Establishing Death in Stranded Odontocetes (Toothed Whales) Using Other Mammals: A Pilot Study

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Abstract

The aim of this study was to investigate and evaluate a new method for determining death in stranded odontocetes (toothed whales). The new method was using the pulsations seen in the retinal blood vessels in the place of the heart rate. The retinal blood vessels can visualized, using an ophthalmoscope, in the fundus of the eye. Initially the procedure was to be testing using animals at a mass stranding, but there were no suitable strandings that took place during the time of the study.

Therefore other mammal species were used to test the procedure. These mammals were cattle, sheep, and dogs, with additional observational testing carried out on seals, sea lions and dolphins. The mammals were chosen because of their availability and supply.

The results showed that there was a strong relationship between the heart rate and the pulsations measured in the retinal blood vessels. This was expected as the cardiovascular system is connected and pulsations of blood vessels must have originated from the heart. The results using dogs, also indicated that there is a relationship between the cessation of the pulsations in the retinal blood vessels and the cessation of the heart beat. Dogs were used as a benchmark by which all other mammals could be compared.

Therefore this study indicates that it is possible to identify the cessation of the heart using the cessation of the pulsations in the retinal blood vessels

General Introduction

Cetacean (whales, dolphins and porpoises) strandings have been recorded since Aristotle 2000 years ago (Geraci 1978) and have provided intrigue and interest for both scientists and the general public since that time. Strandings can be divided into two categories, single strandings and multiple or mass strandings (Geraci 1978, Robson 1984, Dawson 1985). Single strandings occur in many species throughout the world, and have provided valuable scientific information (Odell 1987). But it is mass or multiple strandings, which can involve hundreds of individuals, that rouse the highest level of interest. This type of stranding happens only in certain parts of the world and regularly involves only certain species (Odell 1987), all of which are social odontocetes (toothed whales) (Geraci 1978).

At a mass stranding where seemingly healthy animals came ashore while still alive, 80% of those animals that strand will not survive (Mazzuca *et al* 1999). Therefore it is very important to be able to make accurate judgements about an animal's state of health in order to improve the overall welfare of the animals at a stranding. Unfortunately the 'usual' methods for determining death in mammals are difficult to apply to cetaceans, because of a number of anatomical and physiological features (Pabst *et al* 1999) that they have. This accurate assessment of their state of health is not a straight forward exercise.

The aim of this study is to investigate and evaluate a new method of determining death using pulsations in the retinal blood vessels. The intention was to examine recently stranded whales, however over two years far fewer than the average number of strandings occurred, and the one or two that did were not accessible in time. Accordingly the measurement was tested using dogs, sheep and cattle with additional observational testing carried out on seals, sea lions and dolphins. In order to fully understand how this technique can be assessed it is important to understand the complexity of the cetacean cardiovascular and visual systems, and these are compared with those species used to test the procedure.

References

Dawson S. 1985. *The New Zealand Whale and Dolphin Digest*. Brick Row Publishing Co. Ltd. Auckland

Geraci J. 1978. *The enigma of marine mammal strandings*. Oceanus 21: 38-47

Mazzuca L., Atkinson S., Keating B. & Nitta E. *Cetacean mass stranding in the Hawaiian Archipelago, 1957-1998*. Aquatic Mammals 25: 105 – 114

Odell D. 1987. *The mystery of marine mammal strandings*. Cetus 2-6

Pabst D., Rommel S., & McLellan 1999. *The functional morphology of marine mammals*. In Reynolds J. & Rommel S. (eds) Biology of Marine Mammals. Smithsonian Institution Press. Washington pp 15-72

Robson F. 1984. *Strandings, ways to save whales*. Angus & Robertson Publishers Sydney

Chapter One:

Cetacean Strandings

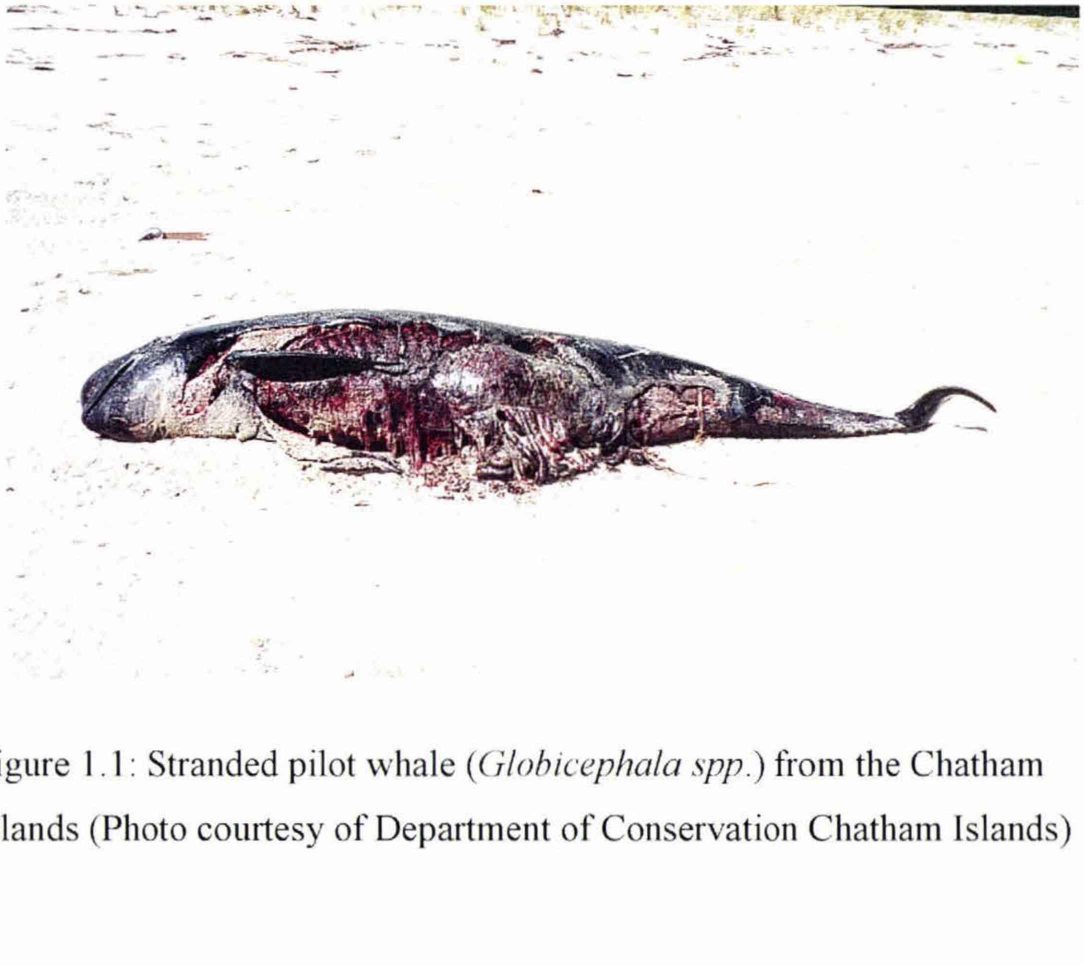

Figure 1.1: Stranded pilot whale (*Globicephala spp.*) from the Chatham Islands (Photo courtesy of Department of Conservation Chatham Islands)

'It is not known why they sometimes run aground on the seashore; for it is asserted that this happens rather frequently when the fancy takes them and without any apparent reason'

Aristotle

(Geraci 1978)

1.1 Introduction

Cetaceans (whales, dolphins and porpoises) make up one of the most popular and well-known groups of animals on earth. Widely considered to be intelligent animals, they nonetheless contain in their behaviours one that is difficult to understand. This is the phenomenon of stranding on the shore, sometimes apparently deliberately. Although there is little direct evidence, whale strandings may have been happening since whales first appeared in the fossil record about 50 million years ago, and the phenomenon was commented on by Aristotle 2000 years ago. It is unclear why seemingly healthy animals sometimes place themselves at extreme risk by entering extremely shallow water at the edge of the sea. This chapter discusses the nature and types of strandings and compares the behaviour in pilot whales and killer whales as special examples.

1.2 Definition

Strandings or beachings have been defined as occurring when marine mammals come ashore and are unable to return to deeper water (Robson 1984). Strandings can be classed as single or solitary, and multiple (Geraci 1978, Robson 1984, Dawson 1985). Multiple refers to two or more animals (excluding mother-calf pairs) coming ashore at the same place and time. As the number of animals increases, the term mass stranding is used (Geraci 1978). Geraci (1978) points out that any marine mammal whether whale, seal or otter can strand singly, whereas only a few species of cetaceans strand in groups.

1.3 Strandings of single individuals

Single or solitary strandings have included all known cetacean species and some of which are known only from the stranding records. For example Shepherd's beaked whale (*Tasmacetus shepherdii*) has never been sighted at sea (Geraci 1978). Additionally Fraser's dolphin (*Lagenodelphis hosei*) was described using a single skull found on a beach in Borneo about 1895 (Odell 1987) and remained mysterious until 1971 when several where accidentally caught in the yellowfin tuna purse seine fishery in the eastern tropical Pacific (Odell 1987). The pygmy killer whale (*Feresa attenuata*) was first described by Gray in 1827, also on the basis of a single skull, which was of unknown origin. The species remained essentially unknown to science until 1952 when, according to an account by M.Yamada, one was caught in Japan (Odell 1987) . *Feresa* is still poorly known to science, and almost all current information has come from stranding records (Odell 1987).

Strandings of single individuals do not always involve live animals, rather, most animals come ashore already dead and are brought by ocean currents while still inflated by the gases resulting from decomposition (Carwadine *et al* 1998). It is sometimes difficult to distinguish between individuals that have died at sea and those which have died after coming ashore (Brabyn 1992). Those that are cast ashore alive are almost always ill (Orr 1984). Orr (1984) suggests that when a whale is ill it may seek shallow water in order to rest and continue breathing. This is very unusual behaviour and only killer whales (*Orcinus orca*) have been reported to spend prolonged intervals in shallow water in so-called 'rubbing areas'. This, however, has not been known to result in strandings of this species, and no other cetacean is recorded as using rubbing areas (Harrison & Bryden 1998).

Single strandings are far more common than multiple and mass strandings, and occur over a much wider range encompassing all kinds of terrain. Single strandings can be used as an approximate indicator of population density and distribution (Sergent 1982).

1.4 Multiple and Mass strandings

One of the most interesting phenomena in animal behavioural ecology is the sudden appearance of a group of whales on a shore. Mass strandings can range from two (excluding mother-calf pairs) to hundreds of animals. The largest recorded stranding was of 800 false killer whales (*Pseudorca crassidens*) in Argentina (Marelli 1953). Unlike single or solitary strandings mass strandings do not occur everywhere, but only in certain locations involving certain species. Frequent stranding sites are known as 'hotspots' and they seem to share certain characteristics. For example, in Hawaii strandings are associated with fringing reefs, shallow water bathymetry, sandy bottoms and/or a gently sloping seafloor gradually ending at the beach (Grace 1974; Campbell 1987, Keating 1994). On Maui four strandings occurred in Mal'alaea Bay bordering the Kihei isthmus with a gently sloping seabed (Mazzuca *et al* 1999). Also, Mazzuca *et al* (1999) suggest that the seafloor in the area may not adequately reflect the approaching landmass sufficiently to allow cetaceans to properly navigate, and as a result they strand.

Figure 1.2 Pilot whale stranding in New Zealand using people and a low-flying helicopter to herd the animals out to sea (Dawson 1985)

Particular stretches of coast can be especially prone to mass strandings. These areas, often referred to as 'whale traps' (Brabyn & McLean 1992) are described as having long sloping beaches and some kind of protrusion of the coastline. Examples of these include Macquarie Harbour in Tasmania (Warneke 1983), Bahia de La Paz in Mexico (Gilmore 1957), Cap Vert in Senegal (Sergeant 1982), Wellfleet Bay in Massachusetts USA (Mead 1979), and Bahia San Bastion in Argentina (Goodall 1978). All of these sites have recorded mass strandings (Brabyn & McLean 1992). Brabyn & Mclean (1992) also found that sites where the beaches were hooked at one end and the surface currents moved towards the beach, experienced more mass strandings. A good example of this is Golden Bay in the north-west corner of the South Island of New Zealand.

Figure 1.3 Sperm whale stranding in the Wellington Region of New Zealand (Photo courtesy of Bruce Dix)

The following 19 species are known to mass strand: short-finned pilot whale (*Globicephala macrorhynchus*), long-finned pilot whale (*Globicephala melaena*), false killer whale (*Pseudorca crassidens*), pygmy killer whale (*Feresa attenuata*), killer whale (*Orcinus orca*), sperm whale (*Physeter macrocephalus*), pygmy sperm whale (*Kogia breviceps*), dwarf sperm whale (*Kogia simus*), spotted dolphin (*Stenella attenuata*), spinner dolphin (*Stenella longirostris*), short-snouted spinner dolphin (*Stenella clymene*), bottlenose dolphin (*Tursiops truncatus*), Fraser's dolphin (*Lagenodelphis hosei*), common dolphin (*Delphinus delphis*), melon-headed whale (*Peponocephala electra*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), scamperdown whale (*Mesoplodon grayi*), strap-toothed whale (*Mesoplodon layardii*), North Atlantic bottlenose whale (*Hyperodon ampullatus*) (Odell 1987). Of these, the four that mass strand most frequently are the two pilot whale species (Figures 1.1, 1.2, & 1.5), the false killer whale and the sperm whale (Figures 1.3 & 1.4) (Odell 1987).

Figure 1.4 Sperm whale stranding in the Chatham Islands New Zealand (Photo courtesy of Department of Conservation Chatham Islands)

Baleen whales rarely, if ever, mass strand, and usually come ashore due to illness or are already dead before being washed ashore. In Hawaiian records, the only baleen whales to mass strand have been 15 humpback whales (*Balaeanoptera novaeangliae*), four minke whales (*Balaeanoptera acutorostrata*) and two fin whales (*Balaenoptera physalus*) (Mazzuca *et al* 1999). In the case of the humpback whales, tests on these animals showed high levels of poisonous biotoxins in the animals that probably caused their deaths (Geraci *et al.* 1989).

Live strandings in general are rare e.g. in 70 years of records of strandings in the United Kingdom only 137 events out of 3000 records could be identified as live strandings. These included 28 group strandings (with 3 or more animals), 96 single and pair strandings and 13 group near-strandings. The latter are cases with all the preliminary features of a live group stranding, but ending in the escape of all or most animals (Klinowska 1986).

1.5 New Zealand Whale Strandings

New Zealand as a whole is recognized as a hot spot for whale strandings. Brabyn (1992) reported that the New Zealand Whale Stranding Database (NZWSD) contained 1140 records of whale strandings representing a total of 8287 individuals, 34 species, 163 mass strandings and 304 known live strandings. This is relatively high compared to stranding databases for other countries.

Of the 34 species found in New Zealand's waters, 33 have stranded at some time during the last 80 years (Orr 1984). The exception is the hourglass dolphin (*Lagenorhynchus cruciger*), an inhabitant of subantarctic waters, that is known to have been in our region, but has not yet been found stranded. The species of whale which most often strand are the pilot whale (Figures 1.1, 1.2 & 1.5), false killer whale, sperm whale (Figures 1.3 & 1.4), scamperdown whale, common dolphin, pygmy sperm whale, dusky dolphin, killer whale (orca) and Hector's dolphin. The first three are common species over New Zealand's continental shelf and travel in large herds or pods, so tend to strand in large numbers.

Figure 1.5 Pilot whale stranding in The Wellington Region of New Zealand (Photo courtesy of Bruce Dix)

Some New Zealand coastlines are particularly associated with strandings (Donoghue & Wheeler 1990) that may be due to shallow sloping shores confusing cetacean sonar systems (Geraci & Lounsbury 1993). According to Dudok van Heel (1962) whales perceive that a sea passage exists where one does not, and become stranded. Dudok van Heel (1962) observed multiple strandings at Whangarei and stated 'It is significant that a bay with beaches exactly fitting our concept on strandings shows so many victims'. Robson (1984) also observed that Mahia Peninsula, the site of multiple pygmy sperm whale (*Kogia breviceps*) strandings, was an excellent example of a gently sloping sandy beach combined with a protrusion of the coastline. New Zealand mass strandings occur primarily at such beaches, for example Houhora, Hokianga, Ruakaka, Ocean Beach Whangarei, Opoutama, Mahia, Manukau, Ngunguru, Wainui, Gisborne, Muriwai, Farewell Spit, Golden Bay, and the Chatham Islands (Orr 1984) (Figure 1.6).

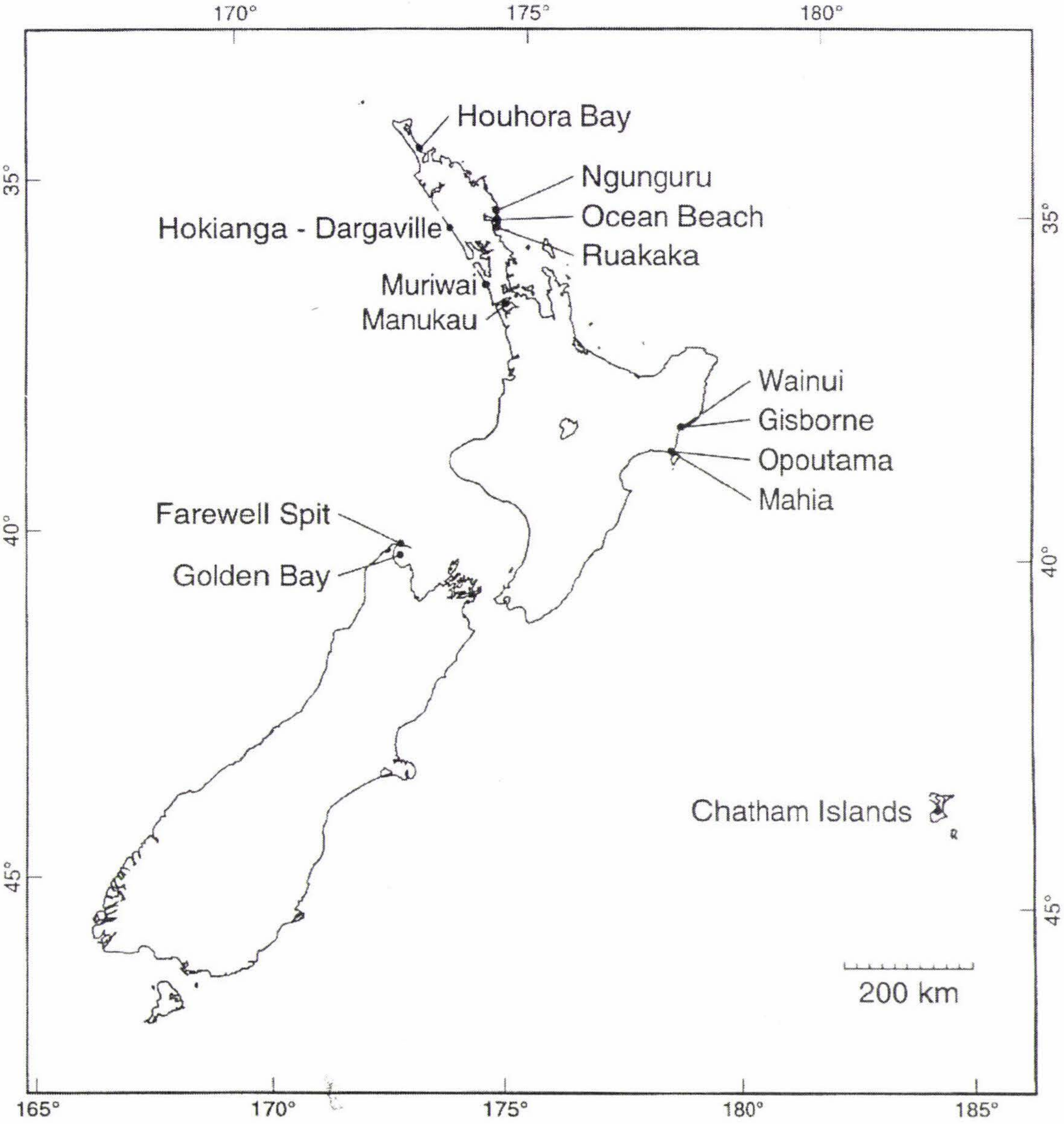

Figure 1.6 Map of New Zealand showing the location of the most frequent stranding sites

1.6 Similarities between Species that Frequently Strand

All the species which mass-strand are social odontocetes (toothed whales) (Geraci 1978) living in sometimes very large groups. According to Klinowska (1986) pilot whales and false killer whales can live in groups numbering in the hundreds. Their highly social nature, and strong social bonds may be the reason why so many animals strand at one time (Carwadine *et al* 1998).

There are numerous reports from early 1900s whaling operations and from drive fisheries of individuals escaping from the boats but returning to the boats and being killed along with the rest of their group (Bonner 1980, Cousteau 1988). This behaviour may not spring from altruism but be selfishly driven i.e. the separated individuals might not be able to survive on their own. For instance evidence from wounds, scarring and shark stomach contents indicate that sharks are significant predators on smaller tropical and temperate odontocetes (Connor *et al* 2000) (Figure 1.7). Tiger sharks (*Galeocerdo cuvieri*), dusky sharks (*Carcharinus obscurus*), bull sharks (*Carcharinus leucas*) and great white sharks (*Carcharodon carcharias*), are the species most often implicated in nearshore attacks on odontocetes such as the bottlenose dolphin (McBride & Hebb 1948; Wood et al 1970; Corkeron *et al* 1987; Cockroft *et al* 1989; Long & Jones 1996; Connor *et al* 2000). White sharks have also been implicated in predation on a wide variety of odontocetes, from the small harbour porpoise to larger beaked whales (Long & Jones 1996).

Figure 1.7 Shark wound healing on a five year old male bottlenose dolphin, Shark Bay Australia (Mann *et al* 2000)

Some odontocetes may attack others. For example killer whales are formidable predators that can successfully hunt even the largest cetaceans (Geraci 1978, Carwadine & Camm 1999). Killer whales have been observed to attack the largest baleen whale (Blue whale *Balaenoptera musculus*, Tarpy 1979), and the largest odontocete (sperm whale, Arnborn *et al* 1987) as well as smaller dolphin species (e.g. Constantine *et al* 1998). The only cetaceans that may be immune to killer whale predation are individuals living in tropical rivers (Jefferson *et al* 1991), or other protected coastal habitats that killer whales do not penetrate. Evidence for killer whale predation attempts come not only from occasional observations of attacks, but also from scars on living cetaceans and from killer whale stomach contents. Scars on the flukes of 20-33% of young humpback whale calves suggest that predation might be focused on young whales and that predation attempts may be much more common than indicated by direct observation (Clapham 2000).

A major factor that affects any wild animal population is the availability of food. All the odontocete species listed above seek very similar foods mostly squid and/or fish. There is evidence to suggest that when fishing catches are low, strandings events are relatively high in number. Using the British stranding records, Odell (1987) found that stranding events gradually increased from 1918 to a peak value in 1935, the year in which the monthly averages of the planktonic stages of teleostean fish were in decline. In contrast Sergent (1982) found in the Newfoundland drive fisheries catch records that although there was a serious decline in the number of pilot whales, however, their main food source squid (*Illex illecebrosus*) did not have a corresponding decline. As squid is also the main food source for sperm whales, as evidenced by squid beaks found in the stomachs of stranded individuals, this might also hold true for them as well (Clarke 1986, Clarke & Young 1998, Smith & Whitehead 2000).

It is believed that all odontocete species have the ability to echolocate by emitting high frequency sounds that are reflected back to the animal from objects (including food) underwater. One of the most popular theories to explain why cetaceans strand relates to failure of their sound reception system leading to false impressions of the seascape (Klinowska 1986; Kirshvink *et al* 1986). This is debatable because the whales' sound reception system is highly specialised – trained dolphins can distinguish between metals of two different kinds and between objects that differ in size by only a few millimetres (Orr 1987). Dudok van Heel (1962) however, showed that gently sloping beaches gave weak echoes, but Geraci (1978) claimed that cetaceans had the ability to detect such a gradually changing profile.

Another theory to explain strandings is that the animals were preoccupied with feeding and thus, ended up inadvertently on the shore (Geraci & Lounsbury 1993). It has been suggested that on sandy shelving beaches a group of whales intent on fishing may stray into shallow water inadvertently because they are not using the frequencies needed for accurate echolocation. The clicks whales emit for echolocation have a wide range of frequencies and volume. The dolphin can deliver loud low frequencies for distant objects and softer, high frequencies for objects nearby. Most sonar hunting sounds are over 10,000 cycles per second (Orr 1987). Orr (1987) also suggests that if they do try to locate the sea bottom, a soft sandy sea bed may be an unsuitable target on which to focus their sonar beams, so the animals perceive the water to be deeper than it is.

Brabyn (1991) however, considers this unlikely because mass strandings involve pelagic (offshore) species whose food species are not found inshore. In areas where the continental shelf is shore (e.g. Kaikoura, New Zealand) there have been no mass strandings. Stomach analysis of stranded whales has shown that most have empty stomachs, but this could be due to regurgitation when under stress. Another theory suggests that when pelagic species that primarily live in deep water away from the coast, come close to shore they are unfamiliar with the surrounding terrain and strand as a result (Gilmore 1957; Dudok van Heel 1962; Warneke 1987).

The following two examples , the pilot whale which is the most frequent mass strander and the killer whale which uses stranding as a hunting technique, exemplify two different aspects of strandings.

1.7 The Pilot Whale (*Globicephala spp.*)

Pilot whales are the most frequent stranders around the world of all whale species. There are two species of pilot whale, the long-finned pilot whale (*Globicephala meleana*) and the short-finned pilot whale (*Globicephala macrorhynchus*) (Figure 1.8), both are widely distributed throughout the world's temperate and tropical oceans while the short-finned pilot whale is found in tropical and warm temperate waters of the Atlantic, Pacific and Indian Oceans (Figure 1.8), the long-finned pilot whale is distributed 'antitropically' (Hubbs 1952; Davies 1963) in the temperate North Atlantic and all southern temperate oceans (Rice 1977) (Figure 1.9). The pilot whales belong to the family Delphinidae, which comprises all dolphin species, and the sub-family Globicephalinae. The Globicephalinae comprises a group known as the 'blackfish' because the members of this group are mostly black in colour, and includes all of the most frequent mass stranders (except sperm whales).

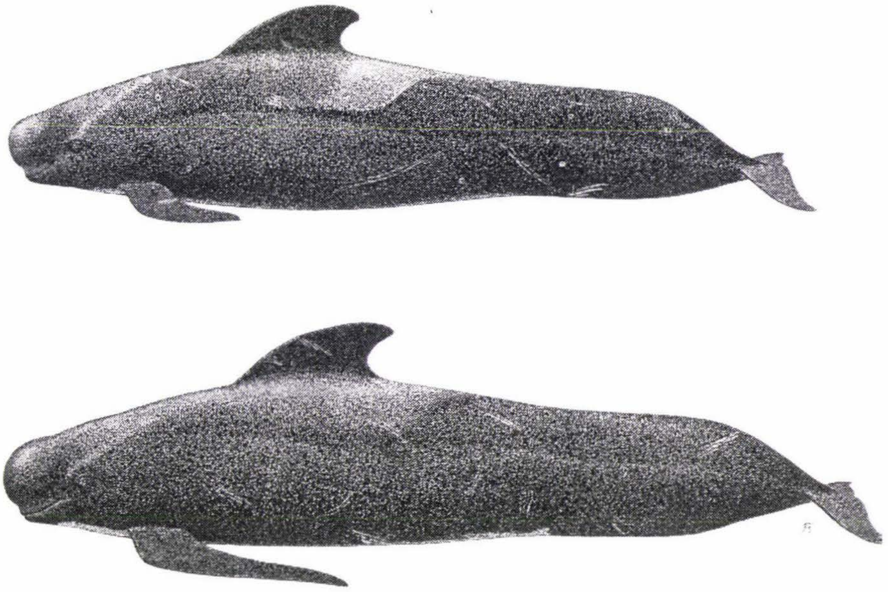

Fig 1.8 Comparison of the short-finned pilot whale (*Globicephala macrorhynchus*)(above), and the long-finned pilot whale (*Globicephala melas*)(below) (Bernard & Reilly 1999)

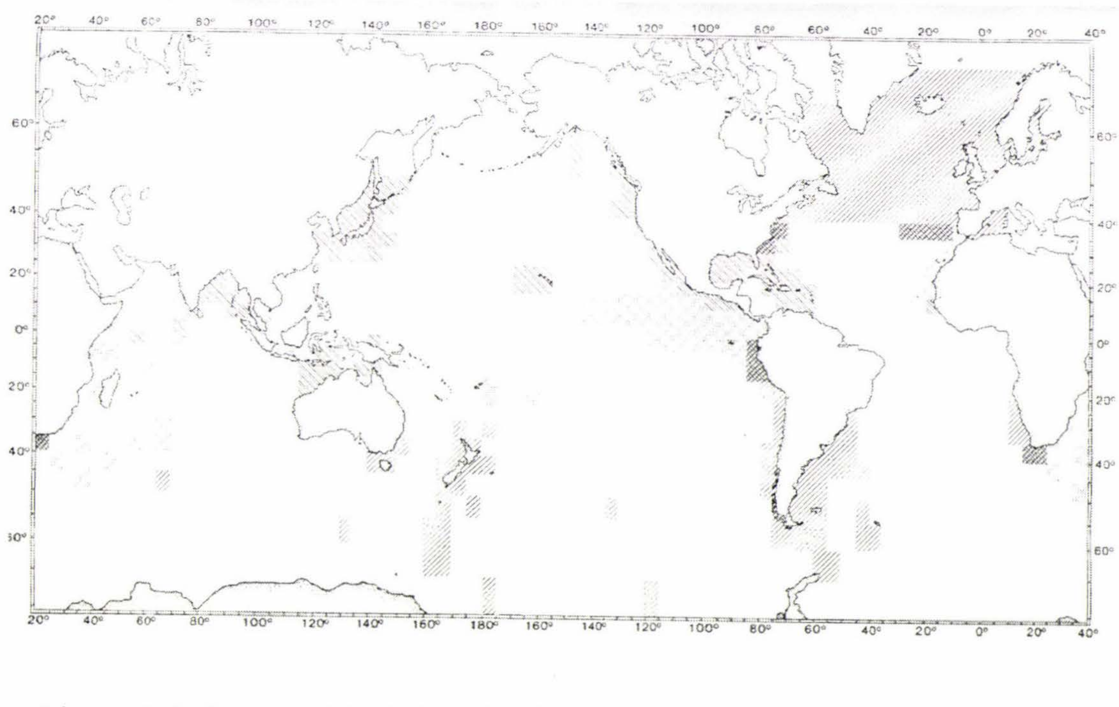

Figure 1.9 Geographical distribution of pilot whales (*Globicephala spp.*) (Bernard & Reilly 1999)

Pilot whales live in pods which vary greatly in size, anywhere from a few to several hundred individuals (Bloch *et al* 1990). They live in possibly the most socially structured groups among odontocetes. Offspring remain with their mother's herd after reaching sexual maturity, but there may be no inbreeding within pods, because DNA evidence from the Faroe Islands indicates a high level of outbreeding (Amos *et al* 1993). Males move between pods when several come together as temporary aggregations (Amos *et al* 1993). There have been three types of social organization described by Norris & Prescott (1961) and Brown & Norris (1956): traveling/hunting groups; feeding groups; and 'loafing' groups. A loafing group is described as an almost stationary aggregation of animals, floating at the surface and nearly or actually touching each other.

1.8 The Killer whale (*Orcinus orca*)

Of all whale species that strand, killer whales are unique in being able to deliberately strand themselves temporarily in the course of predation and then refloat themselves. The killer whale is said to be the most widely distributed mammal on earth (Leatherwood & Dahlheim 1978; Heyning & Dalheim 1988). Although killer whales have been observed in tropical waters and the open ocean, they are most abundant in coastal habitats and high latitudes (Figure 1.10). Killer whales residing in coastal areas often enter shallow bays, estuaries and river mouths (Leatherwood et al 1976). Studies in North America suggest that there are two genetically distinct forms of killer whales, known as 'transients' and 'residents' (Carwadine & Cam 1995). Killer whales are fierce predators and have strong social bonds. One population of killer whales lives in the most stable groups known among mammals, so much so that individuals never disperse from the natal group (Dahlheim & Heyning 1999).

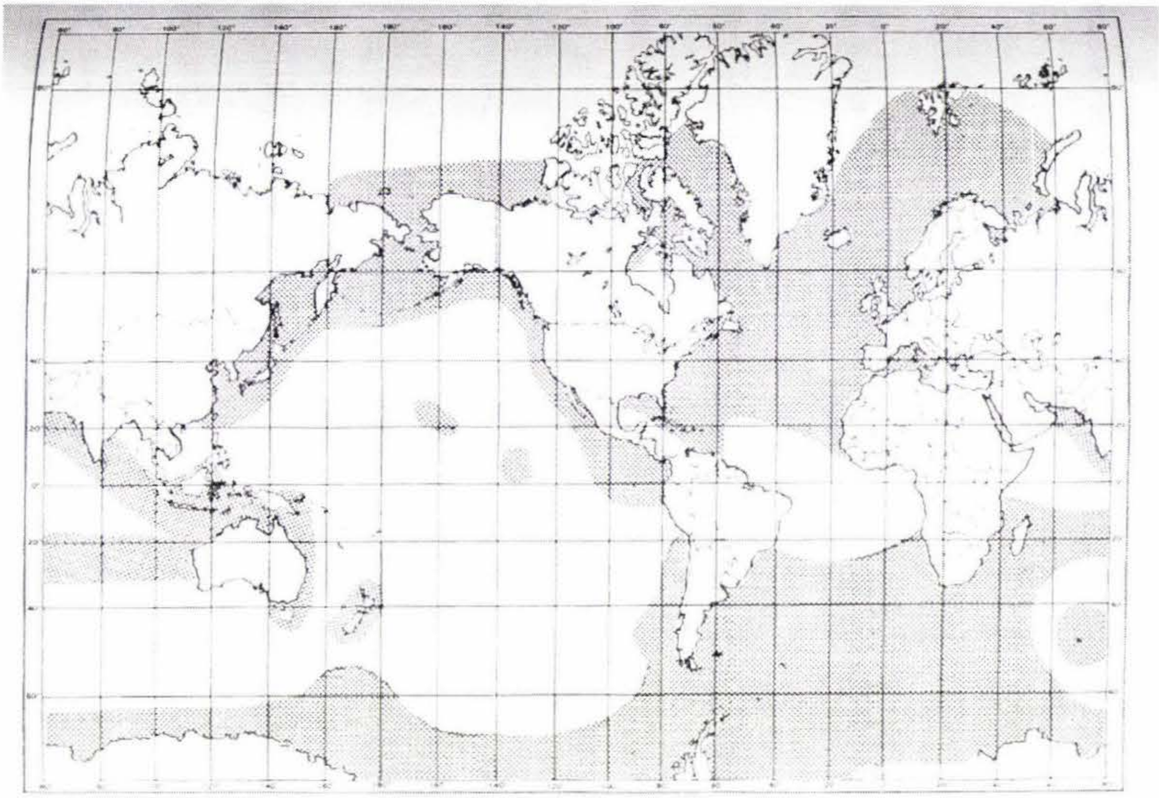

Figure 1.10 Geographical distribution of killer whales (*Orcinus orca*) based on documented records (Dahlheim & Heyning 1999).

Killer whales residing off the coast of Punta Norte, Penninsula Valdes in southern Argentina (Patagonia), have been found to show a curious behaviour in that they intentionally beach themselves in order to catch young and sometimes adult pinnipeds, such as southern elephant seals (*Mirounga leonina*) and southern sea lions (*Otaria flavescens*), on the shores (Lopez & Lopez 1985) (Figure 1.11). Elephant seals give birth mostly in September and October (Scolaro 1976) and sea lions mostly in January and February. Shortly after these times, when pups are beginning to enter the water, killer whales can be observed close to shore (Lopez & Lopez 1985). Lopez & Lopez (1985) give a detailed account of how the killer whales manage to come ashore, capture the seal or sea lion and return to the sea without becoming permanently stranded. This is an interesting behaviour as killer whales belong to the Globicephalinae, which also includes the most frequently stranded species.

Figure 1.11 A male killer whale of Patagonia intentionally beaching in order to catch sea lion pups on the shore (Würtz & Repetto 1998)

1.9 Summary

Cetacean strandings can be divided into two categories, single strandings and multiple or mass strandings. Single strandings involving single or mother-calf individuals occur throughout the world and include a number of different marine mammal species that have provided valuable scientific information. Multiple or mass strandings sometimes involving large numbers of individuals, occur only in certain places and involve 19 species of odontocete (toothed whale). Of those, the most frequent stranders are the pilot whales (*Globicephala spp.*), the false killer whale (*Pseudorca crassidens*), and the sperm whale (*Physeter macrocephalus*). New Zealand is described as a 'hotspot' for stranding due to the relative frequency of multiple or mass strandings as compared to other countries. Stranding has also been employed as a hunting technique by killer whales (*Orcinus orca*) in Patagonia.

1.10 References

Amos B., Schotterer C. & Tauz D. 1993. *Social structure of pilot whales revealed by analytical DNA profiling*. Science 260: 670-672

Arnbom T., Papastavrou V., Weilgart L., & Whitehead H. 1987. *Sperm whales react to an attack by killer whales*. Journal of Mammalogy 68: 450-453

Bernard H. & Reilly S. 1999. *Pilot whales* – Glopicephala. In Ridgway S. & Harrison R. (eds) Handbook of Marine Mammals Vol. 6 The Second Book of Dolphins and Porpoises

Bloch D., Desportes G., HoydalK., & Jean P. 1990. *Pilot whaling in the Faroe Islands: July 1986–July 1988*. North Atlantic Studies 2: 36-44 *not seen*

Bonner N. 1980. *Blandford Mammal Series: Whales*. Blandford Press Ltd. Dorset

Brabyn M. 1991. *An analysis of the New Zealand whale stranding record.* Science & Research Series No. 29 Department of Conservation New Zealand

Brabyn M & McLean I. 1992. *Oceanography and coastal topography of Herd-stranding sites for whales in New Zealand.* Journal of Mammalogy. 73: 469-476

Brown D. & Norris R. 1956. *Observations of captive and wild cetaceans.* Journal of Mammalogy 37: 311-326

Campbell J. 1987. *Bathymetric Atlas of the southeast Hawaiian Island.* Sea Grant Miscellaneous Report. UNIHI – SEAGRANT – MR – 87 – 10 *not seen*

Carwadine M. & Camm 1995. *Whales, Dolphins and Porpoises.* Dorling Kindersley Limited. London

Carwadine M., Hoyt E., Fordyce R.E., & Gill P. 1998. *Whales, Dolphins & Porpoises.* Reader's Digest. Australia Ltd.

