Historical Perspectives

Yasuhiko Naito, Ph.D. (Born 5 February 1941)

Yasuhiko Naito received his bachelor's degree in 1964 and his master's degree in 1968 from Tokyo University of Fisheries. He received his Ph.D. from the University of Tokyo in 1972 through his work on harbor seals in the Sea of Okhotsk and Hokkaido, supervised by Professor Masaharu Nishiwaki.

For his thesis, he voyaged to the Sea of Okhotsk in early to mid spring for several years in the late 1960s, following the pack ice and seals on a sealing vessel. In summer to autumn, he visited several colonies of harbor seals, studying the morphology and ecology of two subspecies, Phoca vitulina largha (ice breeding type) and Phoca vitulina richardii (land breeding type), whose colonies are bordered by the small Nemuro Peninsula and Southern Kurile Islands. He could not find any clear morphological separation between the two subspecies in the cranial characteristics, but he found numerous differences in the hyoid bone system. He also found the breeding isolation between the two types of seals through his investigation of their pupping seasons, lanugo coat development, nursing duration, and sexual dimorphism. His results contributed to the taxonomic separation of the largha seal (Phoca largha) as an independent species from the harbor seal (Phoca vitulina), which breed on land. While working with the harbor seals on board the sealing vessel, he developed a strong interest in the underwater behavior and ecology of the marine mammals, the study of which he pursued when he began his position at the National Institute of Polar Research in 1978.



What Is "Bio-Logging"?

Yasuhiko Naito, Ph.D.

The word "bio-logging" was first used at the International Symposium on Bio-Logging Science, which was held at the National Institute of Polar Research (NIPR) in Tokyo from 17 to 21 March 2003. The term referred to the newly emerging science of animal borne devices (ABDs) (Figure 1). With young colleagues at NIPR, I have conducted studies using ABDs since 1992, and we have compiled a considerable quantity of research data on the diving behavior of marine mammals, marine birds, reptiles, and fishes. Detailed analysis and integration of these findings have revealed some surprising aspects of animal behavior. I envisioned that the introduction of this new technology into the field of biology might be developed into a new science. In point of fact, the methodological concept of this study was not entirely new. Simple animal-borne recorders (ABRs) had already been used in marine mammal research-for example, maximum depth recorders (a dye-coated tube closed at one end) (Scholander, 1940) and mechanical time-depth recorders (TDRs). Devices for biotelemetry, incorporating VHF and acoustic transmitters, were also being developed for tracking animals. In the early 1990s, with the growth of digital innovation in electronics technology, ABRs were digitized. Their use in marine animal studies in the U.S., Japan, and Europe brought about a revolution in terms of the quantity and quality of data generated and its integration from multiple sensors. Our study animals are remote, particularly when they are submerged, and our investigations are completely dependent on these tools. Thus, I believed that these new tools would transform our research and, indeed, the digital ABDs have already provided new insights into marine mammal biology. Consequently, I proposed that we should introduce a new name for this ABD science, a suggestion that received encouraging support from my colleagues, Drs Katsufumi Sato, Akiko Kato, Hideji Tanaka, and Yan Ropert-Coudert. Dr. Ropert-Coudert suggested the new name "Biologging," which, unfortunately, was already in use in the field of molecular biology. Therefore, I modified it to "Bio-Logging." Finally, I decided to organize an international symposium to summarize research activities using ABDs and to discuss future directions for research using this technology with international colleagues. Digital innovation has significantly boosted the development of ABDs in terms of miniaturization of the devices and of integration of the signals. However, these digital innovations were not autonomously

achieved: the foundation for the current status of bio-logging science originated in the ideas and endeavors of scientists who created the first mechanical devices.

Bio-logging was born independently in the U.S., Japan, and Europe, and each "beginning" has its own history. Here, I introduce my own historical perspective based on my experiences.

The Start of My Bio-Logging

Ocean and Space

While I was working on seals in the Sea of Okhotsk, an exciting event for all mankind occurred on 20 July 1969 when three astronauts landed on the moon as part of the United States' Apollo Program. Subsequently, the Apollo Program sent 27 astronauts to the moon or into its orbit. While big challenges were being embarked upon in space, I questioned why people would conceive such dreams about space but not about the ocean depths. At this time, only a few people had visited the deepest regions of the ocean in the Mariana Trench. My view was that differences in the dreams about space and the ocean were related to a difference in visibility-we cannot examine either location by direct touch or by hearing. We readily understand natural phenomena when a visual image is available and, thus, we more easily develop concepts, questions, and hypotheses to study. Visual information is more accessible in space than in the ocean because of the invention of the telescope and other tools of space exploration. This visual accessibility was greatly advantageous for space exploration. In contrast, the ocean was believed, in the past, to be a place inhabited by sea monsters, devils, and terrible creatures-for example, the sea serpent Ketos of Greek mythology (from which the term "cetacean" originates), the Kraken of Viking stories, and others. These beliefs have perhaps negatively influenced aspirations and ambitions for ocean exploration depth.

