Recent Advances in Studies of the Diving Behavior of Marine Birds and Mammals with Micro-data Loggers

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Abstract. The diving behavior and physiology of birds and mammals has been studied for more than a century. From the early 1940s many physiological studies of diving responses in the vascular system were conducted under forced-submerged conditions, despite it being known that the responses differed between voluntary diving and enforced-submerged animals. Accordingly, new attempts to study freely diving animals were begun. The first success was achieved in 1965 by Kooyman, who used a mechanical time depth recorder (TDR) to monitor the diving behavior of Weddell seals, *Leptonychotes weddelli*. Thereafter, in the 1980s marked advances in experimental apparatus revealed many unexpected diving abilities of penguins and seals. More recently, in addition to interest in their physiology, the foraging ecology of free diving animals has attracted considerable interest, and has stimulated the accelerated development and miniaturization of electronic data loggers. Currently, data loggers that record depth, swimming speed, light level, ambient, esophagus and body temperature, acceleration, geo-magnetic field, heart rate, ECG, EMG, visual image, etc., are available as tools to study foraging ecology, physiology and biomechanics. This technology has brought new advances in bio-logging science, which utilizes integrated microsystem technology to study the lives of animals in aquatic and other remote environments. This paper reviews recent technological advances in this field, with special attention to activities in Japan and the roles of these advances in the study of diving by marine animals.

Key words: Behavior measurement, Diving behavior, Diving birds, Diving mammals, Micro-data logger.

Introduction

Marine birds and mammals are breadth holding divers well adapted to the aquatic life and they are also the top predators in the marine ecosystem. How and why they dive for long periods have long been a question of interest to physiologists. At the first stage of the study, biologists made field observations and measured dive durations and where and when they dive. While physiologists have measured physiological responses of seals and ducks under forced submersion in a laboratory since 100 years ago (Scholander 1940). However, responses of animals to forced submersion are known to be different from responses in the natural condition (Kooyman 1989). To further understand diving
behavior and physiology, studies on free ranging animals have been essential. “The lack of technical means to explore this area” (Kooyman 1989) has given rise to a need for useful tools to study physiological responses to voluntary diving.

Simultaneously with increase of physiological interest, animal behavior under water became a matter of concern from point of view of marine ecosystem conservation. Since the 1980s, conservation of the marine ecosystem has become of wide concern because of increasing human activities such as fisheries and ocean pollution. To understand the prey-predator interaction and the process of ecosystem change in the Southern Ocean, many field surveys of the foraging behavior of free ranging marine birds and mammals have been conducted based on various dive depth recording devices and radio tracking techniques. These studies have demonstrated the high diving ability of penguins and seals, which had not been expected before. These studies have also indicated that diving birds and marine mammals are major consumers of epipelagic and coastal fauna and play wide roles in the marine ecosystem. Therefore, the importance of study of diving behavior of marine birds and mammals is strongly suggested (Kooyman et al. 1982, Croxall et al. 1988, Naito et al. 1990a).

For comprehensive understanding of foraging strategy, physiological study on energy system during diving was inevitable. Thus physiology of diving and consumption of prey, a standard procedure for estimating metabolic rate while foraging became essential subject as well as behavior study. Measurement of heart rate during voluntary dives became possible in the early 1990s (Kooyman et al. 1992b) and the relationship between metabolic rate and heart rate has been examined in the laboratory (Butler & Jones 1997). More detailed study of the diving response of the vascular system through nervous control is expected to become possible by using newly developed tools for ECG measurement during diving. For precise measurement of diving behavior, studies on biomechanics of diving animals was encouraged and acceleration data loggers were developed. Yoda et al. (1999) performed first very accurate measurements of flipper movements on free ranging King Penguins, Aptenodytes patagonicus. Thereafter detailed biomechanical analysis has become possible. Not only diving birds but also both flying and diving behavior was measured very precisely.

Animal-attached instruments for measuring diving behavior and physiology of marine bird and mammals have been developed during the last two decades. Thanks to the technological achievement of producing sophisticated instruments, recent studies have obtained a huge amount of information. Both methodological and scientific results obtained using these tools have encouraged us to study more about how marine birds and mammals dive and live in the ocean. Here, I review the history of development of these tools and also recent new directions of these studies focusing on activities in Japan.

**History of development**

For a long time simple diving gauges were used to measure maximum diving depth, especially for small birds due to the light and small size and the low price. A plastic tube with one end closed is coated inside by water-soluble dye that indicates the maximum

In the mid-1980s an electronic multiple maximum depth-gauge was developed and used for penguins and seals (Kooyman et al. 1982, Lishman & Croxall 1983). This multiple maximum depth-gauge records the number times a pre-set threshold depth is exceeded.