Clapham P. 2000. *The Humpback whale: seasonal feeding and breeding in a baleen whale.* In Mann J., Connor R., Tyack P., & Whitehead H. (eds) Cetacean societies: field studies of dolphins and whales. The University of Chicago Press. Chicago pp 173-198

Clarke M. 1986. *A handbook for the identification of cephalopod beaks.* Oxford University Press *not seen*

Clarke M. & Young R. 1998. *Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores.* Journal of the Marine Biological Association of the United Kingdom 78: 623-641 *not seen*

Cockcroft V., Cliff G., & Ross G. 1989. *Shark predation on Indian Ocean bottlenose dolphins* Tursiops truncatus *off Natal, South Africa.* South African Journal of Zoology 24: 305-310 *not seen*

Connor R. 2000. *Group living in whales and dolphins.* In Mann J., Connor R., Tyack P., & Whitehead H. (eds) Cetacean societies: field studies of dolphins and whales. The University of Chicago Press. Chicago pp 199-218

Constantine R., Visser I., Buurman D., Buurman R., & McFadden B. 1998. *Killer whale* (Orcinus orca) *predation on dusky dolphins* (Lagenorhyncus obscurus) *in Kaikoura, New Zealand.* Marine Mammal Science 14: 324-30

Corkeron P., Morris R., & Bryden M. 1987. *Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland.* Aquatic Mammals 13: 109-113 *not seen*

Cousteau J & Paccalet Y. 1988. *Accident or suicide?* In Cousteau J. & Paccalet Y. (eds) Whales. Harry N. Abrams Inc Publishers New York pp 238-241

Dahlheim M. & Heyning J. 1999. *Killer whale –* Orcinus orca. In Ridgway S. & Harrison R. (eds) Handbook of Marine Mammals Vol. 6 The Second Book of Dolphins and Porpoises pp 281-322

Davies J. 1963. *The antitropical factor in cetacean speciation.* Evolution 17: 107-116 *not seen*

Dawson S. 1985. *The New Zealand Whale and Dolphin Digest.* Brick Row Publishing Co. Ltd. Auckland

Donoghue M. & Wheeler A. 1990. *Dolphins, their life and survival.* Blandford (in association with David Bateman). Auckland.

Dudok van Heel W. 1962. *Sound and cetacea.* Netherlands Journal of Sea Research 1 (4): 407-507 *not seen*

Geraci J. 1978. *The enigma of marine mammal strandings.* Oceanus 21: 38-47

Geraci J., Anderson D., Timperi R., St Aubin D., Early G., Prescott J. & Mayo C. 1989. *Humpback whales* (Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin.* Canadian Journal of Fish and Aquatic Science. 46: 1895- 1898 *not seen*

Geraci J. & Lounsbury V. 1993. *Marine Mammals Ashore. – A field guide for Strandings.* Texas A& M University Sea Grant Program Publication. Galveston

Gilmore R. 1959. *On the mass strandings of sperm whales*. Pacific Naturalist 1 (9): 9-16 *not seen*

Goodall R. 1978. *Report on the small cetaceans stranded on the coasts of Tierra del Fuego*. Scientific Report of the Whales Research Institute 30: 197-230 *not seen*

Grace J. 1974. *Marine Atlas of Hawaii*. Sea Grant Miscellaneous Report. UNIHI – SEAGRANT – MR – 74 – 01 *not seen*

Harrison R. & Bryden M. 1998. *Whales, Dolphins & Porpoises*. Intercontinental Publishing Corporation Ltd

Heyning J. & Dalheim M. 1988. Orcinus orca, *Mammalian Species account*. American Society of Mammalogists No 304 pp 9 *not seen*

Hubbs C. 1952. *Antitropical distribution of fishes and other organisms*. In Proceedings of the Seventh Pacific Congress of the Pacific Science Association, Vol III Meterology and Oceanography pp 324-329 *not seen*

Jefferson T., Stacey P., & Baird R. 1991. *A review of killer whale interactions with other marine mammals: Predation to co-existence*. Mammal Review 21: 151-180

Keating B. 1994. *Hawaii Sea floor Atlas*. Hawaii Institute of Geophysics SOEST. University of Hawaii. Honolulu pp 1-21 *not seen*

Kirschvink J., Dizon A. & Westphal J. 1986. *Evidence from strandings for Geomagnetic Sensitivity in Cetaceans*. Journal of Experimental Biology, 120: 1-24

Klinowska M. 1986. *The cetacean magnetic sense – evidence from strandings*. In Bryden M & Harrison R (eds) Research on Dolphins. Oxford University Press. Oxford United Kingdom pp 401-432

Leatherwood J., Caldwell D., & Winn H. 1976. *Whales, dolphins and porpoises of the western North Atlantic: a guide to their identification*. NOAA Technical Report NMFS Circular 396 pp 176 *not seen*

Leatherwood J. & Dalheim M. 1978. *Worldwide distribution of pilot whales and killer whales*. Naval Ocean Systems Center Technical Report 443 pp 39 *not seen*

Long D. & Jones R. 1996. *White shark predation and scavenging on cetaceans in the eastern north Pacific*. In Klimley A. & Ainley D. (eds) Great white sharks: The biology of Caracarodon carcharias. Academic Press San Diego pp 293-307 *not seen*

Lopez J. & Lopez D. 1985. *Killer whales* (Orcinus orca) *of Patagonia and their behaviour of intentional stranding while hunting inshore*. Journal of Mammalogy 66 (1): 181-183

Mann J., Connor R., Tyack P., & Whitehead H. 2000. *Cetacean societies: field studies of dolphins and whales*. The University of Chicago Press. Chicago pp 149

Mazzuca L., Atkinson S., Keating B. & Nitta E. *Cetacean mass stranding in the Hawaiian Archipelago, 1957-1998*. Aquatic Mammals 25: 105 – 114

McBride A. & Hebb D. 1948. 1948. *Behaviour of the captive bottlenose dolphin Tursiops truncatus*. Journal of Comparative Physical Psychology 41: 111-123 *not seen*

Mead J. 1979. *An analysis of cetacean strandings along the eastern coast of the United States*. In Geraci J. & St Aubin D. Insights through strandings U.S. marine mammal commission. Report No. MMC – 77/13. Washington pp 54-68 *not seen*

Norris K. & Prescott J. 1961. *Observations on Pacific cetaceans of California and Mexican waters*. University of California Berkeley Publishing Zoology 63: 291-402 *not seen*

Odell D. 1987. *The mystery of marine mammal strandings*. Cetus 2-6

Orr M. 1984. *Whales and Whale Strandings*. John McIndoe Limited. Dunedin

Rice D. 1977. *A list of marine mammals of the world*. NOAA Technical Report NMFS SSRF – 711 pp 15

Robson F. 1984. *Strandings, ways to save whales*. Angus & Robertson Publishers Sydney

Sergent D. 1982. *Mass strandings of toothed whales (Odontoceti) as a population phenomenon.* Scientific Reports – Whales Research Institute, Tokyo 34: 1-47

Scolaro J. 1976. *Censo de elephants marinas* (Mirounga leonina L.) *en al territorio continente Argentina.* Centro Nae. Patagonica Informe Technico 1.4.2, pp 12

Tarpy C. 1979. *Killer whale attack.* National Geographic 155: 542-45

Smith S. & Whitehead H. 2000. *The diet of Galapagos sperm whales* Physeter macrocephalus *as indicated by fecal sample analysis.* Marine Mammal Science 16(2): 315-325

Warneke R. 1983. *Whale stranding – accident or design?* Australian Natural History 21(2): 43-47 *not seen*

Wood F., Caldwell D., & Caldwell M. 1970 *Behavioural interactions between porpoises and sharks.* In Investigations on Cetacea Vol. 2. Brain Anatomy Institute. Berne *not seen*

Würtz M. & Repetto N. 1998. *Whales and dolphins, guide to the biology and behaviour.* Swan Hill Press England pp 79

Chapter Two:

Handling and Assessment of Cetaceans at a Stranding

Figure 2.1 An air-lifted dolphin (Robson 1984)

2.1 Introduction

This chapter first gives three examples of cetacean strandings and describes legislation relevant to dealing with stranded cetaceans. Then follows a description of marine mammal stranding networks, using the U.S. Marine Mammal Protection Act as an example. Finally there is a description of how best to assess, care for and rescue animals involved in a stranding.

2.2 Conditions of a Typical Stranding

Example One

Fehring & Wells (1976) give an account of a series of strandings of short finned pilot whales (*Globicephala macrorhynchus*) on the lower west coast of Florida. The strandings began on 19 August 1971, and finished six days later on 25 August. The strandings began at 6.00 pm (EDT ; Eastern Standard Time), when three pilot whales came ashore on Manasota Key, Sarasota County, Florida. The animals were returned to the sea with human assistance, and rejoined a larger group approximately 150m offshore. Six pilot whales were then spotted stranding approximately 1km south of the first site, and these animals were also returned to the main herd with human assistance.

The following morning a much larger group stranded on the Gulf side of Gasparilla Island, Lee County, Florida, 18.5km south of the original site. When the animals were discovered two had already perished and the rest were grounded in about 1m of water. A large group of people attempted to push the whales back into deeper water but each time the whales returned to shore. During this episode one of the females gave birth to a stillborn calf. In an attempt to refloat all the animals, some of the large males had ropes tied around their tails and, tethered to boats, were then held about 400m from the shore. This appeared to cause the remaining whales to not return to the shore but instead remain in deeper waters.

During this stranding event a collector for a local Aquarium captured one of the whales and slowly towed it towards the shore. The remaining whales followed the tow boat towards the beach. Close to the beach the boat was stopped to transfer that the captured whale to a van. The accompanying whales then continued on to the beach, stranding on Gasparilla Island 3km south of the site of the earlier stranding. Some of the whales became stuck on rocks and people had difficulty freeing them. When the whales were refloated in small groups they repeatedly came back to the shore, however after all the whales in the pod had been pushed off the shore at the same time, they swam to deeper water.

Five days later thirteen pilot whales stranded in the Marquesa Islands 35km west of Key West Florida, 275km southeast of the original stranding site. These animals were identified as the same whales involved in the original stranding, and included a large male with a distinctive dorsal fin and rope burns in the tail region. Six of the whales, including the one with the distinctive dorsal fin, were successfully refloated but the rest died.

Example Two

Porter (1979) gives an account of a stranding on 25 July 1976 along the shore of the Dry Tortugas, a small group of islands off the Florida coast (Figure 2.2).

Figure 2.2 False killer whales in the Dry Tortugas, in a tight group formation (Porter 1979).

The group comprised 30 false killer whales (*Pseudorca crassidens*), ranging in size from a baby to a large male, eighteen feet in length. It was ascertained that some of the group had beached three days earlier on Captiva

Island in Pine Island Sound, Florida, 140 nautical miles from the Dry Tortugas. One of the large males showed evidence of serious wounds. He lay on his side for three days with his blowhole occasionally submerged, bleeding slowly from his right ear in the shallow water. Eventually he died, flanked on either side by 14-15 whales that kept moving in towards the centre of the aggregation, noses pointing towards the beach. They maintained this wedge-shaped formation for the three days, with only the whales on the outside of the pod leaving occasionally for a few minutes at a time.

In this stranding the animals were very noisy, emitting chirps, squeaks, squawks and squeals that could be heard distinctly 40-50m from the beach, and over a much greater range underwater. Porter (1979) reported that the sounds were very diverse and varied. When attempts were made to push the animals out to deeper waters and individuals were separated from the group they became very agitated and forced their way back to the group. Once they were touching the other whales they became docile again. After three days the large male at the center of the group died and the group was successfully pushed into much deeper water. This event was unusual because the animals never actually stranded. But it indicates the behaviour of the individual animals and the tight social bonds that the animals share (Connor *et al* 2000).

Example Three

The third example is described by Dawson (1985) and occurred on 19 March 1984 at Tryphena Harbour on Great Barrier Island, New Zealand (Figure 2.3).

Figure 2.3 The Tryphena pilot whales with locals attempting to right those whales that are disorientated. Several whales were so disorientated that although they were alive they floated belly up (see middle left of picture) and needed to be turned upright to breathe (Dawson 1985)

The stranding involved 143 long finned pilot whales (*Globicephala melaena*). The stranding started at 10.30pm when an adult female and her calf swam over a sand bar and became stranded on the other side. The rest of the group milled around in the shallows but became beached when the tide receded.

The next morning the animals were refloated in a tight group. During the night 38 whales had drowned as a result of water entering their blowholes when the animals fell onto their sides. The group proceeded from the shore towards the harbour entrance, where 19 whales broke off from the main group and swam out to sea. (This was not observed by those at the stranding site but later there were 19 whales that were unaccounted for). Unexpectedly the whales suddenly turned hard right, and stranded again. They were immediately pushed out to sea but proceeded to swim parallel with the shore. As the tide fell the whales restranded and could not be refloated immediately because of the low tide (Figure 2.4).

Figure 2.4 Shortly after the Tryphena whales were refloated, they restranded at this site on the falling tide. The whales were pushed back off the shore (Dawson 1985)

One group of 35 animals was higher up on the shore than the rest, and were euthanased by shooting, as their chances of survival were considered minimal. This was a difficult task due to the angle of the whales, and the presence of bystanders. The remaining ten died from drowning.

The next morning, the rescuers took a new approach by choosing a large female from the group. This animal was secured using a padded tow rope and gently towed out to sea. Once out from shore, she was secured to a fishing boat to prevent her returning, while another female and two young were towed out and also held offshore. Boats were then used to herd the rest of the group out to sea towards the four secured whales. Once the pod reached all four whales they were released and rejoined the pod continuing out of the harbour towards the open ocean. This time they did not restrand.

2.3 Summary of examples

The examples are of complex strandings and required a lot of time and effort. The examples indicate the role of leadership in their social groups, as the animals seemed to be following certain individuals. Additionally cooperation is seen in example two, as the animals worked together and only left for short periods of time. This also shows the tight social bonds of cetacean groups. Most of the animals were not obviously injured or sick and seemed to be in good physical condition. The need for human assistance and monitoring of stranded individuals after they have been refloated is very important for the welfare of the animals. Therefore there is need for good stranding protocols and networks in order to make sure that the best care is given to stranded animals.

2.4 Current Legislation concerning Cetacean Strandings.

Most countries (particularly those bordering an ocean) have policies concerning marine mammals, and in particular cetacean strandings. For example the USA has The Marine Mammal Protection Act, implemented in 1972 (Bauer *et al* 1999). Australia has the Wildlife Protection Act that includes Part X (Protection of Whales), which was included in the Act in 1981 (Anonymous 1984). New Zealand has The Marine Mammal Protection Act that was implemented in 1978 (NZ Marine Mammal Protection Act

1978). The United Kingdom has the Wildlife Act that was implemented in 1976 (Anonymous 1995). All of the legislation, covers cetacean species which inhabit the waters of these regions.

In some countries the legislation concerning strandings includes all marine mammals, such as the United States, New Zealand and the United Kingdom. Marine mammals are defined by the United States and New Zealand legislation as either, 'any mammal which is morphologically adapted to a marine environment' (including sea otters, and members of the orders Sirenia, Pinnipedia, and Cetacea), or; 'a mammal that primarily inhabits a marine environment' (e.g. a polar bear) (NZ Marine Mammal Protection Act 1978; Bauer *et al* 1999). The New Zealand legislation also includes the progeny of any marine mammal (NZ Marine Mammal Protection Act 1978). However, other countries such as Australia, have legislation that is aimed specifically at cetacean species (Anonymous 1984).

All the legislation is for the protection, conservation and management of marine mammals. It therefore covers not only the animal as a whole, but also any part of the animal including its raw, dressed, or dyed skin, or fur (Bauer *et al* 1999). Thus even when the animal has died there are still laws governing its remains.

International law prohibits the taking of cetaceans for commercial purposes Gambell 1999). However, there are some exceptions to this, such as taking for the purposes of scientific research and taking cetaceans as part of traditional hunts by aboriginal people (Gambell 1993). Some countries also prohibit taking for any purposes except accidental reasons. 'Take' is defined as meaning to 'harass, hunt, capture, collect or kill any marine mammal, or attempt to harass, hunt, capture, collect or kill any marine mammal', including without limitation any of the following; the collection of dead animals or parts thereof; the restraint or detention of a marine mammal, no matter how temporary; tagging a marine mammal; or the negligent or intentional operation of an aircraft or vessel, or the doing of any other negligent or intentional act which results in the disturbing or molesting of a marine mammal' (Bauer *et al* 1999).

Penalties for violations of the national legislation are potentially severe and can range from a maximum fine of $10,000 under New Zealand law to $100,000 under American law. However the maximum fines are usually reserved only for intentional violations of the law and in the United States can carry a prison term (NZ Marine Mammal Protection Act 1978; Bauer *et al* 1999).

2.5 Health Assessment of Stranded Animals

It is important at a stranding to make quick assessments of the animals involved, in order to limit suffering and expense. Under guidelines suggested by the RSPCA, it is necessary first to establish whether the animal is alive, and if it is to assess its general health. There are a number of assessments that can be taken (Anonymous 1993a&b).

2.5.1 Body Condition

The overall body condition of the animal is possibly the most important prognostic feature in determining the health of the animal (Anonymous 1995). Adult animals, especially coastal species, in poor condition have a poor prognosis, but animals that are in moderate to good condition are most likely to survive (Anonymous 1993, Anonymous 1995)(Fig 2.5 & 2.6).

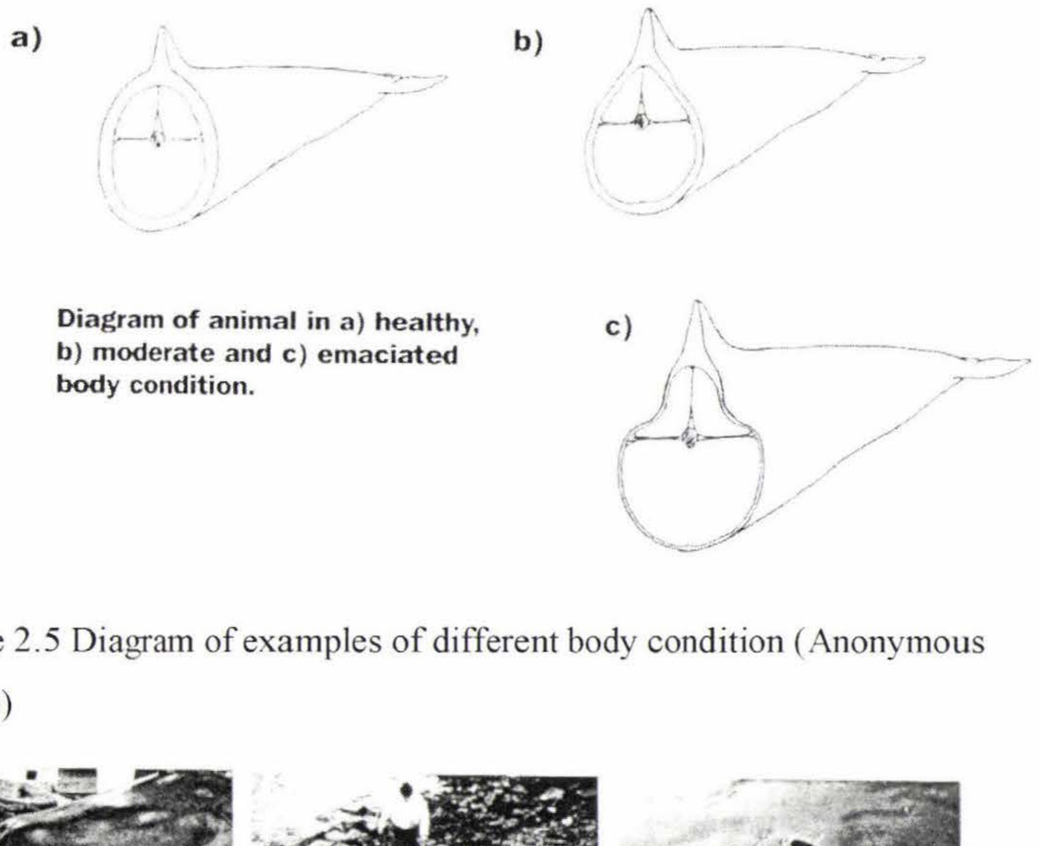

Figure 2.5 Diagram of examples of different body condition (Anonymous 1993b)

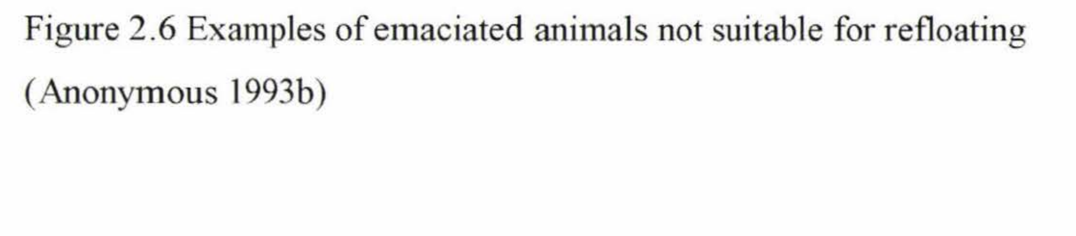

Figure 2.6 Examples of emaciated animals not suitable for refloating (Anonymous 1993b)

2.5.2 Breathing

Whether the animal is breathing or not will indicate whether the animal is alive, as breathing in cetaceans is voluntary and when animals lose consciousness they stop breathing. Some species, such as sperm whales (*Physeter macrocephalus*), are deep divers, however, and therefore can go long periods without breathing (Lockyer 1977, Watkins *et al* 1985; Rice 1989). So under the suggested guidelines, therefore, it may be necessary to observe the animal for approximately 20 minutes (Anonymous 1993a).

If the animal is breathing, then the breathing rate should be monitored. Normal breathing rate is between two and five breath per minute. A breathing rate of above six per minute is indicative of the animal being stressed in some way, and above ten per minute indicates severe stress and is an ominous sign (Anonymous 1995). However, breathing rates may increase to around ten during stressful events, such as being moved, but the breathing rate should return to normal when the stress has been removed. Prolonged periods of elevated breathing rate indicate that the animal is in a poor state of health (Anonymous 1993b).

2.5.3 Discharges

Discharges from the blowhole that are sanguineous or mucopurulent in nature carry a poor prognosis for survival. Also discharges from the mouth or anus that contain blood signal a poor prognosis unless it is the result of superficial cuts sustained during the stranding (Anonymous 1993). Normal cetacean faeces are liquid and dark green in colour (Anonymous 1993b).

2.5.4 Temperature

The temperature of the animal should be taken. This is done by placing a thermistor probe at least 20cm into the rectum. In smaller animals, less than 50kg, it may be possible to obtain an accurate result using a digital thermometer (Anonymous 1993b). Normal deep rectal temperature should be in the range between 36-37.5°C. If the temperature exceeds 42°C the animal is in a terminal condition and will die (Anonymous 1995). Glass thermometers should not be used.

2.5.5 Skin

The skin should be assessed for signs of blistering, cracking and peeling. As this will indicate approximately how long the animals have been stranded, excessive sloughing may indicate a dire state of health (Anonymous 1993b). The presence of numerous ectoparasites, such as whale lice, may indicate that the animal has been ill or injured for some time. If the animals have any deep wounds that penetrate through the skin and blubber, they may prevent the animal from been refloated (Anonymous 1984). Superficial lacerations may be caused by the stranding event and may bleed excessively, taking a long time to clot but this is not a cause for concern (Fig 2.7). However, suturing is not recommended because of the likelihood of dehiscence and lacerations should heal by secondary intention (Anonymous 1993b).

Figure 2.7 A female sperm whale that has drifted in the last stages of a stranding onto a submerged reef. The lacerations and abrasions on her head are typical of wounds sustained in this situation (Robson 1984).

2.5.6 Other signs

Teeth with excessive signs of wear, with loose or missing teeth are commonly associated with advanced age (Anonymous 1993b). The eyes should have a strong palpebral reflex (Anonymous 1993b). Traumatic corneal ulceration is not uncommon in strandings associated with sandy beaches (Anonymous 1993b).

2.4.7 Behaviour

Observations of the behaviour of the animals are also very helpful in making assessments of the overall well being of the animal. Behaviour that indicates good health are: co-ordinated movements returning when supported in water (possibly after several hours) (Anonymous 1993b); vocalization, although not always reliable as high pitched squeals are believed to be signs of stress (Anonymous 1984); and the ability to maintain an upright body position (Anonymous 1993b). Behaviour that indicates a poor state of health are; unco-ordinated movements e.g. twitching, shivering, and major muscle tremors (Anonymous 1993b); lateral or ventral flexion, however muscle stiffness is an expected result of a stranding (ventral flexion is often a sign of abdominal pain) (Anonymous 1993b).

2.6 Current Procedures involving assistance at a Stranding

Cetacean strandings usually attract a number of the general public and it is important that in order to properly assist the animals, people follow the appropriate procedures. Firstly the correct local authority needs to be notified immediately, so that those with experience and expertise can quickly assist the stranded animals (Robson 1987). In some countries it is illegal to give unauthorized first aid to a stranded cetacean (Carwadine & Camm 1995)

At a stranding it is important to keep the animals moist and cool, because they very quickly overheat and their skin starts to dry, harden and crack (Orr 1984). A thin layer of lanolin, zinc ointment or ultraviolet sunscreen, but not suntan lotion can be applied to the skin, (Dawson 1985, Carwadine and Camm 1995). Dawson (1985) found that wet sheets were very effective as they could cover more than one individual at a time but were loose enough not to cover the blowhole (Fig 2.8). It is important not to crowd the animals but to keep the group together, as cetaceans become agitated when separated (Porter 1979). It is also important to return the animals to the sea as quickly as possible, assuming that they are fit to be returned (Robson 1984, Dawson 1985)

Figure 2.8 Example of how sheets can be used to keep the cetacean cool, also note the scooped out mud for easy bucketing of water (Robson 1984)

Stress can be very dangerous, so it is important to always be calm and not to make too much noise (Robson 1984, Dawson 1985 Carwadine & Camm 1995). Cetaceans are prone to acute tension and panic, and those that get caught in nets rarely drown, instead they die from asphyxiation. This happens because when dolphins are in a state of shock they loose muscular control of their blowhole and therefore can not expel spent air from their lungs, and therefore suffocate (Robson 1984). Robson (1984) found through autopsies that 92% of dolphins that had died in nets had no water in their lungs.

It is important to make sure the whales stay upright, by means of air mattresses and foam pads but nothing hard should be placed against the body (Dawson 1985). When the animals are refloated they need to be rocked not dragged, in order to regain their balance, and if they are not rocked they become disorientated (Carwadine & Camm 1995). If the flippers are buried it is important to dig them out and, if possible surround them in water (Dawson 1985). The blood vessels in the flippers are very close to the surface and this is one of the best places to lose heat (Dawson 1985).

At a stranding it is important to not only maintain the safety of the whales but also of the people assisting in the stranding. While cetaceans will not intentionally harm humans (Robson 1984, Dawson 1985), Porter (1979) found that when he tried to approach a mother and her calf he was met by the bared teeth of the mother. Most whales are large and powerful animals, so that a slight nudge can knock a person over, and individuals tend to thrash about (Dawson 1985, May 1990). Geraci (1991) states that even though it is rare, it is possible for cetaceans to transmit disease. Therefore it is important to keep away from the tail and head region, and not to touch the animals unnecessarily (Robson 1984, Dawson 1985, Carwadine & Camm 1995).

2.6 Guidelines for Euthanasia

In most strandings of whales and dolphins euthanasia is difficult to carry out and therefore should be the action of last resort. There are a number of situations that require performing euthanasia on stranded cetaceans, including the following:

(1) The animal has severe external or internal injuries (e.g. bleeding from the mouth, blowhole or anus; deep cuts or other severe injuries)(Anonymous 1993a). (2) The animal is too large to be refloated (e.g. a sperm whale) and a slow uncomfortable death is inevitable (Anonymous. 1993a). (3) The animal is a key whale that can not be refloated quickly enough and may trigger a mass stranding event (Baker 1986). (4) All rescue attempts have failed and the cetacean is suffering intensely (e.g. severe overheating, blistering etc), or treatment is unavailable (Anonymous 1993a). (5) Rescue is not possible because of tidal, sea or weather conditions, the geographical nature of the location, or the lack of available resources (Anonymous 1993a). (6) Veterinary opinion is that the animal is not in good enough condition to be refloated (Anonymous 1993a)(see 2.3).

2.6.1 Methods of Euthanasia

There are several different methods of carrying out euthanasia on whales. Shooting is the most common method (Baker 1986), however, shooting is not suitable for large cetaceans such as the sperm whale, because they are massive and have dense blubber and thick skulls (Baker 1986). It is very difficult to accurately shoot a cetacean and cause a lethal blow but no further harm to the animal, because it is hard to estimate the correct angle and hit the small target area (Baker 1986). Therefore shooting should only be attempted by experienced persons, with a good knowledge of cetacean anatomy (especially of the head area) (Baker 1984). A shotgun or .22 rifle should not be used, and the calibre of the gun should be no less than .30 using solid bullets (Baker 1986, Anonymous 1993a). In New Zealand a firearms license is required and the police must be informed before discharging a firearm in a public place (Baker 1984).

Bleeding or lancing can also be used and if done correctly should kill the animal within a couple of minutes (Baker 1984). The cut should be made as quickly as possible in order to inflict minimum pain. Lancing should only be considered if there are no alternatives, or it is a rare species (e.g. some beaked whales) and the skull is of such scientific value that shooting would damage it (Baker 1984). Lancing involves cutting the arteries that supply the brain, this can be very difficult as the arteries supplying the brain run close to the vertebral column. It is also particularly gory and the public should be shielded from the procedure as much as possible (Baker 1984).

The best method of euthanasia is to inject the animal with drugs, particularly etorphine (Anonymous 1993a). Intravenous drugs should administered by an experienced person, preferably a veterinarian, because of the difficulty associated with the conditions at a stranding. Intravenous injections into the tail flukes are not advised due to the danger of a thrashing tail (Anonymous

1993a). Pentobaribitone can be used on small cetaceans of up to 50-60kg (e.g. harbour porpoise or juvenile common dolphin) and injected into the caudal penduncle vein. Cetaceans of this size can be adequately restrained in order to minimize the danger to the person carrying out the injection (Anonymous 1993a).

2.7 Marine Mammal Stranding Networks

Marine Mammal Stranding Networks exist in various forms around the world. In some countries they are supported by government, but in others they are supported only by academic interest (Wilkinson & Worthy 2000). In Argentina, a single individual, Nathalie Goodall, has functioned as a one-person stranding network (Goodall 1978, 1989). The level of effort involved with strandings can vary between countries. In some countries only cetaceans are recorded while in others, such as the Netherlands, comprehensive efforts have been made to document both cetaceans and pinnipeds (Wilkinson & Worthy 1999). In New Zealand and Australia thorough protocols for handling mass strandings have been prepared (Anonymous 1984, Baker 1986).

Stranding networks face varying problems outlined by Wilkinson & Worthy (1999). Firstly, the care and rescue of marine mammal comes under the authority of the government. Secondly, there is generally little financial assistance available. Thirdly strandings can take place at any time of the day on any day, and for long periods at a time. Fourthly, the smell from a dead stranded cetacean can be almost overpowering, and clings to the person's skin and clothing for many days afterwards.

In the United States, Marine Mammal Stranding networks (Fig 2.9) are well structured and the members of each stranding network receive letters of authorization from the government (Wilkinson & Worthy 1999). The letters have two levels of authorization. At the first level all members are authorized to collect information from dead stranded cetaceans (Wilkinson & Worthy 1999). At the second level only members with facilities suitable for rehabilitation, such as aquaria, have authorization to rehabilitate individuals (Worthy & Wilkinson 1999).

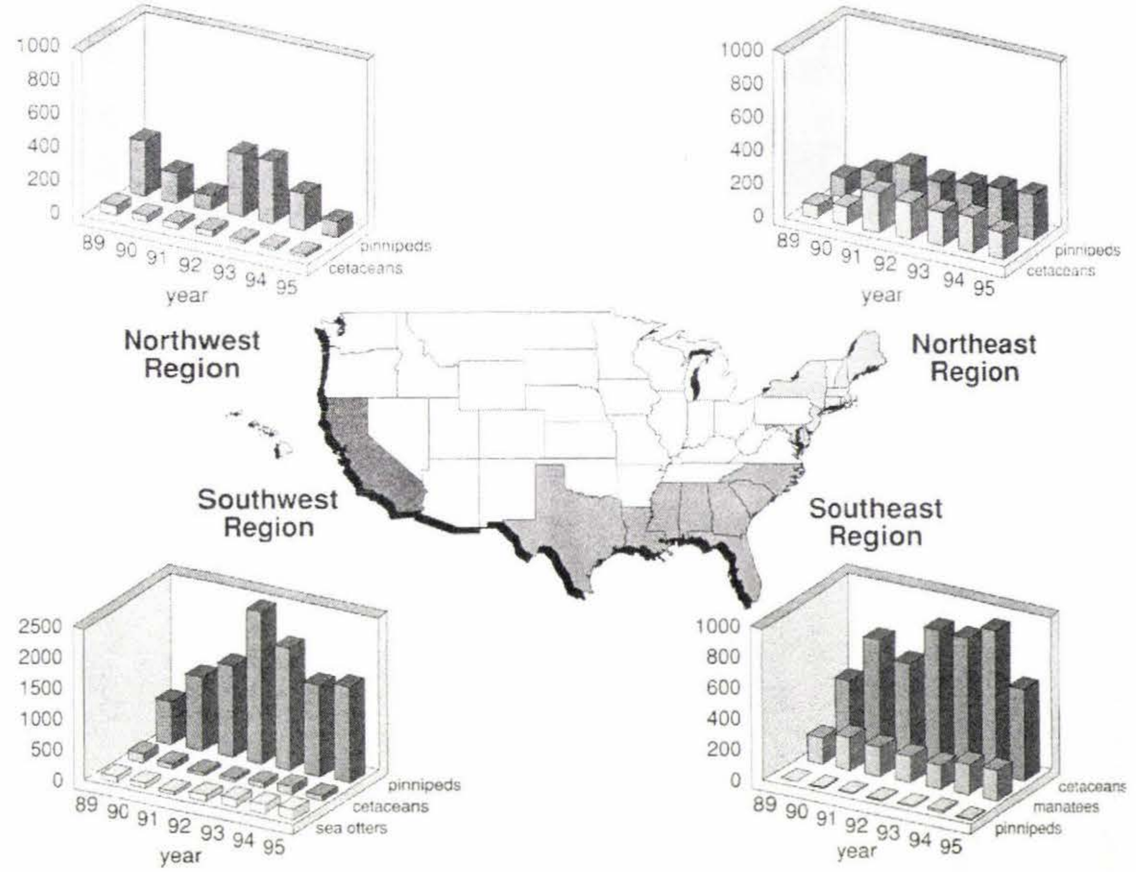

Figure 2.9 Map of the United States showing the four geographic regions that compose the stranding network (Insets illustrate stranding frequency by

taxonomic group and by year, based on data collected through the stranding network) (Worthy & Wilkinson 1999)

A big part of the work of stranding networks is rehabilitation, although the success of rehabilitation is relatively low and therefore does not significantly contribute to the increased survival of wild populations (Wilkinson & Worthy1999). Nevertheless, rehabilitation is seen as an important part of the humane treatment of stranded animals (Wilkinson & Worthy1999). Rehabilitation and release of captive dolphins is also becoming more popular because of public pressure and the financial constraints of holding animals in captivity, and this may increase in the future (Gales & Waples 1993). Release can, however, be difficult because cetaceans have strong social bonds and live in highly organised societies (Connor 2000). Therefore rehabilitated whales can not be released just anywhere, for example the 'Into the Blue' project which released three dolphins in the Turks and Caicos Islands was unable to resight any of the dolphins following their release (McKenna 1992). According to Gales & Waples (1993) this may have occurred because the release site was not the original capture site for these dolphins, and it raised concern amongst scientists about subsequent releases.

Stranding networks provide valuable data that can be used for research purposes (Wilkinson & Worthy 1999). They have also led to better treatment and procedures for dealing with stranded animals, therefore the general welfare of the animals has been increased as a result of stranding networks (Wilkinson & Worthy 1999).

2.7 References

Anonymous 1984. *Victorian whale rescue plan for strandings of cetaceans (whales, dolphins, and porpoises) on the Victorian coastline.* Fisheries and Wildlife Service, Department of Conservation, Forest and Lands, Victoria

Anonymous. 1993a. *Stranded whales, dolphins and porpoises – a first aid guide.* RSPCA. Causeway West Sussex

Anonymous. 1993b. *Stranded cetaceans – guidelines for veterinary surgeons.* RSPCA. Causeway West Sussex

Baker V.(ed). 1986. *Marine mammal rescue.* New Zealand Department of Conservation.

Bauer D., Bean M., & Gosliner M. 1999. *The Laws Governing Marine Mammal Conservation in the United States.* In Twiss J & Reeves R (eds) Conservation and Management of Marine Mammals. Smithsonian Institution Press Washington pp 48-86

Carwadine M. & Camm M. 1995. *Whales, dolphins and porpoises.* Dorling Kindersley Limited. London

Dawson S. 1985. *The New Zealand Whale and Dolphin Digest.* Brick Row Publishing Co. Ltd. Auckland

Fehring W. & Wells R. 1976. *A series of strandings by single herd of pilot whales on the west coast of Florida.* Journal of Mammalogy 57(1) 191-194

Gales N. & Waples K. 1993. *The rehabilitation and release of bottlenose dolphins from Atlantis Marine Park, Western Australia.* Aquatic Mammals 19 : 49-59

Gambell R. 1993. *International management of whales and whaling: An historical review of the regulation of commercial and aboriginal subsistence whaling.* Arctic 46 : 97-107

Gambell R. 1999. *The International Whaling Commission and the contemporary whaling debate.* In Twiss J & Reeves R (eds) Conservation and Management of Marine Mammals. Smithsonian Institution Press Washington pp 179-198

Geraci J. 1991. *On disease transmission between cetaceans and humans.* Marine Mammal Science 7 (2): 191-194

Goodall R. 1978. *Report on the small cetaceans stranded on the coasts of Tierra del Fuego.* Scientific reports of the Whales Research Institute Tokyo 30 : 197-230 *not seen*

Goodall R. 1989. *The lost whales of Tierra del Fuego.* Oceanus 32 (1): 89-95 *not seen*

Lockyer C.1977. *Observations on diving behaviour of the sperm whale* Physeter catodon. In Angel E (ed) A Voyage of Discovery. Pergamon Press Oxford and New York pp 591-609 *not seen*

McKenna V. 1992. *Into the Blue.* The Aquarium Press. London *not seen*

Porter J. 1979. *Pseudorca strandings*. Oceans 10: 8-15

Rice D. 1989. *Sperm Whale (*Physeter macrocephalus *L.).* In Rigway S & Harrison R (eds) Handbook of Marine Mammals. Academic Press Inc. San Diego pp 177-234

Robson F. 1984. *Strandings, ways to save whales.* The Science Press. Johannesburg

Watkins W., Moore K., & Tyack P. 1985. *Sperm whale acoustic behaviours in the southeast Carribean.* Cetology 49:1-15 *not seen*

Wilkinson D. & Worthy G. 1999. *Marine Mammal Stranding Networks.* In Twiss J & Reeves R (eds) Conservation and Management of Marine Mammals. Smithsonian Institution Press Washington pp 396-411

Chapter Three:

Determining Death in Mammals and Features Affecting this Procedure in Cetaceans

Introduction

This chapter is concerned with the usual methods for determining death in mammals and why these methods do not apply to cetaceans.