There is an old Japanese proverb, "Hyakubun wa ikken ni shikazu (百聞は一見にしかず)," which means "to see is to believe" or, in other words, "to see is to recognize for understanding." In this context, the underwater behavior of marine mammals had been in a world unrecognized by our visual senses as noted in the proverb. I have often observed colonies of harbor seals (*Phoca vitulina*) from the tops of cliffs in eastern Hokkaido and considered that those seals were not truly marine mammals but simply mammals breathing at the



Figure 1. Advertising poster for the first symposium on Bio-Logging Science held in March 2003 at the National Institute of Polar Research (NIPR), Tokyo; around 150 scientists and students attended.

water surface since I was unable to visualize most of their life as it was performed underwater. While I was working with these harbor seals in the late 1960s and early 1970s, the striking achievement of human dreams by the Apollo Program strongly inspired me to make a small step, but a giant leap, toward someday visualizing the underwater life of marine mammals.

My Apollo Program—To Make the Diving Behavior of Animals Recognizable for Understanding

Among marine organisms, the top predators are the most difficult to visualize because they are highly mobile. Visualization of their behavior during their movement from one place to another was considered to be quite intractable in the 1970s. One method that I was considering at this time was the development of depth recorders. In fact, TDRs already existed and were called depthtime recorders in the mid-1960s. The recorders were developed by Professor G. L. Kooyman and his collaborators for his pioneering studies of the diving physiology and behavior of free-ranging seals (e.g., Kooyman, 1965). In the 1970s, I was completely ignorant of diving physiology and did not pay attention to his contributions. I therefore missed important information about the TDR he used to study the diving behavior of Weddell seals (Leptonychotes weddellii) in the mid-1960s, and another TDR that was developed later (Kooyman et al., 1976). Without this knowledge, I stepped out on my first challenge to reveal "recognizable underwater behavior" when I participated in the wintering party of the 21st Japanese Antarctic Research Expedition (JARE-21) in 1979. I believed that the depth recorders should be as small as possible so that animals could carry them on their backs within the range of their normal behavior. Searching for manufacturers, I found the Yanagi Keiki Company, which produced depth recorders for fishing nets. Although they seemed very large, I took several of these recorders to Antarctica on this trip. Ultimately, nothing was achieved with these net recorders because they proved too large for the Weddell seals. In 1981, when I returned from 1.4 years overwintering on the JARE-21, I decided to develop a very small device that even penguins could carry because penguins, like seals, seemed to be very adept divers. This meant that the depth recorder should be even smaller than I had originally thought. The challenge proved to be too difficult. Without having any preliminary

knowledge, I thought that the depth recorder should be about 20 mm in diameter and that it should be cylindrical to minimize drag. This idea was promptly rejected by Mr. Shibata, Chief Engineer of the Yanagi Keiki Company, who told me "conventional engineers do not think in this way, and your request is a little crazy." I then told him the story of the awesome challenge of the Apollo Program. Finally, he nodded and was sympathetic to my problem. He gave me some concise instructions: "We need a new concept to build such a small device. If you could provide a new mechanism that facilitates its production, I will collaborate to build a small device." My role in this joint challenge was the invention of a new and practical mechanism for miniaturization, and his role was building the recorder. This challenge seemed to be very hard to me. But the dream of the Apollo Program encouraged me to promote my very small and personal Apollo Program.

First Step: Development of the Time-Depth Recorder In late 1970s and early 1980s, digital microelectronics technology was moving towards prosperity, and digital devices, such as bubble memories, were already available for digital data loggers. However, a large battery was required for these, and this increased the overall size of the TDR so that it would be even larger than the fishing net depth recorders that I had used for the loggerhead turtles (*Caretta caretta*) (Figure 2). I concluded that it was still too early for digital TDR, and I was forced to wait for about a decade before flash memory became available. As the old proverb says, "Mate ba kairo no hiyori ari (待てば海路 の日和あり)" or "Good things come to those who wait (with positive mind)." I started to develop a miniaturized mechanical TDR in 1981.

I tried many revolutionary ideas, including the use of pressure-sensing paper offered by the Fuji Film Corporation. After examination of a bathy-thermograph recorder and seismometer, in which thin lines are scratched onto a carbon-coated glass or drum with a sharp needle, I arrived at the firm conclusion that we should develop a micro pen recorder. In order to produce a high-resolution scratch line, I tested needles made of many materials, including a sapphire needle from an LP record player that could scratch lines as thin as 20 to 30 μ m. Finally, I discovered a diamond needle used in silicon wafer processing, which was able to scratch a 6 to 8 μ m line on thin carbon-coated



Figure 2. At an early stage of development of the time-depth recorder (TDR) and swim-speed recorder (SSR), I used a fishing net recorder, which only turtles were able to carry. Our TDRs recorded depth in arc form, requiring a conversion protocol using a digitizer. Following these experiments, the miniaturization of ABDs was my primary objective.

paper. In other words, it could scratch more than 100 lines in a width of 1 mm, which enabled us to record data for long periods on a short length of paper on a small spool, permitting miniaturization of the whole system (Figure 3). Selection of the recording paper was also important for size reduction of the paper roll. I chose thin carbon-coated nylon paper, less than 10 μ m thick, for the recording paper, and this was later replaced by aluminum-coated paper.