From the mid-1970s to the mid-1980s mechanical type time-depth recorders (TDR), which can record depth continuously, were developed to measure the diving behavior of penguins, seals and sea turtles (Kooyman et al. 1976, Wilson & Bain 1984, Gentry & Kooyman 1986, Naito et al. 1989). The National Institute of Polar Research (NIPR) developed the mechanical TDR targetting miniaturization. First TDR was developed using existing techniques in 1981. A depth recorder for fishing gear (70φ × 310 mm, 1.3 kg) was reduced in size (50φ × 130 mm, 450 g) to study the underwater behavior of loggerhead turtles, Caretta caretta, during the inter-nesting period (Naito et al. 1990a, Sakamoto et al. 1990). This recorder consisted of a motor powered by an alkaline battery (1.5 V AA type), paraffin coated paper, and scratching needle connected to a bellows pressure-gauge, and could work for three months. Another type of mechanical recorder that could record swim speed and diving depth was adapted for loggerhead turtles (Minamikawa et al. 1997). To miniaturize further, we used a diamond needle with 70 degree sharpness, which made it possible to scratch a 6–8 μ fine line on carbon or aluminum coated paper of less than 10–12 μ thickness (Fig. 1, Naito et al. 1990a). This newly developed technique of scratching a fine line on very thin paper allowed us to build
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Fig. 2. Analysis of TDR data from Adelie Penguins at Syowa Station revealed the time, depth and frequency distribution of diving.

A recording system with a very slow rate of recording paper advance (0.04 mm/min) by several gear shifts driven by a very small quartz motor and a 3-volt button-type lithium battery. This system was connected to the bellows depth transducer, and these were assembled in a dome-top cylinder measuring 25 × 80 mm. Total mass including the battery was 80 g in air. This could work for more than 20 days continuously. This smallest was used to record the diving behavior of Adelie Penguins, Pygoscelis adeliae, at Syowa Station, Antarctica (Fig. 2, Naito et al. 1990a); Gentoo Penguins, Pygoscelis papua (Williams et al. 1992); and Macaroni Penguins, Eudyptes chrysolophus (Croxall et al. 1993); and succeeded in obtaining depth data for the first time from 2.6–2.8 kg flying-diving birds, such as the Blue-eyed Shag, Phalacrocorax atriceps (Fig. 3, Croxall et al. 1991, Kato et al. 1992). The same system was also used for northern elephant seal Mirounga angustionstris, and obtained continuous data for more than 80 days, from the seal’s departure to the open sea after breeding to arrival at the colony for molting (Fig. 4, Le Boeuf et al. 1989, Naito et al. 1989).

In the mid-1980s advanced micro-electronic technology became available and Hill and Wildlife Computers developed several type of data loggers (Hill et al. 1987, Bengtson 1993). First they developed a cylinder-shaped maximum depth recorder (30 mm × 125 mm, Model: Mark III) that can measure maximum depth for each dive and record the number of dives according to pre-programmed depth categories. Then they developed the Model: Mark IV, which contains a micro-processor and 512K bytes RAM memory in an epoxy resin pot. The sampling interval of the Mark IV is pre-programmed by a PC. NIPR and Little Leonald Ltd. also jointly developed micro-processor controlled data loggers. They selected an aluminum cylinder case with O-ring measuring 19 × 80 mm. They used
Fig. 3. The first continuous diving record of a flying bird was obtained from the Blue-eyed Shag at Bird Island, South Georgia. Blue-eyed Shag with mechanical TDR (upper), and a part of the diving record (lower).

4 M bytes of flash memory and 12bits AD converter. NIPR and Little Leonald have continued to produce variety of micro data loggers in the last decade.

Studies of foraging behavior

Although the study of animal diving started from a physiological point of view, how
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Fig. 4. TDR data from the Northern Elephant Seal showed the non-stop deep diving performed by three adult female Elephant Seals. A single line represents one dive of which mean duration was 18–22 minutes (Asaga et al. 1994).

marine birds and mammals forage under physiological limitation and how much prey they take while diving are basically crucial questions to understand their foraging strategy in the marine ecosystem. Use of TDRs has greatly contributed to increase of our knowledge of the diving behavior and foraging ecology of diving animals as we could extract information from TDR data such as dive profile, dive depth, dive duration, dive bottom time, descent and ascent rate, surface time, dive bout duration and number of dives in a bout. Thus the TDR is a useful tool for measurement of diving behavior and foraging.

