusing; we have used the definitions:

dive depth = maximum depth of each dive

mean dive depth = mean (maximum depth of dives)

modal dive depth = mode (maximum depth of dives)

modal depth = depth at which most time is spent, based on a cumulative distribution of depth readings

bottom time = time at > 85% maximum depth of dive

daily maximum depth = maximum depth recorded each day

When comparing diving behaviour between species using detailed TDR records, the dive depth and duration are probably the most common and important summary parameters for each dive. Mean or modal values of dive depth and duration are most useful for comparisons between individuals or species (Machlis *et al.*, 1985). An indication of the rate at which dives are performed (the number of dives per day) is a crucial gauge of the energetic expenditure involved. Further to these, the percentage of time spent at the surface (or the percentage of time spent at depth) provides an indication of the time constraints of foraging. Presentation of modal depth is important to assess an animal's use of the water column. Categorization of dive shapes and presentation of the proportion of time spent at the 'bottom' of dives (bottom time) may provide information on the function of dives (Asaga *et al.*, 1994). Ascent and descent rates together with other dive parameters (duration, max. depth, and bottom time) can provide some information on the energetics of diving. Whether or not the study animal is diving to the sea floor is an important consideration for interpopulation differences, since this may be highly dependent on location rather than on a species' capability. Finally,

an overall summary for all individuals of the mean values of these parameters may be of most use in making broad comparisons between species and populations.

While this list sounds quite straightforward, the presentation of these data by different authors varies. Many authors provide detailed statistics for each animal studied (e.g. Westgate *et al.*, 1995), while others fail to provide many of the basic dive statistics suggested above. Others present description of dive types rather than quantification of these types (e.g. Baird, 1994), or provide ranges of dive parameters with no other information to describe the distribution of these parameters (e.g. Martin & Smith, 1992).

Data-downloading TDR studies usually provide mean dive depth recorded, while satellite-linked TDR studies usually provide a histogram of dive-depths. Studies using satellite-derived data often also present the mean of daily maximum depths, and it is worth noting that this is not the same as the daily mean of dive depths and cannot be used as a substitute. Most, but not all, studies provide results for dive rate (the number of dives observed per day), but do not separate this into the rate of dives of different classes, such as the rate of long, deep diving. Ideally, the dive rate should be provided for the classes of dives (depending on the dive definition used) for which basic statistics such as mean depth or duration are given.

Few studies calculate the proportion of bottom time for each dive and present a mean of this. Instead many authors provide mean bottom time and mean dive duration (essentially discarding information about dive shape, e.g. Westgate *et al.*, 1995). However, calculating mean proportion of the dive at the bottom from these is not accurate:

$$(\text{mean bottom time})/(\text{mean dive duration}) \neq \text{mean} (\text{bottom time}/\text{dive duration})$$

For example, if one dive has a total dive duration of 10 min with bottom time of 8 min, i.e. BT/DT = 0.8, while a second dive has total dive duration of 5 min with bottom time of 1 min i.e. BT/DT = 0.2, then

$$(\text{mean bottom time})/(\text{mean dive duration}) = 4.5/7.5 = 0.6 \quad (1)$$

whereas

$$\text{mean} (\text{bottom time}/\text{dive duration}) = \text{mean} (0.8, 0.2) = 0.5 \quad (2)$$

The mean proportion of a dive spent at the bottom, averaged over all dives (2) is more indicative of the 'average' dive shape and is less susceptible to bias from dives of longer duration. This is therefore the more reliable calculation method of the two.

In assessing the proportion of time animals spend at the surface, a wide range of depths (1 m, 2 m, 5 m, 8 m, 10 m) have been used to define 'surface'. This value, calculated from a frequency histogram of the number of depth values recorded within certain ranges, is often determined for use in sighting surveys and so may be defined by reference to the clarity of the surface waters. Alternatively, authors may use '2× instrument resolution'. In order to simplify comparisons with other studies, an indication of time spent at different depth ranges would be helpful (e.g. Table 4). This allows readers to assess the differences in sightability at the surface depending on various factors such as water clarity or surface chop. Further information regarding time spent at depth is also important for consideration of depth-specific threats (such as impact of certain fishing methods, acoustic impacts, etc.). Westgate *et al.* (1995) used an alternative definition of surface time as the sum of the interdive times between dives of deeper than 2 m, divided by the total deployment time. Using the program Dive Analysis (Wildlife Computers, Redmond, WA), this definition is identical to a calculation of time spent as < 2 m depth since the maximum depth of the surface (2 m) is used to define the start and end points for dives.

Table 4. Suggestions regarding data analysis and presentation for future studies (see text for additional explanation).