After many discussions and trials, we succeeded in feeding the recording paper at 0.024 mm/min at which speed the machine was able to record dive depth data continuously for three weeks on a 15-cm length of recording paper. We adapted a bellows pressure sensor as the basis of this mechanical TDR. We finally succeeded in building the world's smallest pen recorder in mid-1984 (depth range, 0 to 200 m; dimensions, 25 mm diameter × 87 mm length; weight, 78 g in air; recording duration, 21 days; Figure 4).

Elephant Seal Experiments Using TDR

The new TDR was first used for Adelie penguins (*Pygoscelis adeliae*) in Antarctica (Naito et al.,

1990a). However, the most exciting results were obtained from an experiment on a northern elephant seal (Mirounga angustirostris) in 1988 in collaboration with Professor B. J. LeBoeuf, University of California-Santa Cruz, using a revised TDR for four months of recording. His previous dive data of two weeks' duration from the northern elephant seals showed continuous diving day and night, and he wanted to examine the length of continuous diving. After receiving his letter inviting collaboration in 1985, I revised the penguin TDR for the northern elephant seal, extending the recording duration up to 130 days. Our first experiment was carried successfully by a seal named "Yel," which migrated for 83 days and returned to the colony with the mechanical TDR in place. A total of 5,024 dives up to a maximum depth of 934 m were recorded (Le Bouef et al., 1989; Naito et al., 1989; Figure 5). This was the first record of the underwater behavior of the northern elephant seal that covered the entire period of oceanic life from start to return to colony (Figure 5). We continued our collaborative study using TDRs for several years, reexamining the surprising diving ability of the female northern elephant seals. They dived



Figure 3. In order to achieve miniaturization, I adapted diamond needles, which allowed us to scratch a very high-resolution line on carbon-coated thin paper or aluminum-evaporated paper. Dive profile data of blue-eyed shag (*Phalacrocorax albiventer*) are shown here.



Figure 4. The first models of the miniaturized mechanical TDRs appeared in 1984 (upper, 130 days; lower, 21days). The first one scratched a line in an arc, which required intricate conversion to a straight line using a digitizer. For easier data reading, straight scratching was attempted, but the paper was too thin and weak and, consequently, needle movements induced paper distortions. To prevent distortion, we added a pressure roller close to the needle.

continuously to about 500 m mean depth for days and nights without any breaks. They spent 90% of their time underwater and stayed only two to three minutes at the surface. These results accelerated our understanding of northern elephant seals but raised several fundamental questions regarding (1) underwater sleep, (2) prey detection and prey capture at depth, (3) tolerance to anoxia in such deep and long dives, and (4) repetitiveness of diving. These questions had already been addressed by Professor Le Boeuf and his team in their previous investigations. They classified the dive profiles into several functional types: foraging dive (pelagic and benthic), transit dive, and processing dive (Le Boeuf et al., 1988; Figure 5). However, there was still much discussion about the function of the dives, and to solve the above questions, we concluded that we needed to build a swim-speed recorder (SSR) in order to examine the activity level during each type of diving.

Do Elephant Seals Dive or Sink? The Swim-Speed Recorder Experiment

To investigate dive profiles in more detail, we decided to incorporate an SSR. We considered that if the swim velocity was known for each segment of each dive type, we could infer the function of these dive types (e.g., foraging or transit) using swim distances and dive angles calculated by vector analysis. While developing the SSR, Mr. Shibata also carried out excellent reliable work for us by adding a propeller for velocity measurement to the Bourdon pressure sensor of the mechanical TDR. Propeller rotation movement was transformed to linear movement of a diamond needle by a gear. After calibration, we used the SSR paired with the TDR on the northern elephant seals in 1989 (Figure 5).

We were able to obtain SSR data paired with TDR data over a period of 29 days for a female northern elephant seal, showing that the seal did



Figure 5. TDR (upper left) and SSR (upper right) were deployed on the back of the seal using marine epoxy resin glue. A continuous dive record was kept of an adult female northern elephant seal (Yel). She left the rookery at Ano Nuevo coast, California, on 18 February and returned 1 May 1988. The single vertical line represents one dive. The dive record showed that the seal did not rest at the surface for long. Enlarged dive profiles (lower left) showed several dive types (lower right; Types A & B: transition, Type C: processing, and Types D & E: foraging).

not swim at the surface. Instead, she swam at an average velocity of 0.9 to 1.6 m/s at an average dive angle of 30° to 60° during descent, and 50° to 80° during ascent. The seal swam faster during descent than during ascent but decreased speed in the second descent segment of a digesting dive type. The SSR data supported our hypothesis of dive type functions. The seal dove at a steeper angle in foraging dives than in digesting dives. Surprisingly, she swam for shorter distances than the dive depth, particularly in the digesting dive, suggesting that she rested during descent (Le Boeuf et al., 1992; Naito, 1992). This nonswim dive hypothesis, based on a single seal experiment, was later reexamined and termed a "drift dive" (Crocker et al., 1997). The discovery of drift diving influenced later studies on northern elephant seals and led to new methods of estimation of body condition during migration, based on simple dive characteristics (Biew et al., 2003). Although the observation of drift diving by northern elephant seals could not answer questions

regarding sleep (Kooyman, 1989) or digestion (Crocker et al., 1997), it provided new insights into the functions of diving.