Foraging studies started by measuring the foraging depth to which animals dive frequently and also the time of day at which animals actively forage (Naito et al. 1990a, Chappell et al. 1993a). Then we compared diving behavior among different seasons, localities and nutritional conditions. Chappell et al. (1993b) and Watanuki et al. (1993, 1997, 2002) showed changes of diving performance through the breeding season in Adelie Penguins and differences of diving performance between areas within and without sea-ice. However, with these early TDRs, prey pursuit, foraging effort and prey capture were not recorded.

Abrupt depth changes often recorded with these TDRs near the bottom of the dives were suspected to be prey pursuits. To prey pursuit, a swim speed recorder was employed. At first, swim distance and change of swim speed during diving and change of descent and ascent swim angles were expected to shed light on feeding behavior. The swim speed recorder was first used for sea turtles and seals owing to their large body size (Ponganis et al. 1990, Le Bouef et al. 1992, Crocker et al. 1994, Minamikawa et al. 1997). Later on the speed recorder was combined with a depth recorder to make a depth-speed data logger for larger penguins, such as Emperor Penguins, *Aptenodytes forsteri*, and King Penguins (Kooyman et al. 1992a, b). Based on abrupt changes in swim speed, King Penguins were assumed to pursue prey at the bottom and during ascent (Ropert-Coudert et al. 2000). However, speed data did not tell us anything about ingestion of prey by these diving
Two methods to estimate feeding ingestion have been proposed. A gastro-temperature recorder detects feeding events by measuring the temperature drop in the stomach by ingestion of prey at seawater temperature. This technique was proposed by Naito (Bengston 1993) and first used for sea turtles and marine birds in the field experiments by Sato et al. (1994), Wilson et al. (1992), Putz (1994) and Kato et al. (1996). It was later modified to detect ingestion of smaller prey by measuring temperature in the esophagus where the temperature drop is more sensitive to prey ingestion than in the stomach (Ropert-Coudert et al. 2000, Charrassin et al. 2001). Another technique was designed to detect prey ingestion by recording mouth opening movements by a magnetic sensor and was first used for Weddell seals, Leptonychotes weddelli, (Bornemann et al. 1998, Plotz et al. 2000).

Ropert-Coudert et al. (2000) measured swim speed, depth and esophagus temperature of free ranging Adelie Penguins, which linked diving and feeding behavior directly (Fig. 5). They suggested that Adelie Penguins ingest prey mostly at the bottom phase of diving or sometimes in the ascent phase, indicating that penguins knew the depth of their prey before diving. Penguins captured prey by upward movement in more than 60% of cases, suggesting that they planned their feeding strategy. When presumably pursuing prey, fish eating African Penguins, Spheniscus demersus, abruptly increased swim speed, while krill-eating Adelie Penguins decreased swim speed, indicating that there are different
prey capture techniques (Wilson et al. 1998, Ropert-Coudert et al. 2002). It is still hard to estimate the amount of prey intake. We need to develop more reliable techniques for estimation of prey type and amount.

Measurement of the energy cost of diving

Physiology studies, starting from forced submersion experiments in laboratories in the early 1940s, have included many experiments on voluntary diving marine mammals with TDRs. Based on these studies, Kooyman et al. (1983) proposed the very important idea of the aerobic dive limit (ADL). This new term was drawn from experiments on the Weddell seal, which identified a critical dive duration beyond which a steep increase of post dive blood lactate concentration was found. ADL can be determined theoretically as the consumption time of stored oxygen. This theoretical ADL is based on some assumptions. Stored oxygen was obtained with the calculated oxygen concentration of various oxygen storage compartments in the body and oxygen consumption rate was also extrapolated from exercise performed in the laboratory or determined as a multiple of resting metabolic rate, usually from an allometric relationship of body mass to resting metabolic rate (Butler & Jones 1997). Consequently theoretical ADL may include errors and lead to misunderstanding about voluntary diving, so that direct measurement of metabolic rate is highly desirable. To measure the metabolic rates of free ranging marine birds and mammals, two methods were developed. One is to estimate metabolic rate by the doubly labeled water (DLW) technique, which indicates metabolic rate by rate of CO2 production (Nagy 1980). The other is the tritiated water method that determine metabolic rate from prey intake estimated by water turnover rate (Kooyman et al. 1982). These methods are useful in evaluating energy or food consumption over a certain period. However, these methods cannot determine metabolic rate continuously. To do this, heart rate was measured by radio-transmitter in voluntary diving Humboldt Penguins, Spheniscus humboldti, in a freshwater pond, where O2 consumption was measured simultaneously with a respirometer (Butler & Woakes 1983). Recently the heart rates of free ranging animals have been measured with implanted data-loggers (Woakes et al. 1995).