3.1 Measuring Death in Mammals

Death can be defined as the "total and irreversible cessation of brain function" (Youngner, *et al* 1999). Therefore, even if respiration and heartbeat were sustained artifically, a mammal could be declared dead if all brain functions were irretrievably lost (Youngner, *et al* 1999).

Death occurs sometime after the cessation of the heart lung activity and is the result of cerebral anoxia. Absence, for a short time, of the heart beat or respiration are not synonymous with death and individuals can be resuscitated after the loss of breathing and heart beat. The key criterion for establishing death is failure to respond to resuscitation (Youngner, *et al* 1999) which means that an irreversible stage has been reached. Loss of brain function is considered to be the most acceptable criterion for establishing death, but heart-lung criteria (i.e. pulse and breathing) are also valid for most cases (Youngner *et al* 1999).

In mammals other than humans death is usually recognized by loss of consciousness and the cessation of breathing followed by cessation of the heart beat (Ewer 1977). Because of the expense not many, if any, mammal species besides humans are ever maintained in a comatose condition, thus loss of brain function as a criterion for death therefore effectively applies only to human patients.

In cetaceans death is characterized by loss of consciousness followed by cessation of breathing and heart beat. This is difficult to assess due to the apparent 'absence' of heart-lung criteria in stranded cetaceans, because of the physical and anatomical features listed below.

3.2 The Effect of Anatomy and Physiology on Determination of Death in Cetaceans

The following six anatomical and physiological features make it difficult to use normal cardiopulmonary (pulse and breathing) measures to assess death in cetaceans.

3.2.1 Bradycardia

Bradycardia is defined as a lowered heart rate (Elsner 1999). Cetaceans experience bradycardia during dives but it is much harder to detect than in other marine mammals, such as seals (Elsner 1999). Bradycardia has been recorded in a wide range of aquatic species including sea lion (Elsner *et al* 1964), fur seal (Elsner 1969), manatee (Scholander & Irving 1941), dugong (Elsner 1969), porpoise (Irving et al 1941), killer whale (Elsner 1969), pilot whales (Elsner 1969), gray whales (Elsner 1969) and hippopotamus (Elsner 1966). The heart slowing in diving animals is developed early in life, but diving ability is not marked in newborn and infant animals (Elsner 1969).

Bradycardia is much less marked in free or trained dives as opposed to enforced dives (Elsner 1965, Jones *et al* 1973, Kooyman & Campbell 1972, Hill *et al* 1987) and it can be conditioned to occur in the absence of diving (Ridgway *et al* 1975).

Bradycardia has also been recorded in terrestrial species that dive (Elsner 1969). Those studied include snakes (Elsner 1969), sloths (Irving *et al* 1942), dogs (Elsner *et al* 1966), and humans (Elsner 1969). As well as in burrowing animals, such as the armadillo (Elsner 1969), pig (Irving *et al* 1956) and humans (Elsner 1969). Terrestrial mammals do not respond as quickly or as noticeably to a lowered heart rate as the aquatic species (Elsner 1969). Fish, including cod (Elsner 1969), grunion and flying fish (Elsner 1969) also exhibit bradycardia when taken out of water.

In a study on the diving capabilities of bottlenose dolphins Elsner *et al* (1966) trained the dolphins to remain touching a target for 5 minutes at the bottom of the pool. At the beginning of the dive the heart rate decreased rapidly from 100 to 12 beats/min, slowly increasing to about 25 beats/min as the trained dive proceeded. Ridgway *et al* (1969) also trained bottlenose dolphins to touch an underwater target attached beneath a boat in the open ocean for increasingly long periods. The study was to determine the duration of aerobic dives, so the dolphin was commanded to exhale underwater into a receptacle for collection of the expired air. The dolphin comfortably endured frequently repeated dives of up to 2.5 minutes in length, but longer dives needed an extended recovery time, suggesting that it had surpassed its aerobic resource limit (Ridgway *et al* 1969).

Recordings demonstrate that the dolphin's heart rate increases each time it surfaces to breathe (Elsner *et al* 1966, Ridgway *et al* 1969). This cycling of heart rate is characteristic of sinus arrhythmia, an oscillation of the heart rate that accompanies most mammals respiratory excursions, showing an increase during inspiration and a decrease at exhalation (Elsner 1999) The excursions are usually exaggerated in marine mammals (Elsner 1999). The oscillating heart rate of dolphins can indicate a lack of diving bradycadia in this species (Kanwisher & Ridgway 1983). The researchers considered the lower heart rate when submerged to be the animal's normal heart rate and the increase at the surface as tachycardia. The results could easily be interpreted in the reverse, as with the earlier results of persisting low heart rates during extended submergence (Elsner 1999).

Further studies on larger cetaceans are needed, but there are problems with their huge size and their relative inaccessibility present problems. Simple observations of diving bradycardia have, however, been made on killer whale (Spencer *et al* 1967), pilot whale and a juvenile gray whale (Elsner 1999).

At a stranding cetaceans revert to diving mode due to stress involved in this situation and indicates that they would experience bradycardia at a stranding (Robson 1984). Voluntary bradycardia has the potential to make assessing of heart activity and death in cetaceans difficult.

3.2.2 Body Size

Cetaceans live in a fluid environment that conducts heat away from the body twenty-five times faster than in air (Elsner 1999). Therefore as a homeothermic mammal, cetaceans must maintain a constant body temperature and some cetaceans live in near freezing water. One solution to this is to decrease the surface area to volume ratio, which would result in animals that are a lot larger in size. Marine mammals in general are much larger than their terrestrial counterparts e.g. the sea otter is twice as large as the largest terrestrial mustelid (Morrison *et al* 1974, Estes 1989), and the polar bear is probably the largest of the ursids (Stirling 1988, Reeves *et al* 1992). Although there are no closely related terrestrial representatives with which to compare cetaceans they include the largest mammals on earth. The extreme example is the blue whale – the largest mammal that has ever lived. In addition, when compared to unrelated terrestrial mammals of similar mass cetaceans have significantly less surface area (Innes *et al* 1990). This creates a larger distance between the heart and the surface of the animal and therefore makes it more difficult to hear the heart. This problem is compounded in a stranding situation as the animals often lie on their stomachs and it is not recommended to roll them on to their backs.

3.2.3 Blubber

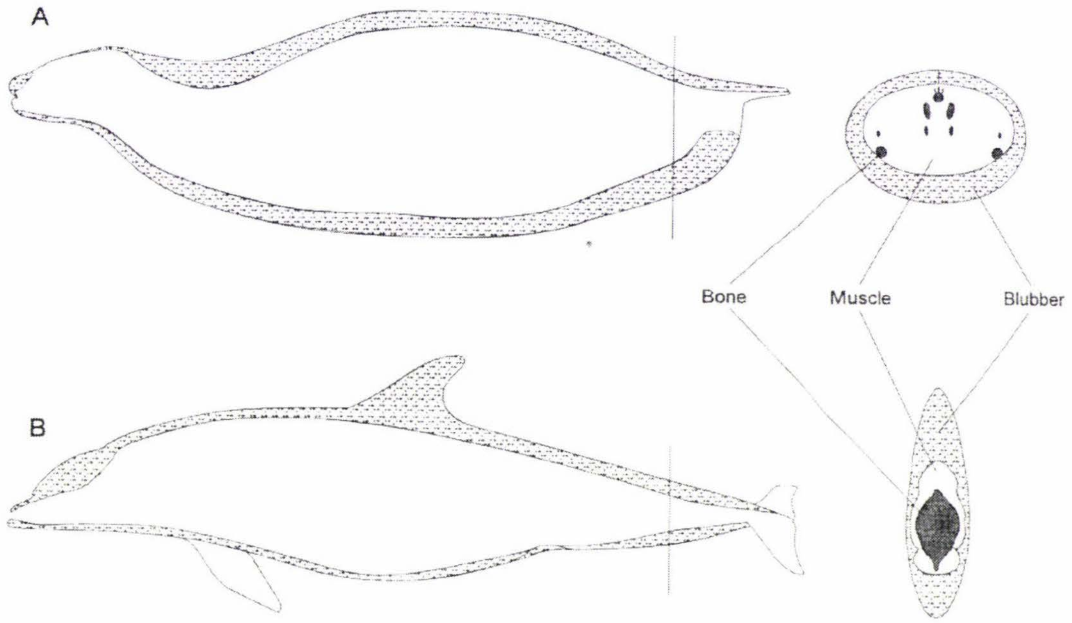

Figure 3.1 Comparison of the blubber between (A) a pinniped and (B) a cetacean (Pabst *et al* 1999).

Cetaceans have a thick layer of subcutaneous fat (blubber) that surrounds their body (Figure 3.1), that provides insulation, increases buoyancy, and constitutes an energy source during lean times (Elsner 2000). Blubber is characterized as a continuous sheet of adipose tissue, reinforced by a network of collagen and elastic fibers (Parry 1949, Sokolov *et al* 1973, Ling 1974, Ackerman *et al* 1975, Lockyer *et al* 1984,1985). The blubber layer usually accounts for a large percentage of the total body mass, often in excess of 30% (Bryden 1964, 1969; Kooyman 1973) (Figure 3.2). Scammon (1874) measured its thickness in bowhead whales as 25cm and gray whales as 18cm. It was highly valued by whalers because it could easily be rendered to whale oil (Elsner 1999). Compared with fur, blubber is from three to seven times faster at conducting heat, especially if the fur becomes wet (Elsner1999).

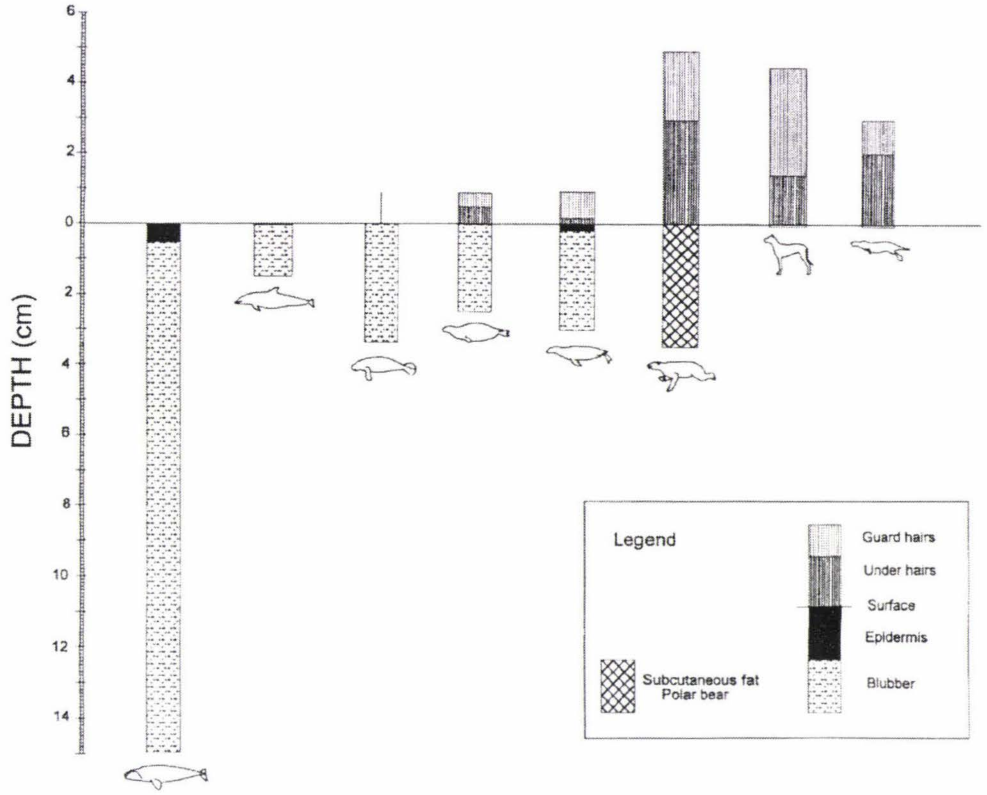

Figure 3.2 Comparison between different marine mammals, and a 'typical' terrestrial mammal (domestic dog, (*Canis familiaris*) of their different insulation structures. From left to right, the right whale (*Eubalaena spp.*), bottlenose dolphin (*Tursiops truncatus*), West Indian manatee (*Trichechus manatus*), harbour seal (*Phoca vitulina*), Californian sea lion (*Zalophus californianus*), polar bear (*Ursus maritimus*), domestic dog (Canis familiaris), and the sea otter (*Enhydra lutris*) (Pabst *et al* 1999)

Blubber can also act as an acoustic barrier to hearing the heart making measurement of the heart beat more difficult, especially in large cetaceans.

3.2.4 The Skeleton

Whales live in conditions were their bodies are wholly and always supported by water. In general the musculoskeletal system acts to define the body shape and gives support and protection to the internal organs (Pabst *et al* 1999). The system consists of bone, muscles, tendons, ligaments and joints and also produces and transmits the mechanical forces required for movement (Pabst *et al* 1999). The density of seawater is almost three orders of magnitude greater, and the viscosity approximately 60 times greater, than air at a similar temperature (Vogl 1994). The cetacean skeleton (Figure 3.3) therefore does not need to provide the same amount of support. This has resulted in cetaceans larger amount of mass than their terrestrial counterparts (Figure 3.4). This bulk creates problems if they come out of the water e.g. in a stranding (Orr 1984).

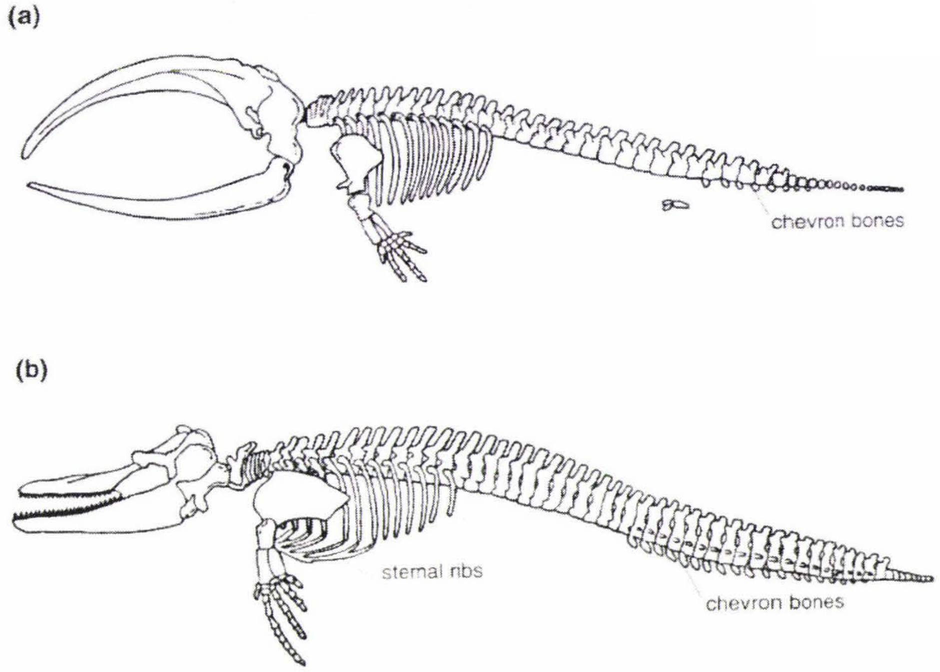

Figure 3.3 Diagram showing the skeletons of (a) a mysticete and (b) an odontocete (Berta & Sumich 1999).

The skeleton creates problems in a stranding situation because it can not fully support the animal's mass on land, and the whales begin to suffocate and crush the lungs making breathing more difficult to assess (Orr 1984).

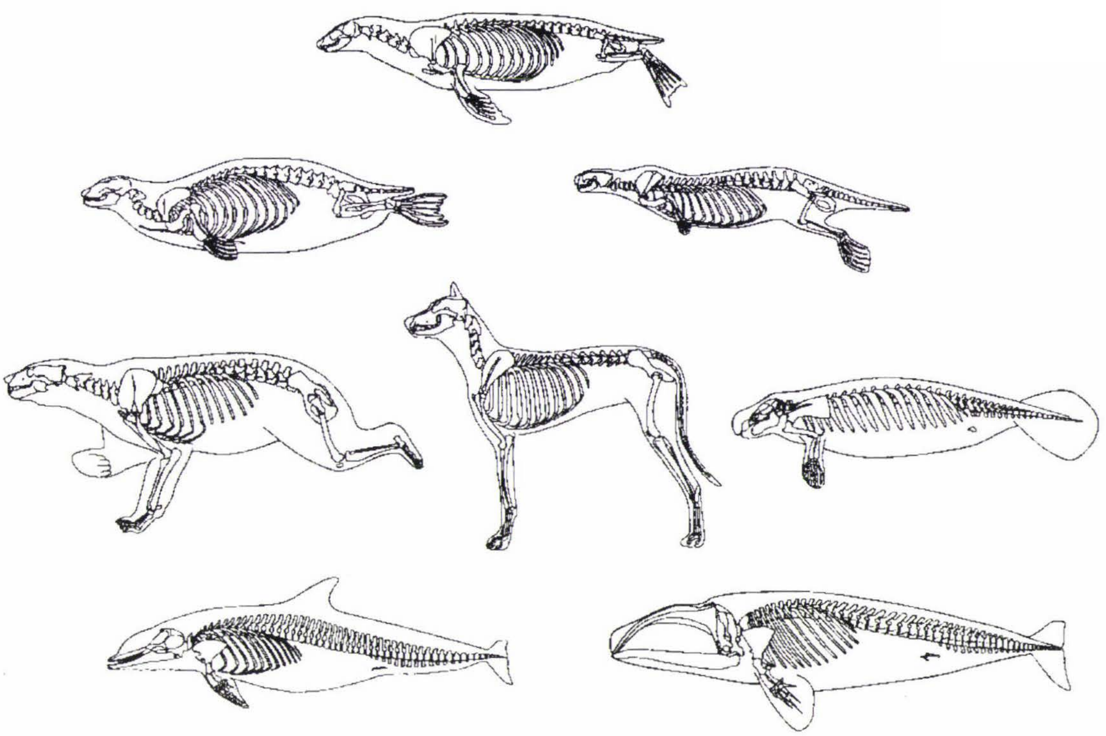

Figure 3.4: Skeletal systems of some representative marine mammals along with the 'typical' terrestrial mammal. Clockwise from the top are the Californian sea lion (*Zalophus californianus*), sea otter (*Enhydra lutris*), West Indian manatee (*Trichechus manatus*), right whale (*Eubalaena spp.*), bottlenose dolphin (*Tursiops truncatus*), polar bear (*Ursus maritimus*), harbour seal (*Phoca vitulina*). The 'typical' terrestrial mammal (domestic dog (*Canis familiaris*) at the centre (Pabst *et al* 1999)

3.2.5 Blowhole

The blowhole of cetaceans varies from species to species, for instance in odontocetes the blowhole is singular, whereas mysticetes have paired blowholes (Reynolds *et al* 2000) (Figure 3.5). The blowhole is located on the top of the head, is usually the first region to make contact with air when the animals surface (Tinker 1988) and comprises the external nares, through which the animals respire. The blowhole is controlled by cranial nerve VII (facial), which is enlarged in comparison to other mammals (Tinker 1988). The blowhole is covered by a muscular flap of tissue, and when relaxed it is closed but opens for breathing.

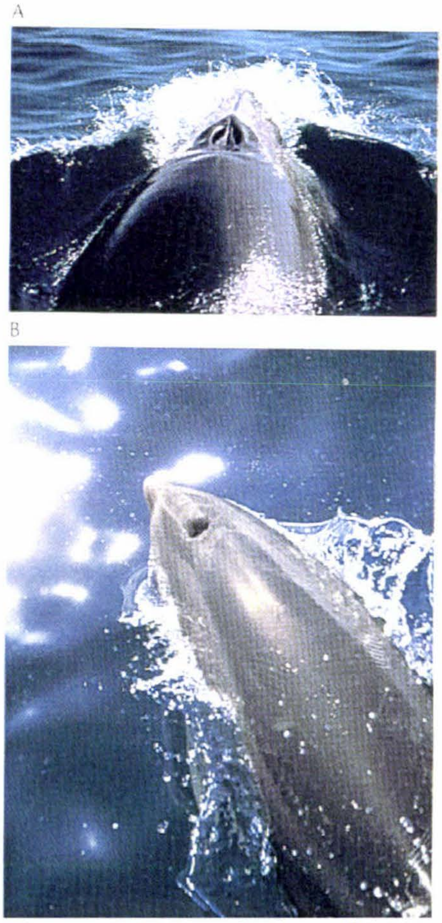

Figure 3.5 Blowholes of (A) a mysticete and (B) an odontocete.

In odontocetes the nasal passages are divided by a bony septum that does not continue to the surface, allowing the nasal passages to join above the skull and become a single passage that continues to the surface to a single blowhole (Figure 3.6). The air passages between the blowhole and the pharynx below show great variation and specialisation, including chambers, ducts, and valves (Tinker 1988). Odontocetes probably have no sense of smell due to the absence of olfactory nerves and receptors (Tinker 1988).

In mysticetes the septum divides the nasal passages into two separate blowholes (Figure 3.6). The blowholes are also surrounded by a ridge of flesh, which keeps water out of them. When closed the blowholes are made water tight by two plugs attached to the septum. Mysticete nasal passages are not as elaborate as those of odontocetes, but they do have olfactory receptors that indicate a sense of smell, although this is probably very rudimentary (Tinker 1988).

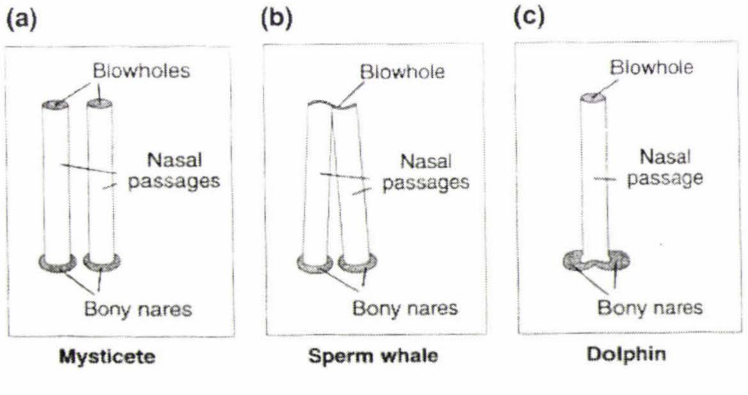

Figure 3.6 Differences in the nasal passages of (a) Mysticete, (b) sperm whale and (c) dolphin. (Berta & Sumich 1999)

The blowholes are important in the determining of death because the blowhole will always respond to an external stimulus by closure, unless the animal is dead or deeply unconscious (Kestin Pers comm).

3.2.6 Breath holding Ability and the Lungs

Cetaceans are deep divers and while diving can hold their breath for long periods. During dives the lungs act as a site for storing of oxygen (Kooyman 1969, 1973, 1985, 1987; Elsner 2000). The gases within the lungs also pose potential threats to a mammal undergoing extended, multiple or deep dives (Pabst *et al* 1999). Humans usually dive with fully inflated lungs that act as a site of oxygen storage throughout the dive, but humans are neither deep nor extended divers (Pabst *et al* 1999). The Weddell seal, one of the most proficient divers, usually exhales before diving (Scholander 1940, Kooyman *et al* 1970), and its lung volume per body weight less than that of comparably sized terrestrial mammals (Kooyman 1973). Evidently, the lung is not the primary site of oxygen storage in the Weddell seal during diving (Pabst *et al* 1999) (Figure 3.7).

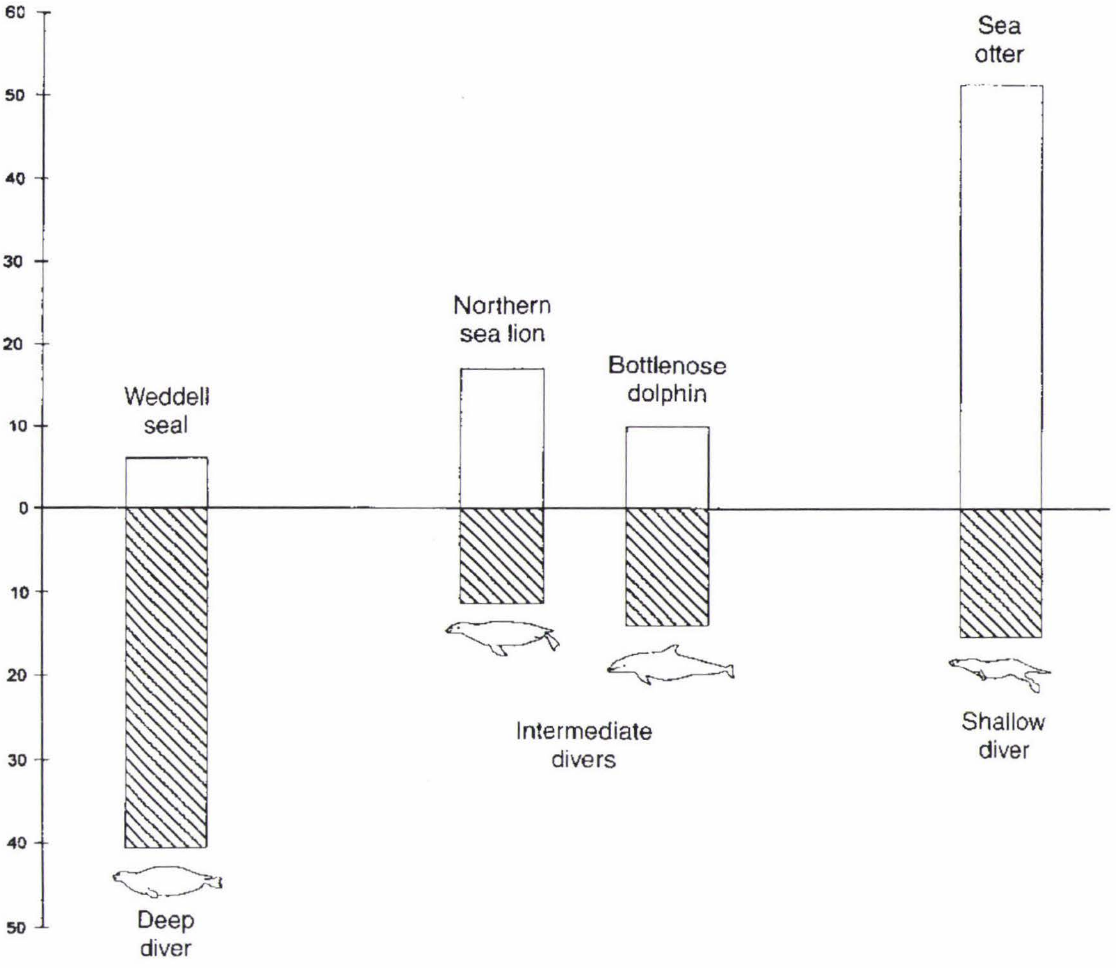

Figure 3.7 Graph showing lung versus oxygen stores in shallow and deep diving mammals

Oxygen is stored and transported in blood by reversibly binding to haemoglobin in the red blood cells and is also stored in muscle, by reversibly binding to myoglobin found within muscle cells (Schmidt-Nielsen 1990). Therefore oxygen can be stored in the lungs, blood and muscle tissues. In deep-diving species the lungs' store of oxygen is a smaller percentage of total on-board oxygen stores, in comparison with shallow diving species. Connected to decreased oxygen stores in the lungs of deep diving mammals of their (1) blood by means of increased blood volume and increased red blood cell concentration, and (2) muscle by means of increased myoglobin stores (Ridgway & Johnston 1966, Hedrick *et al* 1986, Kooyman 1987, Wickham 1989, Thorson & Le Boeuf 1994). Therefore deep diving mammals have larger on-board oxygen stores in their blood and muscles than in their lungs, in comparison to both terrestrial shallow diving mammals (Figure 3.7).

Mammalian lungs comprise numerous gas-filled spaces. The volume of given mass of gas is inversely related to pressure so that if the pressure exerted on a gas is doubled, its volume will be halved (Vogl 1988). Water exerts approximately 1 atmosphere of pressure for every 10m of depth. Therefore, a marine mammal at 10-m depth experiences two times more pressure than it would at the surface, and the air within its lungs occupies one-half its volume at the surface. The lungs occupy just a fraction of their surface volume at the impressive depths achieved by many deep diving mammals – 600 to 740m for Weddell seals (Kooyman 1981, Tests 1994), more than 1500m for elephant seals (Delong & Stewart 1991), and 2000m for sperm whales (Heezen 1957, Watkins *et al* 1993).

Cetaceans dive with their lungs full of air (Ridgway *et al* 1969). In order to avoid the bends, they prevent nitrogen from being able to cross the alveolar membrane by alveolar collapse. When the alveolae collapse air is forced into the upper, non-gas exchanging regions of the respiratory system, therefore the nitrogen is isolated from the bloodstream, and the bends is avoided (Scholander 1940). Alveolar collapse occurs in the lungs of diving mammals as a result of unique morphological and mechanical properties of the terminal airways of the bronchial tree (Figure 3.8).

The functions of the lungs are related to the ability of cetaceans to undergo extended breath holding periods. This is important as breathing is a usual assessment of the vital state of cetaceans, but the sperm whale (which frequently mass strand) can hold its breath for up to 90 minutes and observation of breathing is not a reliable method for assessment of vitality in cetaceans.

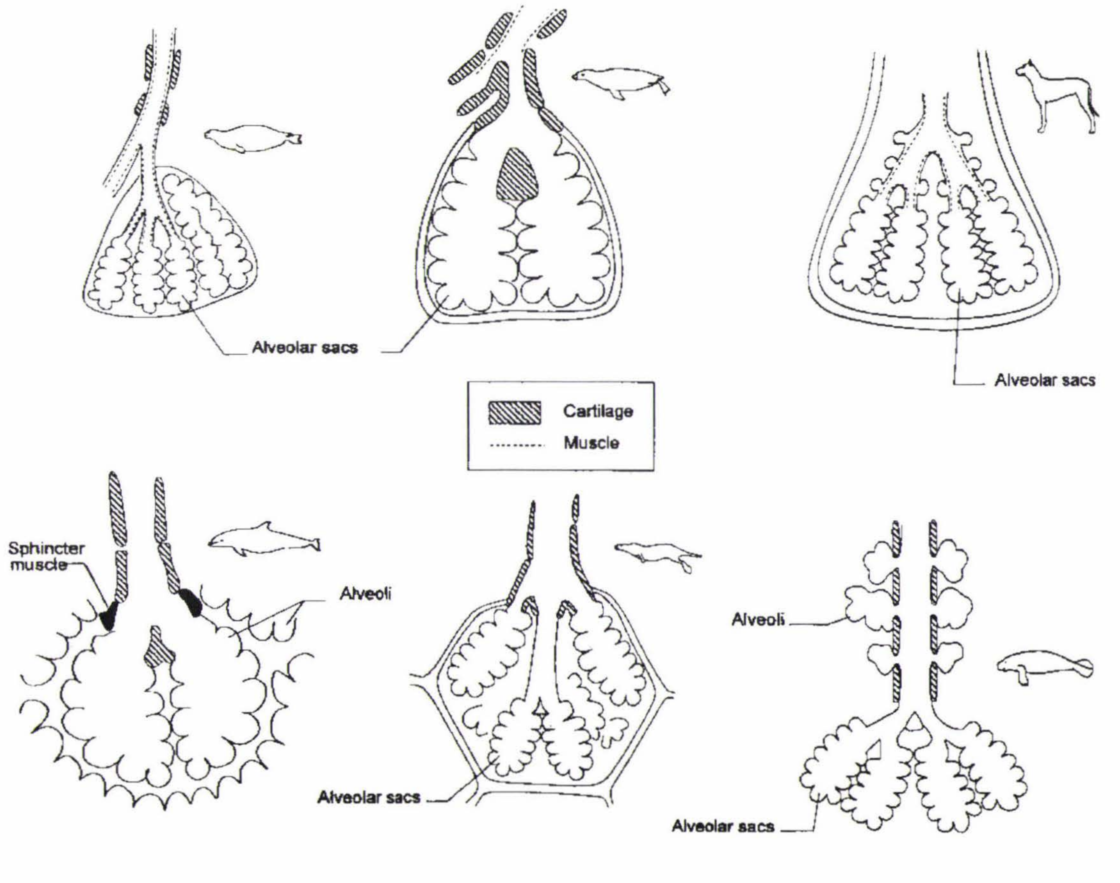

Figure 3.8: Diagram showing the morphology of the airways and the alveoli of different mammals. Clockwise from the top left the harbour seal (*Phoca vitulina*), Californian sea lion (*Zalophus californianus*), domestic dog (*Canis*

familaris), bottlenose dolphin (*Tursiops truncatus*), sea otter (*Enhydra lutris*), and the West Indian manatee (*Trichechus manatus*) (Pabst *et al* 1999)

3.3 Summary of anatomical and physiological features

The anatomical and physiological features considered above make it more difficult to assess death in cetaceans. These features (bradycardia, body size, blubber, blowhole, skeleton, breath holding ability) either create a barrier to detection of the heart beat or make it more difficult to assess breathing in a stranded cetacean. These features alone would make it harder to assess the vitality of an individual or whether it had died. Following the chronology of death, from cessation of breathing to cessation of the heart beating (although individuals can be resuscitated following the loss of breathing and heart beat) to finally the loss of brain function. In animals other than humans, particularly wild animals, cessation of heart beat is normally considered to lead inevitably to death. However, the combination of all of these features contribute difficulty in on making accurate assessment of death and therefore a more accurate measurement is needed.

3.4 References

Ackerman R., Hingley J., Eaton C., Logan V., & Odense P. 1975. *Layering and tissue composition in the blubber of the Northwest Atlantic sei whale* (Balaenoptera borealis). Canadian Journal of Zoology 53: 1340-1344

Bryden M. 1964. *Insulating capacity of the subcutaneous fat of the southern elephant seal*. Nature 203: 1299-1300

Bryden M. 1969. *Relative growth of the major body components of the southern elephant seal* Mirounga leonina (Linnaeus). Australian Journal of Zoology 17: 153-177 *not seen*

DeLong R. & Stewart B. 1991. *Diving patterns of northern elephant seal bulls*. Marine Mammal Science 7: 369-384

Elsner R. 1965. *Heart rate response in forced versus trained experimental dives in pinnipeds*. Hvalrådet Skrifter, Det Norske Videnskaps-Akademi i Oslo *not seen*

Elsner R. 1966. *Diving bradycardia in the unrestrained hippopotamus*. Nature 212: 408

Elsner R. 1969. *Cardiovascular adjustments to diving*. In Andersen H. (ed) The Biology of Marine Mammals. Academic Press New York & London pp 117-143

Elsner R. 1999. *Living in water: solutions to physiological problems*. In Reynolds J. & Rommel S. (eds) Biology of Marine Mammals. Smithsonian Institution Press. Washington pp 73-116

Elsner R., Franklin D., & Van Citters. 1964. *Cardiac output during diving in an unrestrained sea lion*. Nature 202: 809-810

Elsner R., Kenney D., & Burgress K. 1966. *Diving bradycardia in trained dolphin*. Nature 212: 407-408

Estes J. 1989. *Adaptions for aquatic living by carnivores*. In Gittleman J. (ed) Carnivore Behaviour, Ecology and Evolution. Comstock Publishing Associates Ithaca NY pp 242-282 *not seen*

Ewer T. 1977. Science and the practitioner. Veterinary Record. 100(26): 546-548 *not seen*

Hedrick M., Duffield D., & Cornell L. 1986. *Blood viscosity and optimal hematocrit in a deep-diving mammal, the northern elephant seal* (Mirounga angustirostris). Canadian Journal of Zoology. 64: 2081-2085

Heezen B. 1957. *Whales entangled in deep-sea cables*. Deep Sea Research 4: 105-115 *not seen*

Irving L., Scholander P., Grinnell S. 1941. *The significance of the heart rate to the diving ability of seals*. Journal of Cellular and Comparative Physiology 18: 283-297

Jones D., Fisher H., McTaggart S., & West N. 1973. *Heart rate during breath-holding and diving in the unrestrained harbour seal*, Phoca vitulina richardsi. Canadian Journal of Zoology 51: 671-680

Kanwisher J. & Ridgway S. 1983. *The physiological ecology of whales and dolphins*. Scientific American 248: 111-120

Kooyman G. 1973. *Respiratory adaptations in marine mammals.* American Zoologist 13: 457-468 *not seen*

Kooyman G. 1969. *The weddell seal.* Scientific American 221: 101-106

Kooyman G. 1981. *Weddell seal, consummate diver.* Cambridge University Press. Cambridge *not seen*

Kooyman G. 1985. *Physiology without constraint in diving mammals.* Marine Mammal Science 1: 166-178

Kooyman G. 1987. *Free diving in vertebrates.* In Dejours (ed). Comparative Physiology of Environmental Adaptations, Volume 2 8th ESCA Conference Strasbourg, Karger Basel pp 27-37

Kooyman G. & Campbell W. 1972. *Heart rates in freely diving Weddell seals* Leptonychotes weddelli. Comparative Biochemistry and Physiology A 43 : 31-36

Kooyman G., Hammond D., & Schroeder P. 1970. *Brochograms and trachograms of seal under pressure.* Science 1969: 82-84

Ling J. 1974. *The integument of marine mammals.* In Harrison R. (ed) Functional Anatomy of Marine Mammals Vol. 2. Academic Press London pp 387-415

Lockyer C., McConnell L., & Waters T. 1984. *The biochemical composition of fin whale blubber.* Canadian Journal of Zoology 62: 2553-2562

Lockyer C., McConnell L., & Waters T. 1985. *Body condition in terms of anatomical and biochemical assessment of fat in north Atlantic fin and sei whales.* Canadian Journal of Zoology 63: 2328-2338

Morrison P., Rosenmann M., & Estes J. 1974. *Metabolism and thermoregulation in the sea otter.* Physiological Zoology 47: 218-229 *not seen*

Pabst D., Rommel S., & McLellan 1999. *The functional morphology of marine mammals.* In Reynolds J. & Rommel S. (eds) Biology of Marine Mammals. Smithsonian Institution Press. Washington pp 15-72

Parry D. 1949. *The structure of whale blubber, and a description of its thermal properties.* Quarterly Journal of Microscopical Science 90: 13-25 *not seen*

Reeves R., Stewart B., & Leatherwood S. 1992. *Seals and Sirenians.* Sierra Club Books. San Franciso

Ridgway S. & Johnston D. 1966. *Blood oxygen and ecology of porpoises.* Science 151: 456-457

Ridgway S., Carder D., & Clark W. 1975. *Conditioned bradycardia in the sea lion* Zalophus californianus. Nature 256 : 37-38

Ridgway S.H., Scronce B.L., & Kanwisher J. 1969. *Respiration and deep diving in the bottlenose porpoise*. Science 166: 1651-1654

Rommel S. 1990. *Osteology of the bottlenose dolphin*. In Leatherwood S & Reeves R. (eds). The Bottlenose dolphin. Academic Press San Diego CA

Scammon C. 1874. *The marine mammals of the northwest coast of North America together with an account of an American whale fishery*. J.H. Carmany San Francisco, reprinted in 1968, Dover New York p 319 *not seen*

Schmidt-Nielson K.1990. *Animal Physiology: Adaption and Environment*, 4th ed. Cambridge University Press, Cambridge UK *not seen*

Scholander P.F. 1940. *Experimental investigations on the respiratory function in diving mammals and birds*. Hvalrådet Skrifter, Det Norske Videnskaps-Akademi i Oslo 22: 1-131 *not seen*

Scholander P. & Irving L. 1941. *Experimental investigations on the respiration and diving of the Florida manatee*. Journal of Cellular and Comparative Physiology 17: 169-191

Solokov V., Kalashikova M., & Rodinov V. 1973. *Micro- and ultrastructure of the skin the harbour porpoise* (Phocaena phocaena relicta *Abel.*). In Chapskii K. & Sokolov V. (eds) Morphology and Ecology of Marine Mammals. Translated by Mills H. John Wiley & Sons New York pp 82-101 *not seen*

Spencer M., Gornall T., & Poulter T. 1967. Respiration and cardiac activity of killer whales. Journal of Applied Physiology 22 : 974-981 *not seen*

Stirling I. 1988. *Polar Bears*. The University of Michigan Press. Ann Arbour *not seen*

Thorson P. & LeBoeuf B. 1994. *Developmental aspects of diving in northern elephant seal pups*. In LeBoeuf B. & laws R. (eds) Elephant seals: Population Ecology, behaviour, and Physiology. University of California Press Berkley *not seen*

Vogel S. 1988. *Life's Devices: The physical world of animals and plants*. Princeton University Press. Princeton NJ *not seen*

Vogel S. 1994. *Life in moving fluids. The physical biology of flow*, 2nd edition. Princeton University Press. Princeton NJ *not seen*

Youngner S., Arnold R., & Schapiro R. 1999. *The definition of death*. John Hopkins University Press. London & Baltimore

Watkins W., Daher M., Fristup K., Howald T. 1993. *Sperm whales tagged with transponders and tracked underwater by sonar*. Marine Mammal Science 9: 55-67

Chapter Four:

Arterial Blood Supply
In Mammals

4.1 Introduction

The cardiovascular system in mammals is complex and highly specialized. In this chapter only the blood supply to the brain will be considered, in particular how the blood supply to the brain and eyes in cetaceans can compared with that in other selected mammalian species.