Development of the Gastric Temperature Recorder (GTR)

It is generally understood that marine mammals evolved from terrestrial forms to forage in the sea while retaining the inability of the lungs to exchange gases in water. This unique split system of gas exchange at the surface and foraging at depths for energy acquisition led to the evolution of the remarkable diving ability of marine mammals in terms of their tolerance to anoxia and efficient prey capture. That is to say, in order to understand such adaptations, we need to study two principal aspects: (1) physiological adaptation for anoxia and (2) behavioral adaptation for efficient prey acquisition. During the 1970s and 1980s, physiological studies on diving marine mammals were commenced to investigate the mechanisms of tolerance of anoxia using animals

under constrained conditions in the laboratory and unconstrained conditions at sea (Kooyman, 1989). In 1964, Professor Kooyman was the first to measure the diving behavior of free-ranging Weddell seals using TDRs in Antarctica (Kooyman, 1965). Those studies revealed the physiological responses associated with submersion and diving, including bradycardia and body temperature decrease, but provided little information on feeding behavior except for inferences about foraging behavior from the TDR data (Kooyman, 1989; Le Boeuf et al., 1989; Boyd & Croxall, 1996). No direct measurements were made in those days, and it was deemed very difficult to measure feeding behavior.

From my experiences in the development of the TDR, I considered that the word "difficult" should mean "I tried and I found it difficult," but often it seemed to mean "difficult with any trials." So, on the basis that "difficult" in this case meant "not easy," I decided to challenge this difficult subject of feeding behavior measurement. After I finished developing the first miniaturized TDR, I started developing a feeding events recorder in 1985. The idea occurred to me suddenly when I remembered from talks with fishermen that many Steller sea lions (*Eumetopias jubatus*) carry several stones in their stomachs. I hypothesized that if a stone was replaced by a temperature recorder, it could record temperature changes in the stomach caused by cold prey intake. Seals occasionally take in stones together with their prey as part of their natural feeding habit, so I started to build the stomach temperature recorder to study the feeding habits of Steller sea lions. The principle of miniaturization was similar to that of the TDR except that the pressure sensor was changed to a temperature sensor, and it was made heavier than the TDR.

The first test was made at Kamogawa Sea World Aquarium on a juvenile harbor seal. The problem was retrieval of the GTR after measurement. We used a tool, nicknamed the "caw-sucker," which was equipped with a strong magnet on the end of a flexible tube, actually designed for the retrieval of wires accidentally swallowed by cows. We conducted successful trials and verified the usefulness of my idea (Figure 6). A field experiment with the mechanical GTR was carried out with Weddell seals at Syowa Station, Antarctica, in 1987. However, we were unable



Harbor seal (Naito unpublished)

Figure 6. The miniaturized mechanical TDR was transformed into a gastric temperature recorder (GTR) (stomach temperature recorder; upper left), which was tested with a captive harbor seal. When mackerel was given, the stomach temperature quickly dropped and gradually recovered. The integral is supposed to represent the prey mass.





^{© 2004} Bio-Logging Institute

Figure 7. Various animal borne devices (ABDs) were developed starting with analog devices in the 1980s and digital devices in the 1990s in Japan. Digital devices accelerated the degree of data integration and miniaturization, and biologging was born.

to retrieve the GTR due to its being regurgitated. Subsequently, this mechanical GTR was successfully used for the measurement of core body temperature of sea turtles (Naito et al., 1990b; Tanaka et al., 1995), but we were unable to use it with the northern elephant seal because the regurgitation problem had not been solved-that is, the seals regurgitated the GTR at sea and, thus, the device was lost. The stomach temperature method was then successfully used with seabirds (Wilson et al., 1992) and captive harbor seals (Gale & Renouf, 1993). To counter the problem of regurgitation, two approaches were applied to the seal study. The first was to use a radio transmitter to telemeter the stomach temperature data to the data logger on the back (Gale & Renouf, 1993). The other method employed a stomach temperature recorder (STR) within biodegradable ethafoam, which prevented easy regurgitation and extended its retention by the stomach (Austin et al., 2006). Thanks to the efforts of many scientists, the methods have been greatly improved, although problems of accuracy with smaller prey and the effect

of invasion of water into the stomach still need to be solved. More recently, trials have been made using an alternative digital system for monitoring jaw movements (Bornemann et al., 1992; Plötz et al., 2002; Wilson et al., 2002).

Development of Digital Animal Borne Devices

"Mate ba kairo no hiyori ari" eventually proved to be true. In the late 1980s, digital technology entered a prosperous era, and I learned much from talks with upper atmospheric physicists and seismologists among my colleagues at NIPR. The targets of their observations are remote, and they are obliged to depend fully on remote sensing instruments, which were replaced by digital systems in the late 1980s. My conversation with physicists at NIPR was the turning point for shifting the ABDs from mechanical to digital systems. The same shift had occurred at almost the same time in the United States, where the company Wildlife Computers developed the famous Mark series of TDRs. The digital system was revolutionary in terms of its technical utility-that is, easy data



Figure 8. Schematic view of the history of the ABD. A variety of ABDs were developed around the world. Mechanical or analogue ABDs were replaced by digital ABDs in the late 1980s, which made revolutionary changes in the field study of marine mammals in terms of data integration, quality, and quantity. The studies using ABDs provided new insights into diving studies of marine mammals and other marine animals. TDR: Time-Depth Recorder; SSR: Swim-Speed Recorder; 3D logger: three-dimensional dive path logger; ODBA: Overall Dynamic Body Acceleration; GTR: Gastric Temperature Recorder; STR: Stomach Temperature Recorder; IMASEN: Intra-Mandibular Angle Sensor; MAC: Mandible Accelerometer.