Measuring both heart rate and O2 uptake permitted the relationship to be correlated, and it turn out that there is a good relationship (Butler & Jones 1997), though at the time scale of 10 minutes, which is not enough to analyze the energetics of diving. To measure O2 consumption on a fine scale, we need to develop a respirometer data logger.

To determine the metabolic condition of free ranging diving animals, body temperature was measured in several experiments. In order to estimate the heat conductivity of loggerhead turtles, temperature in the stomach, at the carapace surface and in ambient water were measured simultaneously with dive depth and swim speed (Sakamoto et al. 1990, Sakamoto et al. 1993, Sato et al. 1994). Body size had a more important role in maintenance of higher body temperature than ambient temperature (Sato unpublished data). Metabolic level was monitored by measuring body core temperature during diving in King Penguins. Handlich et al. (1997) reported that during a sustained deep diving bout, body temperature in the abdomen decreased to as low as 11°C, which may contribute
to slowing the metabolic rate during the diving. Measurements of core body temperature of flying and diving bird, such as Guillemots, *Uria aagle*, were also made by using miniaturized implanted data-loggers (Niizuma unpublished data). The core body temperature changed in the transition between descent and ascent phases, and showed a decreasing trend until the end of the dive bout.

As far as we know measurements of heart rate and core body temperature by implanted sensors are the only way to monitor the metabolic condition of free ranging animals continuously. However, these methods require special facilities in the field camp for surgical operation. Thus we need to develop non-invasive methods.

**Precise monitoring of diving and other behavior**

To examine the diving behavior precisely and to analyze diving locomotion, we need to measure the movement of the body trunk and flippers, wings and fins. NIPR and Little Leonard Ltd. have developed small and high-resolution data loggers with a 12-bit A/D converter to attain 1/4000 resolution, 5cm per 200m of water depth for example, though resolution does not always guarantee absolute accuracy. It is also important to increase the sampling rate that determines the time resolution. Development of small but large capacity memory (more than 16 M bytes) enables high speed sampling (16 Hz) to be
Fig. 7. Diving record of a King Penguin showing the details of the fluttering efforts in two axes, acceleration data, and the relation between acceleration movement and swim speed affected by buoyancy. When the penguin swims downward it has to stroke its flippers harder to counter the force of buoyancy, and increases swimming speed through buoyancy without doing any stroking.

Fig. 8. The three-dimensional dive path of a Weddell Seal was determined by swim speed, three components of field magnetism and two axes of acceleration. Seals often change the angle of their body axis horizontally and laterally. These changes were compensated for using earth gravity acceleration. The experiment was conducted in December 2000 at McMurdo Station, Antarctica.
continued for a long period (up to 3 days). High-resolution and quick-sampling reveal new aspects of animal diving.

Yoda et al. (1999) first used an acceleration data logger (Model: NIPR-400 D2G) developed by NIPR and Little Leonard Ltd. with swim speed, depth and temperature loggers on Adelie Penguins to test a theoretically proposed hydrodynamic model that predicted that leaping would be energetically cheaper when an animal swims continuously at depths of less than three maximum body diameters below the water surface (Hui 1987). Yoda et al. (1999) suggested that wild penguins reduced drag by swimming deeper than the high drag layer and did not swim continuously in such energetically high cost layer. According to them penguins leapt at higher speed than predicted cost effective speed and distance covered by leaps was only 3.8% of the total distance traveled during porpoising. Conclusion was that energy savings by porpoising were marginal. Yoda et al. (2001) also developed a new method to monitor behavior by Adelie Penguins by measuring acceleration and swim speed, along three axes, and depth, with the Model: UWE-PD2G. They measured surging, heaving and swaying and also measured depth and swim speed, which made it possible to divide behavior automatically into diving, resting at the water surface, walking, standing and lying on land, tobogganing and porpoising with the aid of a macro program operating on a PC with high processing speed (Fig. 6). Sato et al. (2002) used acceleration and other loggers (Model: NIPR-400 D2G and UWE-200 PDT) to study how Adelie and King Penguins control their buoyancy. They found that penguins do not flutter their flippers during the ascending phase, but accelerate their swim speed to the surface by increasing buoyancy (Fig. 7). It appears that based on this acceleration penguins can control the inhaled air volume. Miniaturized acceleration data loggers (Model: UME-D2GT) have also been successfully used to measure both the flying and diving behavior of smaller and flying-diving seabirds including the Rhinoceros Auklet (Cerorhinca monocerata), Guillemot, Brown Booby (Sula leucogaster) and Cape Gannet (Sula capensis) (Kato et al. 2003, Watanuki et al. 2003, Ropert-Coudert et al. 2004). The biomechanical analysis had been done previously using video or movies in a water tank, these were the first direct measurements of acceleration of free ranging animals.

