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The device that revolutionized marine organismal biology

Jeremy Goldbogen and Jessica Meir discuss Gerald Kooyman's classic paper, 'Maximum diving capacities of the Weddell seal, Leptonychotes weddelli', published in *Science* in 1966.

As recently as 50 years ago we had very little information on where marine mammals and seabirds went once they plunged beneath the sea surface. Though at times fortunate enough to catch a glimpse of these animals breathing in between dives, researchers had no systematic way to quantify their underwater behavior. The apparent ability of these animals to migrate long distances and execute long, deep dives begged for an experimental approach. Here we review the first study to measure a continuous time series of diving behavior for a marine animal – Gerald 'Jerry' Kooyman's article titled, 'Maximum diving capacities of the Weddell seal, *Leptonychotes weddelli*', published in *Science* (Kooyman, 1966). This groundbreaking study debuted several scientific innovations including an isolated dive-hole experimental design and the first time–depth recorder (TDR), both of which revolutionized the fields of marine biology and comparative physiology.

Having observed the Weddell seal on his maiden voyage to the Antarctic in the early 1960s, Kooyman realized the potential this species and its ecosystem held as a 'natural' experimental set-up for physiological research. The Weddell seal's sub-ice foraging and diving behavior and its propensity for seeking out, returning to and defending breathing holes offered an open invitation to an inquisitive biologist like Kooyman, presenting a convenient opportunity to attach a dive recorder to (and recover the recorder from) an animal that exhibited extraordinary breath-hold capacity. At the time, diving data for marine mammals at sea were incredibly scarce and primarily observational, with the exception of a few experimental studies that measured only the maximum depth experienced by the animal over the entire attachment duration of a device (Scholander, 1940; Devries and Wohlschlag, 1964; Kooyman, 1965; Kooyman, 1967). The earliest of these studies involved attaching a manometer (pressure gauge) to a fin whale using a harpoon, emphasizing the difficulty of obtaining this type of data on wild animals. Missing from these studies, however, was the coupling of time and depth information to provide a comprehensive assessment of diving capacity. Kooyman recognized that the combination of these parameters was fundamental not only to understanding the diving adaptations of these remarkable creatures, but also perhaps to convincing fellow scientists that the maximum depth data were genuine!

Capitalizing on the novel and still relatively unexplored Antarctic home of this species, Kooyman set out to quantify the diving capacity of the Weddell seal, *Leptonychotes weddellii*. He embarked upon his second of now more than 50 trips to the ice in the austral summer of 1963–1964, marking the debut of his prolific research career on the frosty continent. Though only a graduate student, he ventured there alone in that initial season, a shocking comparison with the elaborate logistics and safety requirements inherent to today's polar research teams (note that for the second season of the project, however, he wisely recruited a fellow graduate student, Charles Drabek, to assist). Based out of McMurdo Station, the US Antarctic base located at McMurdo Sound, Kooyman scouted an area (approximately 3 km^2) of the sea ice that was over water of about 600 m depth and free of cracks and holes. Equipped only with a chainsaw, Kooyman painstakingly cut through the ~2-m-thick ice to create an artificial dive hole, which he covered with a heated hut. Thus emerged a significant innovation in Antarctic science, the isolated dive hole, an experimental design that has been used by numerous researchers (a majority of which are Kooyman's academic progeny) studying the diving behavior and physiology of seals and penguins for five decades since (Kooyman, 2004; Kooyman, 2006).

Kooyman captured 20 adult and subadult Weddell seals over the course of his experiment, brought them to the ice-hole stations (he also co-opted an additional 11 'volunteers' that frequented his ice holes, providing mutually beneficial foraging/tagging opportunities for seal and researcher alike!) and instrumented the animals with one of three different instruments: (1) a Tsurumi–Seiki–Kosakusho (TSK) recorder, which measured solely the maximum depth of the dive, similar to that used in previous studies (Devries and Wohlschlag, 1964; Kooyman, 1965); (2) a manometer tube, which recorded maximum depth only; and (3) a depth–time recorder, which recorded depth against time on a smoked glass disc. This latter device, built to Kooyman's design by a local watch repairman/expert machinist, used an ordinary 60-min kitchen timer, becoming the very first TDR. The limits on recording duration forced Kooyman to change the TDR every hour, putting him in close contact with the seals (Fig. 1).

