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# Historical Perspectives

Melba M. Kooyman and Gerald L. Kooyman

## Melba M. Kooyman

Melba Kooyman has traveled to Antarctica on two occasions and has been an enthusiastic supporter of Jerry's work in field biology over the 47 years of their married life together. While they were living in London in the 1960s, she developed an interest in the history of Antarctic science and exploration under the tutelage of Professor Richard Harrison, FRS, who was Jerry's advisor at the London Hospital Medical College. He arranged special privileges for inquiry and study at the British Museum and the Natural History Museum for both Jerry and Melba during their year-long stay. They maintained a close association with Professor Harrison after he became Chairman of the Anatomy Department at Cambridge University, and spent a summer there while Jerry was a visiting professor at Downing College. Regarding her formal education, she graduated from the University of Utah, *magna cum laude*, and later received a Master of Science degree from the University of California, San Francisco in the field of Nursing Education. While on the faculty of the College of Nursing at the University of Arizona in Tucson, she was a lecturer and clinical instructor from 1962 to 1966. After the family moved to the San Diego area, she became an associate professor at Palomar College, a community college with more than 25,000 students and eight satellite campuses. In 1979, she was named College Teacher of the Year by the Escondido Chamber of Commerce. A few years later, she received the Distinguished Faculty Award, an honor generated by students and affirmed by faculty at Palomar College. The Kooymans are parents of two sons, Carsten and Tory, both of whom have spent extensive time in field camps with their father from the time they were children. Both have had the opportunity to work with Jerry in Antarctica on more than five expeditions as well as in other places, including the Pribilof Islands, Australia, and the Galapagos Islands. The excitement of field biology has been a cornerstone of our family life together.

## Gerald L. Kooyman

Jerry Kooyman holds an AB in Zoology from UCLA, and a Ph.D. in Zoology from the University of Arizona. He is a research professor and professor emeritus at Scripps Institution of Oceanography. He has been at Scripps since 1967 where he came after finishing a one-year National Science Foundation post-doctoral fellowship at the London Hospital Medical School under Sir Richard Harrison, FRS. He held a one-year fellowship under Robert Elsner before becoming a research physiologist in the Physiological Research Laboratory, Scripps Institution of Oceanography. At that time, it was under the directorship of Professor Per F. Scholander.

Kooyman has participated in over 45 expeditions to the Antarctic, for most of which he was the principal investigator and leader of the projects, which have ranged from the diving physiology of Weddell seals to the population trends of emperor penguins. He has also led or collaborated on numerous other field projects on birds, mammals, sea turtles, and whale sharks around the world. His most recent field project in Antarctica took place in November 2006 to conduct aerial surveys of emperor penguin colonies in the Ross Sea. This was the second of two trips to the Antarctic in 2006. The great advantage of semi-retirement is that it allows time for a broader range of intellectual pursuits, and there was no better example than

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his participation as a lecturer and guide during a February cruise to South Georgia Island and the Antarctic Peninsula. The cruise theme was "In the Wake of the Great Explorers," and he learned much from the other explorers on the cruise. The guest lecturers on the cruise were Frans Lanting, Wildlife photographer; Reinhold Messner, arguably the greatest mountain climber of all time; Conrad Anker, world-renowned mountain climber and discoverer of George Mallory on Mt. Everest; and Caroline Alexander, author of *The Endurance* and *The Bounty*. Much was learned from all of them. Kooyman's most recent field expedition was just completed in September 2009 to Raja Ampat and Papua, Indonesia. This involved conducting a survey of possible future research sites for his graduate student, Geoffrey Gearhart. Kooyman's current interest is the application of visual sensing that includes animal-borne to satellite-borne cameras combined with other physical sensors.

Kooyman is a fellow of the American Academy of Arts and Sciences (AAAS) since 1973, a fellow of the Explorers Club since 1976, and a member of Sigma Xi since 1966. He is also a member of the American Physiological Society, and a charter member of The Society for Marine Mammalogy.

In Antarctica, Kooyman Peak in Queen Elizabeth Range was named after him in 1966. In 2005, he was the first recipient of the Kenneth S. Norris Lifetime Achievement Award presented by the Marine Mammal Society, and in March 2006, he was honored with the Quadrienniel Finn Ronne Award from the Explorers Club.

He has published over 160 scientific reports, with numerous national and international co-authors. He is the author of two books: *Weddell Seal: Consummate Diver* (Cambridge University Press) and *Diverse Divers: Behavior and Physiology* (Springer Verlag), and co-editor with Roger Gentry of *Fur Seals: Maternal Strategies on Land and Sea* (Princeton University Press). He has also participated in numerous public exposure of science projects through his activity in photography with cover photographs in several journals and magazines. One photograph was in the book *Celebration of Life; Testimonies of a Commitment* (Gil, 1996, pp. 78-79). His video and motion picture photography has appeared in *Life in the Freezer*, and he has appeared in documentaries such as the Imax movie *Antarctica*, although unrecognizable because he was dressed in a cold water dry suit. More recognizable were his on camera scenes in the National Geographic documentary *Emperors on the Ice*, and most recently the Discovery Studios *Blue Planet, Frozen Seas* and *Journey to the Planet Earth: State of the Ocean's Animals*, which aired on KPBS 28 March 2007.

# The History of Pinniped Studies in Antarctica

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## Introduction

From our perspective and experience, pinnipeds are the only group of mammals endemic to Antarctica. All of those we discuss live much of their life and reproduce in Antarctic waters. Whales, although they may spend substantial parts of the year in the Southern Ocean, mostly give birth to their young further north. Those mammals that we discuss are listed in Table 1.

We divide these species into three groups: (1) the interloper, (2) the commuters, and (3) the residents. The interloper is the Antarctic fur seal, which in recent history has spread from the sub-Antarctic islands but is still within the Southern Ocean, which I define, for the purposes of this commentary, as the northern boundary being the Antarctic Polar Front (APF). However, before the sealers drove this animal to near extinction in the early 1800s, it occurred on islands of the Antarctic Peninsula. It was quickly extirpated from these areas and thought to be extinct until the 1930s. Later, in the 1950s, Nigel Bonner discovered a few animals in Johnson Cove, Bird Island. This island is one of an archipelago that occurs at the northern end of South Georgia Island. Since then, the species has enjoyed an incredible population expansion to other sub-Antarctic islands and a return back to islands of the Antarctic Peninsula. It now resembles an invasive species and is displacing many ground-nesting birds on South Georgia Island and probably in the Antarctic Peninsula, hence the category of interloper.

The commuters are the southern elephant seal and the Ross seal. The reasons for this appellation are detailed later, but suffice it to say that the southern elephant seal reproduces on sub-Antarctic islands and forages in the Southern Ocean. As if a mirror image, the Ross seal reproduces in the heavy pack-ice of the Southern Ocean and forages to the north.

The residents of the Southern Ocean are the Weddell seal, leopard seal, and crabeater seal. In the peregrinations of these species, some are occasional visitors north of the APF. A small population of Weddell seals even reproduces in Larson Harbor, South Georgia Island. Leopard seals also hunt Antarctic fur seal pups from South Georgia Island. All reproduce exclusively in the pack- or on the fast-ice of the Southern Ocean, with the exception of the small breeding group of Weddell seals just mentioned.

## Discovery and Early History of Antarctic Pinnipeds by Melba M. Kooyman

The interlocking relationship of geographic exploration, commercial exploitation, and scientific study is well-illustrated in the story of Antarctic pinnipeds. Harsh climatic conditions have made this region the last place on Earth for men to explore. In few other places is the environment more unforgiving or the margin for error so narrow as when conducting field studies on indigenous Antarctic animal populations. Before scientific success could be achieved, reliable transportation and secure living conditions had to be well-established. The combined and sequential efforts of courageous mariners, keen-eyed collectors, and dedicated scientists using the technology of their day have led to our present state of knowledge about these intriguing animals of the South Polar Region.

The northern limit of Antarctic waters is called the Antarctic Convergence, a natural boundary 32 to 48 kilometers wide that follows an irregular path between 47° and 61° south latitude (Figure 1). The five phocids and one fur seal, which dwell in these waters, include four species in the tribe Lobodontini as well as the southern elephant seal (*Mirounga leonina*) and the Antarctic fur seal (*Arctocephalus gazella*) (Table 1). Because their habitat is remote, subject to extreme polar weather patterns, and experiences long periods of darkness, these animals are relatively new to the study of mammalogy. The story of their discovery, exploitation, scientific study, and conservation has many overlapping features. We describe these events in terms of three historical periods: Exploratory, 1772-1892; Heroic, 1893-1914; and Scientific, 1914-present. These periods provide largely an overview, from the first taxonomic description to more technical studies in recent years, with some more extensive description of physiological and behavioral research of G. Kooyman (which is detailed further in Kooyman, 2006).

A number of explorers, naturalists, and scientists who have worked closely with these marine mammals are mentioned, but they will be

**Table 1.** Six pinnipeds that inhabit the area south of the Antarctic convergence, source of the first collection data, and name of the first person to publish the scientific description

| Name | Collection data | Scientific description |
|---|---|---|
| Antarctic fur seal (*Arctocephalus gazella*) | Kerguelen Islands (German Transit-of-Venus Expedition, 1874) | Peters, 1875 |
| Southern elephant seal (*Mirounga leonina*) | No type specimen, fragments only, Islas Juan Fernandez, Chile (1744, Lord Anson) | Linnaeus, 1758 |
| Crabeater seal (*Lobodon carcinophagus*) | South Sandwich/South Orkney Islands (French Antarctic Expedition, 1837-1840) | Humbron & Jacquinot, 1842 |
| Ross seal (*Ommatophoca rossii*) | Ross Sea (British Antarctic Expedition, 1839-1843) | Gray, 1844 |
| Leopard seal (*Hydrurga leptonyx*) | Falkland Islands, 1820 | Blainville, 1820 |
| Weddell seal (*Leptonychotes weddellii*) | South Orkney Islands, 1823 (James Weddell Expedition) | Lesson, 1826 |
| | Patagonia, Argentina (Fitzroy, 1837) | Gray, 1837 |

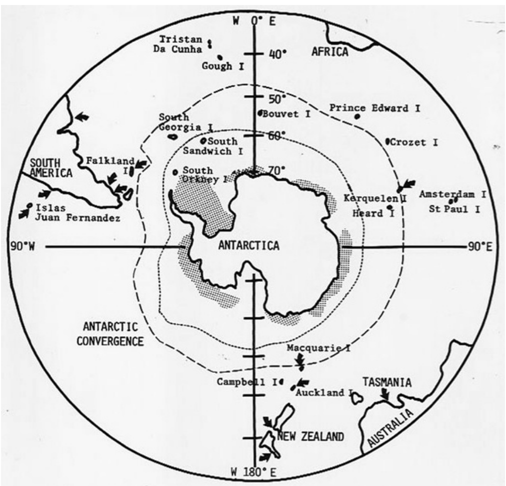


**Figure 1.** The dashed line is the Antarctic Polar Front (APF), also called the Antarctic Convergence. The solid line is the northern edge of the winter pack-ice.

representative of their fields as a complete list of contributors is beyond the scope of this more personal history.

*Exploratory Period*

The Greeks were the first to postulate the existence of a southern land mass. Because of their belief in order and symmetry in nature, it seemed logical that land in the south was present to balance the land in the north. Since the land in the north lay under the constellation *Arcktos* (the bear), it followed that the land in the south be called by the direct opposite, *Antarkticos*, a term attributed to Aristotle. The Greeks had no way of proving that this continent existed, but the logic of the notion persisted in classical scholarship. In 150 AD Ptolemy, the Egyptian geographer, described an enormous landmass to the south and named it *Terra Australia Incognita*, the unknown southern land. It figured prominently in his writings and in his rendering of a world map. Many fanciful ideas emerged about the features and inhabitants of this hypothetical continent, and as the centuries passed into the age of exploration, actual voyages beyond the known world began an era of discovery (Nieder, 1972).

Most of what we know about life below the Antarctic Circle has been learned within the last 200 years. Although this knowledge begins traditionally with the second voyage of Captain James Cook, it is intriguing to consider the experience of one of his contemporaries.

In 1772, Yves Joseph de Kerguélen-Tremarec sailed with orders from the French Government to search for the supposed great southern continent. He discovered a group of 300 icebound islands in the southern Indian Ocean, which are now known as Iles de Kerguelen. Because of fog and high seas, however, he was unable to land or to chart these islands. Naming them *La France Australe*, he returned to France, reporting,

> The lands which I have had the happiness to discover appear to form the central mass of the Antarctic continent. The latitude at which it lies promises all the crops of the Mother Country . . . wood, minerals, diamonds, rubies will be found. . . . If men of a different species are not discovered at least there will be people living in a state of nature. (As quoted in Allen et al., 1985, p. 73)

In 1774, he was given three ships and orders to colonize his discovery. Faced with the inhospitable reality of the islands, he returned to France and a court martial (Allen et al., 1985).

Scientific curiosity about the unknown, though not to be discounted entirely, has seldom been the main object of geographical exploration. As the men and the means to sail uncharted waters appeared and succeeded, their sponsors played an ever-increasing role. Principle motives ranged from political expansion to commercial gain. If the putative southern continent could provide such goods as were being brought to Europe from newly established trade routes in the Americas and the Far East, it was thought to be worth the risk and expense to mount the effort. Little by little, the boundaries of the hypothetical continent were peeled away as sea exploration in the southern oceans advanced. Soon the reality of violent storms, icy waters, and dense fog in the southern latitudes intimidated all but the heartiest. The French explorers Bouvet (1739) and Kerguélen (1772) discovered the sub-Antarctic islands that bear their names, but with the exception of Cook, the stark, inhospitable climate prevented further serious activity in this forbidding territory until the 19th century.