Figure 9. Accelerometers attached to the lower mandible of Weddell seals could detect the feeding event (F.E.). Continuous wavelet transformation to the Y axis data (longitudinal acceleration and pitch angle) was applied for detection of distinct periodicity in spectra using the Spectrum Analysis of the *Ethographer* with *Igor Pro.package* (Sakamoto et al., 2009). Dominant amplitude was applied for filtering the F.E. using the mask manipulation function of the *Ethographer*.

processing (no digitizing needed), multiple sensors on a single board (integration), and low battery drain (miniaturization).

In the 1990s, digital techniques for TDR, and for other ABDs equipped with multiple sensors, emerged as techniques to explore the underwater behavior of diving animals. But this change was not easily achieved in my case because of difficulties in finding suppliers within the industries. There were excellent digital technologies available in Japanese industries, but they were not available to field biologists. The problem was to find a way to introduce these advanced technologies into the field of biology. I believed that the best way was to find an excellent collaborator in industry with whom we could share our challenge. Following my experience with the development of the mechanical TDR, I knew the importance of sharing the dream with collaborators. There were many excellent engineers working in large corporations. I thought that a few engineers might be interested in our scientific exploration. Simultaneously, it seemed likely that university

professors of engineering departments might have a network of human resources within industries and might know such engineers. Professor Akihiko Uchiyama on the Faculty of Science and Engineering at Waseda University, who knew of the miniaturized mechanical TDR through biotelemetry studies, kindly offered me support in finding collaborators from industry and introduced several candidates to me. It took about one year to interview those candidates, and, finally, I met Mr. Suzuki in 1989. He had already resigned from a big company and was the owner of a small company named Little Leonard. Since then, he has been a key player in developing bio-logging tools. His knowledge of the manufacture of the microelectronic products and network of production engineers has promoted our ideas for the development of a new digital ABD. Despite his efforts, our first TDR model was a miserable one. It was handed to us at the airport just before we left for the field experiment and was immediately broken at the airport! Although we experienced many failures, Mr. Suzuki and his Little Leonard

collaborators made progress in manufacturing the ABDs, step-by-step.

With the advent of the digital era, I needed to make another provision simultaneously with the production of digital instrumentation. This was the recruitment of young scientists into the field of bio-logging science. This new discipline would require young, talented people who could work with the new digital tools, which would generate huge quantities of data and require sophisticated techniques of data processing and systems of computer analysis.

After obtaining field data using TDRs, I invited young scientists to my laboratory. First, I invited Dr. Yutaka Watanuki from Hokkaido University. He was not a marine mammal scientist but an excellent young ornithologist. Next, I invited Dr. Akiko Kato because I had known her since her time as a student at the graduate school of Waseda University. Thereafter, Dr. Katsufumi Sato was invited as a Post Doctoral Fellow. These were the core scientists in my laboratory. They worked hard in the field programs and in publication, and they were very adaptable to the promotion of digital field biology. This core group of young scientists attracted other Ph.D. students who were looking for new frontiers in science.

Thus, I was able to successfully transform our biological investigations from analog to digital technology in the early 1990s. But in order to

achieve this, essential conditions had to be satisfied. As our classic precepts dictate, "To achieve the goal, three conditions are required: the time of God, a geographical advantage, and harmony among people." I was very lucky to have the digital era in Japan as the time of God and the geographical advantage, while young scientists and engineers provided harmony among people.

Digital ABDs: Toward Integration

Digital tools allowed us to develop highly sophisticated instruments with a large memory, a CPU, and multiple sensors that enabled us to collect and integrate information on behavior and the ambient environment. After developing the digital TDR and the SSR in the mid-1990s, we started developing a variety of ABDs to understand comprehensive aspects of diving behavior (Figures 7 & 8), including a three-dimensional (3D) dive path logger, acceleration loggers, and digital still image loggers. Using these ABDs, we were able to determine how seals approach the dive bottom and search for prey (Mitani et al., 2003; Watanabe et al., 2003).