First a general description is given of the cerebral blood supply in mammals. Then followed by a detailed description of Carnivora, Artiodactyla and Pinnipedia (see chapter six), and the Sirenia. Finally, a description of the cerebral blood supply in cetaceans is presented.

4.2 Cerebral blood circulation in mammals

Before addressing the anatomy of the cardiovascular system supplying blood to the brain of cetaceans, it is important to discuss the general mammalian cardiovascular system (Figure 4.1, Table 4.1). According to Ask-Upmark (1935) the mammalian brain is supplied with blood in one of the two following ways: anteriorly from the internal carotid and external carotid artery, or posteriorly from the vertebral and occipital arteries. These vessels enter the cranial cavity and anastomose (form a junction, or join together) at the base of the brain forming the circle of Willis which gives rise to the arteries supplying the brain (Cartmill *et al* 1987). In addition, in a few groups such as Cetacea and Sirenia, arterial systems in the vertebral canal may be substituted for the more usual posterior routes. This condition will be discussed more fully.

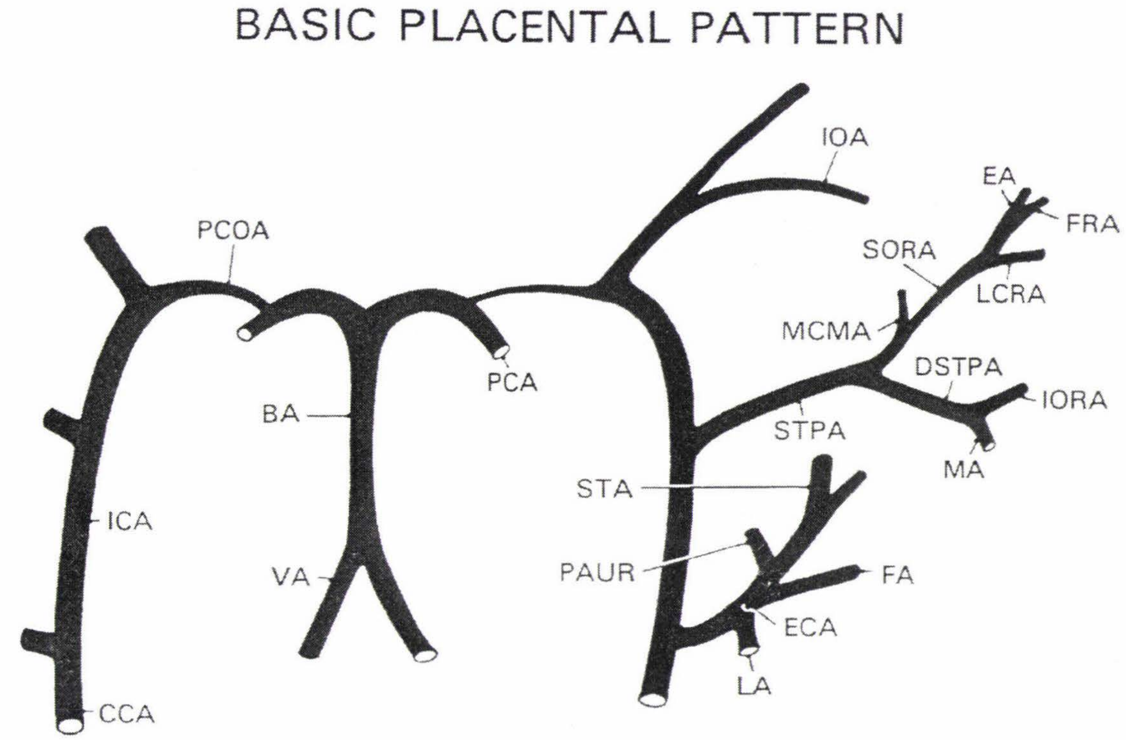

Figure 4.1: Diagram of the blood supply to the brain in a generalized placental mammal (McFarland *et al* 1987) Abbreviations appear in Table 4.1

Table 4.1: List of abbreviations for Fig 4.1

Abbreviation	**Definition**
BA	Basilar Artery
CCA	Common Carotid Artery
DSTPA	Distal Stapedial Artery
EA	Ethmoid Artery
ECA	External Carotid Artery
FA	Facial Artery

FRA	Frontalis Artery
ICA	Internal Carotid Artery
IOA	Internal Ophthalmic Artery
IORA	Infraorbital Artery
LA	Lingual Artery
LCRA	Lacrimal Artery
MA	Mandibular Artery
MCMA	Middle Cerebral Meningeal Artery
PAUR	Posterior Auricular Artery
PCA	Posterior Cerebral Artery
PCOA	Posterior Communicating Artery
SORA	Supraorbital Artery
STA	Superficial Temporal Artery
STPA	Stapedial Artery
VA	Vertebral Artery

Ask-Upmark (1935) presents three extreme patterns of cerebral blood supply among mammals. Firstly the brain is supplied by the internal carotids and no carotid rete mirabile is present, secondly the brain is supplied only by the vertebral arteries, and no carotid artery is present; thirdly the brain is supplied only by the external carotid artery and a carotid rete is always present. In addition to this he described two types of cerebral blood supply where either the blood arrives at the brain without passing through a rete; or blood passes entirely or partially through a rete on its way to the brain. Within the first type of cerebral blood supply pattern where the carotid rete is absent Ask-Upmark (1935) found three sub-types. Firstly,"the internal carotid and vertebral arteries supply about equal proportions of blood to the brain" – groups in this classification include Monotremata, Insectivora, some Rodentia (rats, gophers), Edentata (armadillo), Lemuroidea, Carnivora, Pinnipedia, Anthropoidea; secondly," the internal carotid artery supplies nearly all blood to the brain" – groups in this classification include Marsupialia; and lastly, "the vertebral artery supplies nearly all the blood" – this group includes the Chiroptera, some Edentata, and some Rodentia (porcupine and squirrel).

Within the second type of cerebral blood supply pattern with a rete present, there are two subsystems firstly, all the cerebral blood supply goes through a rete – this group includes some Artiodactyla (cows, sheep and goats) and the Cetacea; or secondly, part of the blood goes through a rete and part goes directly to the brain – the indirect pathway can be the vertebral arteries as in pigs, or the internal carotid, occipital and the vertebral arteries as in the horse.

Ask-Upmark (1935) states that there are three ways by which blood can enter the cranial cavity; "firstly via the external carotid artery entering the cranial cavity through a wide foramen lacerum with an intracranial rete present; secondly via internal carotid, occipital and vertebral arteries entering through relatively narrow bony canals; and thirdly via an internal carotid which forms a cervical extracranial carotid rete and then reforms to enter the skull through a foramen caroticum, as in lemurs (*Loris glacilis* and *Galagos senegalensis*) and the two-toed sloth (*Choloepus hoffmanni*)".

4.3 Marine mammals (excluding Cetacea and Sirenia)

As most marine mammals can cope with extended breath-hold periods during diving when blood oxygen stores are not continually refilled, some specialised arterial supply to the brain to assure an uninterrupted supply of oxygen might be expected. However, species of seals and sea lions that have been investigated, have an arterial supply to the brain, that is more similar to that of terrestrial mammals. The major arterial path to the brain of these animals is through well-developed internal carotid and vertebral arteries, with some contribution from the external carotid arteries (DuBoulay & Verity 1973, Dormer *et al* 1977, King 1977, McFarland *et al* 1979).

Although there are no detailed accounts of the arterial supply to the brain of the sea otter are unknown, the pattern in the river otter (*Lutra lutra*) is similar to that of a terrestrial mammal (DuBoulay & Verity 1973). Therefore, pinnipeds and river otters display 'typical' terrestrial arterial blood supplies to the brain.

4.4 The Rete Mirabile

Among the cetacean specialisations associated with the change to an aquatic environment are the involution of the internal carotid and vertebral arteries and an enormous development of a blood storage system (rete mirabile) in the vertebral canal through which the entire cerebral blood supply of the dolphin passes (McFarland *et al* 1979). 'Rete mirabile' is defined as any vascular vessel (not including capillaries) that divides into multiple branches (Gegenbauer 1898, Weidenreich 1936, Schmidt-Nielsen 1990). Barnett, Harrison & Tomlinson (1958) – divided retia into four types (1) diffuse plexiform anastomoses of arteries and veins in limbs of some animals; (2) vascular bundles of arteries and veins enclosed within a common fibrous sheath; (3) an arterial rete lying retropleurally on the posterior thoracic wall – as seen in Cetacea; (4) an arterial plexus not associated with veins, e.g. the carotid rete (Table 4.2).

Wilson (1879) provided a specific description of retia. He observed that, as an arterial branch enters a rete, its course becomes very tortuous and the artery widens while giving off branches. He found three kinds of vessels in retia: "(1) vasa maxima which are large diameter vessels with thin walls and located primarily in the postero-medial aspect of the rete; (2) vasa media which are smaller vessels than the vasa maxima and whose walls are relatively thicker. The latter are found throughout the rete and take a very tortuous path and; (3) vasa minima which are the smallest vessels in the rete with the thickest walls and are reported to lie deep within the rete. Their paths are only slightly tortuous." These differences in vessel structure may possibly be related to varying haemodynamic functions of the rete though these were not clearly specified by Wilson (1879) (Table 4.3).

Wilson (1879) also noted that the rete mirabile in the thorax of Cetacea is unlike the rete found in any other animal and described the structure of the thoracic rete of the narwhal (*Monodon monoceros*) as a complex maze of sequentially branching arteries following extremely tortuous courses. As an artery proceeded into the rete it was shown to widen and to give off secondary branches, usually of its own size. The secondary branches were found to divide in their turn followed by tertiary branching etc., thus creating a labyrinth of vessels.

Cunningham (1877) noted in his dissections of the porpoise (*Phocaena phocaena*) and the white beaked dolphin (*Lagenorhynchus albirostris*) a 'dense' rete mirabile surrounding the spinal cord. "He ascribed three functions to the rete (1) protection of the spinal cord from mechanical shocks; (2) maintenance of a constant temperature for the spinal cord; and (3) a means of 'equalising' the force of the blood stream before it enters the spinal cord and brain.”

Murie (1874) described retia as being arteriovenous in the harbour porpoise (*Phocaena phocaena*). This is in contrast to most other cetacea where the retia were reported to be purely arterial (Murie 1874, Cunningham 1877, Wilson 1879). In his general comments on retia, Murie (1874) noted that these vascular structures are prominent in cetacea, sirenia, phocidae (seals), and even in some birds, through the various species were not identified in his paper.

Nakajima (1961), utilising dissection, roentgenographic (on dead specimens) and histologic techniques, investigated the retia mirabilia of the bottlenose dolphin (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), the sperm whale (*Physeter macrocephalus*), the sei whale (*Balaenoptera borealis*) and the spotted dolphin (*Stenella caeruleoalbus*) and described several groups of retia. He found these to include a basal cranial rete around each side of the atlas, an internal carotid rete, an orbital rete both inside and outside the orbit, a spinal rete, a dorsal cervical rete extending like horns dorsally from the atlas, a ventral cervical rete, a thoracic rete, a lumbar rete, a pelvic rete dorsolateral to the pelvis, and a caudal rete located ventral to the vertebrae.

Murie (1874) found several retia in his dissections of the pilot whale (*Globicephala spp.*). One was located at the inferior base of the skull extending from the tympanic bone rostral to the maxillary bone where it joined with a rete in the proximal infundibular cavity of the mandible.

Cervical, branchial, thoracic, and spinal retia were also found to be present. This serial arrangement of extracranial arterial rete apparently unique to cetaceans, has been suggested as an adaptation to diving, although Vogl & Fisher (1982) suggest that there are “almost as many functions attributed to the cetacean retial system as there are literary references to its anatomy”.

4.41 Summary Tables

Table 4.2: Descriptions of the different types of rete mirabile

Type of Rete	Description
1	Diffuse plexiform anastomoses of arteries and veins
2	Vascular bundles enclosed within a common fibrous sheath
3	Arterial lying retropleurally on posterior thoracic wall – seen in Cetacea
4	Arterial plexus not associated with veins

Table 4.3: Descriptions of the different vessels found in rete mirabile

Vessels	Description
Vasa maxima	Large diameter with thin walls and located primarily in the posterio-media aspect of the rete
Vasa media	Smaller vessesls with relatively thicker walls found throughout the rete – very tortuous
Vasa minima	Smallest vessels with the thickest walls located lying deep in the rete – slightly tortuous

4.5 Cerebral blood supply in Carnivora

In the dog (*Canis familiaris*) the aorta leaves the heart and branches into the ascending aorta and descending aorta (Figure 4.2). The ascending aorta supplies blood to the brain and neck region. The brachiocephalic trunk is the first artery to branch off the ascending aorta, passing obliquely to the right and cranially across ventral surface of the trachea (Evans & Christensen 1979). The left common carotid is the first branch to leave the branchiocephalic trunk. The branchiocephalic artery terminates in the right common carotid artery and the subclavian arteries. The left common carotid usually arises opposite the vertebral end of the second rib and ventral to the trachea. Its relations are similar to that of the right vessel, as it traverses the neck, except that it is on the left side and loosely bound to the oesophagus dorsomedially by the deep cervical fascia. Its branches and termination are similar to that of the right vessel (Evans & Christensen 1979) (Figure 4.2).

The right common carotid diverges from the left and obliquely crosses the ventrolateral surface of the trachea as it runs toward the head. Throughout the neck it lies in the angle formed by the longus colli or longus capitis muscles dorsally, the trachea ventromedially, and the brachiocephalicus and sternocephalicus muscles laterally (Evans & Christensen 1979). The common carotid artery terminates at or near a transverse plane through the body of the hyoid bone by dividing into the internal and external carotid arteries. The internal carotid, much smaller than the external one, leaves the medial side of the parent vessel and immediately runs through the deep structures of the head to the brain (Evans & Christensen 1979).

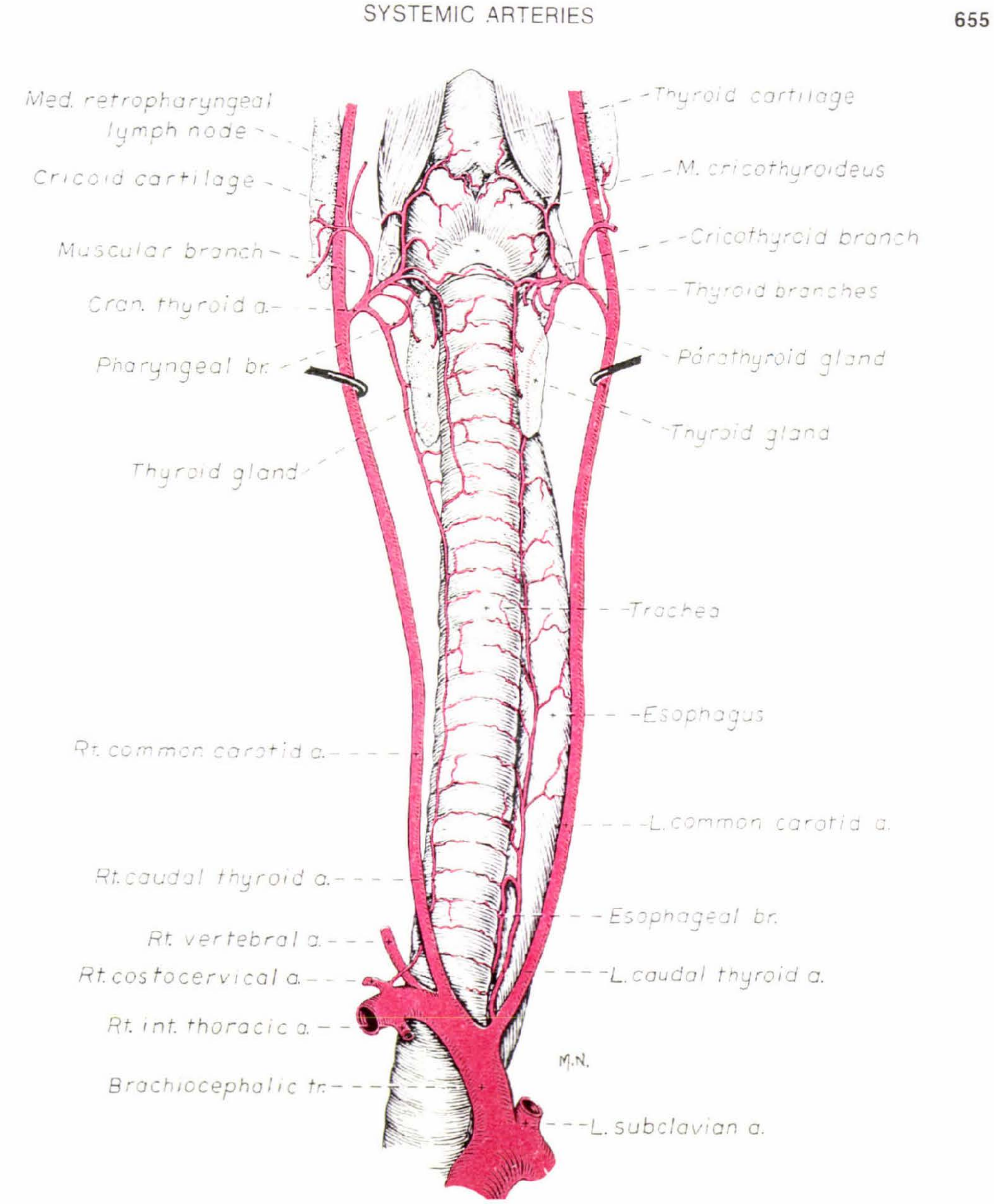

Figure 4.2: Diagram of the Systemic Arteries in the Dog (*Canis familiaris*) (Evans & Christensen 1979).

The external carotid is the main continuation of the common carotid to the head. It forms a sigmoid flexure as it winds its way under the cranial end of the hypoglossal nerve, submandibular salivary gland, and digastric muscle. It is bounded deeply by the muscles of the larynx and pharynx. The following branches leave the external carotid artery after its bifurcation from the internal carotid: occipital, cranial laryngeal, ascending pharyngeal, lingual, facial, caudal auricular, parotid, superficial temporal and maxillary arteries (Evans & Christensen 1979).

The maxillary artery gives off many branches that supply the deep extracranial structures of the head lying outside the braincase (Figure 4.3). It is the larger of the terminal branches of the external carotid, and the main continuation of the external carotid artery (Evans & Christensen 1979). Evans & Christensen (1979) divided it into three parts, the mandibular portion, the pterygoid portion and the pterygopalatine portion. The third part, the pterygopalatine portion, lies on the lateral side of the lateral pterygoid muscle and crosses it obliquely, the following vessels leave the pterygopalatine portion of the maxillary artery: the external ophthalmic, artery of the pterygoid canal, pterygoid branches, rostral deep temporal, buccal, minor palatine and infraorbital arteries, and a trunk that gives rise to the major palatine and sphenopalatine arteries (Evans & Christensen 1979).

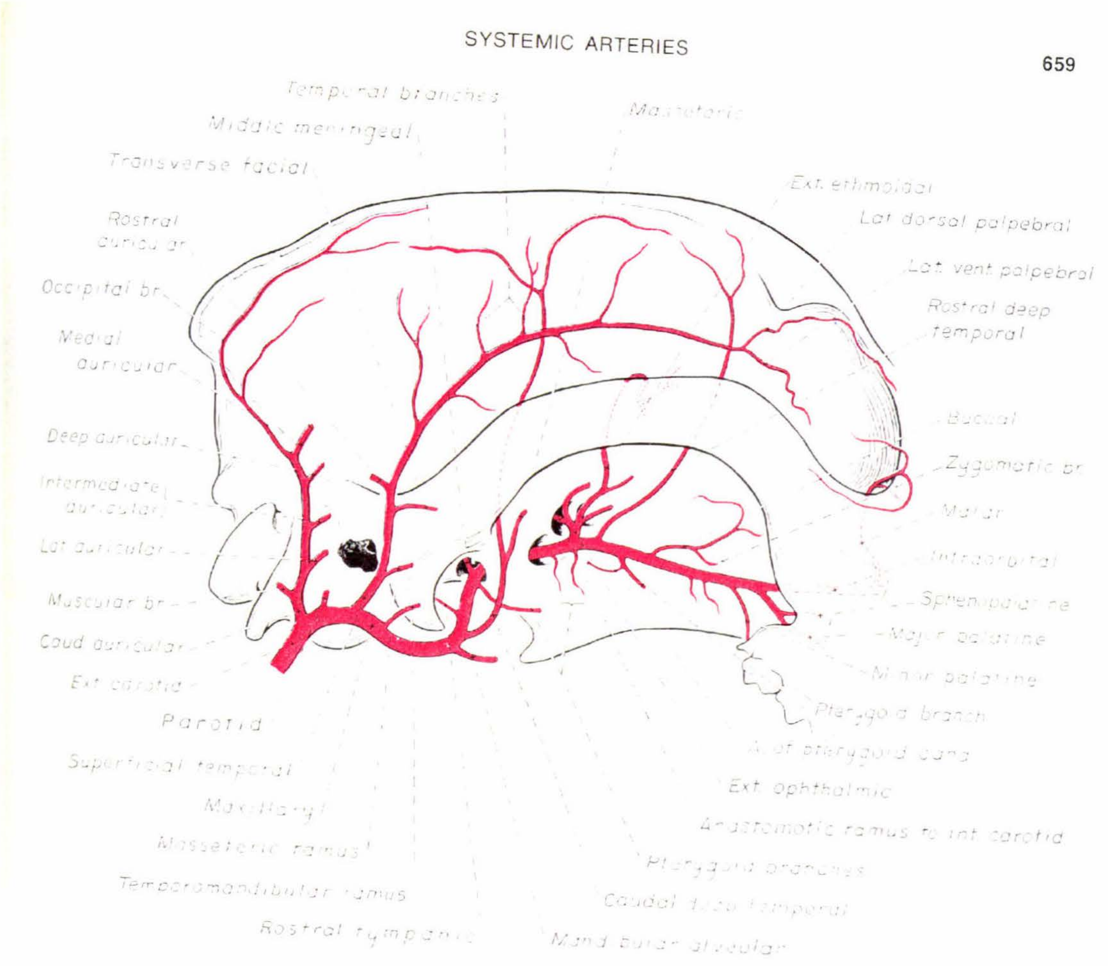

Figure 4.3: Diagram of the Systemic arteries in the Dog (*Canis familiaris*) entering the brain (Evans & Christensen 1979)

The external ophthalmic artery, sometimes called the orbital artery (Tandler 1899, Davis & Story 1943, Jewell 1952), arises from the dorsal surface of the maxillary artery immediately after it leaves the alar canal (Figure 4.4). The external ophthalmic artery typically gives rise to the external ethmoidal and an anastomotic *ramus* to the internal carotid. From the union of the external and internal ophthalmic arteries, two to four ciliary arteries arise and run to the eyeball. On reaching the sclera, which surrounds the optic nerve, the vessels break up into several branches, the posterior ciliary arteries, which extend through the cribiform area and ramify in the choroid part of the vascular coat as the choroid arteries. The retinal arterioles arise as branches of the short posterior ciliary arteries where they penetrate the sclera. Retinal vessels emerge around the periphery of the optic papilla as nine or more arterioles that radiate into the retina (Evans & Christensen 1979), and therefore supply the retinal blood vessels.

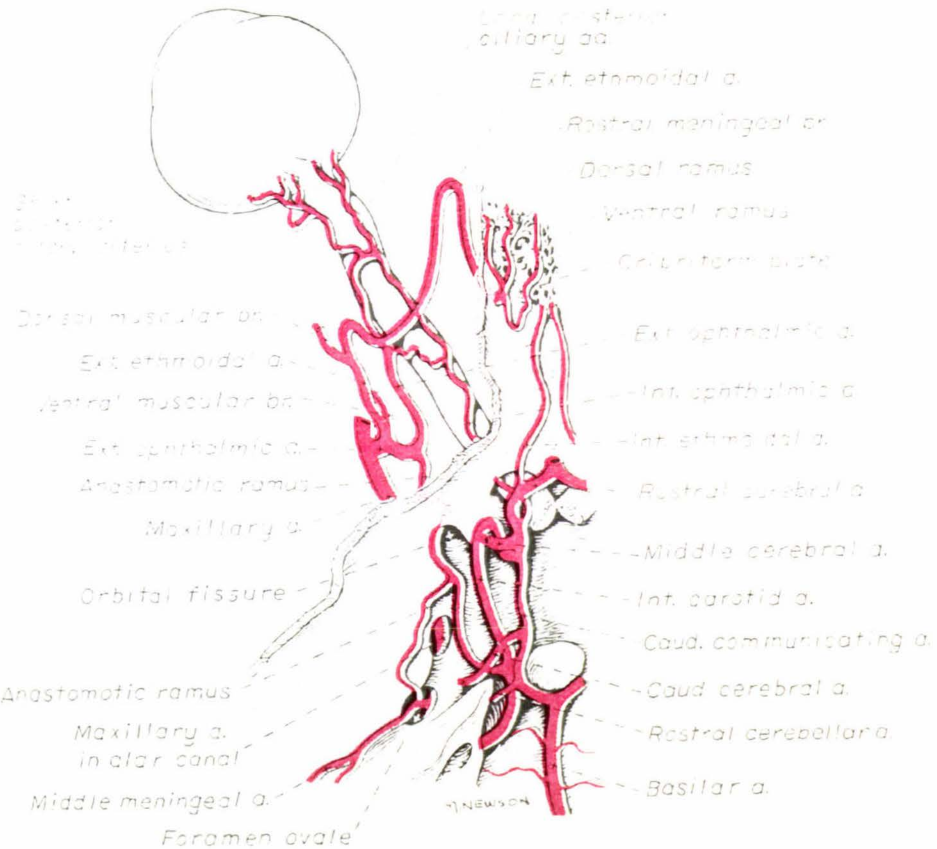

Figure 4.4: Diagram showing the blood vessels supplying the eye in the Dog (*Canis familiaris*) (Evans & Christensen 1979)

4.6 Cerebral blood supply in Pinnipedia

The pinnipedia (e.g. harbour seal, *Phoca vitulina*; southern sea lion, *Otaria flavescens*; walrus, *Odobenus rosmarus*) are aquatic mammals that spend a large part of their life in the water but do come ashore, particularly in the breeding season. As animals that have partially adapted to an aquatic existence it is of interest to determine whether their cerebrovascular system shows any adaptive parallels to the wholly aquatic Cetacea.

DeVriese (1905) noted that the cerebral circulation in the Pinnipedia is largely supplied by the internal carotid artery with anastomoses from the internal maxillary artery (Fig 4.5, Table 4.4). She further noted that the vertebral arteries play an insignificant role in supplying the brain. The cerebrovascular anatomy of the sea lion (*Otaria jubata*) was described by Murie (1874) who observed that the innominate artery arises from the arch of the aorta and divides into a left common carotid and right common carotid and right subclavian artery. The left common carotid artery arises from the arch to the left of the innominate artery origin. A rete in the thorax surrounding the heart was described by Harrison & Tomlinson (1963) in pinnipeds but it is primarily venous and joins with the posterior vena cava. The first branches from the common carotid are reported to be the superior thyroid and the superior laryngeal arteries. At the level of the stylohyoideal muscle, the common carotid artery was found to divide into external and internal carotid arteries of equal diameter. Facial, occipital and internal maxillary arteries branch from the external carotid artery.

Murie (1874) described the internal carotid artery as going ‘backwards’ through the internal groove of the tympanic bone and the periotic canal, crossing the large foramen lacerum medium, going through the carotid groove into the skull cavity and finally assisting in the formation of the circle of Willis. Murie also noted the anterior spinal arteries arise from the vertebral arteries, join, and then form the large anterior median artery of the spinal cord. The vertebral arteries were shown to course rostrad and fuse to form the basilar artery. DuBoulay & Verity (1973) found that, as in most other animals, the brain of the sealion is supplied by both internal carotid and vertebral arteries. Neither spinal nor intracranial cerebral arterial retia mirabilia occur among pinnipedia according to any of these authors. These findings *in toto* indicate that there have been no significant changes from the cerebrovascular supply pattern compared with that of terrestrial mammals in this aquatic order.

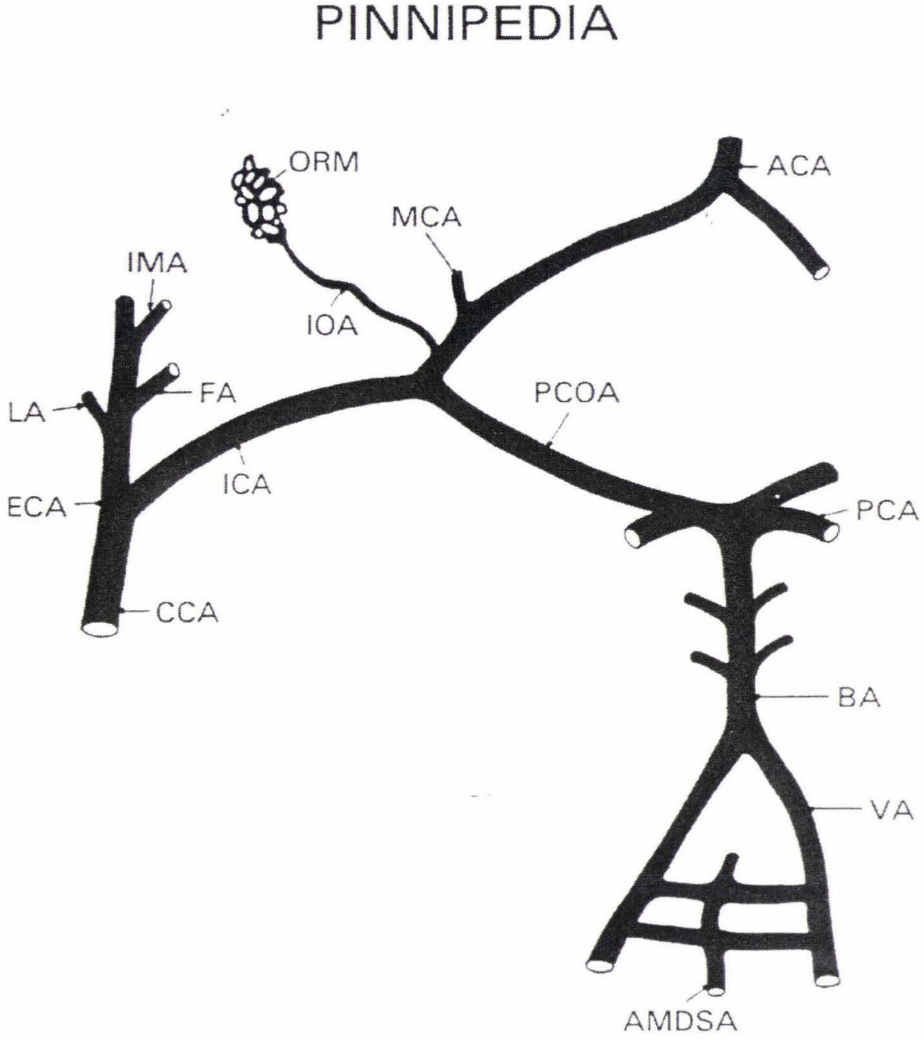

Figure 4.5: Diagram showing the blood supply to the brain in Pinnipedia (McFarland *et al* 1978). Abbreviations appear in Table 4.4

Table 4.4: List of abbreviations for Figure 4.5

Abbreviation	**Definition**
ACA	Anterior Cerebral Artery
AMDSA	Anterior Median Spinal Artery

BA	Basilar Artery
CCA	Common Carotid Artery
ECA	External Carotid Artery
FA	Facial Artery
ICA	Internal Carotid Artery
IMA	Internal Maxillary Artery
IOA	Infraorbital Artery
LA	Lingual Artery
MCA	Middle Cerebral Artery
ORM	Ophthalmic Rete Mirabile
PCA	Posterior Cerebral Artery
PCOA	Posterior Communicating Artery
VA	Vertebral Artery

4.7 Cerebral blood supply in Sirenia

The Sirenia (e.g. Caribbean manatee, *Trichechus manatus*; sea cow, *Dugong dugong*) is an entirely aquatic order of mammals that never leave water. One might expect, therefore, to find some important evolutionary parallels to the cetacean cerebrovascular blood supply pattern. In fact, DuBoulay & Verity (1973) did note that the cerebral vascular pattern of sirenians is similar to that of cetaceans (see Section 4.9 below).

Murie (1874) described the extracranial vascular system of the manatee as beginning with a small vessel that branches from the common carotid at shoulder level and terminates in a "broad radiate rete mirabile" among local muscles (Figure 4.6, Table 4.5). Cranially, at the level of the cricoid cartilage, the common carotid artery was shown to bifurcate into internal and external carotid arteries with the former entering a rete mirabile at the posterior base of the skull. The external carotid was found to have multiple branches, each terminating in retia mirabilia in the jaw, face, snout etc. Spinal, cervical, and thoracic retia are also mentioned but details of their afferent arteries are not given, although the latter two retia are supplied, in part at least, by internal mammary and axillary arteries. Intercostal retia are described as lying between the ribs, supplied by the intercostal arteries (Figure 4.6). Dexler & Eger (1911) have also reported the existence of a rete in the vertebral canal of Indian dugong (*Halicore dugong)*.

Fawcett (1942) also observed the presence of arterial subdivisions in the manatee corresponding to the spinal, cervical, thoracic and carotid retia but refers to them as "vascular bundles" rather than "retia mirabilia". This is because he found the afferent retial arteries in the manatee to divide abruptly into a series of small vessels running parallel to one another with no cross connections (Figure 4.6, Table 4.5). This does not correspond to the complex intertangled and cross-linked arrangement of vessels in true rete mirabile. Hence, it is more appropriate to use the term vascular bundle, a term which was originally coined by Wislocki (1932) and Wislocki & Straus (1932), to describe the vascular arrangements in the limbs of edentates such as the sloth. Fawcett hypothesizes that the true retia mirabilia of Cetacea are a further evolutionary modification of the simpler vascular bundles of Sirenia. The Sirenia are rather slow moving herbivores living in shallow water, in contrast to the more active carnivorous and deep-diving cetacea.