During the age of exploration, it was customary to include some sort of naturalist/scientist on the expedition to identify and collect specimens for the sponsor of the voyage. These acquisitions still enhance the natural history collections in various museums and universities throughout the world and formed the first systematic basis for scientific classification. The ship's surgeon often assumed the role of collector, but trained scientists were occasionally enlisted for the task. Since most voyages of this time were driven by commercial interest rather than scientific discovery, the scientific ability of the collector was not a priority. The few captains who sought competent scientists were often disappointed. A list of the major voyages during the Exploratory Period is shown in Table 2. Where known, the names of the accompanying naturalist/collectors are included. Several of the type specimens for Antarctic seals were collected during this period, and two were named for Captains Weddell and Ross. Many scientific stations and geographic features were named for persons or sailing vessels associated with this period.

As a young botanist, Joseph Banks, age 24, was approached by the Royal Geographic Society to accompany Captain James Cook on his first voyage in 1768. Although their working relationship was effective, their personal association was less than cordial. Banks was appointed as naturalist on Cook's second voyage, but his demands for specially constructed quarters were so excessive that the agreement was terminated by Cook. In his place, Johann Reinhold Forster and his 18-year-old son, George Adam, both native Germans who had relocated to England, joined the expedition. Their perception of the assignment was described in a two-volume account of their experiences published in 1777:

> On the 11th of June, 1772, my father and myself were appointed to embark in this expedition in order to collect, describe and

**Table 2.** Major voyages in the Antarctic seas during the Exploratory Period, 1771-1892; where known, the names of the naturalists are included. Captains Weddell and Ross both had seals named after them.

| Captain/leader | Naturalist/scientist | Ship | Date |
|---|---|---|---|
| James Cook (1728-1779) | J. R. Forster<br>G. A. Forster | *Resolution*<br>*Adventure* | 1772-1775 |
| Thaddeus von Bellingshausen (1778-1852) | Consulted with Joseph Banks* | *Vostok*<br>*Mirny* | 1819-1820 |
| Nathaniel Palmer (1799-1877) | | *Hero* | 1820-1821 |
| Edward Bransfield (c. 1795-1852) | Adam Young, Surgeon | *Williams* | 1820-1822 |
| James Weddell (1787-1834) | Self-taught; consulted with Prof. Robert Jamieson | *Jane*<br>*Beaufoy* | 1822-1824 |
| Nathaniel Palmer (1799-1877) | James Eights, MD | *Scraph*<br>*Annawan* | 1829-1830 |
| John Biscoe (1794-1843) | | *Tula*<br>*Lively* | 1831-1832 |
| Dumont D'Urville (1740-1842) | Two naturalists | *Astrolabe*<br>*Zelee* | 1837-1840 |
| Charles Wilkes (1798-1877) | James Dana + eight other naturalists | *Vincennes*<br>*+ five other ships* | 1838-1842 |
| James Ross (1800-1862) | Joseph Dalton<br>J. D. Hooker | *Erebus*<br>*Terror* | 1839-1843 |
| G. S. Nares (1831-1915) | Wyville Thompson<br>H. N. Mosely | *Challenger* | 1872-1876 |

*Shortly before Bellingshausen's departure, two German naturalists cancelled their contract to sail on the expedition.

> draw the objects of the natural history which we might expect to meet within our course. (As quoted in Chapman, 1965)

These were the kinds of skills expected of naturalists at the time, and they formed the basis for the first descriptive, scientific studies of that era.

Many of the men called to the post of ship's naturalist were collectors only, and they did not do the task of scientific description, so it devolved upon the keepers of museum collections to describe and classify new species using a type specimen sent to them by the collector. These keepers, who rarely traveled beyond the domain of their respective museums, have had a profound effect on the earliest published accounts of pinnipeds collected from the Southern Ocean. It is appropriate to review how their role fits with the more dramatic participation of the on-site discoverers of the southern polar specimens treated in this paper.

The Linnaean system of biological bi-nomenclature was well-established in the 19th century. As the great museums of Europe began to acquire specimens collected on the voyages of exploration, the job of keeper was created to describe, classify, and display the new items or consign them to the storage bins for possible future use. While some were hired as apprentices for "on-the-job" training, many were trained in natural history and became world-renowned experts and their names were attached to the scientific descriptions of type specimens received by their respective museums. Several such keepers made important contributions to polar mammalogy, but we focus on one, John Edward Gray (1800-1875) of the British Museum, as an example of the "type" of man who made significant taxonomic contributions.

Gray was born into a family, which traced its history back to John Ray (1628-1705), one of England's most celebrated early naturalists. Seven members of this family had a tradition of service to the British Museum for over 150 years. Gray began work there at the age of 16 under the patronage of his uncle, Edward W. Gray, who was keeper of natural history. His skill in organization of materials and meticulous examination served him well. In 1843, the extensive documentation of his findings led to publication of the first formal catalog of mammals in the British Museum, *List of the Specimens of Mammalia*. Undoubtedly, his greatest contribution to zoology lay in the class mammalia. His wife, Maria, was a skilled artist and assisted Gray with numerous detailed, beautiful illustrations. She etched thousands of plates of marine mammals between 1857 and 1874, which appeared in his published works (Gunther, 1975).

Although Gray never traveled to Antarctic waters, he was the first to describe the type specimen of the Ross seal, and he clarified the description of the Weddell seal, which initially had not been done using the traditional method. The story of the first description of the Weddell seal illustrates how unscientific collecting could be during the Exploratory Period. Captain James Weddell saw the animal during his 1820-1824 voyage and made what has been described as a "fanciful drawing" of a "sea leopard." Robert Jamieson of the Edinburgh Museum developed a scientific description in 1826 on the basis of Weddell's drawing and the account of the sighting written in his logbook. No type specimen was collected. The first scientific description to be published was done in 1826 by Lesson, who relied on the logbook description as well. Eleven years later, Gray received two specimens at the British Museum from Captain Fitzroy. Gray provided a more accurate description of the Weddell seal, and it was described and illustrated in his catalog of marine mammals published in 1862 (Scheffer, 1958). In this volume, he used the species name of *weddelli*, rather than the more commonly seen *weddellii*, which is probably the result of poor proofreading in later publications (Bonner, 1988).

The Exploratory Period brought together an important coupling of talent and technique. The courage and skill of the early seamen, the choices and preservation methods of the collectors, and the observations and published accounts of the keepers all combined to form a basis for future scientific inquiry. Captain James Cook, the most competent naval man of his generation, initiated this process, but he voiced doubts about the possibility of serious work in the Antarctic. During Cook's epic second voyage in 1772 on the *Resolution*, he crossed the Antarctic Circle at widely different points three times, charted several sub-Antarctic islands, and circumnavigated what is now known as Antarctica. However, its extensive, icy perimeter prevented him or any of his crew from viewing this forbidding land. His account of the voyage was hardly encouraging to other mariners. The following is an excerpt from his journal: Monday, 6th (of February 1774) 58° 15' South, Longitude 21° 34' West:

> It is however true that the greatest part of this Southern Continent (supposing there is one) must lay within the Polar Circile where the Sea is so pestered with ice, that the land is thereby inacessible. The risk one runs in exploring a coast in these unknown and Icy Seas, is so very great, that I can be bold to say that no man will ever venture farther than I have done and that the lands which may lie to the South will never be explored. Thick fogs, Snow storms, Intense Cold and every other thing that can make navigation

> dangerous one has to encounter and these difficulties are greatly heightened by the enexpressible horrid aspect of the Country, a Country doomed by Nature never once to feel the warmth of the Suns rays, but to lie for ever buried under everlasting snow and ice. (As quoted in Chapman, 1965, pp. 34-35)

In summary, he concluded,

> I had now made the circuit of the Southern Ocean in a high Latitude and traversed it in such a manner as to leave not the least room for the Possibility of there being a continent, unless near the Pole and out of reach of Navigation. . . . Thus I flater myself that the intention of the Voyage has in every respect been fully Answered, the Southern Hemisphere sufficiently explored and a final end put to the searching after a Southern Continent. . . . Whoever has resolution and perseverance to clear up this point by proceeding farther that I have done, I shall not envy him the honour of the discovery but I will be bold to say that the world will not be benefited by it. (As quoted in Chapman, 1965, pp. 35, 37)

These dire warnings, so eloquently and confidently expressed, were not to be heeded by his fellow mariners because of another, almost offhand, entry that spurred an onslaught of activity that he could never have predicted. Off the coast of South Georgia Island, he noted, "Seals or Sea Bears were pretty numerous, they were smaller than those at Staten Island: perhaps the most we saw were females for the shores swarm'd with young cubs." Thus began a period of commercial sealing unprecedented for its time. Commercial sealing of an itinerant sort had been developing as an accompaniment to the burgeoning whaling industry during this period. Because a market for seal skins was growing in China, British and American sealers began to explore and harvest seals along the South American coastline and on the Falkland Islands in the late 18th century. Bonner (1982) describes an early example:

> The first recorded vessel to fit out especially for sealing was the ship, *States*, owned by a lady named Haley of Boston. The *States*, a huge ship of a 1,000 tons, set-out soon after the end of the Revolutionary War in 1775 and secured a cargo of 13,000 fur seal skins from the Falklands. These were sold in New York for fifty cents apiece, but were resold in China for five dollars (each). (p. 59)

This profit margin motivated the already adventurous American spirit to further effort. Because of the French Revolution and the subsequent Napoleonic Wars, the Americans had an edge on their prime competitors, the British. Despite this advantage, little is known about their early sealing expeditions. Competitive interests kept ships' logs under wraps lest profitable sealing sites be discovered by other sealers. With the exception of Enderby and Sons, the British Whaling and Sealing Company, few accounts of exploration and discovery were published by any sealers until well after the animals at preferred sites virtually had been exterminated. All species of southern fur seals were ruthlessly hunted and slaughtered in a systematic manner. In this paper, we deal only with the Antarctic fur seal whose range includes those islands south of the APF.

### Antarctic Fur Seal (*Arctocephalus gazella*)

E. Geoffrey St. Hillaire and F. Cuvier proposed the genus name *Arctocephalus* for the Antarctic fur seal in 1826. It is derived from the Greek *Arktos* and *Kephale* meaning "bear-headed." Although Cook described "sea-bears" on South Georgia Island, the center for *A. gazella* populations in 1772, it was more than 100 years later that the type specimen was collected and described. Skin, skeleton, and certain soft parts were collected on Kerguelen Island in 1874 by T. Studer, naturalist on the *SMS Gazelle* of the German Transit-of-Venus Expedition. The first scientific description was published by W. C. H. Peters in 1875.

Sealers began hunting Antarctic fur seals in 1790, not long after published accounts of Cook's *Voyage to the South Pole and Around the World* was in general circulation. It is a tragic commentary on commercialized exploitation of fur seals that a century of slaughter for monetary gain occurred before any serious scientific interest was taken in this species.

Edmund Fanning was the foremost Yankee sealer of this period. During the 1800-1801 sealing season at South Georgia, his ship, *Aspasia*, was among 17 British and American vessels. Of the total catch amounting to 112,000 fur seal skins, Fanning's crew had succeeded in taking 57,000 seals. An example of the extraordinary methods used to conceal information on newly discovered sealing sites is described by Bonner (1982):

> Secrecy was an important ingredient for success (and has considerably hampered research into the history of the industry). When Captain Canning, using the original discoverer's map, rediscovered the Crozet Islands and their fur seal herds, he left at the Prince Edwards Island information regarding their location for the use of another vessel of the same owners. Following instructions from his owners, he erected a marker of stones but buried the record thirty feet to the northeast. The ruse was successful. When the

> ship for whom the information was intended arrived, the crew found that the cairn had been demolished and a deep hole excavated in the place where it had been, but they were able to find the packet easily enough. (p. 61)

One of Fanning's protégés, Nathaniel Palmer, a 20-year-old seaman, became the first American to sight the Antarctic continent while on his quest for undiscovered sealing grounds in 1820. While in command of the *Hero* on this voyage, he also came in contact with a Russian expedition designed for geographical exploration and led by Thaddeus von Bellingshausen. The Russian expedition was the first comprehensive scientific study at these latitudes since Cook's second voyage of 1772-1775. Unfortunately, the Russian Government was dissatisfied with Bellingshausen's work and published a mere 600 copies of his report. It was not translated into English until 1930. Numerous other voyages took place at this time, most of which have been summarized in Table 2.

A word of tribute must be paid to the only commercial organization to make significant contributions to knowledge about Antarctica. Enderby and Sons was a well-established whaling and sealing company based in England. Unlike other commercial enterprises of the time, they encouraged their captains to explore the region, document their discoveries, and publish their findings. Several expeditions returned with empty cargo holds, but with outstanding accounts of geographical exploration. Some of the Enderby captains included John Biscoe, John Balleny, and Peter Kemp.

In 1819, a violent storm and chance sighting of land by William Smith of the brig *Williams* extended the sealers' hunting grounds for a few more years. He discovered the South Shetland Island group and mounted an expedition the following year. Edward Bransfield took command of the *Williams*, with Smith assigned as pilot. Word of this discovery soon passed to other sealers and the "seal-rush" was on again. Bonner (1982) wrote that 47 American and British vessels worked the area in 1821, with another 44 ships arriving the following year only to leave with their holds practically empty.

James Weddell's account stated that during 1821 and 1822, 320,000 fur seals were taken at the South Shetlands. He deplored the loss and described a method of sealing that would promote a sustainable yield such as the one practiced on the Isla de Lobos. In 1822, Weddell estimated that a total of 1,200,000 skins had been taken from that area almost assuring its total elimination (Weddell, 1825).