The studies using acceleration sensors on equipped ABDs have revealed new aspects of diving behavior. Seals do not swim actively using flippers during diving but descend passively in a gliding motion (Williams et al., 2000). This mode contributes to energy saving and consequently extends the duration of the dive. Seals also adjust

Sidebar 1

Professor Gerry Kooyman and His Depth-Time Recorder

In the mid-1960s, there were two reports on the use of a depth recorder for the investigation of the diving behavior of Weddell seals. One was the use of the depth recorder for oceanographic surveys (DeVries & Wohlschlag, 1964), and the other was the time-depth recorder originally developed by G. L. Kooyman, who pursued the study of the diving physiology of animals. He argued about the effect of enforced diving in the estimation of the diving capacity of animals. He noted differences in the diving response of seals under enforced conditions compared with free-ranging or natural conditions and commenced studies of diving physiology and behavior on free-ranging seals and penguins in Antarctica. His first TDR was 7.62 cm (3 inches) in diameter and 8.26 cm (3.25 inches) in length. He used a Bourdon tube for a sensor and a kitchen timer (Kooyman, 1965). He and other collaborators then developed another smaller depth-time recorder, which recorded depth on pressure-sensitive paper using a depth transducer. The depth-time recorder was cylindrical, weighing 650 g in air and measuring 5 cm in diameter and 17 cm in length. This was designed to measure the diving behavior of the northern fur seal (*Callorhinus ursinus*) for long periods (8 days, later modified up to 14 days) with the aim of assessing the potential effect of oil spills. This model of depth-time recorder was broadly used in investigations of the diving behavior of the fur seals (Gentry & Kooyman, 1986). Using these instruments, Kooyman presented dive profiles of many seals prior to other TDR studies. He demonstrated many important aspects of their diving capacity, showing that it is very variable and could not be explained only in terms of simple physiological models but needed to take into account the coupling between physiology, behavior, and ecology (Kooyman, 1989). In order to comprehensively understand the phenomena of animals diving from a variety of aspects, it was necessary to develop more sophisticated tools than the TDR. In this respect, it is possible to conclude that "bio-logging science" needed his contributions as a forerunner.

Sidebar 2

Harness and Epoxy Resin Glue

Columbus's egg refers to a seemingly impossible task that, once tested, is found to be easy. Epoxy resin glue techniques seemed to me like Columbus's egg. I tried to use TDRs for Adelie penguins and Weddell seals in Antarctica in 1984 at JARE-25 and for loggerhead turtles at the Cape Gamouda, Tokushima, in collaboration with Dr. Itaru Uchida, Director of Himeji City Aquarium, and Professor Wataru Sakamoto of Kyoto University. For these experiments, I prepared a type of harness for the animals (Figure 1 & pictures below) after testing them at Kamogawa Sea World Aquarium in Chiba, Japan. All except the loggerhead turtle experiments failed because of the ill design of the harnesses which slipped off after a few dives. I learned from these experiments that the technique of deployment was of equal importance to the TDR design. In fact, the technique of deployment had been solved already by someone in the U.S. using epoxy resin glue in a northern elephant seal study, information I learned through my collaboration with Professor Burney J. Le Boeuf of the University of California-Santa Cruz. I do not know who first invented this method, but the invention is a very simple idea that is equally as valuable as the invention of the TDR itself. The importance of this invention is great, but it has never been mentioned previously. Thus, I would like to say thanks for this invention here. As an alternative to epoxy resin, a method using tesa adhesive tape was devised for the study of seabirds to avoid feather cutting during the retrieval of the devices (Wilson & Wilson, 1989).



A variety of harnesses were tested on captive seals and penguins in order to attach the TDR to the animals. The epoxy resin glue and tesa adhesive tape methods overtook the harness method in seals and seabirds in the late 1980s. These new methods enabled us to attach devices on the lower mandible of seals (lower left) and flying birds (upper right).

their swimming activities according to changes in their buoyancy. The stroke rate of Weddell seals differed with their body conditions (Sato et al., 2003). Similar observations were made on Baikal seals (*Phoca sibirica*) in buoyancy-controlled experiments (Watanabe et al., 2006). Thanks to those studies, we have gained new insights into the diving behavior and diving physiology of pinnipeds (see Sidebar 2).

With regard to the function of the C-type dive of northern elephant seals, dramatic results were obtained in experiments using 3D loggers. Much controversy surrounds the sleep mode of northern elephant seals. It was observed that the seals sank belly-side up without fluttering the flippers during the second segment of the descent phase rather as a looping leaf falls (Mitani et al., 2010). Although this behavior may suggest that the C-type dive represents sleep mode, we need to test this further.

Recently, the acceleration logger was used for visualizing the feeding events of seals by detecting their quick prey capturing or biting motions,