Sampling rate	Differences in sampling rate will cause differences in results. Higher sampling rate will provide more precise results.
Sample size	Individual and seasonal variation may be a problem. Sample size is based on the number of individuals sampled, although the duration of the sampling period will affect the ability to detect temporal trends in the data.
Presentation of ranging data with varying time interval	Displacements should be investigated over time intervals varying from the sampling interval to the study duration, to investigate both short- and long-term displacement rates and patterns.
Definition of dive	There is a need to differentiate objectively between 'respiration' dives and other dives. Possibilities include: – definition of foraging (although subjective) – cluster analysis – three dimensional frequency histogram: depth and duration – log-survivorship plot of dive duration – bimodal plot of cumulative time spent in dives of different durations
Presentation of dive statistics	Dive statistics (independently for dive-types): dive duration (mean, mode, max), dive depth (mean, max.), proportion of time at bottom, ascent rate, descent rate, modal depth. – summary results should be presented for each animal – numerical data description (mean, SD)
Dive rate (no. dives/day)	Present dive rate (for each dive-type).
Proportion of dive at bottom	Presentation of mean proportion of dive at bottom will provide information on general dive shape.
Percentage of time at surface	Present the proportion of time at various depths (dependent on sampling resolution), so that time (%) in top 2, 4, 6, 8, 10 m (for example) of the water can be assessed.
Are dives depth limited?	Dives to the sea floor are likely to differ in dive depths between sites. Sea floor depths in the study area should therefore be presented, and dives to the sea floor noted.
Representativeness	Representativeness of deployments should be discussed. Taggability of animals may vary such that data are not obtained from a random sample of the population, especially for studies of rehabilitated animals.

Finally, for comparisons between populations it is important to consider whether diving is bottom-limited. Results from Narwhal and Beluga studies (Martin & Smith, 1992; Martin *et al.*, 1993; Martin, Kingsley & Ramsey, 1994; Heide-Jorgensen & Dietz, 1995; Heide-Jorgensen, Richard & Rosing-Asvid, 1998; A.R. Martin, pers. comm.) suggest that diving behaviour (especially maximum dive depths) depends to a large extent on the bottom depth of the area in which the studies are conducted. This is likely to be the case for many dive studies (e.g. Baird, 1994), thus reporting bottom depth is important for comparisons between studies.

INTEGRATING DIVING AND RANGING

The two major resources that marine mammals need for survival are air and food. Animals will therefore optimize their diving behaviour in order to gain the maximum food under limitations of oxygen requirements (Kramer, 1988). However, the spatial ranging behaviour of animals will be unaffected by oxygen requirements since oxygen is uniformly distributed at the surface, so we would expect ranging behaviour instead to be governed by maximization of prey. Such correlation between movements and the profitability of foraging has been

shown for Sperm Whales (Whitehead, 1996; Jaquet & Whitehead, 1999). The integration of studies of diving and ranging can therefore provide information concerning the dimensions, concentration and patchiness of prey aggregations, and will allow a more detailed description of the foraging ecology of an animal than studies of either diving or ranging alone.

CONCLUSIONS

Due to the logistical difficulty of deploying time–depth recorders or radio-tags and the often limited attachment durations, studies of the diving and ranging patterns of odontocetes have not progressed at the same rate as those of pinnipeds. Perhaps because so few publications have resulted from this work, and by so few investigators, there is currently little accord in the way data are collected or summary measures reported. We have tried to identify some of the important considerations to keep in mind when designing and undertaking studies of the diving and ranging behaviour of odontocetes, particularly those using time–depth recorders. We have made a number of recommendations on which techniques and sampling regimes are appropriate, depending on the questions being asked and the logistical constraints of the system being studied. Our suggestions for standardization between studies in terms of data analysis and presentation are summarized in Table 4. In particular, an objective discrimination between dive types of odontocetes is needed in order that dive statistics are not biased by the frequent shallow dives made during a surfacing bout and, if more than one dive-type for deep dives is identified, statistics should be presented for each dive-type. Studies using different sampling rates and sensor resolutions will not be strictly comparable and the effect of these will need to be considered in comparisons between studies. Ranging data should be analysed over various time intervals ranging from the sampling interval up to the scale of the study duration to provide information on both short and long-term rates of movement. Certain results are particularly important for management considerations. These include the modal depth and the proportion of each dive spent at the bottom, which are important in assessment of depth-specific (e.g. acoustic) impacts, and the percentage of time at the surface, which is required to establish correction factors for population census analyses. We hope that the adoption of some or all of these recommendations in future studies will aid the comparison of data collected by different investigators, on different species and populations of odontocetes.

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