Restraint was not to be. No authority existed to enforce compliance with any conservation efforts. The logic of such measures was lost on sealers who believed that others would not follow guidelines that would reduce their profits. Because a number of nations were involved, even a national resolution to save the reproducing stocks could not be effective in halting sealers from other countries. Local populations of *A. gazella* were completely wiped out for barely profitable yields, but a few remnants survived. A brief resurgence occurred in

**Table 3.** Major expeditions to Antarctica during the Heroic Period, 1893-1914; note the variety of nationalities represented.

| Leader | Title/major sponsor | Ship | Dates |
|---|---|---|---|
| Henry K. Johan Bull (1844-1930) | Svend Foyn, Norwegian Whaling Expedition | *Antarctic* | 1893-1895 |
| Adrian Victor Gerlache (1866-1934) | Belgian Antarctic Expedition | *Belgica* | 1897-1895 |
| Carsten Egeberg Borchgrevink (1864-1934) | British Antarctic Expedition George Newnes, Newspaper Publisher | *Southern Cross* | 1898-1900 |
| Robert Falcon Scott (1868-1912) | British National Antarctic Expedition | *Discovery* | 1901-1904 |
| Otto Nordenskjold (1869-1928) | Swedish Antarctic Expedition | *Antarctic* | 1901-1903 |
| William Spiers Bruce (1867-1921) | Scottish National Antarctic Expedition | *Scotia* | 1902-1904 |
| Eric von Drygalski (1865-1949) | German Antarctic Expedition | *Gauss* | 1902-1903 |
| Jean-Baptiste Charcot (1867-1936) | French Antarctic Expedition | *Francais*<br>*Pourquoi-Pas?* | 1903-1905<br>1908-1910 |
| Ernest Henry Shackleton (1874-1922) | Private loans and contributions | *Nimrod* | 1907-1909 |
| Robert Falcon Scott (1868-1912) | British National Antarctic Expedition | *Terra Nova* | 1910-1912 |
| Roald Amundsen (1872-1928) | Private contributions; Norwegian sponsors | *Fram* | 1910-1912 |
| Nobu Shirase (1861-1946) | Japanese Antarctic Expedition | *Kainan Maru* | 1910-1911 |
| Douglas Mawson (1882-1958) | Australasian Antarctic Expedition | *Aurora* | 1911-1914 |
| Wilhelm Filchner (1877-1957) | German Antarctic Expedition | *Deutschland* | 1911-1912 |
| Ernest Henry Shackleton (1874-1922) | British Imperial Trans-Antarctic Expedition | *Endurance*<br>*Aurora* | 1914-1917 |

the 1870s, again following the senseless hunting pattern practiced 50 years earlier. The advent of steam-driven whaling ships changed the focus of commercial interests to harvesting the great whale populations, thus effectively providing respite for those small pockets of surviving *A. gazella*.

*Heroic Period*

During the Heroic Period, 1893-1914, very little was published about the Antarctic fur seal. Many believed the species to be extinct. While the heroes of land discovery were staking out their geographic claims further south (Table 3), small pockets of fur seals were gradually beginning what was to become a remarkable recovery. Except for taxonomic descriptions, minimal scientific work was done on this species.

Activities affecting fur seal populations occurred in boardrooms more than in the field during this period. Formal territorial claims by the British were consolidated in 1908, and they were named the Dependencies of the Falkland Islands. The British Colonial Office was placed in charge of all matters related to this area. Although legal regulations on sealing were difficult to monitor and enforce, British administration was aware of the damage being done to fur seal and southern elephant seal populations. Since they had long occupied the area and had a strong naval presence, they issued the first regulatory legislation: The Seal Fishery Ordinance of 1899 (Bonner, 1982). Subsequent legislation would not be forthcoming until the latter part of the next century.

*Scientific Period*

During the Scientific Period (1914-present), further efforts at description and consistent monitoring of resources were made. In 1923, the first cohesive plan for systematic, long-term study was established and titled "Discovery Investigations." Work was primarily concerned with oceanography and marine biology, particularly in connection with the whaling industry. Several Norwegian whaling stations had been established on South Georgia Island and were paying taxes to the British Colonial Office. A portion of these funds was set aside to support the "Discovery Investigations" program (Everson, 1987).

This system was effective in establishing the concept and practice of systematic, scientific investigation in this unique polar region with its remarkable resources. Conflicting territorial claims between Great Britain and Argentina during World War II prompted the Colonial Office to set up a group of bases in the region code-named "Operation Tabarin." Seasoned Antarctic investigators who were serving as advisors also recognized their value as staging areas for scientific research. In the words of Sir Vivian Fuchs (1982), former Director of the British Antarctic Survey (BAS), "Polar advice on both logistics and science was provided by an advisory committee of three: James Wordie, a veteran of Shackletons's *Endurance* expedition of 1914, Dr. Brian Roberts, biologist on the British Graham Land Expedition, 1935-37, and Dr. Neil Mackintosch, Director of Discovery Investigations. Appreciating from the first that bases established for political reasons could also provide platforms for scientific work" (p. 23). This was the origin of the BAS in 1944, and it has had scientific continuity ever since.

The United States actually built the first scientific base on Bird Island, South Georgia, but this now belongs to BAS. Incidentally, the hut lasted until 2004 when it was torn down. From 1981 until its demise, it was used as a shed for a generator.

In the Scientific Period, most of the scientific work on *A. gazella* has centered on ecological studies with an emphasis on population dynamics, breeding behavior, and foraging behavior. One of the first investigators for BAS—or as it was called at that time, FIDS—was Nigel Bonner, who was involved with early studies during the 1950s and 1960s on the natural history of Antarctic fur seals. Since then, he has figured prominently in the conservation efforts on behalf of all Antarctic mammals and has published extensively on the topic. Repenning's work on the taxonomy of all species of fur seals did much to eliminate inconsistencies in previous studies (Repenning et al., 1971).

One individual closely associated with work on *A. gazella* is Michael R. Payne, who contributed the major study over the earlier years of its rapid population growth. Payne's (1977) findings show that the *A. gazella* populations, in part because they are now fully protected, were increasing at a rate of about 15% a year, but that rate probably decreased in later years. The last survey of the seal for South Georgia Island was in 1990 when about 2.7 million animals were estimated. Concurrently, John Croxall, former head of the birds and mammals program of BAS, has published material on the breeding behavior of *A. gazella*. Gerald Kooyman initiated studies of dive times and depths related to feeding behavior of Antarctic fur seals in 1980 (Kooyman et al., 1986). Table 4 contains a list of some investigators who have published recent work on the Antarctic fur seal.

### Southern Elephant Seal (*Mirounga leonina*)

*Exploratory Period*

Another pinniped that was nearly exterminated during the Exploratory Period is the southern elephant seal. This phocid is circumpolar in distribution and found on all sub-Antarctic islands. The first scientific description of this marine mammal, using the genus name *Phoca*, was written by Linnaeus in 1758 and was based on the account given by Lord George Anson who collected a few skull fragments from Isla Más a Tierra, Chile, in 1744. Scheffer (1958) wrote that there is no reason to believe that Linnaeus ever saw these fragments, which are currently held in the British Museum (Natural History). Allen assigned the genus name of *Mirounga* in place of *Phoca* in 1905, crediting Gray as author in 1827. *Mirounga* is the Australian name for the elephant seal (King, 1983).

The history of the southern elephant seal follows a similar and parallel sequence to that of the Antarctic fur seal. While sealers busily hunted fur seals, they could not help but notice the abundant populations of large elephant seals that shared similar habitats. Their pelts were of no interest, but seal oil is similar to whale oil and was used in the same products. They were easier to catch than whales, and each large adult animal when processed provided about two barrels of oil (409 liters). Sealing vessels were often converted from whaling ships and had the structural setup and equipment for processing blubber. Elephant seal oiling thus provided a profitable pastime while the search continued for fur seals. An indiscriminate hunting cycle began, and soon elephant seal stocks were reduced to a low level. In the 1870s, seal-oiling ceased to be a profitable enterprise and was practiced only sporadically after that time.

*Heroic Period*

During the Heroic Period, the advent of steam ships used by the whaling industry shifted the focus to exploitation for large whale populations in the area, giving the elephant seal a chance to recover along with the Antarctic fur seal. Probably the most important contribution to their recovery took place in the political arenas of the time. Although no concerted effort was made to study them for their intrinsic merits, interest in maintaining their population on a sustainable yield basis was considered. The British passed early legislation in an attempt to control harvesting of sea animals in the area that they claimed as part of their colonial territory.

*Scientific Period*

During the early Scientific Period, much significant work on Antarctic pinnipeds was accomplished by Richard M. Laws (Figure 2). Born in 1926, he received his formal education at Cambridge University in England. He has published widely on Antarctic seals and fur seals, but one of his most important findings was on the southern elephant seal. He observed that the pulp cavity of the canine teeth remains open throughout the southern elephant seal's life and continues to lay down dentine at varying rates, creating growth rings that could be examined for age determination (Laws, 1953). Laws' studies appeared in a series of publications from the early 1950s under the auspices of FIDS/BAS. His documented ecological findings on the southern elephant seal formed the basis for a rational harvest of a marine mammal species for the first time since they became a source of commercial exploitation. This was precedent-setting and because of its success, it became a model on which future monitoring and legislative models could be based. Laws has had a distinguished career as a biologist working on other large mammalian species in addition to his Antarctic seal work. He became Director of the British Antarctic Survey in 1973 and was selected as a Fellow of the Royal Society in 1982. He retired from BAS in 1987. Other biologists who have published their work on the southern elephant seal are listed in Table 4.

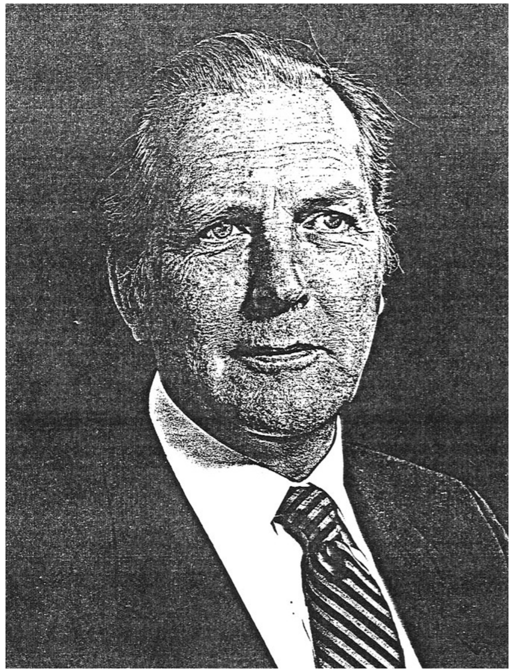

**Figure 2.** Richard M. Laws, Ph.D., FRS; he was the director of the British Antarctic Survey 1973-1987.

## Antarctic Seals, Tribe *Lobodontini*

*Exploratory Period*

Tribe *Lobodontini* refers to the four Antarctic phocids (Table 1). This group of seals, by virtue of their isolated habitat, is among the only marine mammals never commercially exploited by man to near extinction. They were sighted and type specimens were collected during the Exploratory Period. King (1983) summarized the interrelationship among these four seals.

The four genera of truly Antarctic seals share the Antarctic without serious interference with one another because their distribution and food habits hardly overlap. The leopard and Ross seals differ widely in their diets. The leopard seal ranges as far north as some sub-Antarctic islands, while the Ross seal, during the summer, stays in the southerly, heavy pack-ice. The two most abundant seals, the Weddell and crabeater, have been likened to the two most common penguins of the region. The Weddell seal and the emperor penguin (*Aptenodytes forsteri*) are both fish eaters of littoral distribution, and most remain as far south all year as open water will allow. The crabeater and the Adélie penguin (*Pygoscelis adeliae*) feed on crustaceans, which are pelagic. Both the penguin and crabeater seal migrate to the marginal ice zone (MIZ) of the pack-ice.

The following is a brief review of the collection of the type specimen for each species:

*Ross Seal* (*Ommatophoca rossii*)—Because the Ross seal lives mainly in heavy pack-ice during the summer, less is known about it than any of the other Antarctic phocids (Thomas & Rogers, 2009). The type specimens were collected during the British Antarctic Expedition under the direction of James Clark Ross in 1839-1843. It was described by Gray in 1844 and included in his first catalog of marine mammals. In 1940, Bertram wrote that less than 50 of these seals had ever been seen (Laws, 1953, as quoted by Scheffer, 1958).

*Leopard Seal* (*Hydrurga leptonyx*)—Blainville wrote the first published description of the leopard seal in 1920, using a specimen collected in the vicinity of the Falkland Islands. This phocid is the most widely distributed of the *Lobodontini*, but it is mainly solitary and not abundant in numbers (Rogers, 2009). Because of its wide range of distribution, reports of its presence were noted from a number of exploratory groups (Rogers, 2009). One of the first photographs ever taken was of an animal hauled aboard the Dundee Whaler, *Balaena*, in 1892. William Spiers Bruce was aboard this vessel and was later to lead the highly successful *Scotia* expedition in 1902-1904.

**Table 4.** Scientists who published major works on the Antarctic fur seal and the southern elephant seal during the Scientific Period (compiled primarily from Ridgway & Harrison, 1981a, 1981b; see also Bonner, 1981; Ling & Bryden, 1981)

| Behavior | Ecology | Anatomy/ taxonomy |
|---|---|---|
| Angot, M. | Carrick, Robert | Bonner, W. Nigel |
| Bonner, W. Nigel | Condy, Pat R. | Bryden, Michael M. |
| Croxall, John | Ingham, Susan E. | Ling, John K. |
| | Laws, Richard M. | |
| | Nicholls, D. G. | |
| | Pascal, M. | |
| | Payne, Michael | |

*Crabeater Seal* (*Lobodon carcinophaga*)—Most abundant of the Antarctic phocids (Bengtson, 2009), this seal was first described by J. B. Hombron and H. Jacquinot in 1844 using a specimen, including skin and skull that had been collected on the Dumont d'Urville expedition of 1837-1840 in an area between the South Sandwich Islands and the South Orkney Islands. Because of their abundance, this seal has been targeted by some groups for commercial harvesting, but preliminary ventures have been costly and, to date, major efforts have not been forthcoming. Scientists are intrigued by this seal's remarkable tricodont dentition, which has been widely described and discussed. They probably possess the most complex mammalian teeth of any mammal. These teeth are thought to function as sieves to strain invertebrates out of the water.