Sidebar 3

Dive Profiles

Despite the enormous effort, major questions with regard to ecological implications of the diving behavior of the northern elephant seals have remained unsolved because of the robust barrier of water mass. The dive function of northern elephant seals, such as their transit dive, foraging dive, and digesting dive, was first inferred from the dive profiles (dive types A-E; Figure 4) using a TDR (Le Boeuf et al., 1988). Although dive type C was determined as a drift dive using SSRs (Crocker et al., 1997) and possibly a sleep dive using 3D loggers (Mitani et al., 2010), others have not been examined yet. Dive profiles are characterized by the points where seals changed their behavior (changes in descent and ascent and its rate) as shown below. Dive types D and C, for example, have several behavior changing points that took place due to a positive decision by the seals. Dive types A and E are the start points of the dive. Point B is the start point of bottom time for foraging according to the previous inferred foraging hypothesis (Le Boeuf et al., 1988). Point F probably indicates the time of foraging success or result of foraging effort. Point C was not examined yet, but it may suggest that seals decided to ascend, being stimulated by physiological signals, probably the level of the PCO₂, which seals have more sensitivity to than to PO₂. Otherwise, seals may exceed their aerobic dive limit (ADL) easily. Similarly, point G is the time seals decided to ascend, awakened by physiological stimulation, if dive type C corresponds to sleep dive. In order to understand the mechanism that determines points C and D, we need to know how those are different in relation to foraging success, foraging effort, and metabolic rate according to each dive segment of each dive type. Points D and F are more passively determined than points A, B, C, and G. With regard to dive continuity, points A and E are meaningful, but they are the most difficult to explain. Assuming that dive type C is the sleep dive, why do seals need to dive deep for sleep rather than keeping regular surface time? They may prefer to stay in the ocean depth for foraging and visit the surface not as a diver but as a surfacer (Kooyman, 1989); the reason is obscured as to why they need to sleep in the depths. It may be explained by predator avoidance (Le Boeuf et al., 1988). In this case, according to the theoretical dive bout model (Kramer, 1988), seals minimize surface time and maximize bottom time simultaneously to increase foraging opportunity. If this is true, it can be pointed out that northern elephant seals selected the physiological and ecological narrow path to survive. However, this theory and explanation has not yet been tested by observed evidence. We need to observe diving behavior in more detail, particularly in regards to foraging behavior that may explain that mentioned above. We need to continue our effort to observe animals and the ocean as an animal-sphere.





using jaw- or head-deployed acceleration loggers (Suzuki et al., 2009; Naito et al., in press). In this method, a miniaturized acceleration logger was attached externally to the jaw or head, thus providing a very simple and practical field technique compared with previous methods using stomach temperature or the intra-mandibular angle sensor (IMASEN) methods (Wilson et al., 1992; Liebsch et al., 2007). The acceleration logger promises to advance the study of the missing links between the physiology and ecology of diving behavior.

The Goal of My Apollo Program

Bio-Logging of Life and Environments

In the past several decades, numerous studies on the diving behavior of free-ranging marine mammals and marine birds have been made, measuring diving-related parameters such as depth, duration, swim speed, stroke frequency, and heart rate. These studies have revealed their physiological diving capacity, known as the aerobic dive limit (ADL) (Kooyman et al., 1989), and energy-saving mechanisms associated with swim and glide mode (Williams et al., 2000). These investigations have also revealed that seals manipulate stroke rate according to changes in their body condition, such as buoyancy (Biuw et al., 2003; Sato et al., 2003; Watanabe et al., 2006), and that they rest during descent by free fall (Mitani et al., 2010). The above studies that started using TDRs, and then more advanced ABDs, have provided new insights into the diving behavior of marine mammals. However, our studies have only arrived at the halfway post because they have only considered physiological and behavioral mechanisms and have not dealt with ecological and environmental aspects (Figure 9).

The mode of life of marine mammals is unique. They take prey underwater for energy intake, and they take oxygen at the surface for catabolism. Thus, they must balance their foraging requirements against physiological constraints. It is easily understood that marine mammals should have developed effective ways of foraging and unique systems of physiological adaptation. While there have been many studies of their systems of physiological adaptation, foraging behavior has been somewhat neglected, despite its importance, primarily due to the difficulties of underwater observation. Although some of the challenges have now been met, understanding their lives with respect to foraging behavior is still at an immature stage. In order to understand foraging behavior, we need to simultaneously observe feeding effort and feeding success. Effort and success might be determined from their food requirements or body condition, which could vary according to life events and

season. Environment is also an important factor that determines effort and success. Therefore, in relation to foraging behavior, we need to observe their feeding success and effort at a variety of temporal scales as well as in different oceanographic environments. To accomplish this objective, we need to develop new ABDs that will allow us to measure their life events over a variety of time scales from daily to seasonal, or over the course of a whole year. Recalling the saying, "Mate ba kairo no hiyori ari," I waited 30 years to recognize and visualize the underwater life of marine mammals. I am ready to wait still further decades to realize the next stage, "logging life and the environment."

Literature Cited

- Austin, D., Bowen, W. D., McMillan, J. I., & Boness, D. J. (2006). Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology*, 75, 408-420.
- Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H., & Fedak, M. (2003). Blubber and buoyancy: Monitoring the body condition of free ranging seals using simple dive characteristics. *The Journal of Experimental Biology*, 206, 3405-3423.
- Bornemann, H., Mohr, E., & Plötz, J. (1992). Monitoring the feeding-behavior of freely diving Weddell seals (*Leptonychotes weddellii*). Journal of Veterinary Medicine, Series A–Physiology Pathology Clinical Medicine, 39, 228-235.
- Boyd, I. L., & Croxall, J. P. (1996). Dive duration in pinnipeds and seabirds. *Canadian Journal of Zoology*, 74, 1697-1705.
- Crocker, D. E., Le Boeuf, B. J., & Costa, D. P. (1997). Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology*, 75, 27-39.
- DeVries, A. L., & Wohlschlag, D. E. (1964). Diving depths of the Weddell seal. *Science*, 145, 292.
- Gale, R., & Renouf, D. (1993). Detecting and measuring food and water intake in captive seals using temperature telemetry. *Journal of Wildlife Management*, 57, 514-519.
- Gentry, R. L., & Kooyman, G. L. (1986). Fur seals: Maternal strategies on land and at sea. Princeton, NJ: Princeton University Press. 291 pp.
- Kooyman G. L. (1965). Techniques used in measuring diving capacities of Weddell seals. *Polar Record*, 12, 391-394.
- Kooyman, G. L. (1989). Diverse divers: Physiology and behaviour. Berlin: Springer-Verlag.
- Kooyman, G. L., Gentry, R. L., & Urquhart, D. L. (1976). Northern fur seal diving behavior: A new approach to its study. *Science*, 193, 411-412.
- Kramer, D. L. (1988). Behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology*, 66, 89-94.

