A Selection from

Smithsonian at the Poles

Contributions to International Polar Year Science

Igor Krupnik, Michael A. Lang,
and Scott E. Miller
Editors

A Smithsonian Contribution to Knowledge

Smithsonian Institution
Scholarly Press
WASHINGTON, D.C.
2009

This proceedings volume of the Smithsonian at the Poles symposium, sponsored by and convened at the Smithsonian Institution on 3–4 May 2007, is published as part of the International Polar Year 2007–2008, which is sponsored by the International Council for Science (ICSU) and the World Meteorological Organization (WMO).

Published by Smithsonian Institution Scholarly Press

P.O. Box 37012
MRC 957
Washington, D.C. 20013-7012
www.scholarlypress.si.edu

Cover design: Piper F. Wallis

Cover images: (top left) Wave-sculpted iceberg in Svalbard, Norway (Photo by Laurie M. Penland); (top right) Smithsonian Scientific Diving Officer Michael A. Lang prepares to exit from ice dive (Photo by Adam G. Marsh); (main) Kongsfjorden, Svalbard, Norway (Photo by Laurie M. Penland).

Library of Congress Cataloging-in-Publication Data

Smithsonian at the poles : contributions to International Polar Year science / Igor Krupnik,
Michael A. Lang, and Scott E. Miller, editors.
p. cm.
ISBN 978-0-9788460-1-5 (pbk. : alk. paper)
1. International Polar Year, 2007–2008. 2. Polar regions—Research—Congresses.
3. Research—Polar regions—Congresses. 4. Arctic regions—Research—Congresses.
5. Antarctica—Research—Congresses. 6. Polar regions—Environmental
conditions—Congresses. 7. Climatic changes—Detection—Polar regions—Congresses.
I. Krupnik, Igor. II. Lang, Michael A. III. Miller, Scott E.

G587.S65 2009
559.8—dc22 2008042055

ISBN-13: 978-0-9788460-1-5
ISBN-10: 0-9788460-1-X

∞ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48–1992.

Milestones in the Study of Diving Physiology: Antarctic Emperor Penguins and Weddell Seals

Gerald Kooyman

ABSTRACT. McMurdo Sound, Antarctica, is the best place to conduct diving physiology studies on marine birds and mammals under free-diving conditions. Both emperor penguins and Weddell seals live naturally in areas of extensive sea ice under which they dive and hunt for prey. The first experimental diving studies were conducted on Weddell seals in 1964 using the isolated breathing hole protocol for the first time. Sea ice, 2 m thick, covers McMurdo Sound until late December. Below the ice is the deepwater environment where Antarctic predators hunt their prey. Here in the Sound diving studies involve attachment of a recording device to a seal or bird and release of the animal into the hole cut in sea ice. This procedure sets the stage for a bird or mammal to hunt without competition, and the only restrictive condition is that they must return to the release hole to breathe. After the animal surfaces, the attached recording devices can be retrieved and the information downloaded. Results from using this experimental protocol range from determining the first foraging patterns of any diving mammal, to measuring the first blood and muscle chemistry fluctuations during the extended and unrestrained dives. These experiments are the standard for understanding the hypoxic tolerance of diving animals, their aerobic diving limits, and their strategies of foraging, to mention a few. The protocol will continue to be used in 2008 for studies of both emperor penguins and Weddell seals by several investigators.

INTRODUCTION

My goal in this presentation is to engender an understanding of the valuable resource we have next to McMurdo Station, the largest base in Antarctica. That asset is McMurdo Sound itself, which is covered by perhaps the largest and most southerly annual fast-ice sheet in Antarctica. The ice cover most commonly ranges in thickness from 1 to 4 m in thickness, and extends from the McMurdo Ice Shelf to Cape Royds to the north, and east to west from Ross Island to the continent (Figure 1). It covers an oceanic area reaching to depths of 600 m. It is also one of the most stable fast ice areas and it persists until late December. Like almost every first-time visitor, when I arrived in 1961, I was not impressed by the Sound's uniqueness. However, McMurdo Sound may have the only such *annual* fast-ice shelf anywhere in Antarctica where it can be used extensively for innumerable projects. Among the many uses are: (1) the largest and most active airport in Antarctica, (2) "at-sea" marine biological and oceanographic stations