*Weddell Seal* (*Leptonychotes weddellii*)—The Weddell seal is one of the most comprehensively studied marine mammals in the world (Thomas & Terhune, 2008). Living in relative isolation until the turn of the century, this animal has proved to have extraordinary adaptations to its habitat. Because it lives in coastal and fast-ice areas and some do not migrate, it is an ideal study animal. Many biologists have conducted extensive studies on its unique abilities, especially since the International Geophysical Year (IGY), but we will begin with the Exploratory Period.

*Exploratory Period*

During the Exploratory Period, these pinnipeds were viewed primarily from two perspectives: first, potential commercial value, and second, a food source for the exploratory party. This attitude prevailed throughout the Exploratory Period and until well into the Heroic Period. However, by the turn of the century, well-prepared naturalists were more frequently involved in the expeditions. As a result, published scientific work of any substance began in the Heroic Period. Edward A. Wilson, while on Captain Scott's *Discovery* expedition of 1904-1907, made the most thorough study of the natural history of the Weddell and crabeater seals until the 1960s.

Edward Wilson, physician and zoologist, was born in Cheltenham, England, in 1872. In 1891, he entered Gonville and Caius College at Cambridge University to study natural sciences and medicine. Following the successful completion of his exams, he practiced medicine at St. George's Hospital in

London and continued to pursue a variety of other interests, including nature walks, sketching and watercolors, and museum visits. In 1898, he suffered from a recurring fever that was diagnosed as tuberculosis. As part of his cure, he traveled abroad, spending time walking in the mountains of Norway and Switzerland. Refreshed and healed, he returned to work in 1899. Later that year, he was approached by Dr. Philip Sclater, President of the Zoology Society of London, to apply for the junior surgeon's position on Scott's Antarctic Expedition (Thomson, 1977). Despite his history of tuberculosis, Scott approved his application, and he joined the first expedition.

His background in natural history and his skill as an artist combined with his medical preparation made him a strong member of the scientific team. He was the first scientist to describe in detail the natural history of the Antarctic seals. In his published report in the *Voyage of the "Discovery"* (Scott, 1905), he systematically describes all four Antarctic seals as well as an unusual occurrence of a Southern Elephant seal, which was sighted at Cape Royds. Kooyman (1964) noted another such southerly occurrence in 1961:

> Their rookeries were a constant source of interest to us and an ample food supply, from which we drew largely for our needs. The meat was coarse in fiber and very dark, but by no means rank, and although the blubber was immutable the flesh was our greatest stand-by, not only as a preventive of scurvy but a certain cure for the disease. (Wilson, 1907, p. 12)

Eighty-six Weddell seal specimens were prepared for inclusion in the *Discovery* collection. Wilson supplemented these tangible samples with thorough, descriptive accounts of his observations on their behavior, from their manner of locomotion to their unique vocalizations:

> I have already mentioned the Weddell seal as a rival of the Ross in its powers of producing vocal music. It was a constant source of amusement to us to stir up an old bull Weddell and make him sing; he would begin sometimes with a long and musical moan at a high pitch, which gradually got lower and sounded much like the ice-moans that are common on an extensive sheet of ice. This was followed by a series of grunts and gurgles, and a string of plaintive piping notes, which ended up exactly on the call-note of a bullfinch. Then came a long, shrill whistle, and a snort to finish, as though he had for too long held his breath. (Scott, 1905, p. 480)

Wilson's descriptive work on Antarctic mammals was only one part of his contribution to the success of the *Discovery* expedition. He was a key member of the expeditionary team, in every respect. In Scott's words,

> Words must always fail me when I talk of Bill Wilson. I believe he really is the finest character I ever met. . . . Whatever the matter, one knows Bill will be sound, shrewdly practical, intensely loyal and quite unselfish. (As quoted in Allen et al., 1985, p. 195)

During Scott's second expedition, Wilson perished on the return trip from the trek to the South Pole with Scott and three others. His precise and extensive scientific reports, along with his many watercolor illustrations, form a tangible reminder of the gifts and contributions of this early Antarctic biologist.

*Heroic Period*

Other substantial efforts in the Heroic Period to learn more about the Antarctic seals, mainly the Weddell seal, were made by the Bruce Scottish National Antarctic Expedition (Wilton & Brown, 1908).

*Scientific Period*

Early in the Scientific Period, a number of successful scientific expeditions were conducted (Table 5). Much of the work had broad objectives, but all made some contribution to mammalogy. Admiral Richard E. Byrd initiated the lasting U.S. contributions to Antarctic science in the programs he led. On his several *Little America I & II* expeditions to Antarctica beginning in 1929, Byrd was conscious of the need to have competent, well-trained scientists as part of the expeditionary team. One of the first Americans to study Antarctic seals was Alton A. Lindsey, who was born in Monaca, Pennsylvania, in 1907. He studied plant ecology at Allegheny College and received a Ph.D. in Botany from Cornell University. On Byrd's second Antarctic expedition, Lindsey was selected to be a member of the scientific group. Although he was a plant specialist, he was called upon to be a generalist on this occasion. Using unpublished notes on the Weddell seal given to him by Paul Siple, a member of the first expedition, he extended this work, and a thorough descriptive study on the Weddell seal colony in the Bay of Whales was published in the *Journal of Mammalogy* in 1937. He even used a phonograph machine to record sounds of Weddell seals. Skulls of Weddell seals collected by Lindsey reside at the Field Museum of Natural History in Chicago. His career beyond this period was devoted mainly to botany, but the quality of this early study provided important baseline information on this Antarctic seal.

Another landmark expedition that ran concurrently with Byrd's *Little America II* expedition was the British Graham Land Expedition (BGLE)

**Table 5.** Numerous, well-financed, and technically well-equipped expeditions dominated the Scientific Period. Biology remained a minor objective, but the bases that were established and the descriptive studies published formed the basis for present-day, basic research on Antarctic seals.

| Expedition | Leader/sponsor | Years |
|---|---|---|
| *Little America I* (Bay of Whales) | Richard E. Byrd (Private funding) | 1928-1930 |
| British-Australian-New Zealand Expedition (BANSARE) | Douglas Mawson (Australia) | 1929-1931 |
| *Little America II* | Richard E. Byrd (Private funding) | 1933-1935 |
| British Graham Land Expedition (BGLE) | John Rymill (Australia) | 1934-1937 |
| U.S. Services Expedition, *Little America II* | Richard E. Byrd (U.S. Navy) | 1939-1941 |
| Operation Highjump/Operation Windmill | Richard E. Byrd (U.S. Navy) | 1946-1947 |
| Norwegian-British-Swedish Expedition | John Giaever (Norway) | 1949-1952 |
| Australian National Antarctic Research Expedition (ANARE) (Mawson Base) | Phillip Law (Australia) | 1954-1988 |
| Comité Spéciale de l'Année Geophysique Internationale (CSAGI) International Geophysical Year (IGY) | International Council of Scientific Unions | 1957-1958 |

of 1934-1937 led by John Rymill. Funded privately, these young scientists mounted one of the most successful land-based projects in Antarctic history: "The British Graham Land Expedition probably exceeded all others in the ratio of new knowledge to money expended" (Bertram, 1987, p. 56).

Their comprehensive studies and harmonious relationships with one another set a high standard for long-term cooperative ventures in this harsh environment. G. C. L. Bertram, a noted British biologist, was a young BGLE scientist who published a comprehensive study on Antarctic seals during the course of this expedition (Figure 3). Bertram was born in Worcester, England, in 1911. He completed his university studies at St. Johns College, Cambridge University, with a Ph.D. in 1939. He had a distinguished and broadly based career in biology, but we remember him in this paper for his excellent descriptive studies on the Weddell and crabeater seals conducted while serving as a young scientist on the BGLE. His work marked the beginning of more detailed and formalized scientific descriptions. He described his work as follows:

> My thesis was entitled, "The Biology of the Weddell and Crabeater Seals: With a Study of the Comparative Behavior of the Pinnipedia." And, by good fortune and some design, it was published as the first paper in the official series, from the British Museum (Natural History), being the results of the British Graham Land Expedition 1934-1937. Only one volume ever appeared for war intervened, and the Geological and Glaciological results were never published. . . . My seal work was based on a far greater amount of material than ever before collected from any southern seal, and perhaps any seals anywhere at that date. . . . My final paper was a considerable advance on what had gone before and was long, and is still quoted as a basic source of information. The section on comparative behaviour, with an evolutionary theme, was in a way a forerunner on some of the new biology . . . it was the part I most enjoyed writing. (Bertram, 1987, p. 57)

Since the advent of the IGY in 1957-1958 and the Antarctic Treaty, which was ratified in 1961 by 12 participating nations, numerous scientists with specialized and technological skills from many nations have studied the Antarctic seals. The list

**Figure 3.** G. C. L. Bertram conducted one of the first studies on the Weddell and crabeater seals.

in Table 6 was derived from accounts published since 1957 and is not exhaustive. Some investigators have expertise in more than one scientific discipline but have been listed in the category for which they are best known. Ridgway & Harrison (1981a, 1981b) edited a two-volume work, which presents a thorough review of work completed on these animals up to that time. To represent the major areas of research on Weddell seals, we will briefly describe the work of three biologists: Ian Stirling, Donald B. Siniff, and G. L. Kooyman.

Ian Stirling is a Canadian biologist who is currently working for the Canadian Wildlife Service (Figure 4). At present, he is studying ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) interactions and also is involved in various polar conservation activities. While he was a doctoral candidate at Canterbury University in New Zealand under the direction of Professor Bernard Stonehouse, a former FIDS/BAS researcher, he conducted a comprehensive study on the population dynamics of the Weddell seals in McMurdo Sound (Stirling, 1969). This work produced baseline information for subsequent research done by Don Siniff, who developed it into a long-term study, funded by the U.S. National Science Foundation, which is ongoing today.

Donald B. Siniff was born in Bexley, Ohio, in 1935. He received his formal education at Michigan State University and the University of Minnesota. As a faculty member at the University of Minnesota, he has been at the forefront of ecological studies on the Weddell seal in the Antarctic (Figure 5). His population dynamics study, begun in 1969, is one of the longest and most comprehensive studies on any marine mammal. Because of this program, data on reproductive behavior and success have been obtained and a life table has been developed for the McMurdo Sound population, which includes about 1,500 Weddell seals.

Several graduate students have earned degrees under Siniff working on various aspects of the population studies he began in 1969. Some of these students have remained active in Antarctic research and continue to make important contributions to Weddell seal biology. Siniff has been closely involved in committee work related to biology in Antarctica. He has served as a Commissioner and Scientific Adviser to the U.S. Marine Mammal Commission and was active on the Scientific Committee for Antarctic Research (SCAR) where he has made important contributions to U.S. Antarctic policy.

The following historical account is Gerald Kooyman's perspective on Antarctic pinniped research, mainly in McMurdo Sound and mostly about Weddell seals with a few digressions. Those digressions will be memorable stories of work on Antarctic fur seals at South Georgia Island and the Antarctic Pack Ice Seal Cruise of 1999-2000.

**Table 6.** A list of biologists who have published their findings on the Antarctic seals during the Scientific Period are listed below (compiled primarily from Ridgway & Harrison, 1981a, 1981b, and Perrin et al., 2008).

| Behavior | Ecology | Anatomy | Physiology |
|---|---|---|---|
| Cline, D. R. | Bengtson, J. | Bonner, W. N. | Castellini, M. A. |
| Evans, W. E. | Cameron, M. | Boyd, R. B. | Costa, D. |
| Ingham, S. E. | Carrick, R. | Bryden, M. M. | Davis, R. |
| Kooyman, G. L. | Condy, P. R. | Cuello, A. C. | Elsner, R. |
| Krilov, V. I. | Dearborn, J. H. | Denison, D. M. | Hochachka, P. |
| Mansfield, A. W. | DeMaster, D. | Drabek, C. M. | Kooyman, G. L. |
| Marlow, B. J. | Ecklund, C. R. | Ling, J. K. | L'Enfant, C. |
| Müller-Schwarze, D. | Erickson, A. W. | Pieraro, J. | Liggins, M. |
| Poulter, T. C. | Gilbert, J. R. | Polkey, W. | Qvist, J. |
| Ray, G. C. | Hall-Martin, A. J. | | Ponganis, P. |
| Rogers, T. | Hofman, R. J. | | Zapol, W. M. |
| Schevill, W. E. | Laws, R. M. | | |
| Smith, M. S. R. | O'Gorman, F. | | |
| Stirling, I. | Oritsland, T. | | |
| Terhune, J. | Penny, R. L. | | |
| Thomas, J. A. | Siniff, D. B. | | |
| Tikhomirov, E. A. | Stirling, I. | | |
| Watkins, W. A. | Testa, W. | | |
| | Vaz Ferreira, R. | | |

**Figure 4.** Ian Stirling, close friend and student of Bernard Stonehouse, who conducted one of the first comprehensive population studies on Weddell seals in McMurdo Sound during the time that I was studying the behavior and physiology of the Weddell seal.