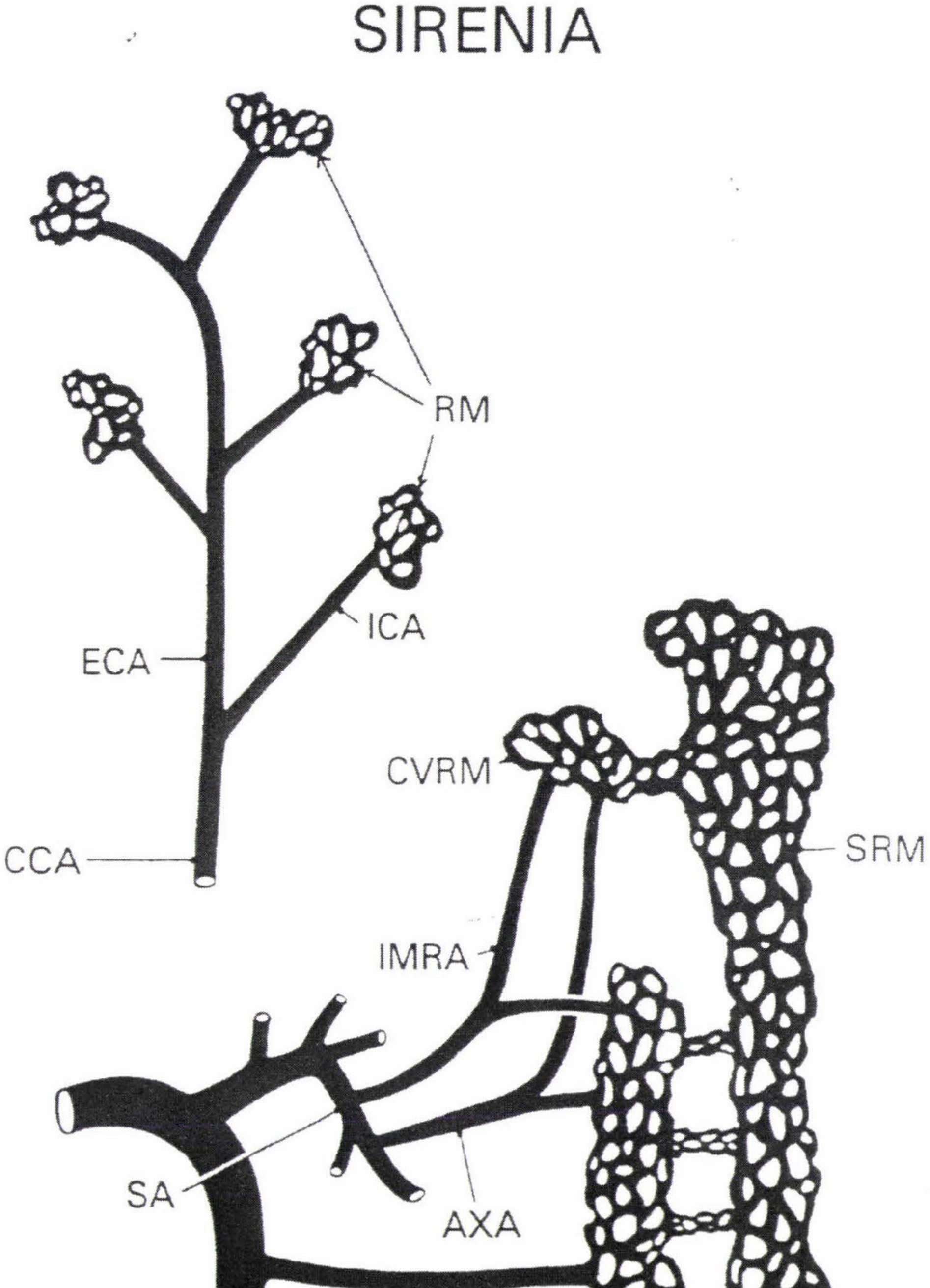

Figure 4.6: Diagram showing the blood supply to the brain in Sirenia (McFarland *et al* 1978). Abbreviations appear in Table 4.5

Table 4.5: List of abbreviations for Figure 4.6

Abbreviation	Definition
A	Aorta
AXA	Axillary Artery
CCA	Common Carotid Artery
CVRM	Cervical Rete Mirabile
ECA	External Carotid Artery
IA	Intercostal Artery
ICA	Internal Carotid Artery
IMRA	Internal Mammary Artery
RM	Retia Mirabile
SA	Subclavian Artery
SRM	Spinal Rete Mirabile
TRM	Thoracic Rete Mirabile

4.8 Cerebral blood supply in Artiodactyla

This group includes even-toed ungulates such as the pig (*Sus scrofa*), ox (*Bos taurus*), goat (*Capra hircus*), and sheep (*Ovis aries*). In this group, according to DeVriese (1905), the internal carotid arteries atrophy during fetal development and the vertebral arteries are also insignificant in providing blood to the brain (supplying up to 20% of the total cerebral blood in cattle, less in pigs, and little in goats and sheep). She notes that there is a rete mirabile at the base of the brain in these ungulates supplied by branches of the external carotid arteries, with rostral and caudal branches arising from the rete to supply the brain with blood (Figure 4.7, Table 4.6). It is also reported by DuBoulay & Verity (1973) that the internal carotid at first develops normally but by the time of birth in artiodactyls has disappeared in the cervical region. There is said to be an intracranial rete near the pituitary fossa lying between skull and dura, hence it is termed an 'extradural' rete i.e. it lies outside all layers of the dura.

The rete is supplied in the pig and in most other artiodactyls by the arteria anastomotica and ramus anastomoticus, both of which arise in artiodactyls from the internal maxillary artery, another branch of the external carotid artery according to these authors. The vertebral arteries reportedly often join with the basilar arteries but instead connect with the occipital arteries. An orbital rete lying medial to the cone of the orbital eye muscles was found to be usually present but there is no direct connection with the intracranial rete. According to Daniel *et al* (1953), this orbital rete is supplied largely by the external ophthalmic artery, a branch of the arteria anastomotica, while the ciliary artery forms the efferent artery of the rete. This rete has been called the 'ophthalmic' rete in the ox by Steven (1964). Chauveau (1898) was the first to describe the ophthalmic rete mirabile in cattle, a rete that is also seen in Cetacea.

Since there are interesting evolutionary parallels to the cetacean cerebrovascular system in even toed ungulates, it is important to give some further details of specific examples in this order. For example, Gillilan (1974) investigated the cerebral arterial supply of pigs, calves and sheep, using for the most part, latex injected heads of a late fetal stage. In the calf (*Bos taurus*), Gillilan found a carotid rete mirabile as in the pig but it was all intracranial. The rostral part of the rete was found to be supplied by the arteria anastomotica as it is in the pig but, in contrast to that species, the caudal part of the rete is supplied by the occipital artery and branches from the vertebral arteries. These findings are similar to those for the lamb (de Boissezon 1941) and the calf (Legait 1944) who also reported trigeminal innervation of the rete.

It is especially interesting in regard to the development of the internal carotid artery in Cetacea that this artery is reported to be well developed in the cervical region of the calf fetus. It passes through the carotid rete giving off branches and then it emerges from it as its efferent artery supplying the circle of willis. With further fetal development, the proximal (cervical) part of the internal carotid atrophies.

Gillilan (1974) did not speculate on the reasons for the devolution of the proximal internal carotid artery. The rostral and caudal division may consist of several branches and the middle cerebral generally has many branches. The posterior cerebral artery, arising from the caudal branch of the internal carotid, also was shown by Gillilan to consist of several branches (Figure 4.7, Table 4.6). The basilar artery was found to be formed by the union of the terminal part of the caudal divisions of the internal carotid arteries (Figure 4.7). The union was often found to be incomplete, leading to a plexiform basilar artery.

The basilar artery was reported by Gillilan (1974) to decrease in diameter caudally and blood flow was shown to be caudad rather than rostrad as in most other mammals. Gillilan found the cerebral pattern in the sheep to have certain similarities with those of the calf. As in those species, the cervical part of the internal carotid artery is atrophied and a carotid rete mirabile was shown to exist within a venous plexus in the cavernous sinus. An arterial configuration similar to that of the calf has been reported in ruminants and pachyderms by Weidner *et al* (1965).

An intracranial rete mirabile has been described by de Boissezon (1941) in the sheep where the afferent arteries are the vertebral and occipital arteries and the efferent arteries are ophthalmic and internal maxillary arteries. He also noted that the rete of the sheep is, embryologically, supplied by arteries derived from the first aortic arch and is homologous to the pseudobranch of fish, as noted by Ask-Upmark (1935, 1953). The pseudobranch is a modified gill arch of fish whose efferent artery is the first efferent gill artery and whose primary efferent artery is the ophthalmic artery. However, there is evidence (Balankura 1954) for the derivation of the rete in sheep from arteries originating from the third arch, rather than the first. It is reported that at the 30mm embryonic stage, the internal carotid artery fragments into smaller vessels in the pituitary region. Branches of the maxillary artery then anastomose with these internal carotid branches to form an intracranial rete and the internal carotid artery caudal to the rete then atrophies in fetal stages. This is an important example of a situation where the internal carotid artery develops in embryogenesis and then atrophies to be replaced by a rete mirabile.

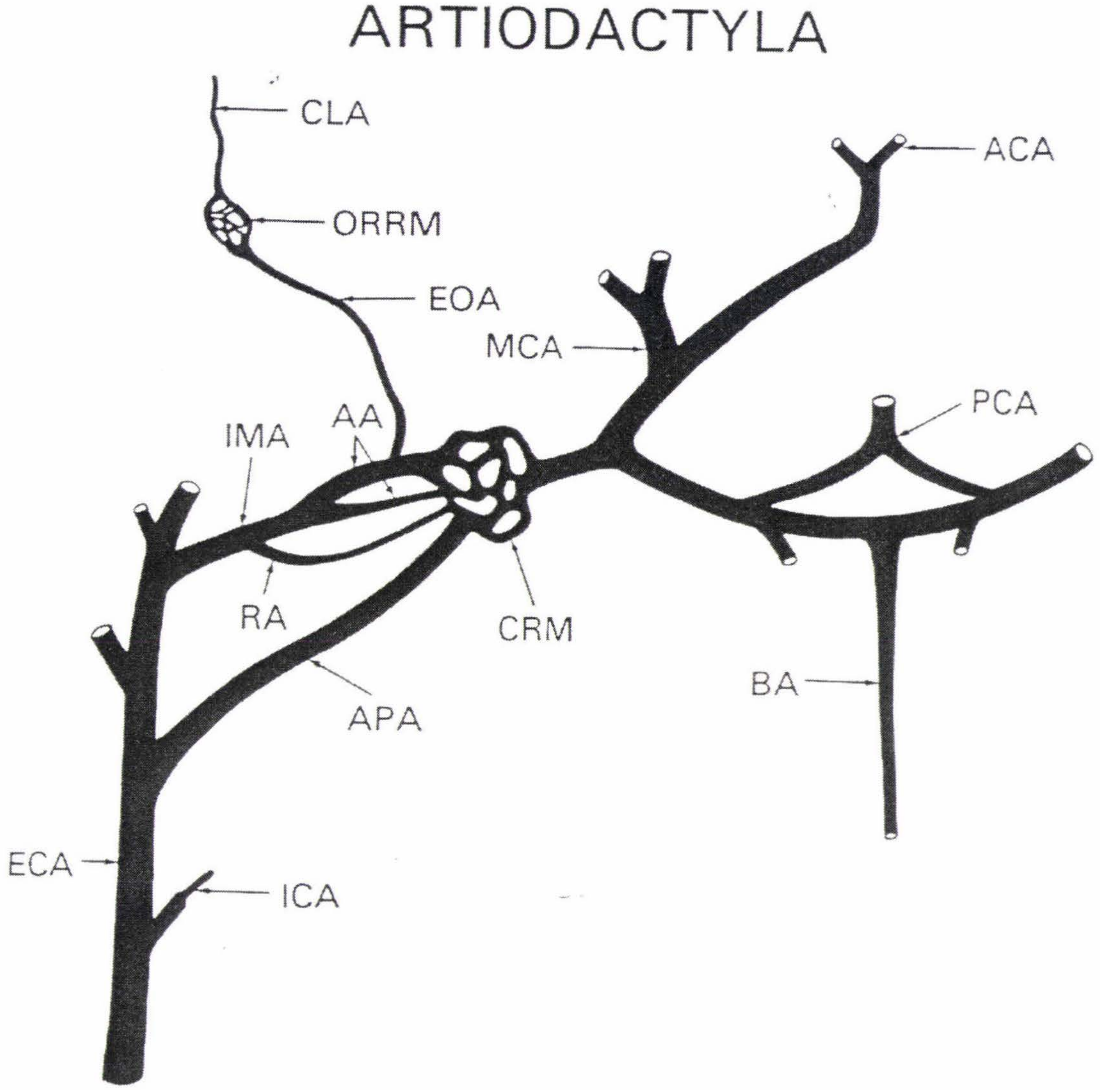

Figure 4.7: Diagram showing the blood supply to the brain in the domestic cattle (*Bos taurus*) (McFarland *et al* 1978). Abbreviations appear in Table 4.7

Table 4.6: List of abbreviations for Figure 4.7

Abbreviation	Definition
AA	Arteria Anastomotica
ACA	Anterior Cerebral Artery
APA	Ascending Palatine Artery
BA	Basilar Artery
CLA	Ciliary Artery
CRM	Carotid Rete Mirabile
ECA	External Carotid Artery
EOA	External Ophthalmic Artery
ICA	Internal Carotid Artery
IMA	Internal Maxillary Artery
MCA	Middle Cerebral Artery
ORRM	Orbital Rete Mirabile
PCA	Posterior Cerebral Artery
RA	Ramus Anastomoticus

4.9 Cetacean Cardiovascular System

The arterial blood supply in cetaceans has many specializations that allow the animals to survive in an aquatic environment. The term 'specialisation' has been defined by Nikitenko (1965) as – "radical structural changes or even development of entirely new structures or organs to permit life in one particular ecological niche". This is in contrast to 'adaptations' which refer to "modifications of structures to allow life in different ecological niches but do not involve fundamental structural reorganisations" e.g. seals are adapted to live on land and in the water but cetacea are specialised to live solely in the water (Nikitenko 1965). Besides sirenia, cetaceans are the only fully aquatic mammals with various adaptations for life under water

Unlike most other marine mammals, cetaceans possess a highly specialised arterial blood supply to the brain (Figure 4.8, Table 4.7). Cetaceans lack vertebral arteries, and their internal carotid arteries are degenerate, often not reaching the cranial cavity (Walmsley 1938, McFarland *et al* 1979, Vogl & Fisher 1981, 1982). Thus, the two major paths of arterial blood supply to the brain seen in many terrestrial mammals do not exist in cetaceans. Rather, arterial blood travels to the brain through a series of arterial retia (Galliano et al 1966; McFarland *et al* 1979; Vogl & Fisher 1981, 1982; Pfeiffer & Kinkead 1990). Arterial blood destined to feed the cetacean brain travels through the thoracic aorta to segmentally arranged intervertebral arteries. These become convoluted anastomotic bundles that are collectively termed the thoracic rete (Ommanney 1932, Barnett *et al* 1958; Galliano *et al* 1966; McFarland *et al* 1979; Vogl & Fisher 1981, 1982) (Figure 4.8).

Slijper (1936) stated the arteries supplying the brain in Cetacea have the following characteristics"(1) the internal carotid artery courses through the tympanic cavity but is obliterated after birth; (2) internal carotid rete and internal ophthalmic rete are present; (3) there is complete regression of the basilar artery during early embryonic life and; (4) the internal carotid rete at the base of the brain and the arteries coming out of it to nourish the brain are supplied exclusively by the extradural spinal meningeal arteries." Slijper (1936) noted that the arterial thoracic rete mirabile was found in all Cetacea he studied but is most prominent in the porpoise, where it lay on either side of the vertebral column and line the whole lateral inner wall of the thorax. It was reported to be associated with adipose tissue and veins and supplied by the supreme intercostal artery, the intercostal arteries and the costocervical artery.

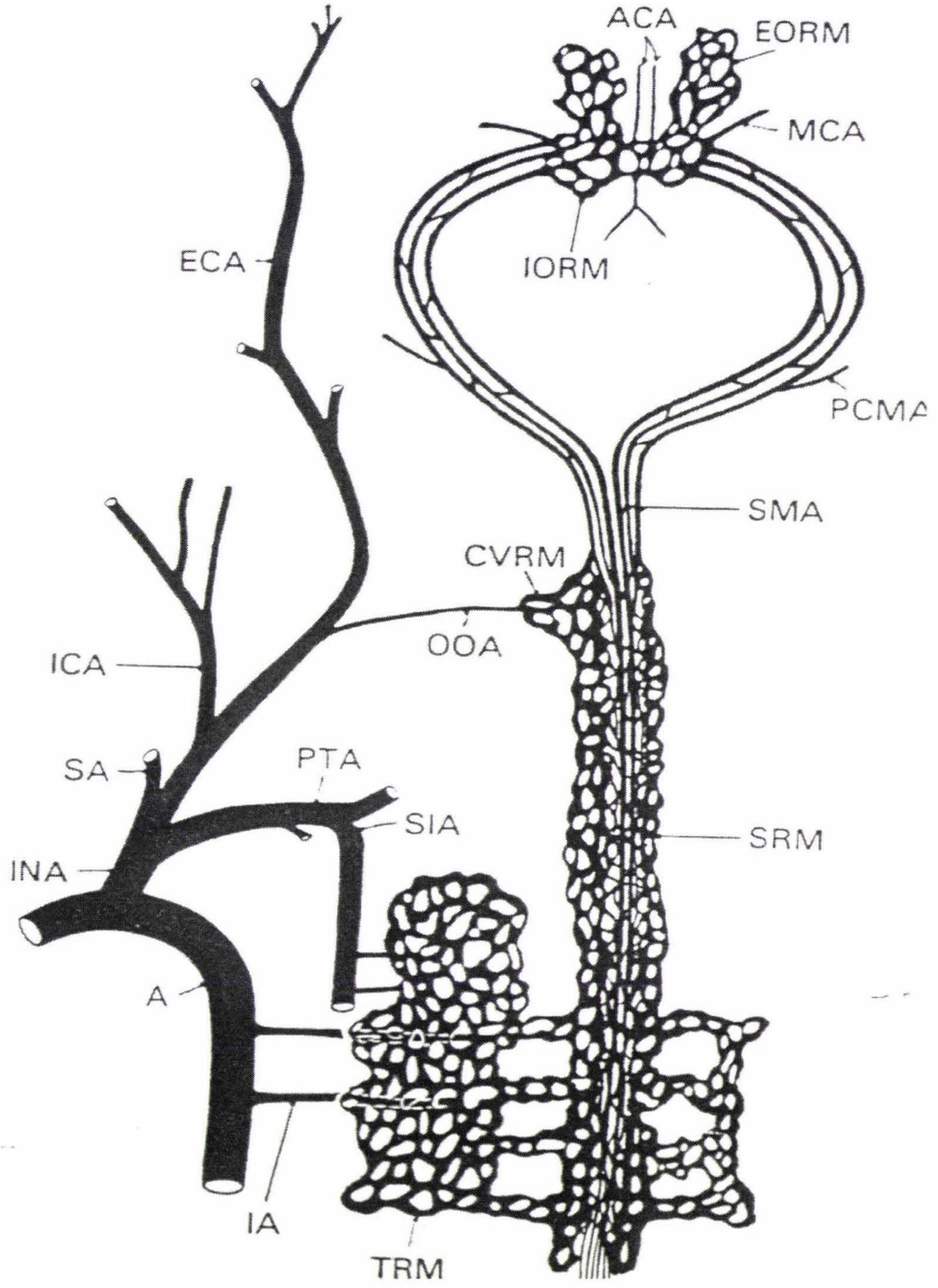

Figure 4.8: Diagram showing the blood supply to the brain in cetacea (McFarland *et al* 1979). Abbreviations appear in Table 4.7

Table 4.7: List of abbreviations for Figure 4.8

Abbreviation	Definition
A	Aorta
ACA	Anterior Cerebral Artery
CVRM	Cervical Rete Mirabile
ECA	External Carotid Artery
EORM	External Ophthalmic Rete Mirabile
IA	Intercostal Artery
ICA	Internal Carotid Artery
INA	Innominate Artery
IORM	Internal Ophthalmic Rete Mirabile
MCA	Middle Cerebral Artery
OOA	Omo-Occipital Artery
PCMA	Posterior Cerebral Meningeal Artery
PTA	Posterior Thoracic Artery
SA	Subclavian Artery
SIA	Supreme Intercostal Artery
SMA	Spinal Meningeal Artery
SRM	Spinal Rete Mirabile
TRM	Thoracic Rete Mirabile

4.9.1 The cervico-thoracic vasculature

The coronary arteries are to be the first two branches of the aorta (Galliano *et al* 1966). The third branch of the right posterior thoracic artery, a branch termed "A rete mirabile cervicalis" by Galliano *et al* (1966), was shown to supply the cervical rete mirabile, while a caudal branch of the artery was found to supply the thoracic rete. The thoracic rete lies between ribs in the dorsal thoracic cavity (McFarland *et al* 1979). And has been found in a number of different cetacean species, including in the fin whale (*Balaenoptera physalus*) by Heddle (1856) and in the bottlenose whale

(*Hyperoodon ampullatus*) by Bouvier (1892) and Hunter (1861). Wyman (1863) reported the existence of the thoracic rete in the beluga whale (*Delpinaptera leucas*) while Murie (1873) found it in the white beaked dolphin (*Lagenorhynchus albirostris gray*) and Wilson (1879) observed it in the narwhal. Slijper (1936, 1958) disagreed with Ommaney (1932) who thought the thoracic rete in the fin whale (*Balaenoptera physalus*) was primarily venous and supplied by the supreme intercostal vein and vertebral column veins.

Galliano *et al* (1966) found that the right posterior thoracic artery terminated in two arteries supplying the cervical muscles and the right subclavian and right common carotid arteries arose from the right branchiocephalic trunk (Figure 4.8). The common carotid artery divided into the internal and external carotid arteries (Figure 4.8). The external carotid was shown to enter the pterygoid fossa medial to the ramus of the mandible. In the pilot whale (*Globicephala spp.*), the external carotid artery branches from the innominate artery on the right side (Turner 1868).

In Slijper's (1936) view the veins described by Ommaney (1932) merely pass through the thoracic rete, which is primarily arterial. Slijper (1936) also found in those species in which it is well developed, to fill the entire space between the vertebral column and the oesophagus and extended further ventrolaterally. Slijper (1936) showed that in the porpoise it joined with the cranial rete and was supplied by the costocervical artery and, via the cranial rete, by the omo-occipital artery. The posterior intercostal arteries originated from the descending aorta and then divided into the right and left posterior intercostal arteries which provided a segmental blood supply to the thoracic rete mirabile (Galliano *et al* 1966).

Vessels extending from the thoracic rete enter the neural canal of the vertebral column and form yet another tortuous, anastomatic plexus called epidural (also named spinal or vertebral) rete (McFarland *et al* 1979) and are connected rostrally with the cervical rete and caudally with the lumbar rete (McFarland *et al* 1979). Barkow (1851) demonstrated that in the porpoise (*Phocaena phocaena*) a thoracic vascular plexus was formed from the posterior intercostal arteries. He further reported a spinal arterial plexus formed by intervertebral branches from thoracic, cervical and lumbar vascular plexus. Mackay (1886) described, on the basis of his dissections of the porpoise anterior, middle, and posterior meningeal branches spreading over the dura from an artery he called the internal carotid. The posterior branches anastomosed with branches from the spinal rete entering the cranium through the foramen magnum. Mackay (1886) noted anterior, middle and posterior cerebral arteries derived from the internal carotid artery, as in other mammals, but the posterior cerebral artery supplied entirely by the internal carotid artery. Mackay (1886) found that the spinal rete is formed by branches of the thoracic rete extending through the intervertebral foramina.

Slijper (1936) described one of the major cetacean retia, the spinal rete, which he termed the rete arterioles columnae vertebralis, as lying largely dorsal to the spinal cord and dura, and supplied through the intervertebral foramina by the thoracic and cervical retia (Figure 4.8). He mentions small branches from this rete that supply the spinal vertebrae and dura mater of the spinal cord. He also described longitudinal arteries, the spinal meningeal arteries, as differentiating from the rete on its dorsal surface and coursing rostrad.

Boenninghaus (1904), in a study primarily devoted to the auditory system of Cetacea, made the important observation that the brain of the porpoise (*Phocaena phocaena*), on which he performed his dissections, is supplied with blood entirely by the spinal meningeal system. Using two severed porpoise heads, he tried to fill the cerebral arteries by injecting the external carotid and occipital arteries, possibly with latex, in the neck. He could find no vertebral arteries in this species. Boenninghaus (1904) failed to reach the cerebral vessels with the injection medium in the carotid and occipital arteries but then proceeded to inject material through the spinal meningeal arteries and did succeeded in filling the cranial vessels. Stannius (1850) first observed that the vertebral artery is absent in the porpoise (*Phocaena phocaena*). He further reported a spinal arterial plexus formed by intervertebral branches from thoracic, cervical and lumbar vascular plexus.

Barkow (1851) homologised the spinal meningeal arteries in the Cetacea with the vertebral arteries in land mammals. DuBoulay & Verity (1973) reported on the cerebral vasculature of the bottlenose dolphin utilising cerebral angiography on dead specimens. While useful in showing gross aspects of the cerebral circulation, the spinal rete was not visualised, but their studies did reveal the extensions of the spinal meningeal arteries proceeding ventrolaterally from the level of the foramen magnum to the intracranial rete at the base of the brain. They, like Slijper (1936), describe both the arteries and the rete as extradural. Two arteries which they identified as the anterior cerebral arteries were shown to extend rostrad from the intracranial rete and join to form a single 'artery of the corpus callosum'. They refer to this arterial arrangement as the 'anterior part of the circle of Willis'.

Boenninghaus (1904) reported that the spinal meningeal arteries enter the foramen magnum and course in a wide convex arc along a channel in the middle cranial fossa, giving off posterior and middle meningeal arteries. The spinal meningeal arteries then were found to turn ventral and medial toward the sella turcica and enter a huge rete mirabile located in the dura. From the retial complex an ophthalmic rete extends around the optic nerve. Boenninghaus (1904) also found an anterior cerebral meningeal artery, an artery of the corpus callosum and a large artery of the Sylvian fossa as efferent arteries of the rete. From the artery of the Sylvian fossa he reported that a deep cerebral artery, a choroidal artery and a superior cerebellar artery arise which, in turn, give rise to the inferior cerebellar artery.

McFarland *et al* (1979) showed in their dissections that these vessels entered the cranial cavity through the foramen magnum, proceed latero-ventrally entirely outside the dura and supply the internal carotid rete, previously described at the base of the brain, which appears to be the rete called the internal ophthalmic rete (McFarland *et al* 1979). Barkow (1851) described, on the basis of his dissections, an arterial internal ophthalmic vascular plexus around the optic nerve. This plexus was also observed in the porpoise, in the narwhal (*Monodon monocerus*) and in the blue whale (*Balaenoptera musculus*) (Mayer 1853; Guldberg 1885; Beauregard &

Boulart 1897). An arterial external ophthalmic plexus has also been reported in the porpoise by Hulke (1867) and Mayer (1853).

The internal ophthalmic arterial rete, also extradural, was shown by Slijper (1936) to arise from the internal carotid rete mirabile. He found it in all his cetacean specimens and it has been reported in the literature by many others, including Barkow (1851), Mayer (1853), Guldberg (1885), Beauregard & Boulart (1897), and Boenninghaus (1904). It was reported to surround the optic nerve, to go through the optic foramen and join with the external ophthalmic rete in the orbit. Hosokawa (1965) found in spotted dolphins (*Stenella caeruleoalbus*) a rete mirabile covering the eye muscles and a retial 'cushion' under the brain that is probably the basal cranial rete of Nakajima (1961).

4.9.2 The internal carotid

Slijper (1936) indicated that the internal carotid rete mirabile is present in all of the species of whale he studied and lies external to the dura on the ventral wall of the skull near or around the pituitary gland. Arteries were shown to arise from this rete, penetrate the dura, and form an intradural network that was less extensive than the extradural rete. It is significant that Slijper found the arteries that form the circle of Willis in other mammals, including the basilar artery, to be entirely absent in the adult whales. He found one component of this circle, the internal carotid artery, to be present in the fetus of several cetacean species but the other component, the vertebrobasilar system, was not.

Slijper (1936) reported that the cranial rete is poorly developed in the porpoise. It lies at the base of the skull ventral to the occipital condyles and consists of intertwined plexiform branches of the external carotid and omo-occipital arteries. The venous parts of these retia were said to be more prominent than the arterial. It joins caudally with the cervical rete and was found to be much better developed in the common dolphin (*Delphinus delphis*) where it receives most of its blood from the omo-occipital artery. In the minke whale (*Balaenoptera acutorostrata*) the cranial rete was reported to be strongly developed caudolaterally but weakly developed dorsally and was not shown to join with the poorly developed cervical rete. It was observed to be supplied exclusively by the external carotid artery or its occipital branch.

Turner (1868) believed that the carotis cerebralis, an older term for the internal carotid artery, is the only blood supply to the brain in the pilot whale even though the artery diminished in diameter as it approached the head. Turner (1868) maintained that the internal carotid artery originated from either the innominate or common carotid artery, which opposes the findings of McFarland *et al* (1979). Boenninghaus (1904) found that the internal carotid artery continued rostrally, passing through the carotid canal of the skull and then emptying into the internal carotid rete mirabile. It then to entered the incisura basiparoccipitalis, a notch in the ventral surface of the skull, and angled somewhat dorsad and outwards to the perioticum (inner ear) under the round window (Slijper 1936; Boenninghaus 1904).

Boenninghaus (1904) makes the interesting point, in regard to the skull openings through which blood vessels and nerves enter the cranium, that in a

68cm embryo of *Phocaena phocaena* these openings are large and even merge with one another (anterior, medial, and posterior lacerated foramina). However, in the adult (150cm) stage these openings are much smaller. This development feature has obvious implications for the manner in which cerebral blood supply vessels are able to enter the skull in the adult. As reported by Flower (1874), in ziphioid whales such as Arnoux's beaked whale (*Berardius arnouxi*), the usual skull foramina are present with one of them near the midline and opposite the tuberculum sellae, ostensibly for the carotid artery. However, no evidence was provided that the carotid artery actually does enter the skull through this foramen.

Boenninghaus (1904) also observed that each internal carotid artery, after entering the skull, distributed branches forwards and outwards to the cerebral lobes, to the tentorial and occipital aspects of the cerebellum, to the pons and medulla, and a posterior branch that joins its opposite to form a median vessel passing caudal to the spinal cord. The internal carotid artery then entered the tympanic space, twists close to the promontorium and then goes through the centre of the corpus cavernosum, becoming even smaller in the process. This is in contrast to the course of the internal carotid artery in primates, for example, where the major part of this artery does not go through the tympanic cavity but only a small caroticotympanic branch continues in the cavity (Luzsa 1974).

DeVriese (1905) reported that the internal carotid artery in the porpoise, forms a network of branches at the base of the skull. The cerebral arteries emerge from this network and, after passing through the dura; branch into the cranial and caudal rami that supply forebrain and cerebellum, respectively. The cranial branches unite in a vascular network rostral to the hypophysis. Two anterior cerebral arteries emerge from this network and, in parallel to one another, pass over the corpus callosum. The two caudal branches then enter an arterial network caudal to the hypophysis (DeVriese 1905).

In summary of the cerebral blood supply to cetaceans, the distribution of the internal carotid artery was clearly visualised: a recurrent branch was found to supply the cervical musculature; a retial branch the carotid rete; and a terminal branch ended blindly. Therefore based on the findings of Viamonte *et al* (1968) the internal carotid was found to extend as far as the base of the skull, but does clearly not supply the brain. Instead the spinal meningeal arteries supply the cerebral arteries, and in particular the ophthalmic arteries, which supply blood to the eyes and therefore the retinal blood vessels.

4.10 References

Ask-Upmark E. 1935. *The carotid sinus and the cerebral circulation.* Acta physiat neurol Supplement 5-7: 1-374 *not seen*

Ask-Upmark E. 1953. *On the entrance of the carotid artery into the cranial cavity in* Stenops gracilis. Acta anatomica. 19: 101-103 *not seen*

Balankura K. 1954. *Observations on the development of the intracranial rete in the sheep.* Journal of Anatomy London 88: 572 *not seen*

Barkow J. 1851. *Über die arterien von Delphinus phocoena.* Anat. Abhandl Breslau 94-100 *not seen*

Barnett C., Harrison R., & Tomlinson J. 1958. *Variations in the venous systems of mammals.* Biological Review 33: 442-487

Beauregard H. & Boulart M. 1897. *Recherches anatomieques sur les balaenides.* Nouvelles archives du Muséum d'histoire naturelle Paris 9: 95 *not seen*

Boenninghaus F. 1904. *Das obr des zahnwales zurgleich ein beitrag zur theorie der scallertung.* Eine biologische Studies Zoology Jahrbach Jena Abtheilang für Anatomie and Oatogenie der Theire 19: 189-360 *not seen*

Bouvier E. 1892. *Quelques observations nouvelles sur l'organisation des cetacés.* Compte rendu sommaire des séances de la Société philom. Paris 5: 2 *not seen*

Chaveau A. 1898. *Comparative anatomy of the domesticated animals.* Second English Ed. Translated by G. Fleming. New York Appleton pp 678-680 *not seen*

Cunningham D. 1877. *The spinal nervous system of the porpoise and dolphin.* Journal Anatomy and Physiology 11: 209-228 *not seen*

Daniel P., Davies J., & Pritchard M. 1953. *Studies of the carotid rete and its associated arteries*. Phill. Trans. Royal Society London Series B. 237: 173-208

Davis D. & Story H. 1943. *The carotid circulation in the domestic cat*. Publ. Field Mus. Nat. Hist. Zool. Series 28: 1-47 *not seen*

DeBoissezon P. 1941. *Le réseau admisable artériel intracranien de l'agneau*. Bulletin Soc. Hist. Nat. Toulouse 76: 299-304 *not seen*

Devriese B. 1905. *Sur la signification morphologiques des artères cérébales*. Arch de Biol (Liege) 21: 359-457 *not seen*

Dexler H. & Egler D. 1911. *Beitrage zur anatomie des saugerrűckenmarkes* Halicore dugong. Morph. Jahrb Leipzig 43: 107-207 *not seen*

Dormer K., Denn M., & Stone H. 1977. *Cerebral blood flow in the sea lion* (Zalophus californianus) *during voluntary dives*. Comparative Biochemistry and Physiology A 58: 11-18

DuBoulay G & Verity P. 1973. *The cranial arteries of mammals*. William Heinemann Medical books Ltd. London pp 1-295

Evans H & Christensen G. 1979. *Miller's anatomy of the dog*. Saunders Philadelphia

Fawcett D. 1942. *A comparative study of blood vascular bundles in the Florida manatee and certain cetaceans and edentates*. Journal of Morphology 71: 105-133

Flower W. 1874. *On the recent ziphioid whales, with a description of the skeleton of* Bernadicus arnouxi. Transactions of the Zoological Society of London. 8: 203 *not seen*

Galliano R., Morgane P., McFarland W., Nagel E., & Catherman R. 1966. *The anatomy of the cervicothoracic arterial system in the bottlenose dolphin (*Tursiops truncatus*) with a surgical approach suitable for guided angiography*. Anatomical Record 155 : 325-338

Gegenbaur C. 1898. *Vergleichende anatomie der wirbelthiere*. L. Wilhelm Engelmann Leipzig pp 978 *not seen*

Gillilan L. 1974. *Blood supply to brains of ungulates with and without a rete mirabile caroticum*. Journal of Comparative Neurology. 153 : 275-290

Guldberg G. 1885. *Über das centralnervensystem der bartenwhale*. Forhandlinger i Videnskabs-selskabet i Christiania. No 4 1-154 *not seen*

Harrison R. & Tomlinson J. 1956. *Observations on the venous systems in certain pinnipedia and cetacea*. Proceedings of the Zoological Society. London 126: 205-233

Heddle R. 1856. *On a whale of the genus* Physalus gray, *captured in Orkney.* Proceedings of the Zoological Society London 24: 187-198 *not seen*

Hulke J. 1867. *Notes on the anatomy of the retina of the common porpoise .* Journal of Anatomy and Physiology. 2: 19-28 *not seen*

Hunter J. 1861. *Essays and observations on Natural History, anatomy, physiology, psychology, and geology.* R. Owen (ed) Volume 2. London *not seen*

Jewell P. 1952. *The anastomoses between internal and external carotid circulations in the dog.* Journal of Anatomy. London 86: 83-94 *not seen*

King J. 1977. *Comparative anatomy of the major blood vessels of sea lions* Neophoca *and* Phocarctos; *with comments on the differences between the* otariid *and* phocid *vascular systems.* Journal of Zoology (London) 181: 69-94

Legait E. 1944. *Anatomoses arterio-veineuses au niveau du réseau admirable carotidien chez le veau.* Am. Endocr. Paris 5: 89-90 *not seen*

Luzsa G. 1974. *X-ray anatomy of the vascular system.* J.B Lippincott Co. Philadelphia and Toronto pp 120-199

McFarland W., Jacobs M., & Morgane P. 1979. *Blood supply to the brain of the dolphin* Tursiops truncatus, *with comparative observations on special* *aspects of the cerebrovascular supply of other vertebrates.* Neuroscience and Biobehavioural Review 3 (Suppl 1): 1-93

Mackay J. 1886. *The arteries of the head and neck and the rete mirabile of the porpoise* (Phocoena communis) Proc. R. Philo. Soc. Glasgow 17: 366-377 *not seen*

Mayer A. 1853. *Anatomische unteruhungen über das auge der cetaceen.* Verhandlungen des Naturhististorische Vereins der Preussischen Rheinlunds and Westphalen 10: 1-55 *not seen*

Murie J. 1874. *On the organization of the caaing whale* (Globicephala melas). Transactions of the Zoological Society of London *not seen*

Nakajima M. 1961. *The study of rete mirabile of the cetacea centered around* Grampidelphis griseus *and* Tursiops truncatus. Toho- Igakukai-Zasshi 8: 1611-1624 (in Japanese) *not seen*

Nikitenko M.1965. *Concerning the paths of adaptation to and of specialisation for aquatic mode of life in different mammals.* In Contributions of the All-Union Conference of Intraspecies Variability of Land-living Vertebrate Animals and Microevolution pp 109-117 *not seen*

Ommaney F. 1932. *The vascular networks (retia mirabilia) of the fin whale* (Balaenoptera physalus). Discovery Reports 5: 327-465 *not seen*

Pfeiffer C. & Kinkead T. 1990. *Microanatomy of retia mirabilia of bowhead whale forman magnum and mandibular foramen.* Acta anatomica 139: 141-150

Schmidt-Nielson K. 1990. *Animal Physiology : adaption and environment.* 4th ed. Cambridge University Press. Cambridge

Slijper E. 1936. *Die cetacean vergleichend-anatomisch und systematisch.* Capita Zoologica Martinus Nijhoff, The Hague 7: 82-96, 102-103, 162-170, 346-348 *not seen*

Stannius H. 1850. *Noveau manual d'anatomie comparee.* Tome H. Animale Vertebres. Spring et Lacardaire Paris *not seen*

Steven D. 1964. *The distribution of external and internal ophthalmic arteries of the ox.* Journal of Anatomy London 98: 429-435

Tandler J. 1899. *Zur vergleichenden anatomie der kopfarterian bei den mammalia.* Denksch. Der kais Akad *not seen*

Turner W. 1886. *The anatomy of the second specimen of Sowerby's whale* (Mesplodon bidens) *from Shetland.* Journal of Anatomy and Physiology 20: 144-188 *not seen*

Vogl A. & Fisher H. 1981. *The internal carotid artery does not directly supply the brain in the* Mondontidae *(order* Cetacea*).* Journal of Morphology 170: 207-214

Vogl A & Fisher H. 1982. *Arterial retia related to supply of the central nervous system in two small toothed whales – narwhal* (Monodon monoceros) *and beluga* (Delphinapterus leucas). Journal of Morphology 171: 41-56

Walmsley R. 1938. *Some observations on the vascular system of a foetal finback*. Contrib. Embryol. Carnegie Institute. 27: 107-178 *not seen*

Weidenreich F. 1936. *Ueber das phylogenetische wachsthum des hominidengehirns*. Kaibôgahn Zasshi Tokyo 5: 1-14 *not seen*

Weidner W., Hanafee W., & Markham C. 1965. *Intracranial collateral circulation via leptomeningeal and rete mirabile anastomoses*. Neurology 15: 39-48 *not seen*

Wilson H. 1879. *The rete mirabile of the narwhale*. Journal of Anatomy & Physiology. 14: 377-400 *not seen*

Wislocki G. & Straus W. 1932. *On the blood vascular bundles in the limbs of certain edentates and lemurs*. Bulletin Mus. Comp. Zool. Harvard 74: 3-15 *not seen*

Wyman J. 1863. *Description of a "white fish" or "white whale"* (Beluga borealis Lesson). Boston Journal of Natural History 7: 603-612 *not seen*

Chapter 5:

Vision in Cetacea

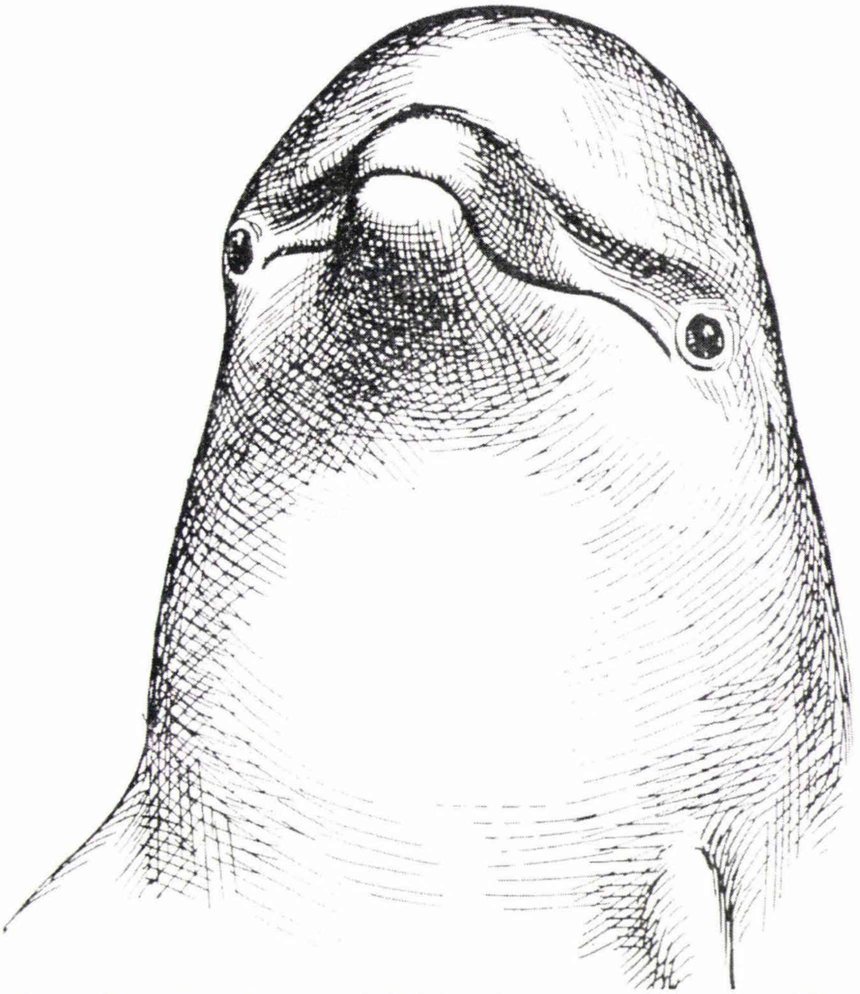

Figure 1: Drawing of bottlenose dolphin (*Tursiops truncatus*), binocularly looking at an object (Dral 1977)

5.1 Introduction

This chapter reviews the anatomy and function of the cetacean eye, with particular reference to the fundus. Comparisons are made to other mammal species, in particular members of the Artiodactyla, which have evolutionary links to whales and to Pinnipedia that live part of their life on land while remaining highly adapted to aquatic, especially marine, habitats.