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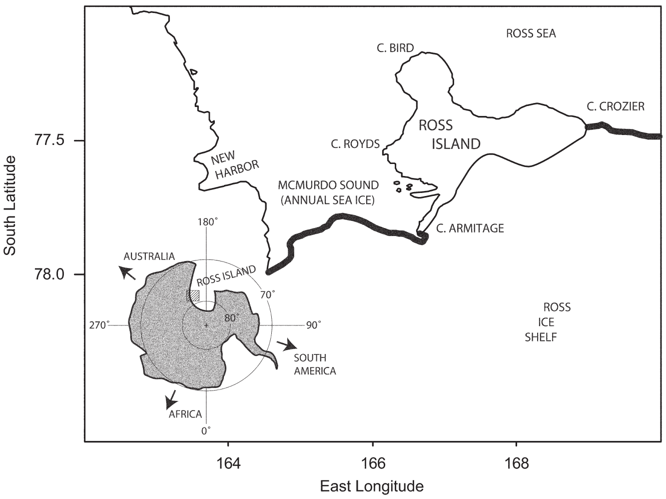

FIGURE 1. Location of McMurdo Sound. The annual sea ice northern limit is usually at Cape Royds, but occasionally extends to Cape Bird. The two major research stations of McMurdo Station (US) and Scott Base (NZ) are near the tip of Cape Armitage.

without the inconveniences and cost of research vessels, (3) scuba diving stations, and (4) at least three to four experimental laboratories for the study of marine organisms. These stations are scattered throughout the Sound in the spring and sometimes in the winter. As an example of the Sound's value as a scientific asset I will describe what is most familiar to me. For the past 43 years, the Sound has been the premier study site for the investigation of diving and behavioral physiology of birds and mammals, and the training of three generations of scientists. These kinds of studies began not long after the station was established in 1957, and there was a surge in scientific endeavor promoted by, and in celebration of the Second International Polar Year, or International Geophysical Year (IGY), as it was called then. The diving studies have been continuous ever since.

The crucial attributes that a plate of fast ice must have to make it useful year-round, is a large surface area of at least 10s of km^2. It must have an ice thickness that will support large vehicles such as Caterpillar D8's, substantial buildings, and large aircraft of at least the size of an LC 130. McMurdo Sound fast ice will support the Boeing C5, the largest aircraft known. Ross Island, where McMurdo Station resides, also provides protection for the Sound from ocean currents and storms so that the annual fast ice persists until early January. In fact, in the last few years, since about 2001 until 2006, little of the Sound ice broke up and departed. This was a result of the added protection given to the Sound by the giant iceberg B15. As a consequence of the Sound's fast-ice stability, the largest airport in Antarctica was built in McMurdo Sound during the IGY (1957), and a new one has been built every spring since that first season. In addition, there is a large, local Weddell seal population in McMurdo Sound that has been the object of intensive ecology and physiology studies since the establishment of the two bases of McMurdo Station and Scott Base.

McMurdo Sound fulfills all the above requirements. It is about 64 km across the Sound from Ross Island to the mainland, and it is about 32 km from Cape Royds to the McMurdo Ice Shelf near Cape Armitage (Figure 1). The sea ice forms in April and decays in January, usually breaking out annually on the eastern half by mid to late February. The ice grows through October at which the maximum is usually about 2 m thick at its southern base next to the McMurdo Ice Shelf, and about 1.5 m thick near the edge at Cape Royds. It is noteworthy to illustrate the variability of the sea ice breakout, formation, and extent. In 1981 during the first overwintering study of Weddell seals, investigators were hampered by the late development of sea ice well into the winter after a previous extensive summer ice breakout to the McMurdo Ice Shelf. In contrast, in 2001 after the arrival of B15 at the northern edge of Ross Island, the annual fast ice became multi-year ice and extended well beyond Beaufort Island. This condition persisted until 2006 when the last remnants of this iceberg drifted north of the zone of influence on McMurdo Sound. Because of the numerous science programs at McMurdo Station and Scott Base, as well as McMurdo Station's function as the logistic center for supplying South Pole Station, the airport, that has hundreds of landings every season, is essential for this region of Antarctica. In addition, sea ice to land access for large vehicles to reach McMurdo Station and Scott Base is ideal with gently sloping land down to the sea ice edge. Finally, the Weddell seal population along the coast of Ross Island from Turtle Rock to Cape Royds (~15 km) harbors about 500 breeding females and it is one of the largest concentrations of seals in the Ross Sea.