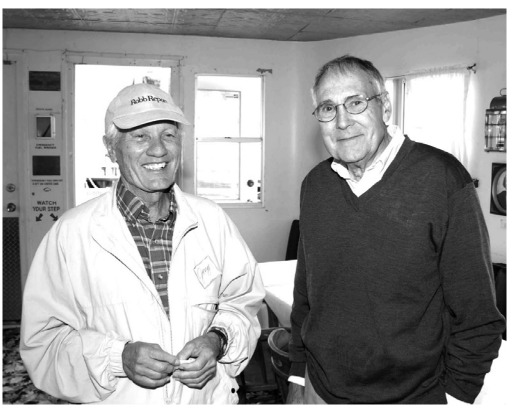

**Figure 5.** Jerry Kooyman and Don Siniff

## Summary of Weddell Seal Behavioral and Physiological Studies in McMurdo Sound (1964-1984) by Gerald L. Kooyman

In early October of 1961, I started working as a technical assistant to Dr. D. E. Wohlschlag on a fish study at McMurdo Station. Shortly after my arrival, John Dearborn took me for a tour on the vast sheet of 2-m thick fast-ice that covers a 2,000 km$^2$ area of McMurdo Sound (Figure 6). As we drove along in a Nodwell tracked vehicle, I got my first look at the Weddell seal. An animal was sleeping on the ice near a hole along a tidal crack, and I knew at first sight that this was an animal I wanted to study. The whole area was like a big, natural laboratory. The seals were unaccustomed to land animals or predators, and although they were uneasy about our presence, they did not retreat or respond aggressively. Two years later, I was able to initiate studies that measured their diving depth and submergence time. Like many such basic experiments, the technique was deceptively simple. The seal was released in an isolated, investigator-made hole in the fast-ice away from seal colonies with a small, time-depth recorder (TDR) attached. It returned with the instrument when it needed to breathe. This was the beginning of the Isolated Hole Protocol (IHP) that is still being used for Weddell seal and emperor penguin experiments. Indeed, as vast as McMurdo Sound is, there is, at times, competition for space to conduct experiments without interfering with other groups. The procedure is to establish a camp with a drilled hole, 1.5 m in diameter, that is at least 2 km distant from any other seal hole, manmade fishing hole, or stress crack in the ice. A seal is collected at one of the local haulout areas, coaxed or coerced into a custom-built sled, and towed by tracked vehicle to the camp. After appropriate sensors are connected to the recorder, it is attached to the animal with epoxy glue and released into the hole. What usually follows are several orientation dives by the seal that are of short duration of about 15 min. These are followed by extended dives, which are for distance exploration and attempts to find a way to another breathing hole. These are the longest dives the seal will make and, on rare occasion, the dives will exceed 1 h. Within a day, the seal accomplishes the three main types of dives, routine 10- to 15-min foraging efforts to mid-water depths of 200 to 400 m. Through the course of all these dives, the seal is observed from the hut that covers the hole, or from an under-ice observation chamber placed 5 to 10 m from the dive hole. Over the years, the recording technology has evolved from a simple, mechanical TDR to the microprocessor archival recorders everyone in the business now uses. In the beginning, these experiments were before personal computers, and miniature microprocessors were still in the future.

*Development of the TDR*

In 1963, Bernard Strothman, a watch repairman, machined the brass case and fittings that I needed to place a stripped-down, one-hour, windup kitchen timer inside. Instead of the usual timer

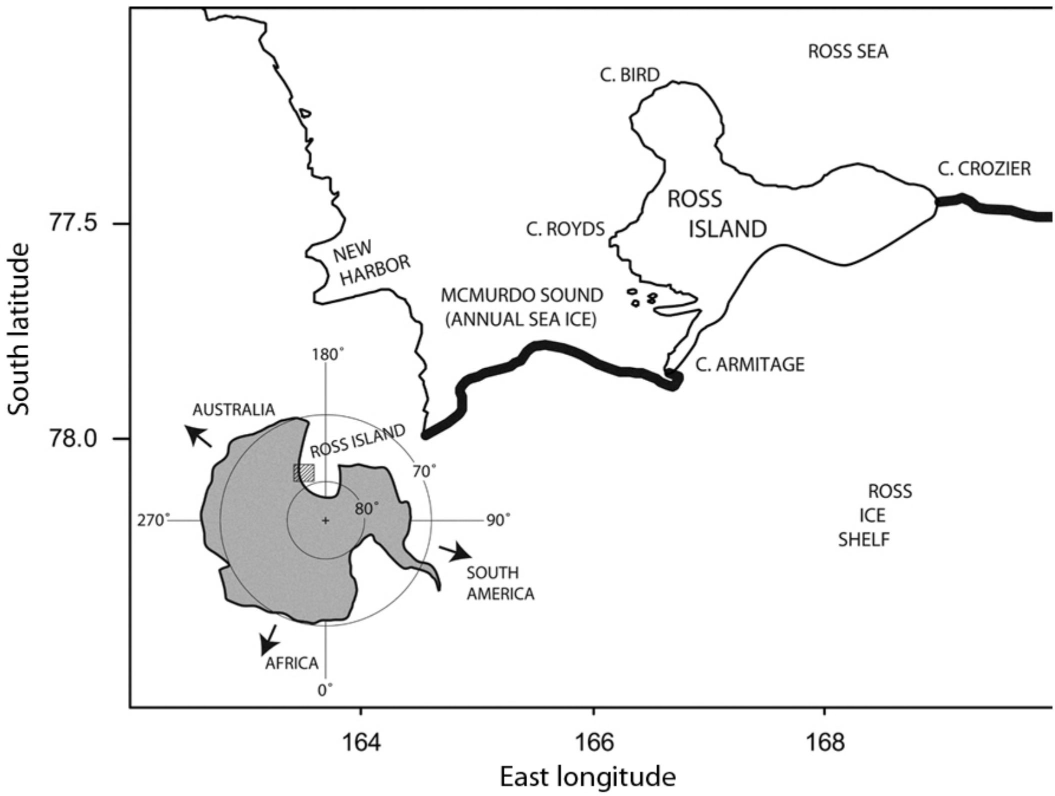


**Figure 6.** The inset shows the location of McMurdo Sound in relation to the Antarctic Continent. The heavy dark line is the northern edge of the Ross Ice Shelf.

face with dial and handle for winding, I mounted a smoked glass disk. Facing the disk was an off-the-shelf bourdon tube type pressure gauge that was extracted from a basic 5-cm diameter gauge. Voilá . . . the TDR (Figure 7). The first pressure range selected for the Weddell seal was equivalent to a depth of 500 m. Time duration of the recorder was a great limitation, and during the experiments, I had to remain at the hole to remove and replace the TDRs regularly. To enable this process, I placed a canvas blind around the hole and would lie down on the hut floor, raise the canvas enough to slip my head and shoulders past the blind, and hang out over the hole. When the seal surfaced and I wanted to remove the TDR, I had to reach down, lightly lift the TDR up, and unsnap the clasp (Figure 8). Usually I had to wait for another dive and return of the seal before attaching another TDR. It did not always go well, and often there was a surprised seal rolling in the hole, occasionally chirping and snapping, and a disgruntled investigator. The first year I worked alone, and in the second year Chuck Drabek, now emeritus professor from Whitman College, joined me as an assistant.

Before the TDR, most studies of pinnipeds dealt with land- or beach-based studies of breeding behavior, reproduction success, and demography. What they did at sea was a virtual "black box," and the TDR was a "window" into the marine world of these animals. Through collaboration with Roger Gentry, and the talent of an excellent designer and machinist in Jim Billups, we constructed a TDR that enabled us to record for two weeks. The limitation in this case was not battery-life, the usual nemesis these days, but the recording medium, which was film. From Kodak, we managed to get the thinnest film available at the time. How we got it, formatted it to our recorders, and what its original use was is another story. In any case, the recorders worked beautifully, and for a few, seemingly short years, I went worldwide in my quest to collaborate with other biologists and learn more about pinniped diving behavior (Figure 9).

During this time, another major technical problem impeded our progress. Our only means of attachment was using harnesses. This limited what type of animals we could put the TDRs on, and we needed a team to accomplish attachment on fur seals (Figures 10a & 10b). The result was


**Figure 7.** The first TDR designed and deployed on a diving animal; the casing is brass, and the kitchen timer is under the mounted smoked glass on the left.

an animal encumbered with a lot of drag (Figure 10c). Despite this handicap, the seals performed well, and we learned the basics about their diving habits. Soon there was a groundbreaking change. It was epoxy glue, and later even faster setting cyanoacrylate adhesives. When these came on the market, many more possibilities of how and on which animals the TDR could be placed became available. It brought an end to the use of harnesses, and soon thereafter the era of the mechanical TDR ended. By then it was the late 1980s, everyone had personal computers, and miniaturized microprocessor-type TDR recorders became commercially available such as the one used for scale in Figure 9. Only the imagination limits the type of sensors that can be incorporated into these devices that are now called archival recorders or biologgers. There are many variations or models of these recorders produced by several companies and individuals. In fact, much of the early telemetry technology was developed through the University of Minnesota by Larry Kuechle and Dick Reichle of Advanced Telemetry Systems in the Antarctic with seals. This technology has had a powerful effect on the research and knowledge accumulated about Antarctic pinnipeds. However, the topics I will discuss in the following relate to the early years of behavior and physiology studies of Weddell seals in McMurdo Sound.

**Figure 8.** G. Kooyman under the blind and in the act of attaching a TDR, which is in a canvas bag with clips for fast attachment, to a Weddell seal resting in the ice hole.

Through the first season of 1963-1964, I spent the full austral summer season (October through December) at McMurdo Sound. The success of the work increased substantially in the second year after Drabek joined me. Most of our time was spent

**Figure 9.** The prototype fur seal TDR on the right; the recording medium was pressure sensitive paper with a steel stylus for inscribing the pressure swings of the helical bourdon tube. On the left is the final TDR designed deployed on fur seals. The recording medium was a specially thin black and white film produced by Kodak. The primary use of the film was classified. The recording arm used a red light emitting diode for recording the pressure trace on the film. For scale, the archival recorder front and center is a Wildlife Mark 9, which is 6.5 cm long.

at the hut deploying and redeploying the TDRs on first one seal and then another. After we had completed measurements on one seal, we would release it and bring another to the site. The recorders logged every dive the seal made, and almost all of these were roundtrips to and from the IHP. As often as possible after the seal returned to the hole to breathe, the instrument was retrieved. When it did not return, the hunt was on around the Sound. Searching on snowmobiles, we usually found the seal, and when we did not, we scheduled a helicopter search. The last dive when the seal left was important because it would be one of the longest dives we would record and also gave us a clue as to how far another hole was from our study site. Our frustration levels often rose because the recorder, with its limited 1-h base, would stop before the seal reached another hole. I remember one profile in particular when the seal was steadily descending and had reached 200 m and it was still descending when the recorder ran out of time at 47 min. No doubt this would have been a record diving duration, and it was frustrating to have such limited recording time. During that season, I was able to determine that the seals routinely dive to depths of 200 m, and one dive was measured at 600 m, the estimated depth of McMurdo Sound. The other astonishing measurement showed a maximal dive time of 43 min, and Figure 11 shows the seal that did it and became a cover girl for *Science* magazine (Kooyman, 1966). Both of these values exceeded by far any predictions for pinnipeds. Since then, the recorded depth has been exceeded by only a few meters to 626 m in McMurdo Sound. Elsewhere, the record now stands at 714 m (Testa, 1994).

Soon after my graduate studies, I continued post-doctoral work first in England with Professor R. J. Harrison, and then at Scripps Institution of Oceanography. Initially, I joined Robert Elsner's lab and almost immediately we went back to McMurdo Sound for more physiological studies. I spent two seasons collaborating with Bob. In the first trip, we studied pregnant seal diving capabilities (Figure 12). On the second trip, the maximum dive duration record reached 87 min, measured by my colleagues and me in 1969 (Kooyman et al., 1971) (Figure 13). However, we may have given the seal an unnatural boost because we were attempting to measure lung volume by the nitrogen washout method in which the subject ventilates on 100% oxygen until a washout occurs. In this case, the seal dived before we switched back to normal air. The longest profile obtained on normal air, which gave us much information about the character of the dive, was obtained from a near-term pregnant female that made a 58-min dive. There was also another at 60 min with no profile (Elsner et al., 1970). We also obtained the entire ventilation variable of minute volume and tidal volume from a seal after a 70-min dive (Kooyman et al., 1971). This was an important observation because it indicated how long it takes for recovery back to normal blood chemistry levels after a dive. Finally, after years of work with Weddell seals, we summarized the frequency distribution of dives from the IHP and from free-ranging animals. Of 1,100 dives measured from the IHP, only 82 (8%) exceeded 26 min. From 4,600 dives measured from free-ranging seals, only 123 (2.7%) exceeded 26 min (Kooyman et al., 1980). Since then, there have been many studies of Weddell seals in McMurdo Sound and some results have probably superseded these records, but the basic information showed that Weddell seals are a conservative diver when compared to southern elephant seals, the studies of which began in the 1980s by Burney LeBoeuf and Dan Costa's group at the University of California, Santa Cruz.

During this period of time, we also were the first to obtain heart rates, a variety of pulmonary function values, and metabolic rates using the conventional way of measuring oxygen consumption, all from free-diving seals. Here, I make the distinction between free-"diving" and free-"ranging" to differentiate between seals diving from an IHP and those on their own around McMurdo Sound, or anywhere else for that matter. Most of these physiological measurements must use an IHP because of the methodology, the need for access to the instruments after short intervals of time, and for the respirometry measurements. Since the advent of the microprocessor, heart rates can be and have been obtained from free-ranging

**Figure 10a.** The first fur seal proof of concept group that visited Bird Island in 1977 from the *NSF R/V Hero*; standing from left to right in front of the original NSF-USARP hut are unknown, unknown, Peter Prince, Randall Davis, Frank Todd, Sean McCann, John Croxall, unknown seaman, and sitting is Jim Billups, designer and builder of the TDR (Photo by G. Kooyman).

**Figure 10b.** The first deployment team of the TDR on an Antarctic fur seal in 1980. Standing from left to right are Randall Davis, Steve Hunter, and Colin Pennycuick. Seated from left to right are Ian Hunter, Jerry Kooyman, and John Croxall. Note the fur seal pups and light mantled sooty albatross.