5.2 The cetacean eye

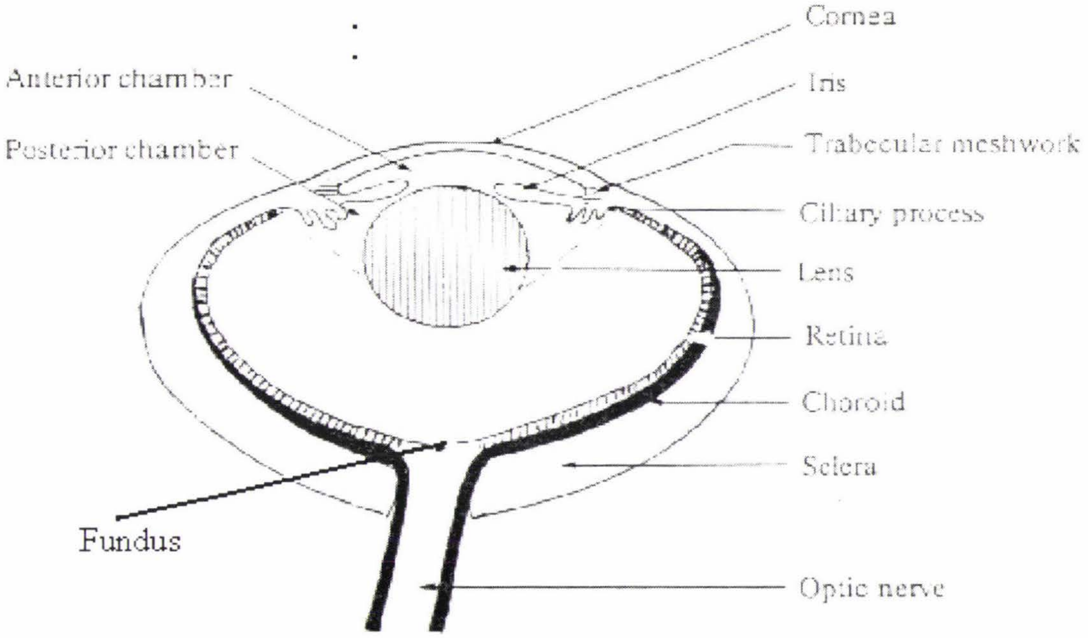

Figure 5.2: Diagram of a cross section of the eye of a harbour porpoise (*Phocoena phocoena*) (Kastelein *et al* 1990)

The cetacean eye (Figure 5.2 & Figure 5.3) has undergone a number of changes to adapt to aquatic environments, while retaining an ability to adequately see in air. In the first study on eye structure in cetaceans Walls (1942) believed that cetaceans had fish like eyes, and that they would not be able to rotate their eyeballs. He was quite incorrect in this belief as cetaceans are able to rotate their eyeballs (Nachtigall 1986). Walls (1942) did, however, provide a basic structural description of the eyes. They are ellipsoidal with a spherical lens and with a cornea that is thickened at its margins. A reflective tapetum is located behind the retina. Dral (1972) examined seven dolphin eyes and found that contrary to Walls' assumptions, not all of the lenses were spherical and some had a distinct oval shape. He also noted that the iris operculum has strong muscles and lies close against the lens and therefore could provide a mechanism for accommodation similar to that found in otters. He also noted that in-air bright-light conditions "the operculum is lowered by which action, together with a small lowering of the iris and the pupil is divided into two apertures, a nasal and temporal one." Dawson *et al* (1972) examined both living and fixed dolphin eyes with a retinoscope, ophthalmoscope and fundus camera and found in contrast to Dral (1972) found that the pupil closes down into a U-shaped slit and not into two distinct apertures. On the basis of this pupillary slit and the adaptations for dim-light sensitivity (e.g. large pupil and tapetum), Dawson *et al* (1972) proposed that the dolphin overcomes in-air myopia by focusing with a very narrow opening, analogous to that of a pinhole camera.

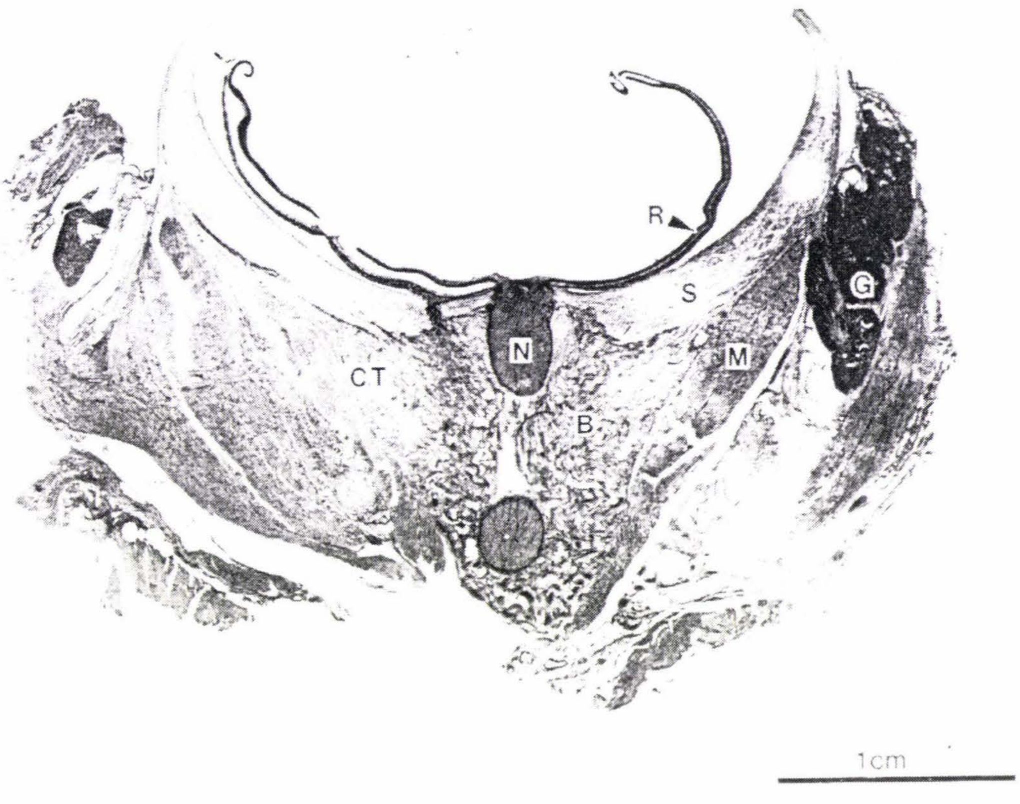

Figure 5.3: Anterior part of the eye with surrounding tissue. Retina (R), sclera (S), optic nerve (N), blood vessels (B), eye muscles (M), connective tissue (CT), and eye gland (G) (Kastelein *et al* 1990)

Eyes of cetaceans must collect information from a world characterised by low light levels and temperature and pressure conditions that fluctuate widely between the surface and deeper waters. Cetacean eyes, have a thick sclera for protection against increased pressure (Yablokov *et al* 1972), and in cold water prevent excessive heat loss by the ophthalmic rete (a highly efficient vascular radiator) and fatty insulation in the eyelids (Dawson 1980; Dawson *et al* 1987).

The environment immediately surrounding the eye is subject to hostile biochemical and immunological conditions from dissolved ions, particulate matter and microorganisms, as well as to hydrodynamic deformation due to swimming and variation in pressure (Dawson 1980; Fobes & Smock 1981; Watkins & Wartzok 1985; Natchtigall 1986). Secretions from the Harderian glands continuously bathe the eyes with a layer of fluid which probably reduces hydrodynamic distortion of the cornea by coming off easily and in doing so flushes away any irritants which may have settled onto the eye (Yablokov *et al* 1972; Dawson 1980; Dawson *et al* 1987a; Dawson *et al* 1987b).

Terrestrial mammals' eyes utilise two focusing structures (Figure 5.4) to project a clear image upon the photosensitive retina. The cornea provides gross focus as a product of refraction, which is not under control of the ciliary muscles and contraction which flexes the lens, producing a change in focus. In contrast to the general terrestrial model, the cetacean cornea functionally is absent in water because it has nearly the same index of refraction as water. Examination of corneas of *Tursiops* suggests that the corneas have irregular surfaces with uneven radii of curvature (Dral 1974; Dawson *et al* 1987b). The uneven quality of the cetacean cornea is pertinent only to discussions of in-air vision because functionally it is nonexistent underwater.

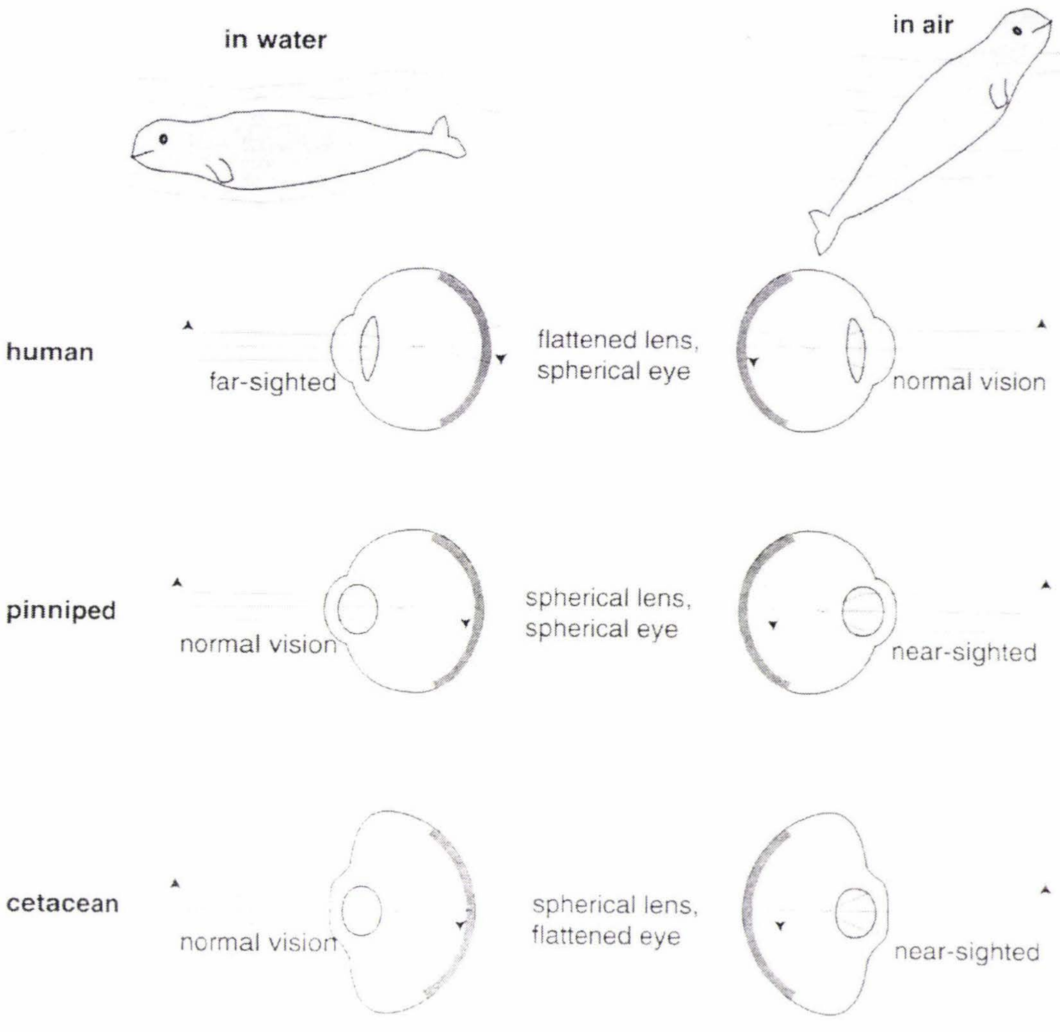

Figure 5.4: Diagram showing the comparison of the eye and lens shape of a human, pinniped, and cetacean; optics in air and water (Berta & Sumich 1999).

Lenses in terrestrial eyes tend to be ellipsoidal but may be nearly spherical in the eyes of cetaceans (Yablokov *et al* 1972). The possibility of dynamic accommodation (i.e. change in focal length through muscular deformation of the lens) has been discounted at least in *Tursiops*, due to the absence of ciliary muscles surrounding the lens (Yablokov *et al* 1972; Dral 1975) and the lack of any observed accommodative muscles during ophthalmoscopic observations (Dawson 1980). As a result, many authors have been quick to conclude that this characteristic, in combination with the irregularly shaped cornea, necessarily produce an animal with both severe in-air myopia and astigmatism (Walls 1942, Fobes & Smock 1981). However, these observations contrast with behavioural evidence for delphinid species that suggest relatively good visual acuity for those species tested (Mobley & Helweg 1990).

The tapetum lucidum is a reflective structure that maximises the ability of the retina to function under low light conditions by reflecting light onto the photoreceptors with minimal scattering, thereby functionally increasing light levels available for vision with minimal loss of resolution (Mobley & Helweg 1990). This type of structure is useful for cetaceans that live in dim or aphotic light conditions. The cetacean retina is completely tapetalised whereas the tapeta in terrestrial species normally lie only on the upper visual field of the retina (Young *et al* 1988). This characteristic of the cetacean eye presumably is more effective at capturing available light (Mobley & Helweg 1990).

Histological examinations of the tapeta from a pygmy sperm whale (*Kogia breviceps*) and a bottlenose dolphin (*Tursiops truncatus*) indicate that the tapeta provided extremely pure reflectance of bluish light near the centre of the optic fundus and more greenish wavelengths at the superiotemporal aspect of the fundus (Young *et al* 1988). Examination of the ocular fundus of two species of cetaceans provided evidence of uniform tapetal reflectance, with that of the pelagic Risso's dolphin (*Grampus griseus*) transmitting more bluish wavelengths than that of the neritic *Tursiops* (Dawson *et al* 1987a). Parenthetically, Young *et al* (1988) made the observation that cetaceans are the only carnivores with a tapetum fibrosum, (a layer of fibrous tissue of a highly reflecting nature, situated just beyond the choroidal layer of choriocapillaries, and encircling the globe for an area of from one sixth to one half, mainly upper quadrants(Prince 1956), which is found in terrestrial ungulates. Carnivore eyes typically are lined with a tapetum cellulosum (layer of cells, endothelial, and probably of the choroidal origin arranged just beyond the choriocapillaries (Prince 1956). This observation increases the evidence for a common phylogenetic ancestry among cetaceans and ungulates.

5.3 Visual Acuity

Walls (1963) believed that the cetacean eye would be 'completely useless in air'. However Kellogg & Rice (1963, 1966) showed that the cetacean eye is not completely useless in air. Although not a parametric examination of visual acuity, their study on bottlenose dolphins (*Tursiops truncatus*), showed that these animals could distinguish between two-dimensional shapes both in air and underwater.

It is obvious to anyone who has observed a captive bottlenose dolphin that their eyes are readily moveable (Nachtigall 1986). Dral (1972) observed this ocular mobility and examined a living dolphin's eyes. He noted that when the dolphin looks underwater it often views an object to the side with a single eye but when the animal views an object in air it 'faces' the object in a nasal-ventral direction. `Dral's ophthalmoscopic measurements indicated that the dolphin may see quite well in a dorso- or ventro-temporal direction (through the thickened portion of the cornea) in air. He concluded that "underwater the animal can use the whole range of its eye, whereas in air its vision is restricted to its nasoventral part".

Dawson *et al* (1972) were apparently unaware of Dral's (1972) work and formulated an independent, but different, view of the focussing mechanism of the dolphin eye in air. On the basis of their calculations of the curvature of the cornea and the distances within the eye, they determined that the dolphin would require 5.1 diopters of lens accommodation which would correct for the additional power provided by the cornea in air, indicating that optically a dolphin is strongly myopic when it is out of water. They did specify precisely which part of the cornea the animal would presumably be viewing through but did not mention its irregular shape, as Dral (1972) had, but the calculations were based on a radius of curvature of approximately 14.8m which implies a regularly curved cornea. Dawson *et al* (1972) proposed that the dolphin overcomes it myopia in air the same way that the sea lion compensates for its astigmatism by focusing with a very narrow opening analogus to a pinhole camera.

Madsen (1972) examined both aerial and under-water visual acuity in the bottlenose dolphin and found the minimum angle of resolution (MAR) in water to be about 12 min, and in air about 22 min. She was, however not particularly confident in her results, noting that part of the experiment was performed hastily and before the animal was fully trained to the new discrimination. Madsen used Ronchi grid patterns (Nachtigall 1986) presented simultaneously and collected data by a combined method of descending limits and tracking (Nachtigall 1986). In spite of Madsen's trepidation concerning her results, another study of bottlenose dolphin aerial acuity (Pepper *et al* 1972), using Ronchi rulings successively presented by a method of constants, indicated that the bottlenose dolphin has a MAR of 18 min in air under bright light conditions – not very different from Madsen's 22 min.

It should be noted that all three of the aforementioned studies of aerial vision (Kellogg & Rice 1966, Madsen 1972 and Pepper *et al* 1972) conducted with bottlenose dolphins were carried out with some difficulty. For example it is quite difficult to get a dolphin to attend to static visual stimuli presented in air. Kellogg & Rice (1966), for instance, report that aerial discrimination could only be accomplished after the animal had learned the task underwater. A great deal of training was required before Pepper *et al*'s (1972) animal properly attended to the visual stimuli. Despite such difficulties, the results generally indicate that cetaceans are capable of resolving the details of objects in air fairly well.

Spong & White (1971) attempted to examine the visual acuity of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) underwater. The task consisted of a simultaneous discrimination between two stimuli presented on a white background. Each variable stimulus was made up of two black vertical lines separated by a gap, while the standard was a black rectangle equal in area to the sum of the vertical lines on each variable target. The animal was trained to choose the variable target containing the gap. The MAR determined by the method of constant stimuli was found to be 6 min in bright light. White *et al* (1971) examined underwater visual acuity of the killer whale (*Orcinus orca*) using a task and methods similar to that used with the white-sided dolphin (Nachtigall 1986), in an attempt to control for possible brightness differences, White *et al* (1971) changed the standard target from a solid black rectangle to two vertical black lines with a gap width well below the presumed acuity of the whale. The MAR was estimated to be 5.5 min of arc in relatively bright light. Although the procedures in both these underwater acuity studies appear sound, the MARs may be an overestimate of the true underwater acuity for these animals.

When Schusterman (1968) presented a similar task to sea lions he found a MAR of about 2 min and subsequent testing of sea lions with Ronchi patterns indicated an actual MAR of 6min. Schusterman (1971) stated that it seems quite probable that the underwater acuity of at least the Pacific white-sided dolphin had been overestimated in Spong & White's (1971) work. Herman *et al* (1975) examined the visual acuity of the bottlenose dolphin in air and underwater using Ronchi grid targets presented either 1 or 2.5m away. They found that 1m aerial vision was poor, as compared with underwater vision, but that at 2.5m the acuity in air and underwater was about the same at 12.5min of arc. Expanding on Dral's and Dawson's earlier hypothesis, Herman *et al* (1975) postulated that the vision of the dolphin's eye was equally good in the two media due to a double slit pupil in bright light conditions.

5.4 Colour Perception in Cetaceans

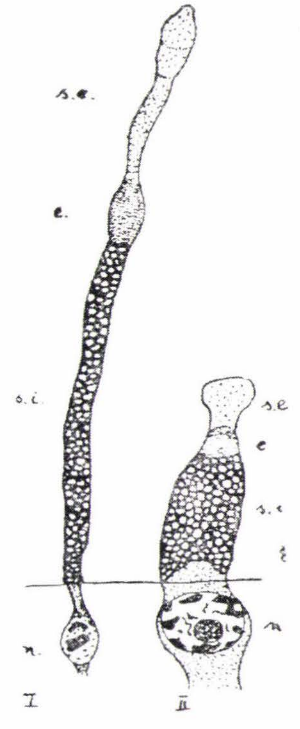

Figure 5.5: A rod (I) and a cone (II) as found in the retina of *Balaneoptera physalus* (Dral 1977).

In order for an animal to have colour vision it must possess more than one type of photoreceptor (cone, Figure 5.5) with different visual pigments (opsins) and therefore different spectral sensitivities (Peichl *et al* 2001). Most terrestrial mammals are cone dichromats (Peichl *et al* 2001), having long-to-middle- short-wave-sensitive (L-) cones (green to red-sensitive, depending on the species) and short-wave-sensitive (S-) cones (blue to near UV-sensitive, depending on species)(Jacobs 1993; Alnelt & Kolb 2000). Cone trichromacy is seen in humans and some primates, where the L-opsin gene has duplicated resulting red and green cones as well as blue ones Peicl *et al* 2001). Cone monochromacy is very rare among terrestrial mammals and has been recorded in only two primates, owl monkey (*Simia trivirgata*) and bushbaby (*Otolemur crassicaudatus*) (Wikler & Rakic 1990; Jacobs *et al* 1993, 1996); three carnivores, common raccoon (*Procyon lotor*), crab-eating raccoon (*Procyon cancrivorous*) and kinkajou (*Poto flavus*); (Jacobs & Degan 1992, Peichl & Pohl 2000); and a few rodents that lack S-cones (Jacobs 1993; Szel *et al* 1996; Crognale *et al* 1998; Peichl & Moutairou 1998; Ahnelt & Kolb 2000). All of these species are nocturnal, and being colour blind would not unduly affect their fitness for survival (Peichl *et al* 2001). However, all other nocturnal terrestrial mammals are cone dichromats (Peichl *et al* 2001).

Peichl *et al* (2001) investigated seven species of cetacean and found that cetaceans have no S-cones and therefore are monochromats. This means that they would be unable to recognize colour. As noted above, this is very unusual among mammals and in terrestrial mammals is associated with a nocturnal lifestyle (Peichl *et al* 2001). This is interesting because it implies that patterns and contrast play a more important role in visual communication in these animals and probably explains the lack of obvious skin colouration. Behavioural tests in the bottlenose dolphin have found no inclination of colour discrimination (Madsen & Herman 1980). As well as examining cetaceans, Peichl *et al* (2001) investigated five species of

Pinnipedia, (three species of eared seals, and two species of earless seals) and found that they lack S-opsin and are therefore monochromats. But unlike the cetaceans behavioural tests revealed that several pinniped species including harp seal (Phoca groenlandica), (Lavigne & Ronald 1972); larga (spotted) seal (*Phoca largha*), (Wartzok & McCormick 1978); South American & Australian Fur Seal (*Arctocephalus australis*, *Arctocephalus pusillus*), (Busch & Dücker 1987); California sea lion (*Zalophus californianus)*, (Griebel & Schmid 1992) may be able to discriminate colour. However, the spectral sensitivities were unusual. They are not consistent with the expected performance of two spectral cone types, nor could they be easily explained by the interaction of L-cones and rods. Thus these behavioural findings have met with criticism (Jacobs 1993; Crognale *et al* 1998).

5.5 The Fundus of the Eye

The fundus is the posterior part of the eye where the optic nerve and retinal blood vessels enter the eye (Natchtigall 1986). The vessels of the fundus enter the cetacean eye through the optic nerve head or papilla (Figure 5.6) and join to form two major vessels, the central retinal vein and artery (Dawson 1980). These vessels travel through the optic nerve for several millimeters, then exit into the orbit. They do not pass through the optic foramen with the optic nerve (Dawson 1980). Dawson (1980) did not see their exact destination, for they tended to become lost in a large vascular region at the rear of the eye, which fills a good portion of the orbit in the vicinity of the optic nerve. This appears to be an ophthalmic division of the rete mirabilia (Ridgway 1972). According to Ridgway the function of the retia are not fully understood, but the close association between the ophthalmic retia and optic nerve is interesting. When fixed the tissues of the retia become very white and hard (Burne 1952, Yablokov *et al* 1972). This is probably the 'thick, stiff sheath of the optic nerve' described by Walls (1942). Walls blamed the mechanical properties of this sheath for eye 'immobility', which he incorrectly reported in whales. In fresh tissue the optic nerve of whales is very pliable and typically mammalian. In the deep-diving mammals the high volume and surface area of the ophthalmic rete could serve both as a biological thermostat by stabilising the temperature of the retina and optic nerve and to fill relatively void areas of the orbit.

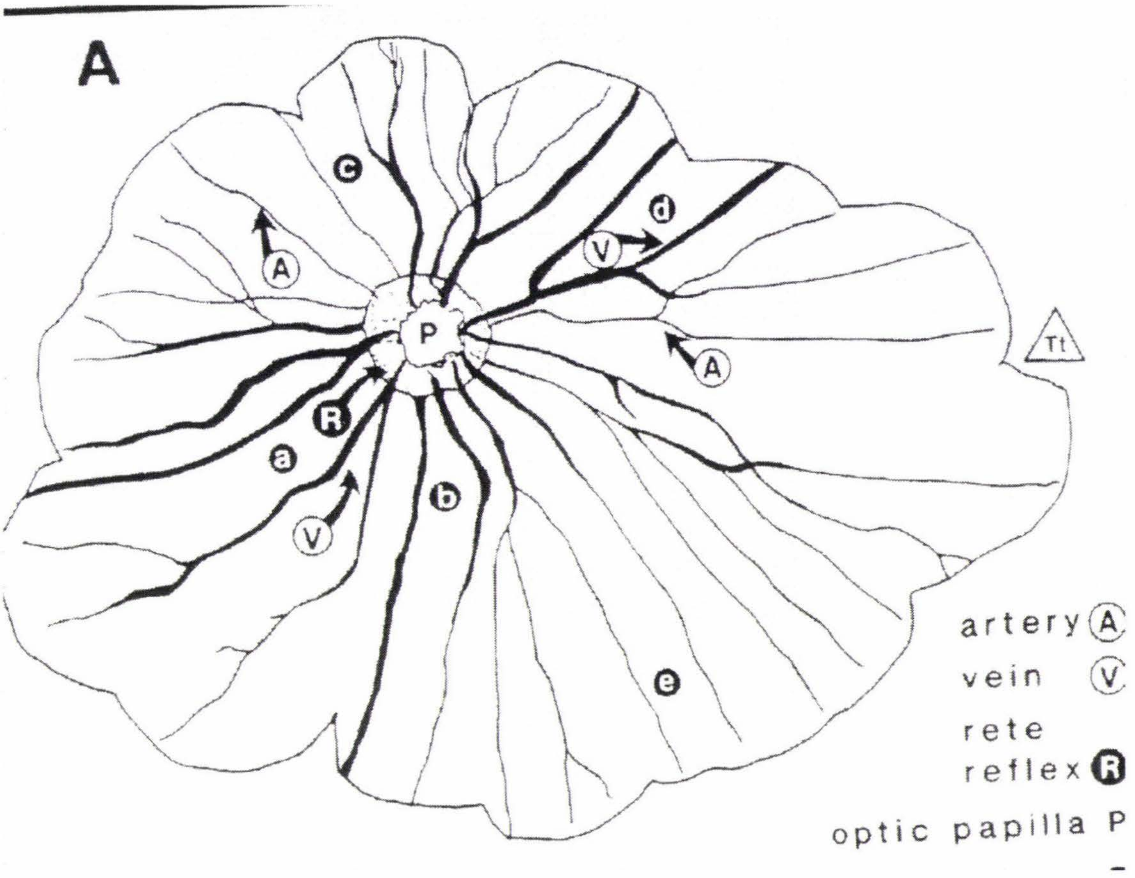

Figure 5.6: Diagram of the fundus of a bottlenose dolphin (*Tursiops truncatus*) (Dawson *et al* 1987)

Observations of the ocular fundus of cetacean species have failed to reveal clear evidence of an area centralis (the retinal area found in many terrestrial mammals that appears to be specialised for high resolution of detail (Mobley & Helweg 1990). Dral (1977, 1983), examining specimens of *Tursiops truncatus* and *Delphinus delphis*, outlined two areas possessing relatively high ganglion cell densities (an area temporalis and area centralis) that showed maximum ganglion cell densities around 500 mm^{-2}. (Mass *et al* 1986) similarly found two such areas in retinal preparations obtained from

Phocoena phocoena, one in the nasal region (500mm^{-2}) and an area of greatest concentration in the temporal region with a cell density of about 700mm^{-2}. However, the estimates of both authors are relatively low when compared to estimates for domestic cats of 4000mm^{2}, (Stone 1965) and 10,000mm^{-2} in domestic rabbits, (Rodieck 1973). Recent examinations of the ocular fundus of *Tursiops truncatus* and *Grampus griseus* failed to show the reduced vascularisation in these areas normally characteristic of an area centralis, thus suggesting that the areas proposed by Dral and Mass *et al* may not function as areas of high resolution (Dawson *et al* 1987a).

The cetacean ocular vascular patterns of the fundus are classed as holiangiotic (Dawson *et al* 1987a). "This is described as a vascular pattern showing a direct blood supply from the main arteries, in which the veins enter the eye through the optic nerve head and then branch out through the retina in most directions" (Prince 1956). However, they do not fully meet the requirement, that the blood vessels "enter the eye through the optic nerve head" (Dawson *et al* 1987a). Of the nineteen blood vessels that enter the *Tursiops* fundus, careful examination shows that at least eight enter from the perineural ophthalmic rete rather than through the head of the nerve (Dawson *et al* 1987a). In *Grampus griseus*, five of the ten originate in the rete, and the remainder clearly originate from within the white nerve head and cross the rete (Dawson *et al* 1987a). Many of the terminal vessels that originate in the rete appear to come off their stem almost at right angles. This tendency is often used as an arterial marker in terrestrial mammal central nervous system anatomy (Wise *et al* 1971). If this convention is applied to cetaceans, all or most of the vessels originating from the rete are arteries, and those from the nerve head are veins, and the vein-artery ratio is about 50/50 in each species (Dawson *et al* 1987a). It is these blood vessels that are of particular relevance for later work (chapter six).

The colour of the 'background' of the fundus montages is produced by a highly reflective retroretinal layer of rod-like, plane-orientated intracellular structures (tapetum cellulosum) that can only be resolved at the electron microscope level (Dawson *et al* 1987a). Light with the emphasis on some spectral regions is reflected back into the receptor cells ('eyeshine') by constructive and destructive interference between the wave fronts that strike critically spaced tapetal elements (Young *et al* 1983). The physical size and spacing of the reflective rodlets are in agreement with the waveguide/antenna theory. The crucial spacing may be unpredictably and slightly affected by the uneven shrinking during fixation of specimens, accounting for varied reports on tapetal colour in cetaceans (e.g. Dawson 1980). This may partially explain Walls (1967) observation that tapetal colour varies within relatively homogeneous species. Dawson *et al* (1987a) found no variation in apparent colour of the tapetal reflection in the eyes of eleven living *Tursiops truncatus*. The fully tapetalised fundus employed by cetaceans (Dawson 1980) may be unique among vertebrates. Prince (1956) states that the "tapetum never lies far ventrally to the horizontal equator of the eye".

5.6 The Importance of Vision in Cetacean Lives

According to Madsen & Herman (1980) it was thought in the past (Walls 1963, Herman & Tavolga 1980, Popper 1980) that because cetaceans have echolocation, vision would not play an important role in their lives. But this is untrue, since cetaceans have excellent vision that is important for avoiding predators and finding prey, as well as for social communication and signalling (Madsen & Herman 1980).

Visual communication has not been explored in detail for cetaceans (Wursig *et al* 1990). One of the major reasons is that visual communication and sound communication have been difficult to separate because underwater acoustic data have not been recorded consistently with behavioural observations (Würsig *et al* 1990). Furthermore, from the observer's standpoint, subtle posturing and movements that reflect flash patterns of communicative light are often obscured by distance and various properties of the aqueous environment (e.g. refraction, turbidity, wave-induced surface scatter); and even when the animals are within close range for behavioural observations, these and hydrophone recordings often are difficult to synchronise (Würsig *et al* 1990). Also, it is not always possible to separate the visual from the tactile modes often used by cetaceans (Würsig *et al* 1990). Yet, it is interesting to attempt to separate these sensory modes, for each has it's advantages and disadvantages; and the relative use of each mode may suggest the behavioural states of these interacting animals (Würsig *et al* 1990).

Very few successful behavioural observations have been carried out underwater, where cetaceans spend most of their time. Generally the observations made by human observers are made from above sea level, so that in most cases the only interactions observed are those made when the cetaceans are at the surface. More long-term underwater observational studies need to be conducted, like those on Hawaiian spinner dolphins

(*Stenella longirostris*) (Norris & Dohl 1980a; Norris *et al* 1985) and those now being carried out by several research groups working with Atlantic white-sided dolphins (*Stenella frontalis*) in the Bahamas (Würsig *et al* 1990). The difficulty with this kind of work is the need for the water to be clear and the species to consistently allow human approach. However, momentary glimpses of underwater visual communication have been recorded for humpback whales (*Megaptera noveangliae*) (Madsen & Herman 1980; Tyack 1981; Tyack & Whitehead 1983; Baker & Herman 1984; Bauer 1986). Very little is known about visual communication between other large whales.

5.6.1 Detection of Predators

The lateral and downward visual field of delphinids, is apparently well suited for detecting sharks or other predators charging from below or approaching from the side and fills in sensory gaps in the dolphins forward directed sonar scan (Madsen & Herman 1980). The passive nature of vision and the wide visual field of the delphinids (and other cetaceans) provide an environmental monitoring system with little energy cost and many benefits in promoting survival (Madsen & Herman 1980). Furthermore, an echolocation system can be disadvantageous in interactions with predators able to localise acoustic information accurately (Madsen & Herman 1980). It is not suprising therefore, that belugas and some other cetaceans cease vocalising in the presence of killer whales (Kleinenberg *et al* 1964). When threatened by predators, the line of sensory defence may shift to vision and passive listening (Madsen & Herman 1980).