The above-described attributes of McMurdo Sound are matchless. There are no other stations throughout Antarctica that have the air support or base size and support of McMurdo Station. Consider the rest of the Ross Sea. There are two possibilities: Terra Nova Bay (TNB) and Moubray Bay both of which have extensive fast ice sheets. In the southern end of Terra Nova Bay resides the Italian base of Zuchelli Station. The Campbell Ice Tongue bisects the bay. The small southern section would be feasible for only limited bird and mammal work. Here there is a small airstrip and a few offshore marine stations. The northern portion of TNB is much larger and has both a large population of Weddell seals, and one of the largest known emperor penguin colonies. This part of the bay is bordered by high ice cliffs and is not accessible from land. There is also a large perennial ice crack that bisects the eastern part of TNB from east to west that limits its usefulness for bird and mammal studies. There is also no access to land so that a shore station could not be established to support the kind of programs that are carried out from McMurdo Station and, at least for seals, it would be difficult to establish a functional sea ice station where the isolated hole protocol (IHP) would work. Wood Bay to the north of Cape Washington has no bases except for a small field camp at Edmonston Point for Adélie penguin research, and there is no good site for a station. Little is known about this area, but it appears to have a substantial seal population.

The only accessible land to sea ice in Moubray Bay is on Hallett Peninsula where a large Adélie penguin colony occupies the entire land surface area, and consequently is not an option for a research station now, although there was a research station there in the past. In the eastern Ross Sea adjacent to Cape Colbeck, Bartlett Inlet forms about a 15 km bight into an embayment of fast ice, which at the most southern extension is found a large emperor penguin colony. Little is known about this very isolated region that is notorious for foul weather and extensive pack ice. There is no easy access to land where a permanent station might be established. All of the described areas are small compared to McMurdo Sound and would provide a much more limited program of research than is possible at McMurdo Sound. These are the areas that I have first hand knowledge. As far as the rest of Antarctica is concerned, to my knowledge, there are no areas with air strips to handle routine air support from outside of Antarctica, with the exception of the Antarctic Peninsula, and none of those in the peninsula have extensive fast-ice sounds for the conduct of marine research. In short, there are no other places in the Antarctica or the world, where marine research, especially on birds and mammals can be conducted in the way I describe below.

METHODS

With a 2-meter-thick layer of ice over the Sound, the first objective is to pierce through it to reach the marine environment below. In the early days, this was a major, backbreaking task to cut a hole through the ice with a chainsaw and lift out the cut blocks from the developing hole with ice tongs. Depending upon the number of laborers and the thickness of the ice, the task of penetration could take from a few hours to several days. Thankfully, soon after the cutting task was assisted by using explosives and the sea ice landscape began to be peppered with marine stations. However, this was not ideal for several reasons one of which was the potential harm to seals diving under the ice. By the early 1970s, a 1.2 m diameter augur was employed for hole cutting. Because the holes even in the thickest ice can be cut in about 20 min, this has become one of the most valuable assets in the toolbox of marine work in McMurdo Sound.