**Figure 10c.** Antarctic fur seal with TDR and harness (Photo by C. Pennycuick)

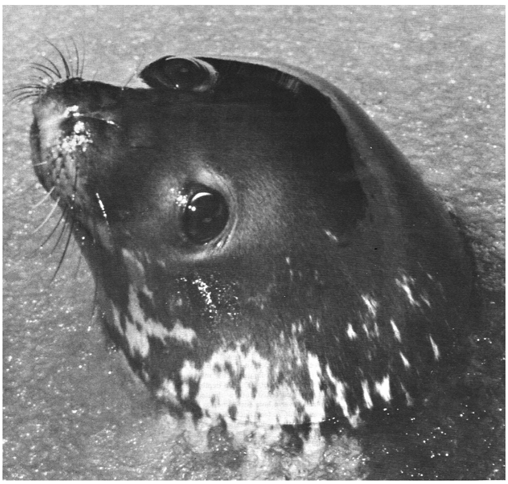

**Figure 11.** Weddell seal on the cover of *Science* magazine for the publication of the first detailed report on diving behavior in a marine mammal. The photo was taken while the seal was in the hut with the isolated diving hole described in the text.

animals, but in those paleo-physiology years of the 1960s and 1970s, such devices were not available. Instead, we used very long (10 to 70 m) electrode leads attached to breakaway connectors. These connectors were part of the mount that we used to attach the electrode plates to the chest of the seal and then waterproofed with neoprene covers. In this way, we were able to obtain the first 3 to 5 min of a serious dive and the entire dive of an animal resting under the ice. Like the TDR work, we got very "close and personal" with the seal for hours at a time. For me, these were some of the finest hours of working with a wild animal. When devices became more automated and recordings more remote, there was a loss in the connection with the animals that I have missed ever since, even though the animals were probably pretty irritated with us most of the time. The heart rate work gave some insights into the energy expenditure of the animals, and more importantly, some insights about the diving response of the seals. Prior work on the diving response dealt with forced submersions, and what we were doing was determining how it differs from "free" diving. Indeed, even though the term *diving* is used throughout the literature on studies of forced submersion, I think it

**Figure 12.** The physiology and behavior team led by Robert Elsner to McMurdo Sound in 1968. Standing left to right are Robert Elsner, Charles Drabek, and Claude Lenfant. Kneeling is Jerry Kooyman.

**Figure 13.** The 1969 team of Walton Campbell, Dan Kerem, and Jerry Kooyman working in McMurdo Sound to determine the pulmonary function variables of the Weddell seal.

is inappropriate to use the term for these types of experiments. Results from free-diving experiments were intriguing because the bradycardia was not nearly as dramatic as in the forced submersion, and to us at the time, this suggested a more open circulation during the dive. It has taken decades, and some very sophisticated instrumentation, to resolve this mystery of how diving animals use their oxygen stores, and it has been accomplished just recently with the work of Paul Ponganis and his graduate students (Ponganis et al., 2003; Stockard et al., 2005; Ponganis, 2007a, 2007b, 2009; Meir & Ponganis, 2009; Meir et al., 2009). That is another story worth telling, and I leave that to Paul Ponganis. For now, I will tell of another element in the free-diving story that began with studies in the late 1970s, and in one way or another continues into this new millennium of 2000.

*Physiology*

This critical question of the difference between forced submersion and free-diving took research beyond the basic parameter of heart rate variation during the dive. Most fundamental of all was the question of the degree of anaerobic metabolism during the dive. The basic element was the abrupt rise in lactate at the end of a forced submersion. The lactate surge always occurred, even on the shortest of forced submersions, and was sometimes called the "hallmark" of diving. Well, it is not. What we found during our, again, very simple technical procedures was that an increase of blood lactate is seldom seen. Indeed, that was the main reason for doing the analysis in the 1980 paper showing how many dives occurred in excess of 26 min. Less than 3% of dives by Weddell seals are beyond this special number. Mike Castellini, Dan Costa, and I determined the frequency distribution of free-ranging Weddell seals not because we were especially interested in the foraging behavior of Weddell seals, which we were, but because of the relationship it held to the previously determined lactate to dive duration curve.

Construction of the curve was obtained from multiple seals and blood samples. These samples were obtained by placing an arterial catheter in the fore-flipper of the Weddell seal, putting an extension tube on the catheter and a float on the end. We were under the blind again. This time to retrieve the catheter tip, floating at the surface next to the seal's head, and then drawing a blood sample. Most of this and the results are detailed in Kooyman (2006). The float was necessary so that the end of the catheter would be at the surface and within easy reach of the sampler. Again, we were working from behind a blind and "up close and personal" to the animal. Since the seal was diving in freezing water at a surface water temperature of -2° C, the flush in the catheter tubing could not be normal saline, which freezes at -0.5° C. We had to use a nontoxic flush in case some was injected into the animal. Easily available was ethanol, which we diluted to about 10%. From all of our samples we constructed the lactate/endurance curve that showed that Weddell seals seldom make a dive that has a significant anaerobic metabolism component (Figure 14) (Kooyman et al., 1980, 1983). The threshold at which there is an increase in blood lactate occurs at about 26 min, and thus the significance of that dive duration to the natural history of the Weddell seal. To accomplish these experiments, I had an exceptionally good team of experimentalists (Figures 15a & 15b). Since then, very detailed and elegant study of foraging behavior and physiology of the Weddell seal (Williams et al., 2004) confirmed the curve by similar measurements, except their threshold is at 23 min. This shorter aerobic limit could exist for a variety of reasons, including the possibility that the seals were more encumbered, increasing drag because of extra gear, including a camera, which may have added extra work to their diving.

Later, we coined the term *aerobic diving limit* (ADL), a term which was later modified by Butler (2006) to the *diving lactate threshold* (DLT); they are now used interchangeably. For me, I tend to still call it the ADL. With this concept, a whole range of studies suddenly developed within the community of physiologists and ecologists interested in the foraging behavior of marine mammals. We wanted to know more about the diving metabolic rate and the oxygen store of these animals so that we could calculate the cADL. The Weddell

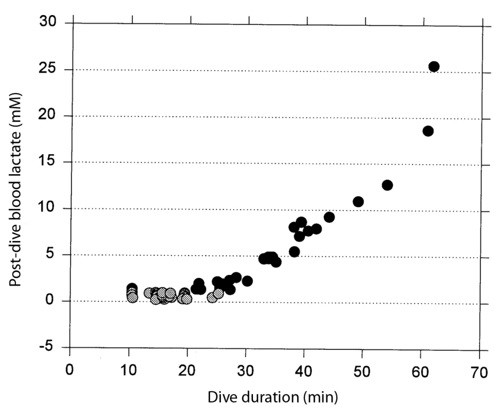


**Figure 14.** One of the main results of the expedition was the plot of lactate endurance curve. The gray dots indicate dive durations for which there was no increase in post-dive lactate above that of the resting seal. The black dots are for when an increase in blood lactate occurred indicating a net production of lactate and anaerobiosis during the dive.

**Figure 15a.** The 1977 team working in McMurdo Sound to determine the blood chemistry of freely diving Weddell seals. The team consisted from left to right of Jerry Kooyman, Michael Castellini, Randall Davis, Eric Wahrenbrock, and Everett Sinnett.

**Figure 15b.** The enlarged team to conduct more detailed and extensive studies of physiological processes of diving seals of different ages in 1981. Standing from left to right are Randall Davis, Jerry Kooyman, Eric Wahrenbrock, and Charles Parkos; and seated from left to right are Michael Castellini, Maria Davis, Robert Maui, and Markus Horning.

seal would be the "truthing animal" because in few other diving animals could we determine the ADL as directly as with the Weddell seal.

Other variables that could only be measured in the Weddell seal were the recovery time in relation to arterial lactate concentration and how Weddell seals managed an oxygen debt after a very long dive. Possibly the only species and circumstance where this could be measured was on the Weddell seal. For example, we obtained the complete recovery of a seal that obligingly remained at the surface for 50 min after a 43-min dive (Figure 16). We also constructed a summary of recoveries from several dives (Figure 17). This is possible only in the Weddell seal because the IHP allows the researcher to follow closely the diving activity of the animal while collecting blood samples when appropriate. These results have important implications for other diving species. For example, what was the blood chemistry of southern elephant seal #1423 that made a 120-min dive and followed this long dive with several, nearly hour-long dives (Hindell et al., 1992)? We can only guess, but using the results of the Weddell seal study may help understand the southern elephant seal better.

What we have learned from the unique set of data on recovery is that for dives only slightly exceeding the ADL, it takes about a 10-min surface time to return the blood lactate to resting levels (Figure 17). That is slightly more than three times the surface recovery normally required during foraging diving bouts of Weddell seals to restore oxygen stores between dives. To take this a step further and apply yet another unique set of data, we learned that Weddell seals will not necessarily stay on the surface for extended periods of time in order to return blood lactate to resting levels. Instead, they may continue to dive probably within their ADL and use the excess lactate as a fuel during the aerobic dives that follow. It may take longer to get their blood chemistry back to normal values, but during the process, they can continue to dive and hunt (Kooyman, 1987; Castellini et al., 1988). All of this is explained in more detail in Kooyman (2006) as well as in Kooyman (1989).

Once the ADL of a diving mammal was measured, it became clear that with a few simple calculations, a cADL could be determined for any diving animal if the diving oxygen consumption rate and the oxygen store were known. The oxygen store could be obtained through a sampling program of blood volume, hematocrit, and myoglobin concentration. All of these variables can be determined in the field from any captive and restrained animal. In addition, the lung or air sac (if working with birds) volume, as well as the diving oxygen consumption, could be estimated from scaling equations. Armed with these possibilities, ecologists have made estimates of many diving species to determine their foraging abilities and how good a match they are with the cADL. From these results, all sorts of hypotheses can be derived, and I address one dealing with southern elephant seal #1423 in the section on southern elephant seal later.

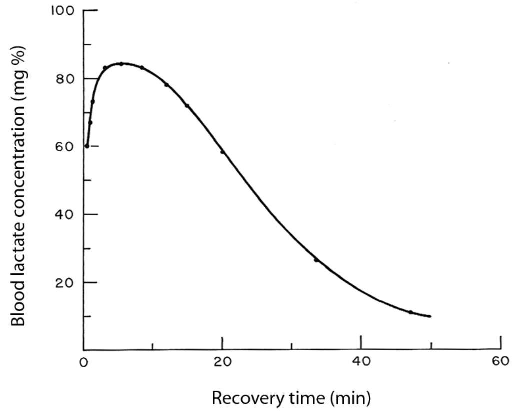


**Figure 16.** The complete recovery of arterial blood lactate of a Weddell seal that had previously made a 43-min dive

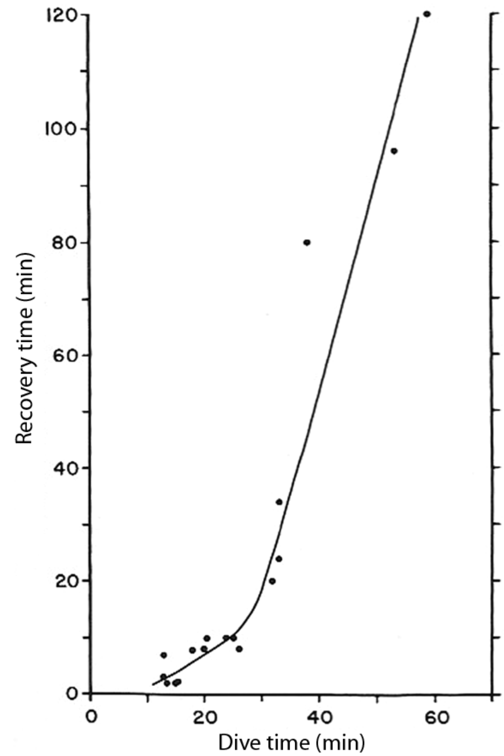


**Figure 17.** The overall blood lactate recovery curve as a composite of several dives and seals

While my team was in the midst of conducting many of the studies just discussed, Warren Zapol and his team from Harvard and elsewhere were conducting experiments in the laboratory at McMurdo Station on forced submersions of pregnant Weddell seals, and later on diving responses of freely diving Weddell seals in McMurdo Sound (Figure 18). In the former experiments, the results were a good foil for us in comparison with our free-diving experiments. In the later experiments, they applied submersible microprocessor technology for the first time to a diving animal. The engineer for this work was Roger Hill, an Oxford physicist, who later turned the technology into a commercial product, the archival recorder (i.e., Wildlife Computers Inc.). All of us in the field of diving animals are grateful to Roger for doing this, especially me, because it eliminated the necessity of designing and constructing our own TDRs, which was always a major task and distraction from our scientific research.

With these programmable recorders onboard the Weddell seal, the Zapol group could obtain blood samples throughout the dive. In doing this, they noted that there was a marked rise in hematocrit during the dive. This raised the blood oxygen-carrying capacity significantly during the dive bout. Through dissections, they showed that the spleen of the Weddell seal was exceptionally large and confirmed the hypothesis first proposed by Bryden & Lim (1969) that the spleen was an important blood cell reservoir for enhancing the body oxygen store. Zapol (1987) called it the "SCUBA" tank effect. However, we disagreed with that model because it assumes the tank (spleen) is filled after every dive. Concurrently with the Zapol investigations, we were working with changes in blood chemistry of freely diving Weddell seals and found that during a diving bout, the spleen initially contracts and raises the hematocrit to its elevated level noted by Zapol, but it remains there through the course of the bout. In the Zapol experiments, they were working with single or a few dives and did not have the data from diving bouts. The hematocrit returns to resting levels after the bout and essentially saves the work of the heart because of the higher viscosity resulting from the increased hematocrit (Castellini et al., 1988).