Defensive responses to a predator vary, depending on species and circumstances, but may include diving, fleeing, evading, group defence, counter threat or fighting (Madsen & Herman 1980). A complex of sensory cues, including vision, may play a part in closing ranks or the placing of vulnerable calves in the centre of the delphinid group (Leatherwood 1977). Charges at the predator by peripheral animals may be mainly visually guided (Wood *et al* 1970). Mysticetes as well as odontocetes may be attacked by killer whales (Tomlin 1967). In response the mysticete may turn on its back and slash out with its powerful tail. Chittleborough (1953) observed a humpback whale successfully warding off an attacking group of killer whales in this manner. Cummings *et al* (1971) observed two southern right whales defending themselves against five killer whales by "endless slashing with flukes and pectoral fins."

5.6.2 Finding and Capturing Prey

Cetaceans eat a wide variety of prey including fish, crustaceans, cephalopods, pinnipeds and other cetaceans (Carwadine and Camm 1995), and vision is very important in helping cetaceans to find and capture prey, particularly in the regions above and below the animal, as these areas are not well-covered by their sonar system (Norris *et al* 1961). Also, as noted above, killer whales are unable to successfully use echolocation to hunt other marine mammal species. In British Columbia and Washington State, for example, resident killer whales that feed on salmon are quite noisy, while transient killer whales that feed largely on pinnipeds tend to be quiet (Ford & Fisher 1983). The assumption is that finding and capturing prey is mostly by sight.

Cetaceans seem to rely almost solely on vision at the end of the pursuit of prey. A blindfolded dolphin has great difficulty finding fish at a close range despite vigorous echolocation attempts (Nachtigall 1986). Also vision is very important in capturing prey out of the water – dolphins are known to leap out of the water and catch fish in mid air (Madsen & Herman 1980). Pacific bottlenose dolphins are able to detect and track flying fish when these are in flight. The dolphins may also be able to signal to others by their leaps out of the water accompanying catching the fish (Würsig & Würsig 1980). Bottlenose dolphins have also been noted to herding shoals of mullet on to steep banks. Once the fish are trapped, they begin leaping out of the water to escape the dolphins but are in some cases caught in mid-flight by the dolphins (Caldwell & Caldwell 1972) (Figure 5.7). Aerial vision may also be used to scan the surface for circling seabirds and 'white water' created by schooling fish (Madsen & Herman 1980).

Figure 5.7: Bottlenose dolphins (*Tursiops truncatus*) chasing fish onto mud banks in South Carolina (Mann *et al* 2000).

Vision is very important for predators that employ a sit and wait strategy, but this is a strategy which is not made use of by many cetaceans, as most species tend to capture prey by pursuit. Clarke (1970, 1979) however, hypothesized that sperm whales may use a sit and wait strategy to hunt squid. This is accomplished by taking in water through the blowhole which cools the oil in the spermaceti organ and increases its density and thus creating neutral buoyancy (Clarke 1970). The whale is then able to remain motionless with its jaws apart waiting for the bioluminescent squid to swim past. The squid may also be attracted to the reflection from the white lining around the mouth of the whale. The whale then snaps closed its lower jaw capturing the helpless squid. It is a very interesting hypothesis, but not all agree with Clarke's (1970) views on the function of the spermaceti organ (Norris & Harvey 1972).

5.6.3 Social Communication and Interaction

Cetaceans have relatively non-expressive faces, shaped during evolution towards streamlining in water. Also, most species lack flexibility of the neck and forelimbs, body parts that are used expressively in many terrestrial vertebrates. Yet visual communication is important to cetaceans (Würsig *et al* 1990), and this is likely to be true especially for social cetaceans in clear surface waters, where highly complex colouration patterns can transmit refined information (Figure 8). Cetaceans have remarkable abilities to communicate and to scan their environment by using sound. However, it is potentially disadvantageous to make sounds that prey or predators might hear (Myrberg 1981); and Würsig *et al* (1990) have found that in Hawaiian spinner dolphins (*Stenella longirostris*), dusky dolphins (*Lagenorhynchus obscurus*), and killer whale (*Orcinus orca*) all can be remarkably silent during the daytime. This is especially true when dolphins are resting and when killer whales are travelling in apparent search of marine mammal prey.

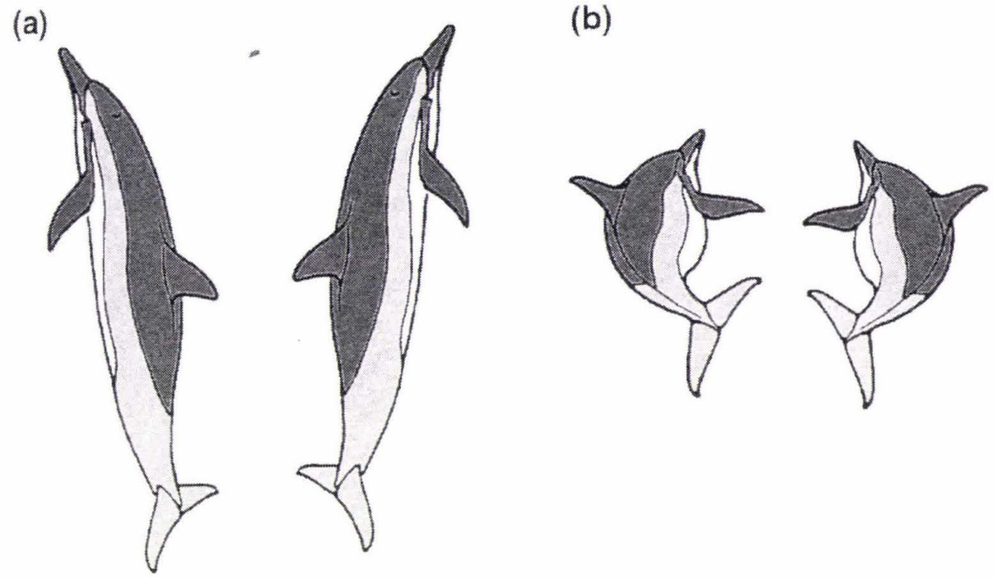

Figure 5.8: Rotating pairs of Hawaiian spinner dolphins (*Stenella longirostris*) illustrating the use of pigment patterns in signaling (a) tilt away (b) tilt-toward (Norris *et al* 1994).

During migration, as well as in the terminal breeding and feeding grounds, some of the mysticetes species may 'spy-hop' (Figure 9) by raising themselves headfirst vertically out of the water (Madsen & Herman 1980). While in this posture, the whale may sometimes rotate on its longitudinal axis, as if visually scanning a 360° sector. Most often spy-hopping among cetaceans seems to orient the cetacean to nearby or distant surface features, although it may have social functions, as well. Scammon's (1874) account of 19th century whaling included a sketch of gray whales spy-hopping among a field of ice floes. Among odontocete species, in addition to the Atlantic bottlenosed dolphin, spy-hopping has been reported for the sperm whale, the pilot whale, the Pacific bottlenose dolphin (Norris 1974) and the killer whale (MacAskie 1966).

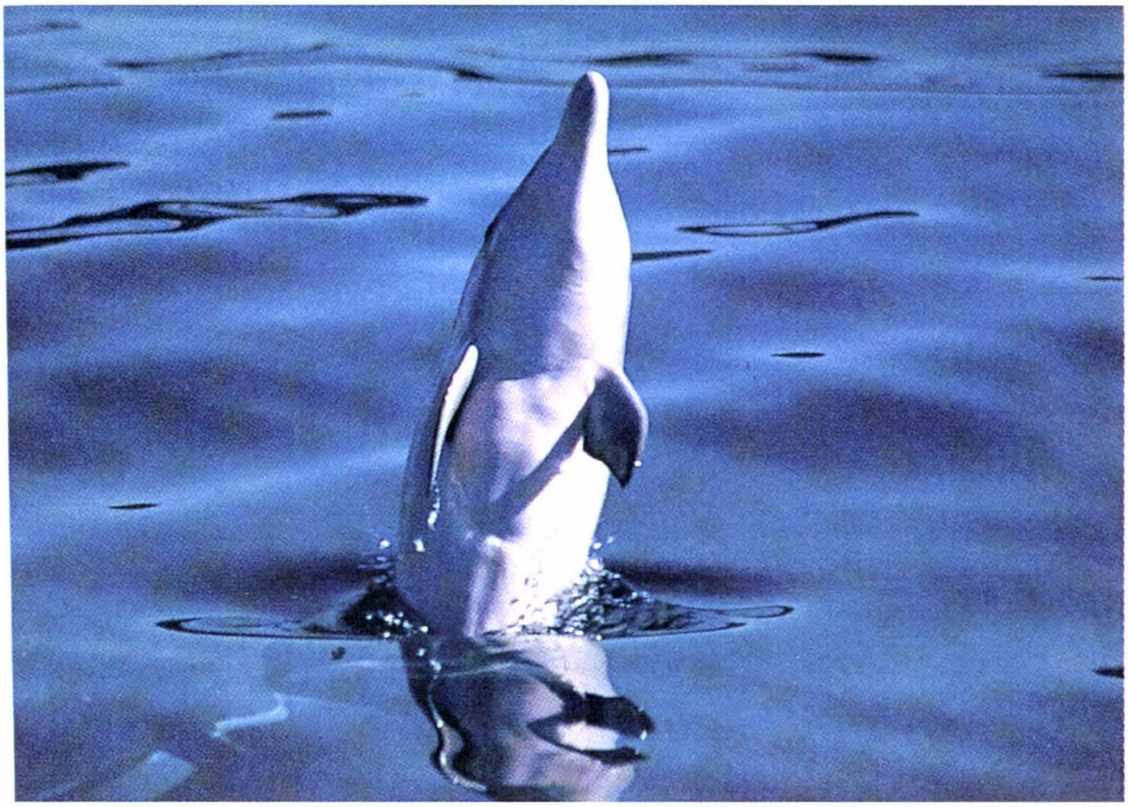

Figure 5.9: Shark bay bottlenose dolphin (*Tursiops truncatus*) calf spy-hops during play (Mann *et al* 2000).

Visual communication is affected by the interactive traits of morphology, colouration and postures (Würsig *et al* 1990) (Figure 10). For visual communication to be useful, water clarity, light level and visual acuity must be sufficient for efficient transfer of messages (Lythgoe 1979). All cetaceans have a functional sense of sight (Würsig *et al* 1990). It is reduced in the plantanistoids, but even the Amazon river dolphin (*Inia geoffrensis*), can see flash patterns of contrasting white and black, and its yellow eye lens (Dawson 1980) is believed to filter out the glare and dazzle of back-scattered light in murky water (Lythgoe 1979; Walls 1967). The Ganges and Indus river dolphins (*Platanista spp*) often are referred to as blind because they have no lens at all (Dawson 1980), nevertheless, their eyes are thought to be capable of light detection and possibly forming crude images, since the eye opening is extremely small and may operate like a pinhole camera (Purves & Pilleri 1973).

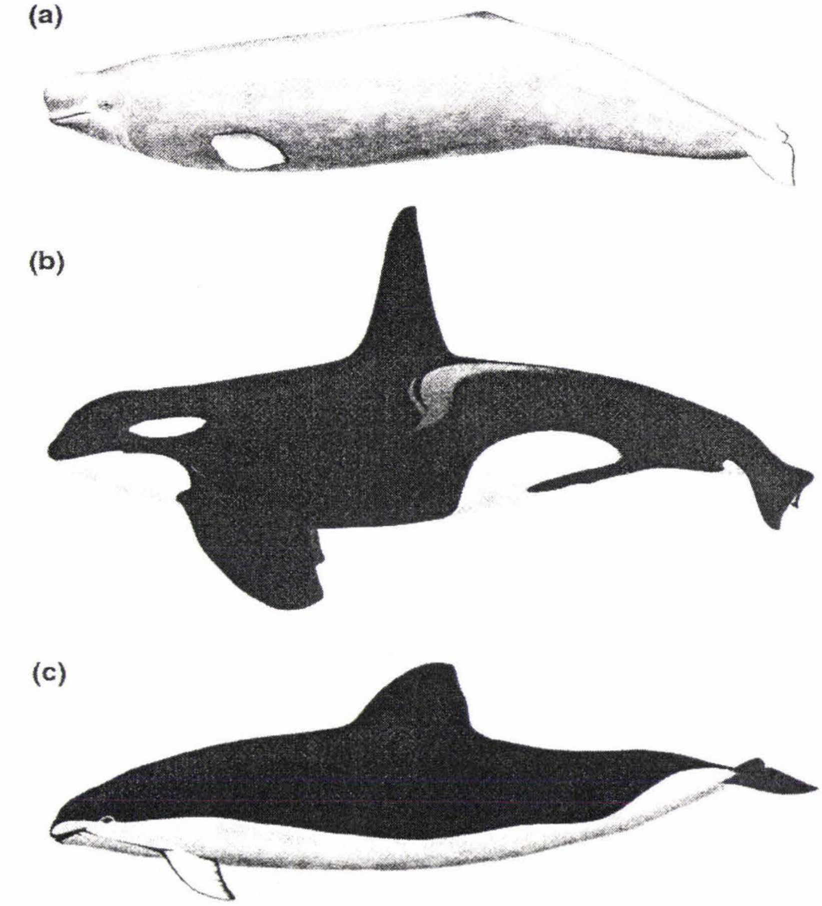

Figure 5.10: Examples of cetacean pigmentation patterns (a) Beluga *Delphinapterus leucas* (b) killer whale *Orcinus orca* (c) Spectacled porpoise *Phocoena dioptrica* (Leatherwood & Reeves 1983)

In some environments sight is probably useful only above the surface and at extremely close range. The Chinese river dolphin, or baiji (*Lipotes vexillifer*), for example, lives in water that is essentially opaque. It often brings its head and eyes out of water when surfacing to breathe, possibly scanning the shoreline, river vessel traffic, and conspecifics while doing so (Würsig *et al* 1990). However, the assumption is that cetaceans living in murky waters use visual communication in a more refined way than those that live in clearer water.

Cetaceans lack some of the underwater sensing mechanisms used by many other vertebrates (Würsig *et al* 1990). Such mechanisms include, sophisticated chemical and electrical sensing systems, and a very sensitive hydrodynamic sense that are common to many fishes and amphibians (Würsig *et al* 1990). Würsig *et al* (1990) made the assumption that without the availability of a wide range of sensory capabilities, cetacean communication by sight would have evolved to its highest degree within the constraints of the environment.

5.7 Summary

The cetacean eye is adapted to see well through two different mediums. This is indicated by both their anatomy and their behaviour, as cetaceans are able to adequately capture prey both underwater and in the air. This indicates that they must have a good blood supply to the eyes and that diseases of the eye would be uncommon, as individuals that developed diseases that affect their vision would be unable to either capture prey or defend themselves against predators. The fundus of the eye is where these blood vessels can be seen, and the vascular pattern is holiangiotic. This indicates that the blood vessels should be able to be visualized using an ophthalmoscope.

5.8 References

Alnelt P. & Kolb H. 2000. *The mammalian photoreceptor mosaic – adaptive design*. Progress in Retinal and Eye research. 19 711-777 *not seen*

Baker C. & Herman L. 1984. *Aggressive behaviour between humpback whales* (Megaptera noveangliae) *wintering in Hawaiian waters*. Canadian Journal of Zoology. 62 1922-1937 *not s*een

Bauer G. 1986. *The behaviour of humpback whales in Hawaii and modifications of behaviour induced by human interventions*. PhD dissertation. University of Hawaii. Honolulu pp 314 *not seen*

Berta A., & Sumich J. 1999. *Marine mammals evolutionary biology*. Academic Press. San Diego.

Burne R. 1952. *Handbook of R.H. Burne's Cetacean Dissections*. London: British Museum *not seen*

Busch & Dűcker. 1987. *Das visuelle Leitungsrermőgen der Seebären* (Arctocephalus pusillus und Arctocephalus australis). Zoologischer Anzeiger. 219 197-224 *not seen*

Caldwell D. & Caldwell M. 1972. The world of the bottlenosed dolphin. Philadelphia Lippincott *not seen*

Chittleborough R. 1953. *Aerial observations on the humpback whale* Megaptera novodosa *(Bonnaterre).* Australian Journal of Marine and Freshwater Research. 4: 219-226 *not seen*

Clarke M. 1970. *Function of the spermaceti organ of the sperm whale.* Nature. 228: 873-874

Clarke M. 1979. *The head of the sperm whale.* Scientific American. 240: 128-141

Crognale M., Levenson D., Ponganis P., Deacon J., & Jacobs G. 1998. *Cone spectral sensitivity in the harbour seal* (Phoca vitulina*) and implications for colour vision.* Canadian Journal of Zoology. 76: 2114-2118

Cummings W., Fish J., & Thompson P. 1971. *Bioacoustics of marine mammals off Argentina.* R/V Herd Cruise 71-3. Antarctic Journal of the United States. 6: 266-268 *not seen*

Dawson W. 1980. *The cetacean eye.* In Herman L. (ed) Cetacean Behaviour. Mechanisms and Functions. John Wiley and Sons. New York NY pp 54-99

Dawson W., Birndorf L., & Perez J. 1972. *Gross Anatomy and Optics of the Dolphin Eye* (Tursiops truncatus). Cetology 10: 1-12

Dawson W., Schroeder& Dawson J. 1987a. *The ocular fundus of two cetaceans.* Marine Mammal Science. 3 (1) 1-13

Dawson W., Schroeder J., & Sharpe S. 1987b. *Corneal surface properties of two marine mammal species.* Marine Mammal Science. 3: 186-197

Dral A. 1972. *Aquatic and aerial vision in the bottlenosed dolphin.* Netherland Journal of Sea Research. 5: 510-513 *not seen*

Dral A. 1977. *On the retinal anatomy of cetacea.* In Harrison R. (ed) Functional Anatomy of Marine Mammals Vol. 3 Academic Press Inc. London pp 81-135

Fobes J. & Smock C. 1981. *Sensory capabilities of marine mammals.* Psychological Bulletin. 89: 288-307 *not seen*

Ford J. & Fisher H. 1983. *Group-specific dialects of killer whales* (Orcinus orca) *in British Columbia.* AAAS Sel Symposium. 76: 129-161 *not seen*

Griebel U. & Schmid A. 1992. *Colour vision in the California sea lion* (Zalophus californianus). Vision Research. 32: 477-482 *not seen*

Herman L., Peacock M., Yunker M., & Madsen C. 1975. *Bottle-nosed dolphin: Double-slit pupil yields equivalent aerial and underwater diurnal acuity.* Science 189: 650-652

Jacobs G. & Deegan J. 1992. *Cone photopigments in nocturnal and diurnal procyonids.* Journal of Comparative Physiology A. 171: 351-358

Jacobs, G.H., Deegan Ii, J.F., Neitz, J., Crognale, M.A. & Neitz, M. 1993. *Photopigments and color vision in the nocturnal monkey.* Aotus. Vision Res, 33: 1773-1783 *not seen.*

Jacobs G., Neitz M. & Neitz J. 1996. *Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate.* Proceedings of the Royal Society of London. Series B. 263: 705-710

Kastelein R., Bakker M., & Dokter T. 1990. The rehabilitation of 3 stranded harbour porpoises (*Phocoena phocoena*). Aquatic Mammals. 15(4)

Kastelein R., Ruud C., Zweypfenning, & Spekreijse H. 1990. *Anatomical and histological characteristics of the eye of a month-old and an adult harbour porpoise* (Phocoena phocoena). In Thomas & Kastelein (eds). Sensory abilities of cetaceans. Plenum Press. New York NY pp 519-536

Kellogg W. & Rice C. 1963. *Visual discrimination in a bottlenose porpoise.* Psychological Record. 13: 483-498 *not seen*

Kellogg W. & Rice C. 1966. *Visual discrimination and problem solving in a bottlenosed dolphin.* Norris K (ed) Whales and Dolphins. University of California Press. Berkeley pp 731-754

Kleinenberg S., Yablokov A., Bel'kovich B., & Tarasevich M. 1964. *Beluga* (Delphinapterus leucas): Investigations of the Species. Jerusalem: Israel Program for Scientific Translations.

Lavigne D. & Ronald K. 1972. *The harp seal* Pagophilus groenlandicus *(Exleben 1777). Spectral sensitivity.* Canadian Journal of Zoology. 50 1197-1206

Leatherwood J. 1977. *Mother-infant interactions of bottlenosed dolphins in captivity and at sea.* In Ridgway S. & Benirschke K. (eds) Breeding Dolphins: Present status suggestions for the future. Washington DC U.S. Marine Mammal Commission Report MMC 76/07 pp 143-167

Leatherwood J., & Reeves R. 1983. *The sierra club handbook of whales and dolphins.* Sierra Club Book. San Franciso

Lythgoe J. 1979. *Vision through scattering media.* In Lythgoe J. (ed) The Ecology of Vision. Clarendon Press Oxford pp 104-147

MacAskie I. 1966. *Unusual example of group behaviour by killer whales* (Orcinus rectipinna). Murrelet. 47 38

Madsen C. 1972. *Visual acuity in marine mammals.* Paper presented at the American Psychological Association meeting Honolulu.

Madsen C. & Herman L. 1980. *Social and Ecological correlates of cetacean vision and visual appearance.* In Herman L. (ed) Cetacean Behaviour. Mechanisms and Functions. John Wiley and Sons. New York NY pp 101-147

Mann J., Connor R., Tyack P., & Whitehead H. 2000. *Cetacean societies: field studies of dolphins and whales.* The University of Chicago Press. Chicago pp 148

Mass A., Supin A., & Severtsov A. 1986. *Topographic distribution of sizes and density of ganglion cells in the retina of a porpoise* Phocoena phocoena. Aquatic Mammals. 12 95-102

Mobley J. & Helweg D. 1990. *Visual ecology and cognition in cetaceans*. In Thomas & Kastelein (eds). Sensory abilities of cetaceans. Plenum Press. New York NY pp 519-536

Myrberg A. 1981. *Sound communication and interception in fishes*. In Tavolga W., Popper A., & Fay R. (eds). Hearing and Sound Communication in Fishes. Springer-Verlag New York pp 365-426

Nachtigall P. 1986. *Vision, audition and chemoreception in dolphins and other marine mammals*. In Schusterman R., Thomas J., & Woods F (eds). Dolphin cognition and behaviour: A comparative approach. Lawrance Erlbaum Associates. Hillsdale NJ pp 79-114

Norris K. 1974. *The porpoise watcher*. Norton New York

Norris K. & Dohl T. 1980. *The behaviour of spinner porpoise* Stenella longirostris *(Schlegel, 1841)*. Fish bulletin. 77 821-849

Norris K. & Harvey G. 1972. *A theory for the function of the spermaceti organ of the sperm whale* (Physeter catodon L.). NASA Special Publication SP – 262 pp 397-417

Norris K., Prescott J., Asa-Dorian P., & Perkins P. 1961. *An experimental demonstration of echolocation in the porpoise,* Tursiops truncatus *(Montagu)*. Biologiae Bulletin 120 163-176

Norris K., Wells R., & Johnson C. 1994. *The visual domain.* In Norris K., Würsig B., Wells R., & Würsig M. (eds) The Hawaiian Spinner Dolphin. University of California Press. Berkeley pp 141-160

Norris K., Würsig B., Wells R., Würsig M., Brownlee S., Johnson C., & Solow J. 1985. *The behaviour of the Hawaiian spinner dolphin,* Stenella longirostris. Southwest Fisheries Center Adminstration Report. LJ-85-06C pp 213

Peichl L., Behrmann G. & Krőger R. 2001. *For whales and seals the ocean is not blue: a visual pigment loss in marine mammals.* European Journal of Neuroscience. Vol 13 (8) 1520-1530

Peichl L. & Moutairou K. 1998. *Absence of short-wavelength sensitive cones in the retinae of seals (Carnivora) and African giant rats (Rodentia).* European Journal of Neuroscience. 10 2586-2594

Peichl L & Pohl B.2000. *Cone types and cone/rod ratios in the crab-eating raccoon and coati (Procyonidae).* Invest. Ophthalmol. Vis. Science 41 S494

Pepper R., Simmons J., Beach F., & Nachtigall P. 1972. *In-air visual acuity of the bottlenose dolphin.* Proceedings of the 9th Annual Conference on Biology Sonar and Diving Mammal. Freemont California.

Prince J. 1956. *Comparative anatomy of the eye.* C. Thomas. Springfield, IL pp 83-97, 252-259

Purves P. & Pilleri G. 1973. *Observations on the ear, nose and throat and eye of* Platanista indi. In Pilleri (ed) Investigations on Cetacea Vol 11. Berne Switzerland Institute of Brain Anatomy University of Berne pp 13-57

Ridgway S. 1972. *Homeostasis in the aquatic environment.* In Ridgway S. (ed) Mammals of the Sea. C. Thomas Springfield IL pp 691

Rodieck R. 1973. *The vertebrate retina.* Freeman San Franciso. California

Scammon C. 1874. *The marine mammals of the northwestern coast of North America.* Putnam New York. (Republished in 1968).

Szel A., Röhlich P., Caffé A., & vanVeen T. 1996. *Distribution of cone photoreceptors in the mammalian retina.* Microscopy Research and Technique. 35 445-462

Schusterman R. 1968. *Experimental laboratory studies of pinniped behaviour.* In Harrison R., Hubbard R., Peterson R., Rice C., & Schusterman R. (eds). The Behaviour and Physiology of Pinnipeds. Apple-Century Crofts. New York pp 87-171

Spong P. & White D. 1971. *Visual acuity and discrimination learning in the dolphin* (Lagenorhynchus obliquidens). Experimental Neurology. 32 431-436

Stone J. 1965. *A quantitative analysis of the distribution of ganglion cells in the cat's retina.* Journal of Comparative Neurology. 124 95-352

Tomlin A. 1967. *Mammals of USSR and adjacent countries.* Vol IX. Cetacea. Jerusalem: Israel Program for Scientific Translations.

Tyack P. 1981. I*nteractions between singing Hawaiian humpback whales and conspecifics nearby.* Behavioural Ecology and Sociobiology. 8 105-116

Tyack P. & Whitehead H. 1983. *Male competition in large groups of wintering humpback whales.* Behaviour. 83 132-154

Walls G. 1942. *The vertebrate eye and its adaptive radiation.* McGraw-Hill. New York

Watkins W. & Wartzok D. 1985. *Sensory biophysics of marine mammals.* Marine Mammal Science. 1(3) 219-260

Wartzok D. & McCormick M. 1978. *Colour discrimination by a Bering Sea spotted seal,* Phoca largha. Vision Research. 18 781-784

White D., Cameron N., Spong P., & Bradford J. 1971. *Visual acuity of the killer whale* Orcinus orca. Experimental Neurology. 32 230-236

Wikler K & Rakic P. 1990. *Distribution of photoreceptor subtypes in the retina of diurnal and nocturnal primates.* Journal of Neuroscience. 10 3390-3401

Wise G., Dollery C., & Henkind P. 1971. *The retinal circulation.* Harper and Row. New York NY pp 20-31

Wood F., Caldwell D., & Caldwell M. 1970. *Behavioural interactions between porpoises and sharks.* In Pilleri (ed) Investigations on Cetacea Vol 11. Berne Switzerland Institute of Brain Anatomy University of Berne pp 264-277

Würsig B., Kieckhefer T., & Jefferson T. 1990. Visual displays for communication in cetaceans. In Thomas J.& Kastelein (eds). Sensory abilities of cetaceans. Plenum Press. New York NY

Würsig B. & Würsig M. 1980. *Behavioural and ecology of dusky porpoises* Lagenorhynchus obscuris *in the South Atlantic.* Fish Bulletin 77 871-890

Yablokov A., Bel'kovich V. & Borisov V. 1972. *Whales and dolphins.* Jerusalem: Israel Program for Scientific Translations.

Young N., Hope G., Dawson W., & Jenkins R. 1988. *The tapetum fibrosum in the eyes of two whales.* Marine Mammal Science. 4 281-290

Chapter Six:

The Retinal Pulse as a method for Determining Death

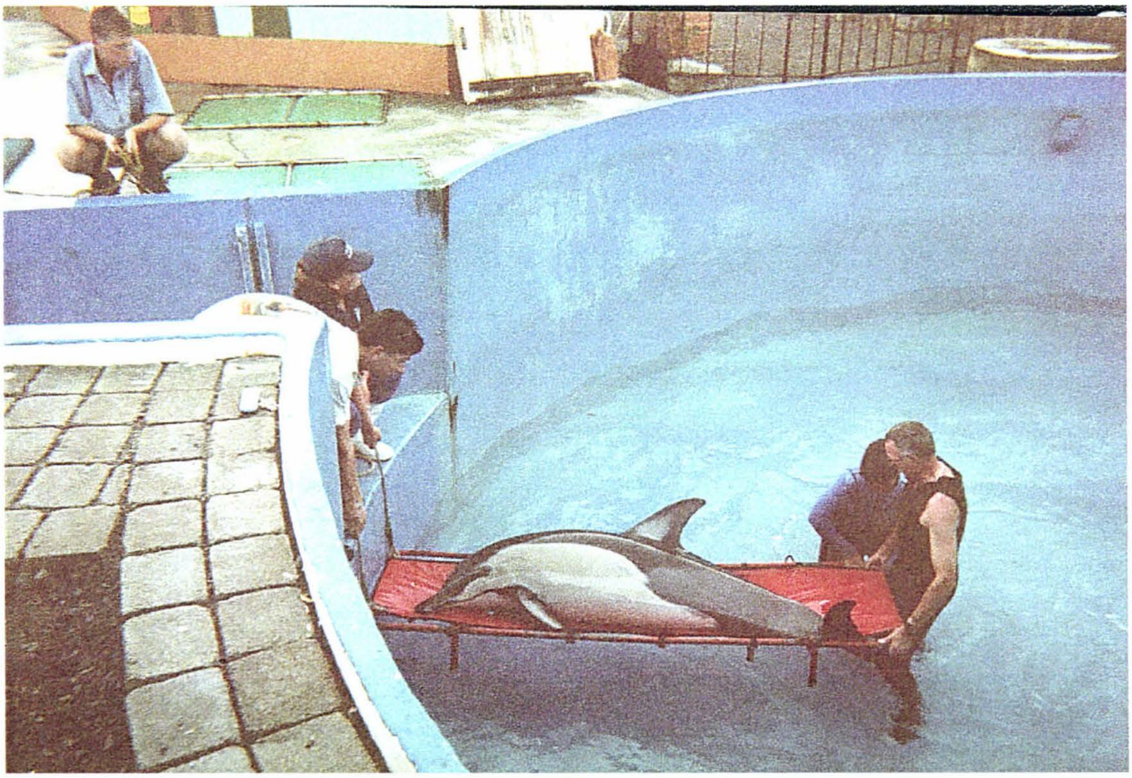

Figure 6.1 A common dolphin (Kelly) at Marineland being lifted from its pool

6.1 Introduction

Death is defined in chapter 3 as the total and irreversible loss of brain function (Younger *et al* 1999). However, in animals other than humans the loss of cardiopulmonary (heart rate and breathing) signals are usually the best indicators of death. In the past it has been difficult to accurately assess these cardiopulmonary signals in cetaceans (especially large cetaceans) and therefore the health of stranded animals, due to a number of physiological and anatomical features that these species possess, including bradycardia, body size, skeleton, blubber and breath holding ability (chapter 3). Therefore a new method that would accurately assess their vital state is needed so that the welfare of these animals can be improved and their survival increased. This chapter provides the observational and experimental basis on which a new method could be implemented, involving measurement of the pulse in the retinal blood vessels in the eye as an indicator of vitality.

6.2 Study Animals and Methods

A number of different mammals were used for the observational and experimental part of the research. They were dogs (*Canis familiaris*), sheep (*Ovis aries*), cattle (*Bos taurus*), New Zealand fur seal, *Arctocephalus forsteri*, California sealion, *Zalophus californianus*, and the common dolphin (*Delphinus delphis*). The animals were all examined using a Welch Allyn (REF 11720) ophthalmoscope) using the direct method where by the fundus was visualized by directly looking through the pupil of the eye.

The cattle were provided by the Massey University Large Animal Teaching Unit (LATU) and were held in pens in a large shed at the facility. The cattle were observed alive with the ophthalmoscope on two occasions (25 January 2002, and 20 March 2002), and were not euthanased after the procedure. The observation of each animal took one minute, and during this time a count was taken of the heart rate and the pulsation of the retinal blood vessels. The heart beat was measured by an assistant listening with a stethoscope and the retinal pulse was measured directly by means of the ophthalmoscope.

The dogs were provided by the Palmerston North City Council Dog Pound and were scheduled for euthanasia between the end of September and the beginning of November 2001. The dogs, ranging from puppies to elderly animals of both sexes, were grouped as Young (dogs two years or under) or Old (dogs over two years of age). Dogs in the latter category were usually nine years of age, or older.

Euthanasia of these animals required three separate injections by a veterinarian. The first was a sedative, and the second by an anaesthetic (magnesium sulphate), which was followed by a lethal dose of sodium pentobarbitol. The dogs were observed from the end of the last injection until the heart stopped beating and the pulses in the retinal blood vessels ceased. The observations were made with two stop watches timed from the same start point; one recorded the cessation of heart beating which was timed by listening with a stethoscope, while the other recorded the cessation of the pulsations in the retinal blood vessels by watching through the ophthalmoscope. The measurements of the heart where done by an assistant

The sheep were measured between July and September 2001 in a Veterinary Physiology teaching laboratory at Massey University where, at the conclusion of the laboratory work the animals were euthananased with magnesium sulphate. The sheep were therefore under anaesthetic throughout the whole procedure of measuring the cessation of the retinal pulse and never regained consciousness.

Marineland of New Zealand in Napier, and Auckland Zoological Park provided the pinnipeds. The pinnipeds at Marineland were an eleven year old male New Zealand Fur seal (Figure 6.2) and a six year old male Californian sealion. The animals at Marineland were observed live on 27 August 2001 at approximately 1600 hours when light intensity was still high.

Figure 6.2 Looking into the eyes of an adult male New Zealand fur seal (Angel) using an ophthalmoscope and showing the light shield

The pinniped at Auckland was a mature male Californian sea lion (Figure 6.3). The sea lion was observed live on 16 December 2001 and again on 22 March 2002. Both these days were overcast, so although the animal was observed at midday, ambient light levels were low. All the pinnipeds were observed to see if pulsations in the retinal blood vessels were visible. No further investigations were possible because the animals were wild, and safety protocols did not allow the heart rate and retinal pulse rate to be measured simultaneously. In general the pinnipeds were not used to the procedure, so they tended to move around and close their eyes.

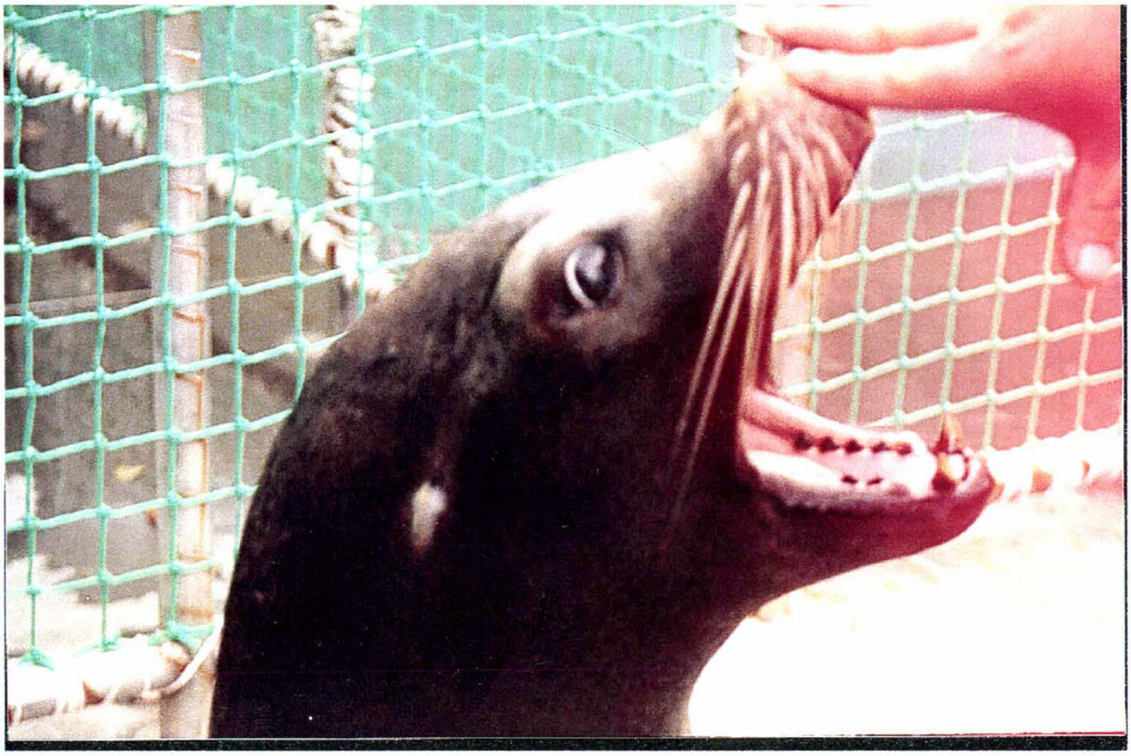

Figure 6.3 An adult male Californian sea lion (Skuttles) at Auckland Zoo

Marineland of New Zealand in Napier provided two common dolphins that had been at the facility since December 1974. Both female, the dolphins were aged 31 (Kelly) and 33 (Shona) years respectively, which is approximately fifteen years past the usual lifespan of 15-18 years for this species. Because of their advanced age minimizing stress to the animals was, therefore, very important. The animals were examined live on two separate occasions, 28 May 2001 and 27 August 2001, about 1700 hours after the park had closed and ambient light levels were low.

First the animals were coaxed into a small holding pool (Figure 6.1) and the water was gradually removed until approximately knee deep. The handlers corralled one dolphin at a time into a sling that was then lifted out of the water. The sling was designed to fully support the animal while out of the water. The animal was placed on the side of the pool but was tilted slightly off the ground, so that the head was lower than the tail and they would keep their eyes open. The dolphins remained fully supported throughout the procedure. Both dolphins were examined with an ophthalmoscope to see if pulsations could be observed in the retinal blood vessels (Figures 6.4 & 6.5).

Figure 6.4 Looking into the eye of a common dolphin (Kelly) at Marineland using an ophthalmoscope

Figure 6.5 Tilting of the dolphin during the procedure to observe a retinal pulse.