The sea ice stations have a range of functions. Some are platforms for setting fish and invertebrate traps to capture benthic specimens for ecology and physiology studies. Others are used for setting up a long-line to capture the large Antarctic cod, *Dissostichus mawsoni*, which may weigh greater than 100 kg. From these specimens much has been learned about anti-freeze properties of the body fluids, their physiology, and their natural history. My own personal experience has been to use the sea ice stations for conducting detailed diving studies on unrestrained Weddell seals and emperor penguins. For these kinds of experiments there is no match for the situation. In 1964 I established the isolated hole protocol wherein the dive hole was established a distance of 1 to 4 km from any other hole, either manmade or natural. Under these circumstances a penguin or seal released into the isolated hole had to return to this same breathing hole, and therefore, instruments could be deployed and recovered after each or a series of subsequent dives. Normally the diving seals would remain and use the hole for hours to days. During this period the hole was covered with a heated hut for the convenience of the investigators. The emperor penguins were peculiar because they would never surface in a hole covered with a hut if they had an option to go to a hole in the open. At the open air hole they would leave the water after almost every dive. The IHP has been used continuously by a variety of investigators over the past 43 years (as of 2007), and several projects are planned for the future. A great deal of information has been collected during these studies and the following are a few highlights most familiar to me.

RESULTS (BIRDS AND MAMMALS)

BEHAVIOR—WEDDELL SEALS

The first diving studies ever conducted on a diving animal, in which detailed diving information was obtained, occurred in 1964 in McMurdo Sound. Using time-depth recorders full advantage of the IHP was used to determine the behavior and physiology of Weddell seals (Kooyman, 1968). Investigations of this kind have been in progress ever since. The first results broke new ground in many ways, and one of the most significant was to show that we had been far too conservative in assumptions about marine mammal diving capacities. Indeed, even the first two publications on Weddell seals were too conservative on the estimates of what these animals could do (DeVries and Wohlschlag, 1964; Kooyman, 1966). In the latter report it was proposed that the maximum depths and durations were proposed to be 600 m and 46 min, respectively. At present the depth and duration records for Weddell seals now stand at 714 m (Testa, 1994), and 96 min (Zapol, Harvard Medical School, personal communication). Seals accomplished all of these exceptionally long dives while diving from an isolated hole. This procedure brings out the extremes in breath holding of these animals. Presumably they are responding to the trauma of capture and transport to the hole, and are trying to find an escape route from the new environment. However, within a few hours they settle in to routine hunting dives, and take advantage of the isolation and being away from competition with other seals. This provides to the investigator the best of both worlds. One is the discovery of some of the limits the seals may press themselves toward followed by the ordinary kind of effort that they do routinely. Both are of interest to the behaviorist and physiologist.

Behavior—Emperor Penguins

Emperor penguins have responded in a somewhat different way from Weddell seals to the IHP. They still achieve some of the longest dives recorded by emperor penguins and this record stands at 23 min (P. J. Ponganis, Scripps Institution of Oceanography, personal communication) compared to 21.8 min obtained from a free ranging bird (Wienecke et al., 2007). However, emperor penguins seldom make deep dives during the IHP compared to animals foraging under more natural conditions of the pack ice. The maximum depth of the IHP is 250 m (Ponganis et al., 2004), while that of the free ranging animals is 560 m (Wienecke et al., 2007). At least part of the reason for the shallow dives by emperor penguins during IHP is the lack of incentive. Free ranging birds feed primarily on Antarctic silver fish at mid-water depths in the Ross Sea. However, birds hunting under thick fast ice of the Sound switch from silver fish, even though these are abundant and the primary prey of Weddell seals, to another fish, *Pagothenia borchgrevinki*, which is present in large numbers just under the ice. This has been a frustration to the physiologist who wants to explore the responses of the animals under extreme conditions. However, deep dives are so rare that it is purely by chance when physiological protocols are in place when the animals dive to extremes.

Indeed, in the many thousands of dives observed in Weddell seals only once were some of the responses made. In one case, a blood lactate sample was obtained after a 66 min dive (Kooyman et al., 1980), and pulmonary function measurements were obtained from a seal that made an 82 min dive (Kooyman et al., 1971). However, a benefit for the behaviorist and ecologist working in McMurdo Sound is that it has been possible to deploy "Crittercams" or "VDAPS" on emperor penguins and Weddell seals, respectively. These are animal borne imaging devices that have made it possible to observe their hunting tactics. With the Crittercam on emperor penguins taped images show how the birds catch *P. borchgrevinki* hiding in ice crystals attached to the fast ice undersurface (Ponganis et al., 2000). Similarly, with the VDAP Weddell seals' captures of Antarctic silverfish and Antarctic cod were documented (Davis et al., 1999). All of these imaging results proved exciting both to the scientific community and the media.