**Figure 18.** Warren Zapol at the command console of a deep-diving submarine (From *Anesthesiology* [1999], *91*, 917-919)

Another elegant experiment of the Zapol team was the measurement of blood $N_2$ levels during the dive. Drawing blood samples at various intervals throughout the dive, they showed that the arterial blood $N_2$ during dives as deep as 280 m never exceeded 3 Atmospheres Absolute (ATA) (Falke et al., 1985). I was delighted to see this result because it matched, as closely as could be expected, the values we obtained from northern elephant seal diving experiments at Guadalupe Island, Mexico, in 1970 and published two years later (Kooyman et al., 1972). More detail on these pressure studies and the effects of pressure on diving mammals is in Kooyman (2006).

*Foraging Behavior*

The first foraging behavior of any diving animal was conducted at McMurdo Sound by Drabek and me as described earlier. We could do those studies because of the mellow behavior of Weddell seals, which at that time showed little response to humans and seldom took flight at our approach. In addition to the seal, the environment was ideal with the stable fast-ice, which remained intact well into January—mid-summer in the Antarctic. I described this unique polar setting and how these attributes created a hot-bed for foraging studies of Weddell seals, but also for many programs of marine polar biology at a recent Smithsonian conference (Kooyman, 2009b). Numerous studies of different aspects of Weddell seal ecology have come from McMurdo Sound. Several former students and I have conducted and are conducting a variety of studies on the foraging ecology of Weddell seals. Both Terrie Williams and I have written books about Weddell seals at McMurdo Sound (Kooyman, 1981; Williams, 2004). With few exceptions, all have dealt with Weddell seals during the summer. The exceptions are a study in late winter that I conducted with the assistance of W. Campbell and D. Kerem in 1968 and 1969 at McMurdo Sound. Then, a decade later, my team did another winter study in 1981 at White Island, which in this case included an overwinter study both at the Island and in McMurdo Sound. This may have been the first and perhaps will be the last study conducted through the entire winter at a remote camp with intermittent support from McMurdo Station.

We established the camp in January 1981 (Figure 19a). It was a major undertaking with the following camp components: (1) a living hut; (2) a garage consisting of a Jamesway for the Spryte, a tracked all weather and terrain vehicle, and four snowmobiles; and (3) a laboratory hut which had an aluminum lined ice hole that extended about 50 ft through 4 m of sea ice and 15 m of platelet ice. The winter crew of Michael Castellini, Randall Davis, Maria Davis, and Markus Horning were seldom there all at the same time (Figure 19b). They rotated through the winter night, making the long drive to the camp about every three weeks. There is not space to tell of the wild experiences they had at White Island, tracking down seals to attach or retrieve TDRs, nor of sea ice experiences in McMurdo Sound during the winter. It is enough to say that the camp was placed directly in the path of the winter storms called Herbies that came down from the polar plateau, blew through the camp, and out to sea over McMurdo Sound. To quote Douglas Mawson (no better description fits this place although described for his base at Cape Denison, on record as the windiest place in Antarctica): "We dwelt on the fringe of an unspanned continent, where the chill breath of a vast polar wilderness, quickening to the rushing-might of eternal blizzards, surged to the northern seas. We had discovered an accursed country. We had found the home of the blizzard." In this case, the accursed place was White Island.

Suffice it to say they survived this place, although during the winter a rescue of the camp had to be organized because, unknown to anyone, the snow deposition in the area was great and depressed the sea ice surface below sea level. The camp structures exacerbated the situation as they behaved like snow fences and accumulated major amounts of snow. The outcome was that the huts were buried, and the weight of the snow so depressed the ice that major flooding from the nearby tidal crack put the camp awash and it had to be moved. This required a team of workers and heavy equipment. To everyone's credit, the move was achieved after great effort, and the camp remained in place until late into the following summer.

During the winter and summer studies at White Island and McMurdo Sound, we learned in regard to White Island much about the benthic fauna, how infrequently the seals come to the surface, how many seals were in the population, the number of pups born, the food habits of the seals, and the character of their diving behavior. All of this was especially interesting because the seals, and the rest of the fauna, are isolated and they live under very thick ice. Based on snow cover, storm patterns, and light levels below the ice, summer never comes to White Island. While existing under conditions of eternal winter, there is little above-ice activity by Weddell seals, and below the ice the seals do not dive below 200 m or far from the tidal crack along the shore line. The crack provides their only access to air, and sometimes they must burrow through several meters of platelet ice to get to the surface and to return below the sea ice. Some of the study results obtained were similar to the previous winter study in McMurdo Sound (Kooyman, 1975). At White Island, there were no extended dives by Weddell seals. Since the earlier study in McMurdo Sound was conducted at the IHP, it influenced some seals to make exploratory dives. In these cases, they were the shallowest exploratory dives ever recorded and were usually less than 50 m. During early winter of April to June 1981, the frequency of dives were evenly distributed throughout the 24-h period, whereas in January, a period of 24-h daylight, most dives were at "night" or low sun. This was also true for the seals in McMurdo Sound. In the course of these studies in the Sound, a female Weddell seal set a new diving depth record of 626 m. This broke the previous record set nearly 15 years earlier. In this record, the entire dive profile was obtained as well as the series of dives in which it occurred. In the course of 4.5 h, the seal made 12 dives, four of which exceeded 600 m, and all but one were deeper than 500 m. This was an exceptional record for a pinniped until some years later when elephant seal diving behavior studies began.

In summary, the reason for dwelling on this single, singular species, the Weddell seal, through these many paragraphs is that numerous landmark studies were accomplished. In doing so, the Weddell seal has become and continues to be the most studied and best known of any single species of pinniped. It was the first animal to carry a TDR and, later, a biologger attached and deployed to learn more about the diving characteristics of the animal. There is probably more detailed information on the natural history of this seal than any other, and there is certainly more about its diving physiology than any other. There continue to be numerous studies of Weddell seal diving biology by second and third generation investigators that use the IHP and/or McMurdo Sound as a platform to conduct these studies. These range from the diving physiology studies of Ponganis (Horning & Hill, 2005; Ponganis, 2007a), through the consequences of aging and diving of Horning (Horning & Hill, 2005), to the natural history and detailed tactics of hunting Weddell seals of Davis and Williams (Davis et al., 1999; Williams, 2004). Pleasing to me, as this perspective is being written

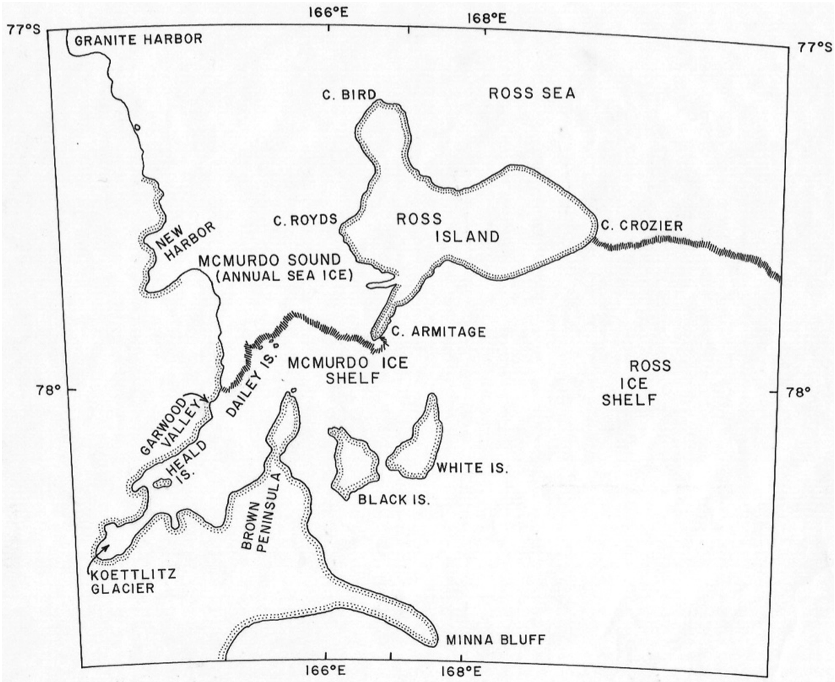


**Figure 19a.** The location of White Island in relation to McMurdo Sound. This site is one of only two where Weddell seals breed as far south as 78° S. This is the most southerly breeding area of any mammal.

**Figure 19b.** The White Island research team from left to right: William Stockton, Markus Horning, Robert Maui, Jerry Kooyman, Michael Castellini, Randall Davis, and Maria Davis. The three who did not winter over were W.S., R.M., and J.K.

(July/August, 2009), the latter authors are conducting a detailed late winter study of diving in Weddell seals in McMurdo Sound in which they are employing an attached video camera as well as the additional hardware to record numerous characteristics of each dive in three dimensions. Sigh . . . It makes me weep to think of all the wonderful toys my scientific "children" and "grandchildren" possess to pursue elegant inquiries into the mysteries of the deep.

## Antarctic Seal Research Since 1990

*Antarctic Fur Seal*

The decades following the original work with TDRs were an exceptional time for pinniped studies, and the arrival on the scene of a means to go beyond attendance and breeding behavior in fur seals and sea lions was timely. The Antarctic fur seal was in rapid expansion from a remnant population of about 100 animals in the 1930s to a few hundred thousand by the mid-1970s. In 1984, Laws published a review chapter on Antarctic seals, and it contains a curve that is prophetic. He extrapolated the population trajectory of the Antarctic fur seal to the year 2000. His last data point was 1980, and the projection was for a population of about 2.5 million by 1990, and 4 million by 2000. The last coarse estimate of the Antarctic fur seal population was made in 1990 at South Georgia Island, and the total population was estimated at 1.5 million (Boyd, 1993). Laws' projection seems an overestimate, but considering that at one time the species was thought to be extinct, the 1980s and 1990s were really good times to be a fur seal biologist or tourist in the sub-Antarctic or Antarctic. Not only was the Antarctic fur seal population growing at South Georgia Island, but it was spreading to other sub-Antarctic islands and to the Antarctic.

Therefore, when Roger Gentry and I decided to develop a new TDR that would have a much longer time base than my original recorder, the plan was to deploy it on fur seals. The two-week duration was the primary specification to fit with the known foraging cycle of the northern fur seal, but by luck it also fit well with the Antarctic fur seal. We tested the prototype on the northern fur seal in the summer of 1975. At that time, for all we knew, fur seals grazed at the surface, and we would not get any dive records. But we did, and my son, Carsten, was there to enjoy the thrill of it all when the first northern fur seal returned and we felt we had discovered the Mother Lode. Still, Roger's and my enthusiasm was not contagious enough for him, and years later, despite a Zoology degree, my son became a pilot and went flying. This vocation was another love and seemed more stable than my existence on grants. I now kid him about the stable airline industry that he joined.

Roger and I quickly followed the prototype test with a revised and final TDR model which we employed on South African fur seals in January 1976 with technical help from Mike Meyer and the political help of Peter Best. It is not easy to get permission to put foreigners onto the premises of a South African diamond mine near Kleinsee where the fur seal colony resided (Figure 20). After the African experience, I mixed Weddell seal diving behavior studies, as described above, with Antarctic fur seal work, and Roger went back to his work on northern fur seals.

In 1980, Randy Davis and I traveled to South Georgia Island to do the first study of diving on the Antarctic fur seal. It was no ordinary expedition as we met Richard Laws on the crossing from South America to South Georgia Island, and then we teamed up with John Croxall at Bird Island. These were luminaries of the BAS, and we were pleased to cement lasting friendships during that work. In the end, our modest first attempts to understand the Antarctic fur seal's foraging behavior became part of a chapter in a book Roger and I edited and published in 1986 (Gentry & Kooyman, 1986). The book contains chapters on the attendance and foraging behavior of six species of otariids: five fur seals and one species of sea lion. Of these species, I was a co-author on all species—not by design, but it just worked out that I played a key role in getting the diving data. Researching and writing the book was a great experience that allowed me to get to know well

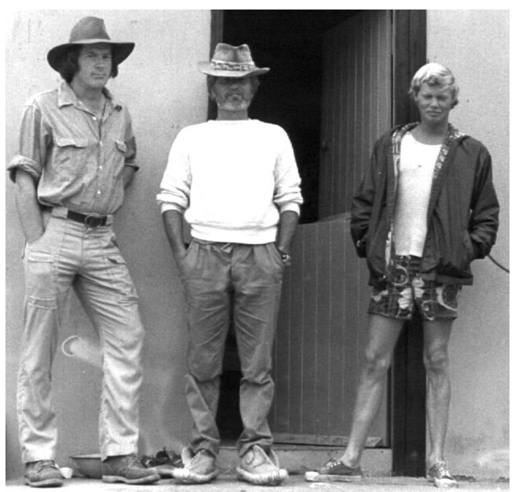

**Figure 20.** The South African fur seal research team that performed the first study and final test of the development of the TDR. From left to right are Roger Gentry, G. Kooyman, and Mike Meyer at the Kleinsee diamond mine site.

so many colleagues and different kinds of marine mammals. Since that time, Dan Costa has told me that he has now studied all species of otariids. That is a major accomplishment, and it pleases me that his work also began in my laboratory at Scripps Institution of Oceanography.

In the last 20 years, studies on the Antarctic fur seal at sea have, since the inception of such investigations, expanded to unimaginable levels. A few examples will illustrate my point. One of the earliest reports, after the publication of the fur seal book, was the determination of a close correlation with the Antarctic fur seal diving behavior and the diurnal movement of krill from the depths to the surface (Croxall et al., 1985). Then, Ian Boyd's group reported on the foraging response of Antarctic fur seal to environmental changes. They used only TDRs (McCafferty et al., 1998). In a later paper, they tracked the distribution of the Antarctic fur seal using both TDRs and satellite transmitters to determine the whereabouts of the fur seals during their foraging trips (Boyd et al., 2002). This was one of the first studies on fur seals using the new technology of satellite tracking, and it is one of the greatest ever leaps forward on understanding animals at sea, with the bonus that the recorder does not have to be retrieved to get the data. Almost concurrent with this study, but from one conducted at Kerguelen Island, Antarctic fur seals were tracked by TDR and satellite telemetry to determine where they were foraging. This study was the first to coordinate fur seal foraging data with the collection of oceanographic variables and determining fish abundance by trawling from a research vessel (Guinet et al., 2001). Lastly, Bailleul showed the difference in foraging areas of two sympatrically breeding species, the Antarctic fur seal and the sub-Antarctic fur seal (*A. tropicalis*) (Bailleul et al., 2005). In this case, they used both TDRs and satellite transmitters to determine depth of dive and geographical distribution of the seals.