With the placement of isolated dive holes far from natural cracks in the ice, the instrumented seals were forced to return to the entry site, where Kooyman eagerly awaited the return of his instruments. Although a majority of the dives recorded by the tags were short and shallow, longer dive durations of 6–15 min were correlated with depths of more than 100 m and often greater than 300 m. Kooyman recorded dives greater than 20 min, with the longest single dive lasting an impressive 43 min 20 s. He found that the animals made many dives to mid-water depths (300–400 m), but rarely dived deeper than 400 m. The deepest dive recorded was made by an adult male carrying a TSK depth recorder. Kooyman recounts almost choking on a

Classics is an occasional column, featuring historic publications from the literature. These articles, written by modern experts in the field, discuss each classic paper's impact on the field of biology and their own work.

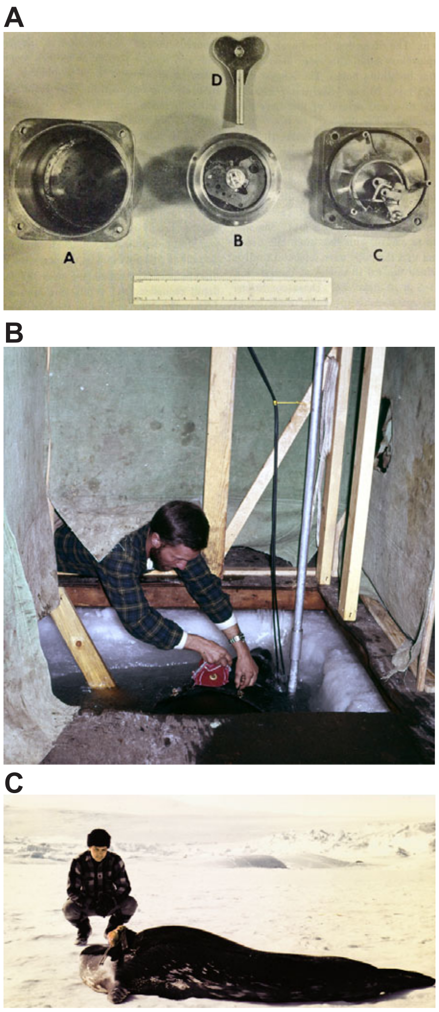

Fig. 1. Time-depth recorder (TDR) and attachment to a Weddell seal in McMurdo Sound, Antarctica. (A) Core components of the TDR, including a modified 60-min kitchen timer (from Kooyman, 1967). (B) Kooyman attaches the TDR to a surfacing Weddell seal (photo credit: Charles Drebek). (C) Peter Koerwitz inspects a tagged Weddell seal hauled out on sea ice (from Kooyman, 1966).

dried biscuit when he observed that the reading went far beyond the calibrated 500 m mark on this device. As the instrument was undamaged, he conducted a subsequent test drop to match the trace of the seal's dive, revealing an astounding depth of 600 m for this dive.

Kooyman measured hundreds of Weddell seal dive profiles, an impressive dataset, which provided a solid foundation for understanding the dive capacity and behavior of what we now recognize as one of the consummate diving animals.

But perhaps the most important impact of this pioneering work was the debut of the TDR, an instrument that is an integral part of nearly all studies on the behavior and physiological ecology of free-ranging aquatic vertebrates. Even the most sophisticated tags used in contemporary studies to measure kinematic, physiological, acoustic and oceanographic data still rely heavily on a TDR to provide key information on behavior and ecological context (Madsen et al., 2002; Johnson and Tyack, 2003; Biuw et al., 2007). For these reasons, this classic paper by Kooyman represents a milestone in the field of biologging, a diverse and rapidly growing discipline driven by the perpetual miniaturization of electronic tag technology. Since Kooyman's innovation in the 1960s, the TDR has been modified and equipped with other sensors for a wide range of studies focused on diving physiology (Williams et al., 2004; Ponganis et al., 2011), locomotor performance and energetics (Wilson et al., 2006; Watanabe et al., 2011; Gilly et al., 2012), the echolocation and feeding of the world's deepest diving whales (Madsen et al., 2002; Johnson and Tyack, 2003; Tyack et al., 2006), and the migratory behavior of apex predators across ocean basins (Block et al., 2011; Costa et al., 2012). Biologging has come of age to represent a new type of natural history that provides novel time-series data, which, in combination with other biological and physical assessments, can offer experimental insights into how animals operate in their natural environment (Rutz and Hays, 2009; Ropert-Coudert et al., 2010). As field studies begin to merge with traditional laboratory techniques in comparative physiology, we will always look back to Kooyman's classic contribution and how it transformed the way we study marine animals in the open ocean.