Physiology—Weddell Seals

For the comparative physiologist working on diving physiology McMurdo Sound has been a magnet because of the IHP. This protocol has made possible the attachment of complex instruments to record heart rate, measure blood chemistry, and to determine oxygen and nitrogen tension in blood at known depths and times in the dive. Some of the results have been the generation of the lactate endurance curve from blood samplings of several different seals (Kooyman et al., 1980). This curve has defined the aerobic diving limit (ADL) of Weddell seals by the inflection area within the curve (Figure 2). The concept was defined by Kooyman (1985), and states that "The ADL is defined as the maximum breath hold that is possible without any increase in blood LA concentration during or after the dive." It was further explained that the calculated ADL (cADL) could be estimated if the body oxygen store and diving metabolic rate were known. This concept has motivated many research projects to make estimates of the ADL in a variety of diving animals. Several of these studies have been done on Antarctic divers including the emperor penguin using the IHP for the study in McMurdo Sound.

Another landmark study on Weddell seals, among the many that have occurred, was the determination of blood N_2 levels while Weddell seals were diving to depth

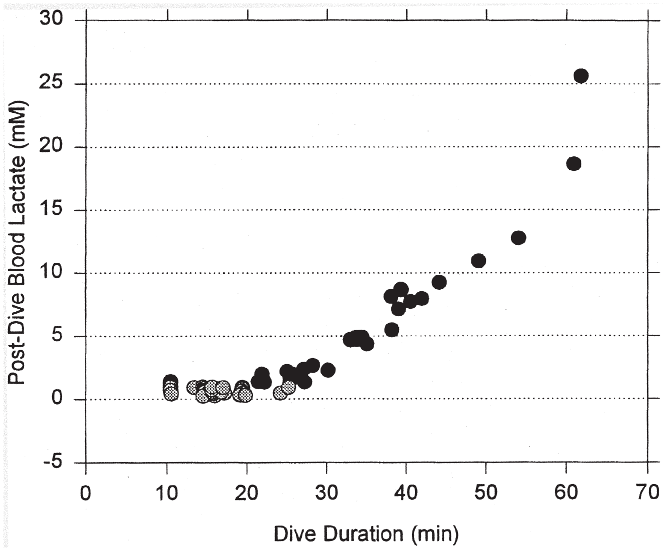

FIGURE 2. Lactate endurance curve of the Weddell seal. The gray dots are peak arterial post-dive lactic acid concentrations of aerobic dives. The black dots are the peak arterial post-dive lactic acid concentrations after dives with a lactate accumulation above resting levels (modified from Kooyman et al., 1980).

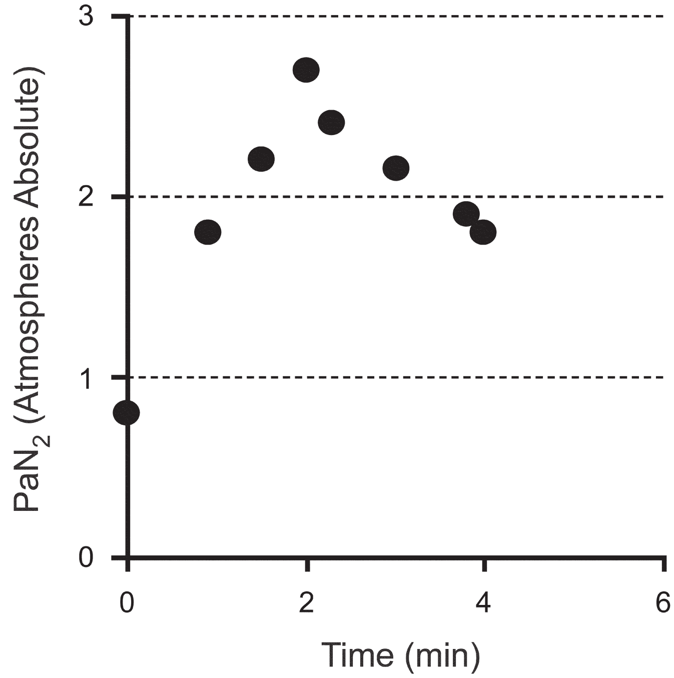

FIGURE 3. Arterial N_2 tensions in a Weddell seal. The seal made a free dive to 89 m under McMurdo Sound fast ice. The dive began at zero on the abscissa, reached a maximum depth at 5 min, and the dive ended after 8 min.