One field problem was that under full light intensity i.e. direct sunlight, the blood vessels in the fundus were not easily visualized, but this was overcome by the use of a shield (Figure 6.2) that prevented excess light from entering both the observer's eye, and the eye of the animal being observed. The shield was made from flexible plastic and cardboard and was worn over the eyes of the observer. The ophthalmoscope fitted into the shield that did not touch the animal. The shield was used only at Marineland to observe pinniped eyes, as this was the only time when the animals were in direct sunlight. All other observations were either indoors under artificial light, or under low light conditions outdoors.

6.3 Results

6.3.1 Domestic Cattle

Measurements of the retinal pulse rate and the heart rate were taken from 16 individuals (Table 6.1). The eyes were relatively clear so the retinal blood vessels were observable and the retinal pulse could be identified. However, the animals were observed without anaesthetic so they were slightly restless and were not as still as animals observed under anaesthetic. This meant that the retinal pulse was not easily observed because the animals tended to move around at critical moments.

The measurements of the frequency of the retinal pulse rate and heart rate showed little variation within individuals and in one animal no variation at all. The average for the heart rate was 69.13 beats/min with a standard error of 1.73 and the average for the retinal pulse rate was 66.63 beats/min with a standard error of 1.70. The standard errors for the data set overlap, which indicates that they are not significantly different. A mean between the two measurements was recorded which ranged from 53.5 to 74.5 beats/min with a mean of 55.72. The difference between the retinal pulse rate and the heart rate, ranged from –2 to +7 with a mean of 2.38. These results indicate that there is a very close relationship between the two measurements and that the difference between them is not significant. This is represented graphically in Figure 6.6. The relationship is also shown as a regression analysis (Figure 6.7). The R squared value (0.827) shows there is a significant, direct relationship between the two values, i.e. if the heart rate is slow then the retinal pulse rate will also be slow and if the heart rate is fast so will be the retinal pulse rate.

Table 6.1: Mean of the retinal pulse rate (beats/min) and the heart rate (beats/min) in live cattle (*Bos taurus*), and the difference between these measures.

Heart Rate (beats/min)	Retinal Pulse (beats/min)	Mean	Difference
68	63	65.5	5
68	70	69	-2
57	56	56.5	1
79	70	74.5	9
70	70	70	0
80	78	79	2
75	74	74.5	1
62	55	58.5	7
70	68	69	2
71	69	70	2
70	68	69	2
68	65	66.5	3
72	70	71	2
68	69	68.5	-1
74	68	71	6
54	53	53.5	1
Mean 69.13 ± 1.73	Mean 66.63 ± 1.70	Mean 67.88 ± 1.68	Mean 2.5 ± 0.73

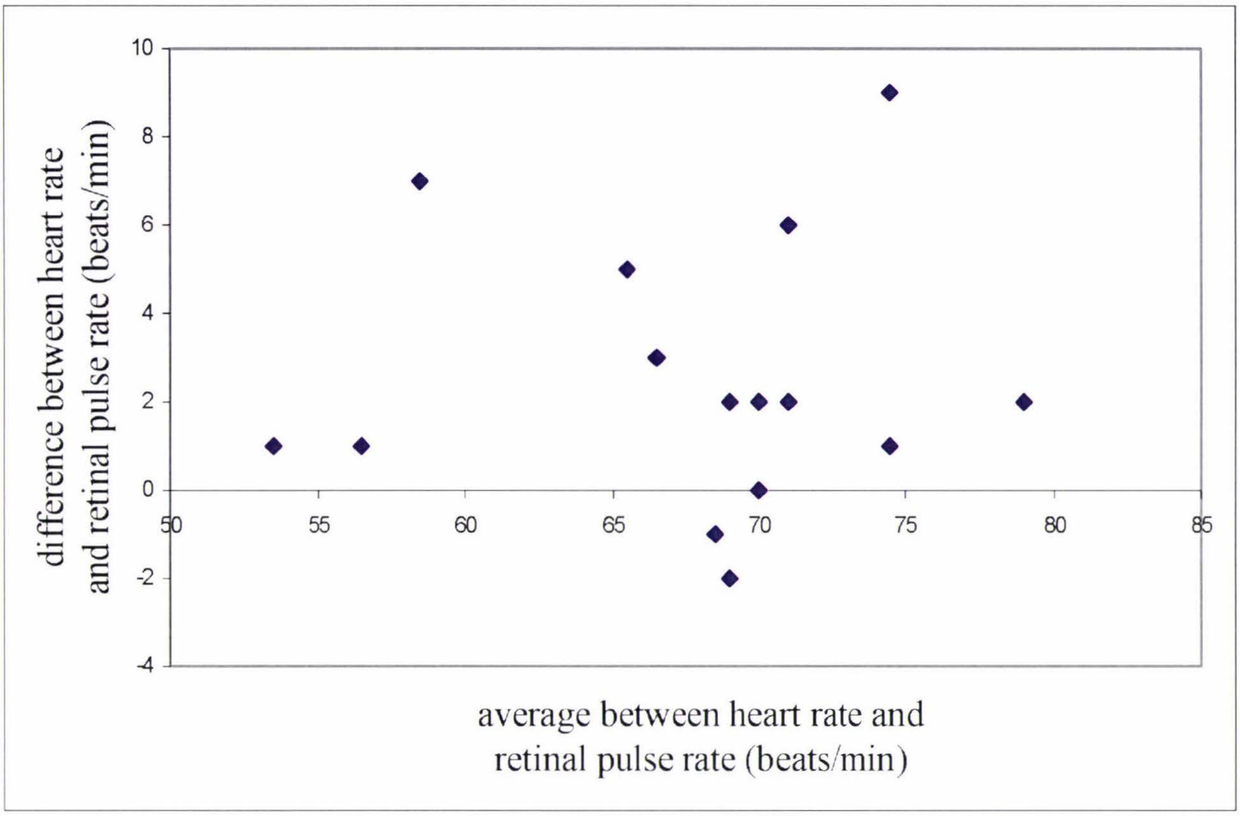

Figure 6.6: Relationship of the difference between retinal pulse rate and heart rate and the mean of these two measures.

In Figure 6.7 the regression line shows that there is a strong relationship between the retinal pulse rate and heart rate and that they are essentially the same measurement and therefore the retinal pulse rate can be substituted for the heart rate when the heart rate is unknown.

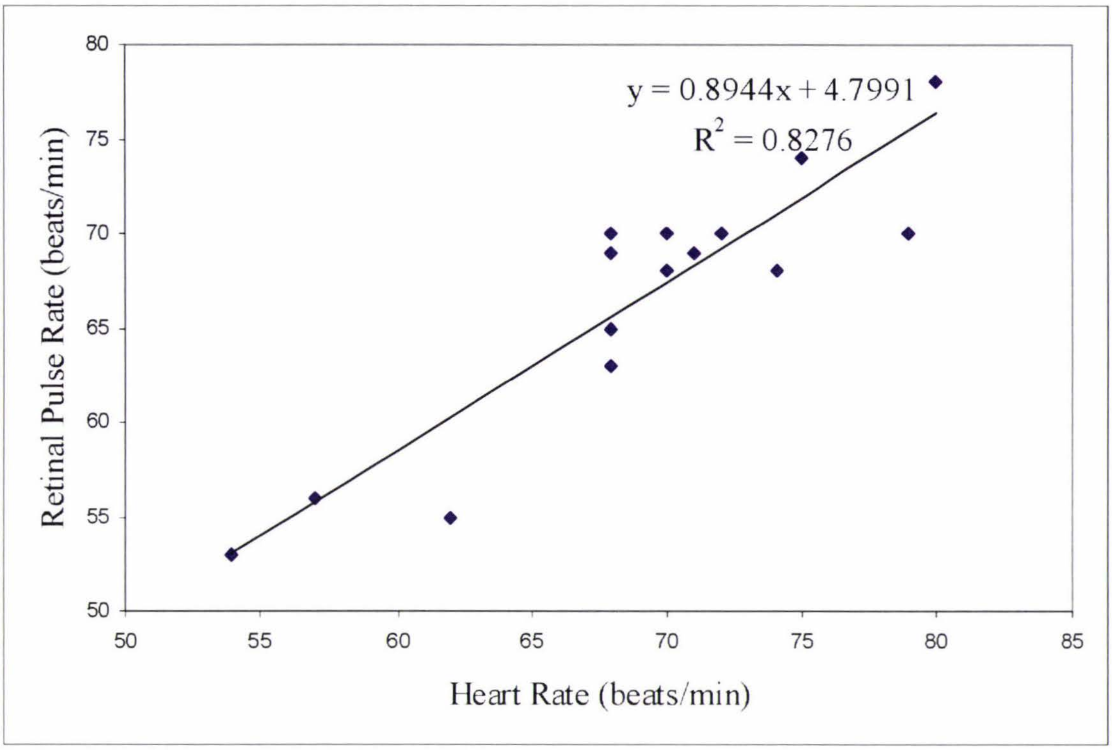

Figure 6.7: Relationship between retinal pulse rate and heart rate in cattle using a regression line

	df	SS	MS	F	Significance F
Regression	1	5.95.6365	595.6365	67.1878	0.000
Residual	14	124.1135	8.8653		
Total	15	719.7500			

The ANOVA for these data show that the regression is significant at a 95% level. This means that there is a strong relationship between the two measurements and that they are measuring the same phenomenon (cardiac activity). There is no significant variation between the two measurements.

The results were then used to investigate whether the retinal pulse rate can accurately predict the heart rate of an individual where the heart rate is unknown and can not be measured directly. Figure 6.8 shows that most of the values range from +3 to –3 with two values outside this range. This indicates that the retinal pulse can be accurately used to assess the heart rate when the heart rate is unknown.

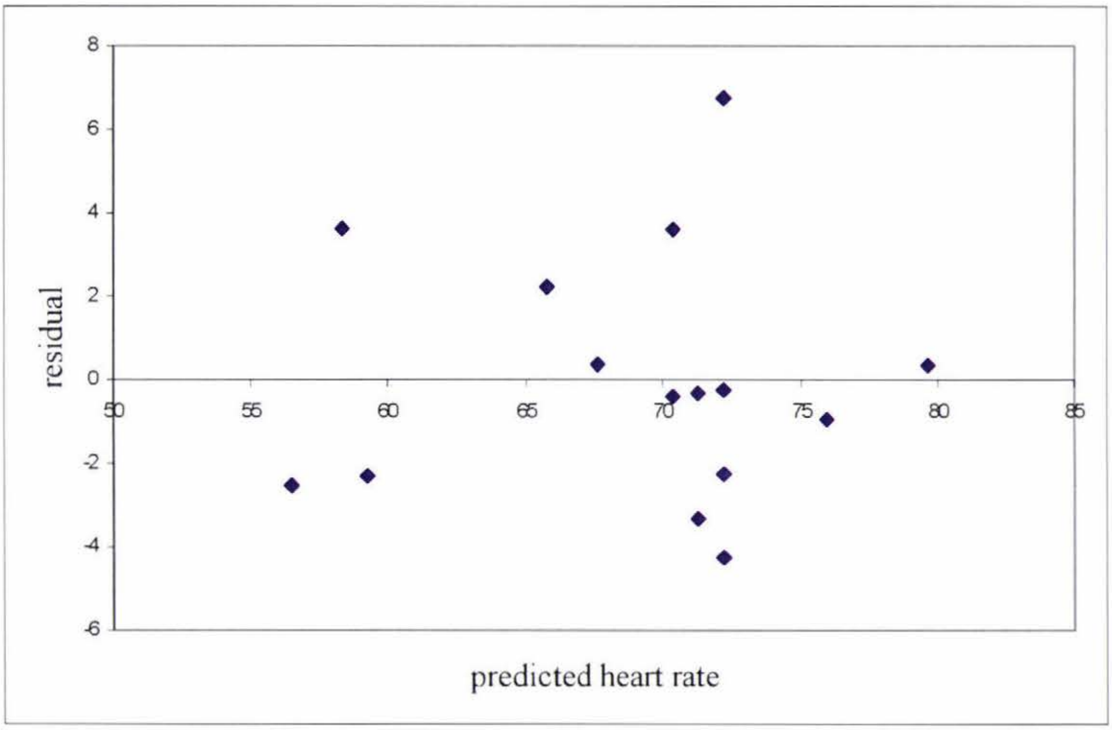

Figure 6.8: The predicted heart rate of cattle using the retinal pulse rate

6.3.2 Domestic Dogs

Measurements were taken from 27 dogs after they were euthanased (Table 6.2). This involved recording the time of cessation of the heart beat and the time of cessation of the retinal pulse suing the end of the last injection as the start point of both measurements. The time of cessation of the heart beat ranged from 1.01 minutes to 7.35 with a mean of 1.78 minutes. The time of cessation of the retinal pulse ranged from 1.01 to 7.54 with a mean of 2.36. The difference between the two mean was 58 seconds, and all the measurements, except one, show that there is a difference between the two measurements. This indicates that there is an apparent lag between the time the heart stops beating and the time the retinal pulse stops beating. The eyes of the dog were very clear in comparison with other species and in one case the individual blood corpuscles could be seen moving along the retinal blood vessels. As the dogs were under anesthetic there was no eye movement, which made measurement of the retinal blood vessels less difficult than in those animals observed or measured without anesthesia.

Table 6.2 Table showing the time of cessation of the heart beat and the time of cessation of the retinal pulse in 27 dogs (*Canis familiaris*)

Time of Cessation of the heart beat (mins)	Time of Cessation of the retinal pulse (mins)
1.18	1.31
1.19	1.32
1.24	1.41
1.25	1.34

1.07	1.13
1.12	1.22
1.17	1.38
1.27	1.32
1.59	2.05
1.45	2.06
1.03	1.1
1.26	1.26
1.26	1.36
1.33	1.45
1.49	1.52
1.49	1.53
1.59	2.08
2.21	2.32
2.38	2.49
1.04	1.22
1.01	1.01
1.1	1.13
3.56	4.21
4.49	4.59
1.51	7.23
1.48	7.31
7.23	7.54
Mean 1.78 minutes	Mean 2.36 minutes

The data for the measurements recorded from the dogs (Figure 6.9) were strongly influenced by three outliers. This graph also indicates a positive relationship between the retinal pulse and the heart beat and that the retinal pulse is dependent on the heart beating

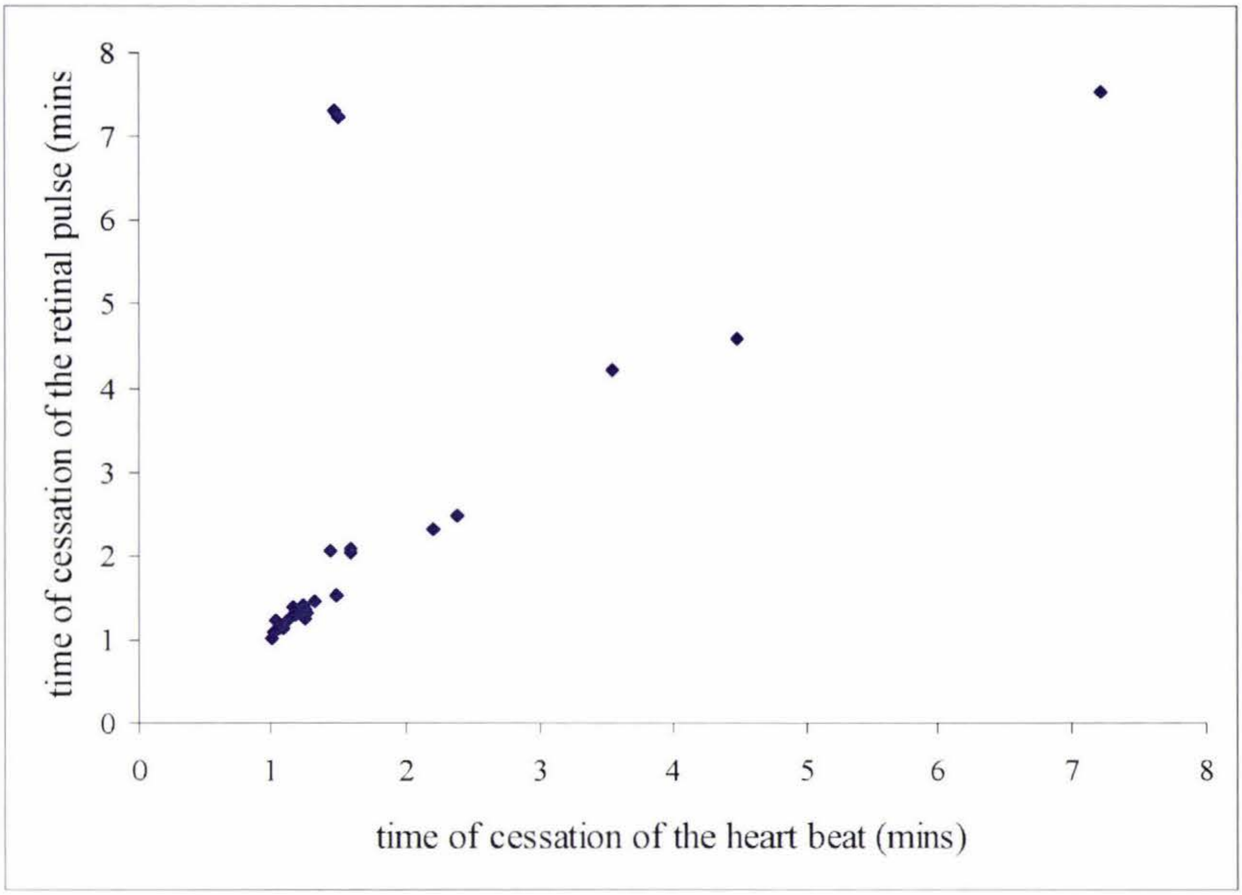

Figure 6.9: Time to death in dogs (*Canis familiaris*) showing the relationship between the retinal pulse rate and heart rate

Figure 6.10 does not include the outlying results for three individuals which are considered to be atypical. In two individuals the heart beat apparently stopped a relatively long time before the retinal pulse, probably because of recording errors, and in the third the individual took a relatively long time to die following problems with the anaesthetic.

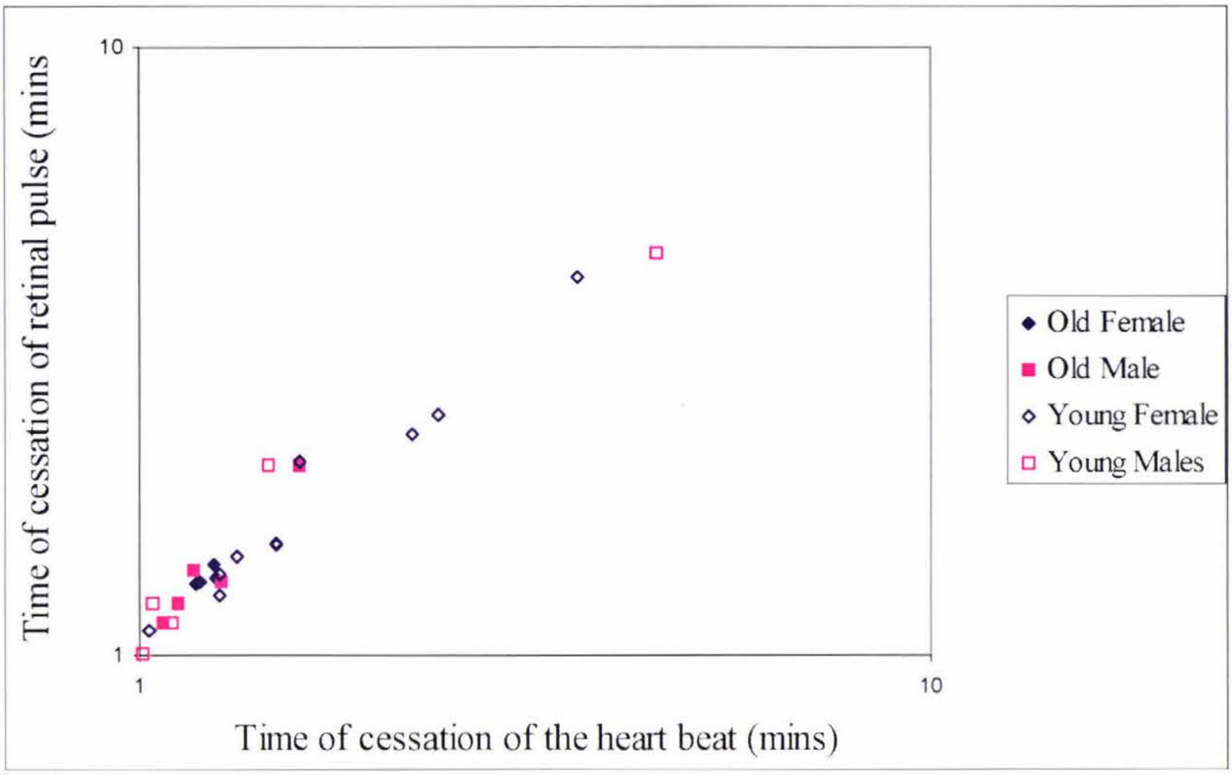

Figure 6.10: Relationship between retinal pulse and heart beat in the times to death in dogs (*Canis familiaris*)

A Scatter plot of the whole data set (Figure 6.11) shows the data not uniformly scattered around the axis, instead they were bunched, indicating that the data were strongly affected by the outliers. In the second scatter plot (Figure 6.12) where the outliers were not included, the data were evenly distributed around the axis. This indicates that the outliers had a large effect on the data set, which became more uniform when they were removed.

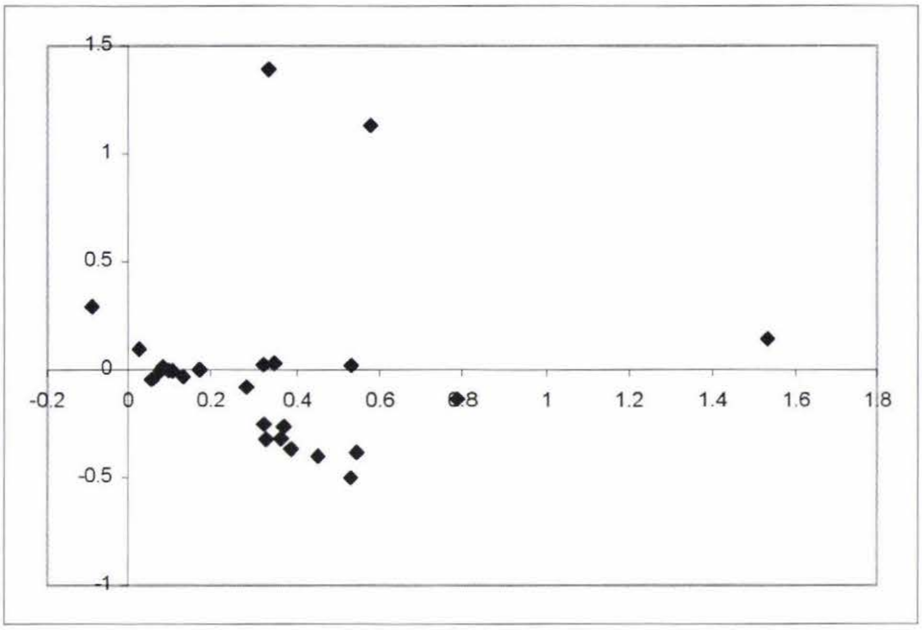

Figure 6.11: Scatter graph of the entire data set

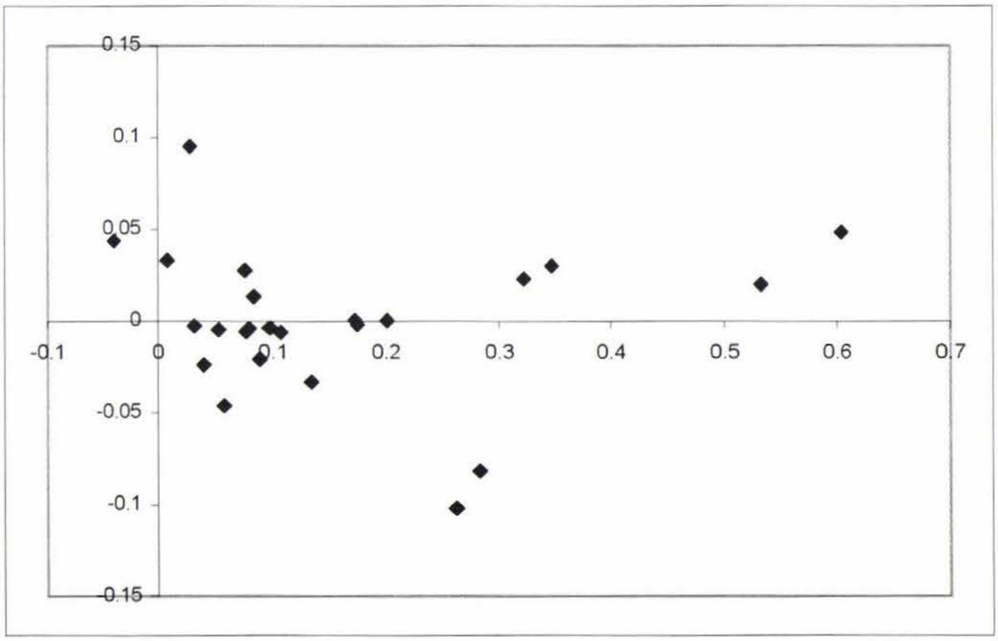

Figure 6.12: Scatter graph for the data set excluding the three outliers (see Figure 6.9 and accompanying text).

Because the data were non-parametric in distribution a Spearman rank correlation was carried out to see if there was a relationship between the retinal pulse rate and heart rate. The Spearman rank correlation was 0.5338, which is a significant at a 95% level and this indicates that there is a relationship between the retinal pulse rate and heart rate at the 95% confidence level. Spearman rank correlations were also carried out on the data for each individual category to see if there was any effect attributable to sex or age. Only the young female category result was significant (S.R.C.= 0.9207) and showed a relationship between the two measurements. The results therefore indicate that there is a significant relationship between the retinal pulse rate and heart rate over the whole sample of dogs, and a significant relationship for these measures in the young female category. This is a somewhat suprising result and probably reflects the small sample size of the other age/sex categories, rather than the likelihood that there was no underlying relationship between the two measurements in these categories.

Category	**Spearman rank correlation**
Young female	0.9207
Young male	0.4286
Old female	0.8
Old male	0.0857

6.3.3 Sheep

Measurements of the retinal pulse were taken in 18 individuals (Table 6.3) undergoing euthanasia to determine whether it could be accurately monitored in the animals. The eyes of the test sheep were clear and the retinal pulse could be seen clearly as the animals succumbed to euthanasia. Initially the retinal pulse was steady, but as the animals entered the final stages of life their eyes became blurred and unclear. In some cases the eyes rolled at the point of death. However, it was possible to calculate time of death using the retinal pulse.

Table 6.3: Observational data of the time of cessation of the retinal pulse in the sheep

Sheep Number	Time of cessation of the retinal pulse (mins)
1	6.17
2	6.14
3	6.39
4	6.54
5	6.46
6	7.69
7	6.64
8	6.71
9	6.17
10	7.73
11	6.28
12	6.32
13	7.67
14	6.68
15	6.13
16	6.19
17	6.17
18	6.12
	Mean 6.57

6.3.4 Seals and sea lions

The retinal pulse could be observed in the retinal blood vessels of both the seal and the sea lions, but pinniped eyes were not as clear as those in the cattle, sheep and dogs. In addition the retinal blood vessels were slightly blurred and more ill-defined then those in the cattle, sheep and dogs. However rhythmical movement was observed in the blood vessels and this was almost certainly the retinal pulse. Also the seal and sea lions observed were not under anaesthetic so they could move around relatively freely, accordingly the eyes were not as still as in those animals that were not conscious.

6.3.5 Dolphins

The animals were observed to see if the retinal pulse was observable in the retinal blood vessels. Like the pinnipeds the eyes in the two dolphins were not as clear as those in cattle, sheep and dogs and the definition of the vessels was about the same as that observed in the seal and sea lion eyes. The retinal pulse was, however, observable as rhythmical movement of the retinal blood vessels. This indicates that the retinal pulse is observable in the common dolphin and should be able to be seen in other cetacean species.

6.4 Discussion

The results indicate that there is a strong relationship between the heart rate and the retinal pulse rate and that the retinal pulse is dependent on the heart beat. The strength of this relationship, shown firstly in the cattle, is an expected result. As the cardiovascular system is connected, the pulse seen in the blood vessels must have originated from the heart. The results from the work done on cattle indicates that it is possible to use the retinal pulse rate to predict the heart rate. This indicates that in animals where the activity of the heart can not be determined the retinal pulse can be used as a substitute.

Heart rate and retinal pulse rate are measured in quite different ways, the former are taken with a stethoscope and recorded by listening, while the latter is taken with an ophthalmoscope and recorded visually. They are, however, measuring the same phenomenon, namely the circulation of blood around the body. The ophthalmoscope is more difficult to use than the stethoscope because it requires skill to identify the pulsations and it is relatively easier to make mistakes in recording. Therefore some of the difference between the two measures can probably be attributed to recording difficulties, including coping with the movement of the animals.

The results from the practical work on dogs reinforces the relationship between heart rate and retinal pulse rate. It also establishes that it is possible to establish time of death using the pulsations in the retinal blood vessels in dogs. The results show that there is a lag between the apparent cessation of the heart beat and cessation of the retinal pulse. This should be expected because it takes time for the blood to reach the retinal blood vessels from the heart, therefore it will also take time for the pulsations to cease in the retinal blood vessels after the heart has appeared to cease beating. As the heart beat may become so faint that it is unable to be picked up but has not actually stopped, however, in the situation with the dogs they did not recover.

Because dogs and dolphins are both eutherians they share some ancestral lineage (Kemp 1982, Savage & Long 1986), and as a part of this they both have closed, complex, circulatory systems (Kemp 1982). But dogs are terrestrial mammals adapted to land life with none of the adaptations possessed by entirely aquatic mammals, like dolphins, and this is reflected in their circulatory system. For instance dogs are carnivores and do not possess any of the rete mirabile that are a major feature of the cetacean circulation (Evans & Christensen 1979), and it has been suggested by Mc Farland *et al* (1979) that these rete mirabile would cause the pulsations in the retinal blood vessels to disappear, due to the effect of damping. Also vision of dogs is that of a terrestrial mammal since it has no adaptation for sight through more than one medium. Therefore the fundus of the eye is a lot clearer than that seen in the more aquatic mammals (seals, sea lions and dolphins). However, the retinal pulse is still visible in the aquatic mammals and was recorded successfully.

There are obvious differences between cetaceans and dogs and of the mammals investigated these two groups have the least in common in terms of lifestyle and evolutionary lineage. They are, however, used here as a benchmark against which all others can be compared. Pabst *et al* (1999) characterize dogs as the 'typical' mammal and use them describe the morphological specialisations which marine mammals possess that make them different from the 'typical' mammal. Carnivora possess a circulatory system which is complex, but possesses none of the complexity of the circulation in cetaceans (Evans & Christensen 1979, McFarland *et al* 1979). Therefore it is easier to do the initial testing of the procedure on them. Moreover, dogs are in ready supply.

The observational data obtained from the sheep, seals, sea lions and dolphins confirm that a retinal pulse can be seen in the eyes of these animals. The observational data from the sheep confirms that death can be established using only the retinal pulse. The observational data from the seals, sea lions and dolphins confirms that a retinal pulse can be seen and that the procedure can most likely be used to determine death.

The difficulty experienced with terrestrial mammals moving their heads around while under observation, will probably be minimized in cetacean species, because nearly all cetacean species have no noticeable neck and cannot move their head around very easily (Würsig *et al* 1990). This, therefore, limits the amount of movement experienced when looking into the animal's eyes, compared with looking in the eyes of a terrestrial mammal. A significant difficulty with cetaceans is the lack of eyelids which makes it relatively harder to induce the animals open their eyes. In the other mammals looked at, closed eyes could be easily reopened by touching the eyelids, and physically moving the eyelids apart. With dolphins, however, this is impossible because they have no eyelids and shut their eyes by squeezing together the skin surrounding the eyes. In the present study this was compensated for by tilting the dolphin, head down, which induced the animal to open its eyes. At a stranding this would be difficult, but individuals that were in a bad state of health would possibly be less inclined to keep their eyes closed.

The practical work carried out here was aimed at establishing a method for determining death in cetacean species, using dogs as a benchmark. The observations indicate that in dogs the retinal pulse rate can be used in place of measuring the heart rate to determine cessation of heart activity.

6.5 References

Evans H & Christensen G. 1979. *Miller's anatomy of the dog.* Saunders Philadelphia

Kemp T. 1982. *Mammal-like reptiles and the origin of mammals.* Academic Press. London

McFarland W., Jacobs M., & Morgane P. 1979. *Blood supply to the brain of the dolphin* Tursiops truncatus, *with comparative observations on special aspects of the cerebrovascular supply of other vertebrates.* Neuroscience and Biobehavioural Review 3 (Suppl 1): 1-93

Pabst D., Rommel S., & McLellan 1999. *The functional morphology of marine mammals.* In Reynolds J. & Rommel S. (eds) Biology of Marine Mammals. Smithsonian Institution Press. Washington pp 15-72

Savage R. & Savage M. 1986. *Mammal evolution – an illustrated guide.* British Museum (Natural History). London

Würsig B., Kieckhefer T., & Jefferson T. 1990. *Visual displays for communication in cetaceans.* In Thomas J.& Kastelein (eds). Sensory abilities of cetaceans. Plenum Press. New York NY

Youngner S., Arnold R., & Schapiro R. 1999. *The definition of death.* John Hopkins University Press. London & Baltimore

General Discussion

The aim of this study was to investigate and evaluate the use of the pulsations of the retinal blood vessels as an indicator overall vitality in odontocetes. Initially, the testing of the procedure was to be carried out at mass strandings where there would be individuals in various stages of declining health. However, this was not possible because there were no suitable strandings during the study. Therefore an alternative to test for the technique and this was found in terrestrial mammals (cattle, dogs and sheep). Supplementary observations were made on captive seals, sea lions, and dolphins.

Cattle, sheep, and dogs were chosen as subjects because of their accessibility and supply. The results using these mammals indicated that there was a strong relationship between the pulsations seen in the retinal blood vessels and the heart beat. The heart beat is a significant measure for determining vitality in mammals and, for mammals other than humans, loss of the heart beat is usually indicative of inevitable death. Therefore establishing that these two measures are closely related is important in evaluating the retinal pulse as an indicator of inevitable death. The strong relationship indicated in the results was expected because the cardiovascular system in mammals is connected, and pulses occurring throughout the body must have originated at the heart.

The arterial blood supply in mammals (such as pinnipeds and cetaceans) is highly variable (Ask-Upmark 1935, 1953) especially when comparisons are made between terrestrial species and those adapted to a more aquatic lifestyle. Suprisingly, however, pinnipeds have an arterial blood supply system which more closely resembles that of terrestrial mammals than cetaceans (DuBoulay & Verity, Dormer *et al* 1977, King 1977, McFarland *et al* 1979). The main reason for this is that cetaceans have a series of rete mirabile that increase the complexity of their cardiovascular system (McFarland *et al* 1979) and compared with the 'typical' cardiovascular system seen in most mammals. However, artiodactyls (cattle and sheep) also have rete in their cardiovascular system, although not as many as cetaceans (DeVriese 1905, DuBoulay & Verity 1973), and these animals were used in the initial testing of this procedure, and the retinal pulse was clearly seen in them. There was more difficulty in visualising the retinal pulse in the aquatic pinnipeds and dolphins. This is probably because in both groups vision is adapted to both air and water.

Dogs were chosen as a benchmark because of their availability and they have been characterised as the 'typical' mammal by other authors (Pabst *et al* 1999). Tests with euthanased dogs established clearly that the time of cessation of the heart beat and the retinal pulse could be used to pinpoint death. Even though dogs are carnivores and do not have any rete mirabile in their cardiovascular system (Evans & Christensen 1979), they are still valuable to use for this research as a benchmark to which all other mammals can be compared. McFarland *et al* (1979) suggested that the presence of a rete would cause the disappearance of pulsations in blood vessels that came after the rete in blood vascular system. But retinal pulses were detected in all the species (cattle, sheep, dolphins) that have rete mirabile. Therefore retinal pulses were detected in animals with and without (dogs) rete mirabile.

Future studies should focus on testing the procedure on cetaceans, particularly mass stranded odontocetes. Possibly future studies should be done over a longer time and be based in closer proximity to likely stranding sites, although that is hard to predict. Additionally, further research should be carried out to show that the technique can be used to establish death in a wide variety of mammals.

References

Ask-Upmark E. 1935. *The carotid sinus and the cerebral circulation.* Acta physiat neurol Supplement 5-7: 1-374 *not seen*

Ask-Upmark E. 1953. *On the entrance of the carotid artery into the cranial cavity in* Stenops gracilis. Acta anatomica. 19: 101-103 *not seen*

Dawson W., Schroeder& Dawson J. 1987. *The ocular fundus of two cetaceans.* Marine Mammal Science. 3 (1) 1-13

Devriese B. 1905. *Sur la signification morphologiques des artères cérébales.* Arch de Biol (Liege) 21: 359-457 *not seen*

Dormer K., Denn M., & Stone H. 1977. *Cerebral blood flow in the sea lion* (Zalophus californianus) *during voluntary dives.* Comparative Biochemistry and Physiology A 58: 11-18

DuBoulay G & Verity P. 1973. *The cranial arteries of mammals.* William Heinemann Medical books Ltd. London pp 1-295

Evans H & Christensen G. 1979. *Miller's anatomy of the dog*. Saunders Philadelphia

King J. 1977. *Comparative anatomy of the major blood vessels of sea lions* Neophoca *and* Phocarctos*; with comments on the differences between the* otariid *and* phocid *vascular systems*. Journal of Zoology (London) 181: 69-94

McFarland W., Jacobs M., & Morgane P. 1979. *Blood supply to the brain of the dolphin* Tursiops truncatus*, with comparative observations on special aspects of the cerebrovascular supply of other vertebrates*. Neuroscience and Biobehavioural Review 3 (Suppl 1): 1-93

Madsen C. & Herman L. 1980. *Social and Ecological correlates of cetacean vision and visual appearance*. In Herman L. (ed) Cetacean Behaviour. Mechanisms and Functions. John Wiley and Sons. New York NY pp 101-147

Nachtigall P. 1986. *Vision, audition and chemoreception in dolphins and other marine mammals*. In Schusterman R., Thomas J., & Woods F (eds). Dolphin cognition and behaviour: A comparative approach. Lawrance Erlbaum Associates. Hillsdale NJ pp 79-114

Pabst D., Rommel S., & McLellan 1999. *The functional morphology of marine mammals*. In Reynolds J. & Rommel S. (eds) Biology of Marine Mammals. Smithsonian Institution Press. Washington pp 15-72