Now we have succeeded in making fine scale measurements and classifying the motions by aid of computer techniques. If it becomes possible to obtain data over a longer duration, it is possible to monitor behavior precisely over a long term by computer classification. Computerized behavior science will soon link to simulation science and will contribute to the study of the behavior ecology model.

**Future prospects of bio-logging science**

Recent animal tracking techniques by satellite have made tremendous contributions to determining activity patterns during foraging trips, migration routes and speed (Le Boeuf et al. 2000). In the case of marine birds, VHF and satellite telemetry techniques have been successfully used both while the birds are flying and on the water surface. A geolocation technique by measuring light intensity and recording it with a data logger has been developed (Hill 1994) and applied to northern elephant seals (Stewart & DeLong
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Fig. 9. Digital still picture logger (DSL) used on a Weddell Seal in December 2000 at McMurdo Station, Antarctica. The logger can take and store about 700 pictures. DSL equipped with both flush light and preset interval controller photographed organisms distributed along the dive path of the seal at 30 second intervals. An image analyzer analyzed data and determined the prey index along the seal's dive path. The upper figure shows the points of DSL shots and prey index distribution shown by symbols. The lower picture shows a patch of prey fish at 290 m depth.

1994) to determine the foraging area. Although satellite tracking is useful for determination of large scale to meso-scale movements, it is not effective to determine micro-scale movements under water.

To do this, geomagnetic direction has been measured along with swim distance in Weddell seals (Fig. 8, Davis et al. 1999, Mitani et al. 2003). In same way smaller data loggers could be used to determine diving paths of diving birds. With similar animal-borne data logging systems it is possible to collect data on their environment where they are moving. Ambient temperature light level and conductivity of seawater were successfully measured. However it is still difficult to measure, for example, accurate salinity, level of
Recent data loggers developed by the National Institute of Polar Research and Little Leonard Co. Ltd. There are two main types of data loggers; the smaller M series and the larger W series. Logger types are named W380M-DT, W380L-DT, M190-DT, etc., with the numbers in name indicating the depth range in metres. Both the W and M series have several variations according to the equipped sensors, e.g. W380M-DT showing DT; depth and temperature, PDT; speed, depth and temperature, PD2GT; speed, depth, two accelerations and temperature, ECG; electrocardiograph, 2T; two temperatures. For highly accurate measurements all types of loggers are equipped with a 12 bit AC/DC converter, giving 1/4098 data resolution. Sampling interval can be preset by PC commands in 255 steps by each channel independently. Weight in air varies from 16 g to 40 g.

chlorophyll $a$ concentration and distribution of prey organisms. A new trial has been done on the Weddell seal to measure prey distribution using image data loggers (3.4 kg in water and 1.6 kg in air). The still picture loggers sample 510 by 492 pixel images at 30 s intervals with synchronized flash, and these images show the relative abundance of potential prey through the diving paths of animals. Preliminary experiments have indicated that the density of organisms is greater in deep water where seals concentrate efforts (Fig. 9, Watanabe et al. 2003). The camera system was miniaturized was tentatively used for penguins (Takahashi unpublished data). With regard to camera system further miniaturization and increase of memory size is possible and it will allow us to measure prey distribution along dive path together with environmental data.

Integration of multiple parameters measured precisely by an advanced data logger system as described above will contribute to our understanding of foraging behavior, physiology and ecology in the field where animals are living (Fig. 10). During the course
of developing the data loggers for animal behavior studies the primary effort was focused on miniaturization. This will be key point in the future as well in future, because we have to minimize the effect of devices on animals under natural conditions. Miniaturization will expand the possibilities to study smaller species. Increase of memory size is required to store data obtained by multiple sensors. The large memory size will permit high speed sampling and long data records. On the other hand researchers need to take initiatives in developing sensors that will meet the requirements of the research and also requirements for integration of information about under water lives and ocean, which are left unstudied.

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