(Falke et al., 1985) (Figure 3). This result corroborated the more artificial studies conducted on elephant seals forcibly submerged and compressed in a hyperbaric chamber (Kooyman et al., 1971) a number of years earlier. The salient feature of these blood pN_2 results was that no matter the depth of the dive the N_2 tensions do not rise above a relatively low value that is unlikely to cause decompression sickness. The only similar measurements on other species diving under unrestrained conditions are those of the emperor penguin using the IHP in McMurdo Sound (Ponganis, personal communication).

Physiology—Emperor Penguins

Using the same procedures as applied to the Weddell seal, the ADL of emperor penguins has been determined (Ponganis et al., 1997), and it has equally important implications for diving birds as the studies of Weddell seals had for diving mammals. To probe this problem further a recent study has asked the question of how emperor penguins manage their oxygen stores. This question is of exceptional importance to understanding the physiological principles of how diving animals overcome the problems of limited oxygen and endure hypoxia on a routine basis. In the course of these studies the investigators have shown that emperor penguins can tolerate exceptionally low arterial O_2 tensions in the range of 5–10 mmHg (Ponganis, personal communication). These values are at levels below what could maintain consciousness in most terrestrial birds and mammals, including humans. Indeed they are substantially below the expected arterial O_2 tension of a person standing on Mt. Everest (Chomolungma), and they raise a series of questions about how this diving bird overcomes such extreme hypoxia.

DISCUSSION

I have briefly mentioned several types of studies on birds and mammals that have had a significant impact on diving behavior and physiology of marine animals. If this were a comprehensive review of work accomplished in McMurdo Sound there would be many disciplines and investigators represented and the number of publications would be in the hundreds if not thousands. Many of the studies could not have been done anywhere other than in McMurdo Sound. As for the birds and mammals studies there are at least three generations of investigators, spanning 45 years that have found the greatest contributions to their field in McMurdo Sound. In regard to the diving studies mentioned above, many of the results are fundamental to the field of behavior and physiology of diving.

Reflecting on these accomplishments and many others such as the long-term works of Siniff's trends in Weddell seal populations (Siniff et al., 1977), DeVries's range of work on ecology to the molecular nature of antifreeze compounds in fish (DeVries, 1971) and long term catch data on the highly sought after Antarctic cod (DeVries, University of Illinois, unpublished data), and Dayton's cage exclusion studies of benthic organisms (Dayton et al., 1974; Dayton, 1985), I wonder if McMurdo Sound is not underappreciated. In the early days it was not coveted at all, and was used as a dumping ground for human waste and many harmful inorganic and organic products. Thankfully those "bad old days" ended a long time ago, and like Antarctica in general, it is treated by a much softer human footprint. Still, to recognize the distinct value of McMurdo Sound it should be given some sanctuary or museum status as the great contributor to biological sciences, because as I hoped to achieve in this review, there is no other place like it. We do not know what specific effects the changing climate in Antarctica will have on the seas that surround the continent, but with the long-term history of science in McMurdo Sound, it will be one of the areas invaluable in assessing some of the changes. Especially with the large modern laboratory of Crary Center adjacent to the Sound where researchers can study the animals with some of the most sophisticated techniques in the world.

Acknowledgments

Thanks to Smithsonian for making this symposium possible and providing the travel funds to attend. All my work over the past 45 years at McMurdo Sound has been supported by numerous NSF OPP grants for which I will always be grateful. I give thanks, as well, to the many support contractors and their staff on land, sea, and air that have made the journeys such a fine experience. In the background always has been my wife Melba and my sons, Carsten and Tory. It was also an inestimable joy to see both sons become the best field assistants one could ever want.

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