*Southern Elephant Seal*

The southern elephant seal is a special case of a commuter and deep diver. The only species even closely resembling what this species does is the northern elephant seal, its congener. Their diving habits seem to be duplicates of each other, and their commuting is a mirror image. Both were hunted to near extinction for their blubber oil; both made amazing population recoveries; both made this recovery from small, isolated islands; they both have amazing diving habits; and their commuting patterns are mirror images, with the northern species migrating to the west and/or north and the southern species migrating east and/or south, which they do twice a year. In both cases, their natural history at sea might not have been guessed if it were not for the brilliant combination of using satellite transmitters and TDRs (SLTDRs). One of the first such reports was that of McConnell of the BAS (McConnell et al., 1992). They attached SLTDRs to three female southern elephant seals at South Georgia Island, and one of those migrated deep along the Antarctic Peninsula coast 2,650 km from its starting point. The other two approached, but never quite reached, the Antarctic Peninsula. Other studies followed in which males were included in the experiment (McConnell & Fedak, 1996). The males remained near South Georgia Island, but again the females either went south to the Antarctic Peninsula or they went east. One reached a maximum distance of 3,085 km from South Georgia Island. Building up a large data set that they obtained from 1,785 days of tracking, a recorded maximum dive of 1,585 m was recorded, and it was found that 90% of the seal's time was spent under water with an average dive time of 21 min. There were examples of favored locations to which some migrated over successive seasons.

Almost concurrently, the Australians were conducting similar studies from Macquarie Island on 23 female and 16 male southern elephant seals using TDRs. In over 50,000 dives, they obtained a 120-min dive from famous female #1423. Apparently, she was not so famous to the Australian ecologists in their first paper because they barely mention her, and no profile of the dive nor the following dives were described (Hindell et al., 1991). Unlike the study of McConnell, they did not use satellite tracking, but instead estimated the location of the seals from water temperature obtained from the temperature thermister imbedded in the TDR. From this, they determined that some fed along the APF, while others went to the Antarctic continental shelf. Southern elephant seal #1423 is of special interest to diving physiologists because it raises several questions about not only why a seal would make such a long dive, but how long it took to recover from what must have been a great oxygen debt.

To their credit, a year later, the authors published a detailed report of #1423 and 13 other seals that exceeded their cADL routinely (Hindell et al., 1992). They suggested that these animals could exceed the cADL by becoming hypometabolic. I do not think this is necessary in most cases, and much of how such long dives are performed are an enigma. However, some of the answers are now available that were not available in 1992. First, almost all of the seals were pregnant females, and the blood volume is greater during pregnancy than otherwise. For this reason, the oxygen store is larger. Also, it has been shown recently in northern elephant seals that blood oxygen utilization is much greater than in earlier estimates. In addition, it has also been shown that northern elephant seals, and presumably southern elephant seals, glide for extended periods, which is close to resting metabolic rate and not necessarily hypometabolic. As a result, the cADL used for the estimates on these southern elephant seals is too low. Therefore, many of the dives thought to exceed the ADL do not, and there is no lactate accumulation. Finally, for the exceptional 120-min dive, there may be a reduction in metabolism; the seal may have been resting throughout the entire dive, and even with following dives, swimming may have been minimal as the seal was still in recovery. A hypothetical case of this type of recovery was posited for the northern elephant seal (Kooyman, 1988). Unlike the Weddell seal that has a calm platform of sea ice with a breathing hole where it can rest, the elephant seals are diving in some of the roughest seas in the world. In addition, the Weddell seal has no predators of concern, but the elephant seals have both shark and killer whales (*Orcinus orca*) as predators, thus, remaining at the surface is not a good option compared to the calm conditions below the surface. And finally, why would a seal make such a long dive? Perhaps a long, deep dive is the best strategy for an elephant seal to avoid predation by killer whales.

Back to the topic of monitoring southern elephant seals at sea. In a later, but similar study (Campagna et al., 2000), TDRs were attached to 23 southern elephant seals, 21 of which were females, at the breeding colony of Peninsula Valdes, Argentina. In this case, the seals had to travel over a very broad continental shelf to reach deep water. Campagna and his team not only measured water temperature with the TDR, but also used the time of sunrise and sunset to determine their geographic location. He was also one of the first to mention the use of seals as oceanographic platforms for collecting data usually left to the physical oceanographers.

Not long after, a serious study using southern elephant seals as oceanographic samplers (SEaOS) was launched. This was a circumpolar study where 85 Conductivity Temperature Depth (CTD)-SRTDLs were deployed from various sites around the Southern Ocean on seals just after the elephant seals' molt, and they were tracked through the winter. The result was a paper with almost as many authors as there were seals in the study (Biuw et al., 2007). It provided data in ice-covered areas that would have been hard to come by using conventional means on oceanographic ships. However, there were large gaps in the two mystery seas of the world, the Ross Sea and the Weddell Sea, simply because southern elephant seals apparently do not go there in the winter. Indeed, from my own personal experience during a winter cruise to the Ross Sea, I can tell you there are no birds nor mammals there except for breeding emperor penguins, Weddell seals, and snow petrels (*Pagodroma nivea*) (Van Dam & Kooyman, 2004).

*Ross Seal*

It is quoted by Thomas & Rogers (2009) that "Less is known about the Ross seal than any other pinnipeds" (p. 988). This was thought to be true based on the paucity of sightings of this species. It was believed to be extremely rare. Happily, I participated in a cruise that showed it was not so rare but, rather, has a cryptic natural history. During this Antarctic Pack Ice Seals (APIS) 1999-2000 sojourn, we spotted over 70 Ross seals during about 40 days of transects in the Amundsen and Ross Seas. Much of this was through heavy pack-ice with large floes. All of the seals were in molt, and all were alone in the middle of large floes. According to Ian Stirling, who was obtaining underwater recordings, there were many Ross seals in the water within recording distance of his hydrophone.

In 1997, the duo of Bengtson & Stewart (1997) published the first preliminary report on the results they obtained from one Ross seal in the Antarctic Peninsula. They attached a TDR and recovered the same two days later. There was little learned from this short record in which the maximum depth was only 212 m. The more sensational aspects of this species was to follow using the later technology of SLTDRs from which they obtained tracks and dive records. In 2000, Bengtson and others deployed some SLTDRs on a few seals in the Ross Sea (Boveng, pers. comm.). They confirmed what was measured by Norwegians working offshore from the opposite side of the Antarctic near Queen Maud Land. Ross seal breeding habits are the reverse of the southern elephant seal. Blix & Nordøy (2007) deployed SLTDRs on 10 post-molt Ross seals in February and obtained data from six. The seals made about 100 dives/day, and the hunting range was from 100 to 500 m with the deepest dive at 792 m. However, the most interesting result, by far, is that after their molt, Ross seals travel up to 2,000 km north into open water and out of the Southern Ocean. They return south of the APF in about October. By following three pregnant females, they learned exactly where in mid-November the seals pup and that nursing lasts 13 days. Natural history through remote recording does not get any better. Should the Ross seal be classified as an Antarctic seal or a sub-Antarctic seal? We also now understand why sightings are so uncommon. When they are in the Antarctic, they dwell in such heavy pack-ice that few ships ever dare or are capable of entering in search of those solitary molters. Otherwise, the rest of the year is spent in some of the most remote waters of the world, where few ships, except fishers, have an interest in sailing, let alone being lucky enough to see a Ross seal at sea. Such an event has probably never occurred.

*Crabeater Seal*

The crabeater seal is arguably the most abundant pinniped in the world (Bengtson, 2009). How abundant is an area of dispute which I will leave to the population ecologist who writes a perspective for this series. Again, the coworkers of Bengtson and Stewart were one of the first to obtain diving records of this species (Bengtson & Stewart, 1992). In 1986, they applied TDRs to six seals that were recovered four days later. In this preliminary report, they found that 90% of the dives were < 50 m. Again, the Norwegians followed them with the technically more capable SLTDR attached to eight crabeater seals, which transmitted for up to 5 months. The seals stayed close to the shelf within the pack-ice and moved north as the sea ice expanded with the onset of autumn. They made about 150 dives/day and recorded the maximum depth for this species of 528 m. However, most dives were less than 50 m. They were active mostly at night in March, but with the lengthening of the night in April and May, there was no diurnal pattern (Nordøy et al., 1995). Soon after the Nordøy study, the Australians conducted another crabeater seal study in eastern Antarctica, and consistent with their approach to a study, the sample size was large with 23 seals involved over a 5-year period. The tagging was done from September to December, and the tags last < 3 months. The seals traveled about 400 to 600 km from the place of release in a meandering track. They were off the continental shelf and in pack-ice 86% of the time. From 92 to 98% of the time, dives were to depths of < 20 m. Overall, they were probably grazing on krill, and in regard to diving, it is perhaps the most boring natural history of any pinniped.

*Leopard Seal*

The diving natural history of the leopard seal is perhaps even more boring than the crabeater seal is, except for one significant difference. Like flying, their time at sea is filled with hours of boredom with brief moments of stark terror; in this case, not for the seal, but for the victim be it another seal or a penguin. Some of the most gripping studies are a result of shore-based observations of leopard seal tactics for catching arriving or departing penguins (Kooyman, 1965a; Penney & Lowry, 1967). Some of my most thrilling times in Antarctica have been watching leopard seals stalk emperor penguins at the ice edge near a large colony of these birds. These observations were done both at the ice edge and below the sea ice. As for diving studies, they are limited, and I know of only two. Kuhn et al. (2006) attached a SLTDR to a juvenile leopard seal and recorded diving behavior during most of August near Adelaide Island, Antarctic Peninsula. The maximum depth of dive was 425 m, but most of the dives were < 50 m, and the seal did not travel more than 60 km from the original capture site. In a more detailed study with two adult animals, Nordøy tracked and recorded dives from February to September using SLTDRs (Nordøy & Blix, 2009). During June/July, the seals made fewer than 50 dives/day, and were hauled-out as much as 11 h/day. From the 24,000 dives recorded, only one was > 15 min, and the maximum depth of all dives was only 304 m. Most of their time was spent in pack-ice.

## Summary

From my perspective, of having a strong interest in both the behavioral and physiological aspects of diving, such as externally what part of the environment they exploit and internally what are the physiological adaptations to diving, and my wife's interest in the history of exploration, we have given thumbnail sketches. First, about the early explorers, followed by a long exposition about the Weddell seal. Finally, we have told something of the frenetic exploits of fur seals, to the incredible journeys of southern elephant seals and Ross seals, to the laid-back life of crabeater and leopard seals. Overriding all of this is the amazing adaptations of Weddell seals to live year-round under fast-ice in the most southern reaches of the southern seas, and sometimes under very thick ice during the dark nights of the Antarctic winter. This habitat of sea ice which allowed us to set up laboratories and learn some of the most amazing adaptations of an air breathing animal are the blessings from the Weddell seal. From this unabashed bias, I give you my top 10 most influential studies and technology in chronological order. My wife claims no part in this section.

## The Top 10

1. IHP (Isolated Hole Protocol) – A technology based on the unusual properties of McMurdo Sound, which has allowed the conduct of a host of different behavioral and physiological experiments on Weddell seals (Kooyman, 2009a).
2. TDR (Time depth recorder) – The IHP facilitated the design and inauguration of the first TDR experiments, which began to open a door

into the mystery of animals at sea (Kooyman, 1965b, 1968).

3. Weddell seal diving physiology – This was only possible because of the IHP in the early days, and until recently was the only way to unravel some of the mysteries in regard to diving physiology without restraint (Kooyman, 1985).
4. ADL (aerobic diving limit) – From the physiological studies on Weddell seals, the concept of the ADL was defined and then applied along with the TDR to many other species of diving animals (Kooyman, 2004).
5. Microprocessor-based TDR – With the new technology coming of age in the late 1980s, the TDRs were much easier and cheaper to build, many more sensors could be easily incorporated, and data were now digital and much easier to retrieve and analyze (Hill, 1950; Hill, 1986).
6. Commercialized TDR – With a readily available commercial TDR, the tool was put into the hands of many laboratories, especially ecologists, to gain the large databases necessary to test hypotheses on foraging theory and habitat use.
7. cADL – The ecology of animals at sea developed from the use of TDRs and the calculated ADL. Now it is possible to gain some idea of the strain of foraging on the forager by having some idea if the diver is working close to its physiological limit (Costa et al., 2001).
8. SLTDR – In combination with the TDR, and many additional sensors besides pressure, satellite tracking opened a major new horizon in our understanding of habitat use and has become a major conservation tool by helping to define the critical habitat of a species (see earlier references on southern elephant seals, Ross seals, crabeater seals, and leopard seals).
9. Blood nitrogen measurements – This single experiment on free-diving Weddell seals using the IHP confirmed earlier experiments performed on northern elephant seals in a compression chamber. These results showed the protection diving seals enjoy from decompression sickness (Kooyman et al., 1972; Falke et al., 1984, 1985). Many of the details of how this protection works and how it applies to other species are still being worked out.
10. PTDR – The physiological TDR first developed in the 1980s for timed mechanical sampling (Hill, 1986) was expanded in the early part of this millennium to add electronic sampling of physiological variables. Those are blood and muscle oxygen tension, blood and muscle temperature, pH, and, still in progress, the crown jewel of diving physiology, blood lactate (Ponganis et al., 2002, 2003, 2004; Ponganis, 2007b, 2009; Meir et al., 2009).

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and trials of Washington, DC. He and his ethical standards are and will continue to be missed.

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