Jeremy A. Goldbogen
Stanford University
jergold@stanford.edu

Jessica U. Meir
NASA Johnson Space Center and Harvard Medical School/Massachusetts General Hospital
jmeir@mgh.harvard.edu

References

Biuw, M., Boehme, L., Guinet, C., Hindell, M., Costa, D., Charrassin, J. B., Roquet, F., Bailleul, F., Meredith, M., Thorpe, S. et al. (2007). Variations in behavior and condition of a Southern Ocean top predator in relation to *in situ* oceanographic conditions. *Proc. Natl. Acad. Sci. USA* **104**, 13705-13710.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A. L. et al. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86-90.

Costa, D. P., Breed, G. A. and Robinson, P. W. (2012). New insights into pelagic migrations: implications for ecology and conservation. *Annu. Rev. Ecol. Evol. Syst.* **43**, 73-96.

Devries, A. L. and Wohlschlag, D. E. (1964). Diving depths of the Weddell seal. *Science* **145**, 292.

Gilly, W. F., Zeidberg, L. D., Booth, J. A. T., Stewart, J. S., Marshall, G., Abernathy, K. and Bell, L. E. (2012). Locomotion and behavior of Humboldt squid, *Dosidicus gigas*, in relation to natural hypoxia in the Gulf of California, Mexico. *J. Exp. Biol.* **215**, 3175-3190.

Johnson, M. and Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Oceanic Eng.* **28**, 3-12.

Kooyman, G. L. (1965). Techniques used in measuring diving capacities of Weddell seals. *Polar Rec.* **12**, 391-394.

Kooyman, G. L. (1966). Maximum diving capacities of the Weddell seal, *Leptonychotes weddelli. Science* **151**, 1553-1554.

Kooyman, G. L. (1967). An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. In *Antarctic Research Series: Biology of the Antarctic Seas III*, Vol. 11 (ed. G. A. Llano and W. L. Schmitt), pp. 227-261. Washington, DC: American Geophysical Union.

Kooyman, G. L. (2004). Genesis and evolution of bio-logging devices: 1963–2002. *Mem. Natl. Inst. Polar Res.* **58**, 15-22.

Kooyman, G. L. (2006). Mysteries of adaptation to hypoxia and pressure in marine mammals. The Kenneth S. Norris lifetime achievement award lecture. Presented on 12 December 2005, San Diego, California. *Mar. Mamm. Sci.* **22**, 507-526.

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I. and Mohl, B. (2002). Sperm whale sound production studied with ultrasound time/depth-recording tags. *J. Exp. Biol.* **205**, 1899-1906.

Ponganis, P. J., Meir, J. U. and Williams, C. L. (2011). In pursuit of Irving and Scholander: a review of oxygen store management in seals and penguins. *J. Exp. Biol.* **214**, 3325-3339.

Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. and Kato, A. (2010). Diving into the world of biologging. *Endanger. Species Res.* **10**, 21-27.

Rutz, C. and Hays, G. C. (2009). New frontiers in biologging science. *Biol. Lett.* **5**, 289-292.

Scholander, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**, 1-131.

Tyack, P. L., Johnson, M., Soto, N. A., Sturlese, A. and Madsen, P. T. (2006). Extreme diving of beaked whales. *J. Exp. Biol.* **209**, 4238-4253.

Watanabe, Y. Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Iwata, T., Minamikawa, S. et al. (2011). Scaling of swim speed in breath-hold divers. *J. Anim. Ecol.* **80**, 57-68.

Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973-982.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081-1090.