- Le Boeuf, B. J., Costa, D. P., Huntley, A. C., & Feldkamp, S. D. (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris. Canadian Journal of Zoology*, 66, 446-458.
- Le Boeuf, B. J., Naito, Y., Huntley, A. C., & Asaga, T. (1989). Prolonged, continuous, deep diving by northern elephant seals. *Canadian Journal of Zoology*, 67, 2514-2519.
- Le Boeuf, B. J., Naito, Y., Asaga, T., Crocker, D., & Costa, D. P. (1992). Swim speed in a female northern elephant seal: Metabolic and foraging implications. *Canadian Journal of Zoology*, 70, 786-795.
- Liebsch, N., Wilson, R. P., Bornemann, H., Adelung, D., & Plötz, J. (2007). Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep Sea Research, Part II*, 54, 256-269.
- Mitani, Y., Russel, A. D., Katsufumi, S., Kato, A., Naito, Y., & Costa, D. P. (2010). Three-dimensional resting behavior of northern elephant seals: Drifting like a falling leaf. *Biology Letters*, 6(2), 163-166.
- Mitani, Y., Sato, K., Ito, S., Cameron, M. F., Siniff, D. B., & Naito, Y. (2003). A method for reconstructing three dimensional dive profiles of marine mammals using geomagnetic intensity data: Results from two lactating Weddell seals. *Polar Biology*, 26, 311-317.
- Naito, Y. (1992, October). When does northern elephant seal sleep? Kagaku Asahi, 40-44. (In Japanese).
- Naito, Y., Asaga, T., & Ohyama, Y. (1990a). Diving behavior of Adelie penguins determined by time depth recorder. *Condor*, 92, 582-586.
- Naito, Y., Le Boeuf, B. J., Asaga, T., & Huntry, A. C. (1989). Long-term diving record of an adult female northern elephant seal. *Antarctic Record*, 33, 1-9.
- Naito, Y., Bornemann, H., Takahashi, A., McIintyre, T., & Plötz, J. (in press). Fine-scale feeding behavior of Weddell seals revealed by mandible accelerometer. *Polar Science*.
- Naito, Y., Sakamoto, W., Uchida, I., Kureha, K., & Ebisawa, T. (1990b). Estimation of migration route of logger-head turtle *Caretta caretta* around nesting ground. *Nippon Suisan Gakkai shi*, 56(2), 255-262.
- Plötz, J., Bornemann, H., Knust, R., Schroder, A., & Bester, M. (2001). Foraging behavior of Weddell seals, and its implications. *Polar Biology*, 24, 901-909.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi A., Daunt, F., et al. (2009). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE*, 4(4), e5379.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B., & Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *The Journal of Experimental Biology*, 206, 1461-1470.
- Scholander, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrdets Skrifter Norske Videnskaps-Akad (Oslo)*, 22, 1-131.
- Suzuki, I., Naito, Y., Folkow, L. P., Miyazaki, N., & Blix, A. S. (2009). Validation of a device for accurate timing

of feeding events in marine mammals. *Polar Biology*, 32, 667-671.

- Tanaka, H., Sato, K., Matsuzawa, Y., Sakamoto, W., Naito, Y., & Kuroyanagi, K. (1995). Analysis of possibility of feeding of logger-head turtles during internesting periods based on stomach temperature measurements. *Nippon Suisan Gakkai shi*, 61, 339-345.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y., & Miyazaki, N. (2006). Body density affects stroke patterns in Baikal seals. *The Journal of Experimental Biology*, 209, 3269-3280.
- Watanabe, Y., Mitani, Y., Sato, K., Cameron, M. F., & Naito, Y. (2003). Dive depths of weddell saels in relation to vertical prey distribution as estimated by image data. *Marine Ecology Progress Series*, 252, 283-288.
- Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., LeBouef, B. J., Horning, M., et al. (2000). Sink or swim strategies for cost-efficient diving by marine mammals. *Science*, 288, 133-136.
- Wilson, R. P., & Wilson, M. T. (1989) Tape: A packageattachment technique for penguins. *Wildlife Society Bulletin*, 17, 75-79.
- Wilson, R. P., Cooper, J., & Plötz, J. (1992). Can we determine when marine endotherm feed? A case study with seabirds. *Journal of Experimental Biology*, 167, 267-275.
- Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A., & Kurita, M. (2002). Lip-reading in remote subjects: An attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, 140, 17-27.