INTRODUCTION
The turn of the twenty-first century has seen a major leap forward in Earth sciences, with simultaneous improvements in numerical modeling and truly global observing capabilities. Combining satellite observations with coordinated ship cruises and autonomous sampling devices has proved effective for monitoring most of the world ocean at relevant temporal and spatial scales, with the notable exception of marginal sea ice zones in polar regions where limitations include ice, logistics, and rough weather. Sparse coverage of the polar oceans is particularly alarming because of the important role they play in regulating Earth’s climate system (Macdonald and Wunsch, 1996) and the amplified environmental change currently evident in polar regions (Schofield et al., 2010). Biologging science, based on the use of miniaturized animal-borne loggers to study free-ranging animals in their natural environments, is revolutionizing the field of marine biology (Hussey et al., 2015). While tags were first developed simply to track animals at sea, over time it has become possible to add sensors that measure environmental parameters.

The realization that valuable information about water masses could be obtained from remote areas frequented by animals led to the development of conductivity-temperature-depth satellite relay data loggers (CTD-SLDRs; Box 1; Fedak, 2013). The potential for observational cooperation between biologists interested in CTD-SLDR data from a habitat perspective and oceanographers interested in the water masses themselves rapidly became obvious. Places visited by the animals proved to be generally important in describing the state of the global ocean as data could be logged in ice-covered areas during the winter season when there are virtually no other in situ data (Charrassin et al., 2008; Roquet et al., 2013).

Since 2002, instrumented animals have generated an exceptionally large CTD data set, especially in polar regions (Figure 1). First started as independent national programs, the efforts to collect animal behavior and oceanographic data rapidly required some level of international coordination. In this context, the Marine Mammals Exploring the Oceans Pole to Pole (MEOP) consortium
BOX 1. THE CTD-SRDL TAGS

The CTD-satellite relay data logger (CTD-SRDL; Figure B1) is an autonomous tag that records location with vertical profiles of conductivity, temperature, and pressure to a maximum depth of ~2,000 m, depending on the species involved (Boehme et al., 2009; Photopoulou et al., 2015). Vertical profiles of salinity and density can be inferred from this information. These physical properties are among the most important for seawater as they can be used to determine the circulation patterns and climate variability of the ocean.

The CTD-SRDLs are built at the Sea Mammal Research Unit at the University of St Andrews (UK), incorporating the miniaturized CTD unit manufactured by Valeport Ltd. (Devon, UK). The sensor head consists of a pressure transducer, a platinum resistance thermometer, and an inductive cell for measuring conductivity. The temperature and conductivity sensors have a precision (repeatability) of 0.005°C and 0.005 mS cm⁻¹, respectively. Before being taken into the field, devices are calibrated in the laboratory.

The loggers are noninvasive (Field et al., 2012); they are glued to the animal’s hair (Figure B2) and fall off when the animal molts. Loggers have also been attached to non-mammals such as turtles (Figure B2). CTD-SRDLs record hydrographic profiles during the ascent of the animals (Boehme et al., 2009; Roquet et al., 2011; Photopoulou et al., 2015) at a 0.5 Hz sampling frequency, retaining only the deepest dive in each six-hour time interval. Profiles are then telemetered in a compressed form (between 10 and 25 data points per profile, depending on the tag program) through the Advanced Research and Global Observation Satellite (ARGOS) system. Geolocation is determined by satellite triangulation with a typical accuracy of a few kilometers. The transmission occurs up to four times per day.

It is also possible to include a fluorometer, an oxygen sensor, or a Fastloc GPS in the instruments; the latter instrument greatly improves location precision. A post-processing procedure is applied to hydrographic data to ensure the best possible data quality (Roquet et al., 2014). New CTD-SRDLs include enhanced data collection capabilities. For example, it is now possible to store all logged data in a flash memory unit inside a CTD-SRDL. If a tag is retrieved, the entire archived data set can be recovered.

The MEOP data portal distributes data mainly from CTD-SRDL tags because it is currently the only available tag that incorporates both temperature and salinity measurements with a precision suitable for oceanographic studies (~0.02°C for temperature, ~0.03 psu for salinity). A secondary database (the MEOP-TDR database) has recently been released that incorporates temperature profiles using the popular MK9/MK10 Wildlife Computers tags with lower accuracy (~0.5°C) but higher spatial resolution (~60 profiles/day).

New sensor capabilities are also being added. The Cyclops 7 fluorometer is a compact cylinder (110 mm × 25 mm after removal of the end cap), low-energy-consumption, single-channel fluorescence detector that can be integrated into the CTD-SRDL tag (Guinet et al., 2013). It has been attached to elephant seal tags deployed in the Indian sector of the Southern Ocean since 2007, yielding a unique data set of in situ chlorophyll measurements in this extremely data poor, highly productive region. Also, an oxygen optode sensor has been successfully incorporated into a few CTD-SRDLs (Baillieux et al., 2015). While this technology is still in early development, it has great potential for the future of integrated biophysical and biogeochemical research, as oxygen provides a fundamental link between physical and biogeochemical processes.

**FIGURE B1.** Photograph of a CTD-SRDL, with visible hardware components labeled. The tag is housed in normal solid epoxy rated either to 500 m or 2,000 m depth. Standard sensors include pressure, a wet/dry saltwater switch, temperature, and conductivity. The tag has a PC interface and is powered by a primary cell (battery), and the standard version includes an antenna. From Photopoulou et al. (2015); photo by Lars Boehme, SMRU

**FIGURE B2.** Examples of deployments on (a) a southern elephant seal. Image provided by Anne M. Treasure, University of Pretoria (b) a Weddell seal. Image provided by Daniel Costa, University of California, Santa Cruz (c) a hooded seal. Image provided by Kit M. Kovacs and Christian Lydersen, Norwegian Polar Institute (d) an olive ridley sea turtle. Image provided by Damien Chevallier, Université de Strasbourg
was launched in 2007 during the International Polar Year. The consortium acts as an international discussion forum for scientists who tag marine animals, as well as a platform for fostering the use of animal-derived data for scientific and operational applications. MEOP has historically focused mainly on CTD data, because these physical data are most readily useful for physical oceanographers. However, the consortium has started to broaden its emphasis to include other types of data (Box 1). The core missions of the MEOP consortium include (1) producing a comprehensive quality-controlled database of oceanographic data obtained from instrumented marine animals, and (2) maintaining a data portal from where information and data can be accessed easily. MEOP is now a large consortium that acts as a bridge between the scientific teams that deploy the tags and the scientists who use the data. So far, this consortium includes participants from 13 countries; other countries that have researchers deploying oceanographic tags on marine animals are welcome to join this research effort.

THE DATA AND THE MEOP-CTD DATABASE

Animal-borne loggers have provided extensive circumpolar oceanographic sampling of the Southern Ocean (Figure 1a,b), supplying about 70% of all oceanographic profiles for the region south of 60°S (Fedak, 2013). In the north, marine mammals have also provided significant coverage for the North Pacific (e.g., Robinson et al., 2012), North Atlantic (e.g., Grist et al., 2011), Nordic Seas (e.g., Isachsen et al., 2014), and Arctic (e.g., Lydersen et al., 2002; Blanchet et al., 2015) regions (Figure 1a,c). This coverage of polar regions has dramatically extended our spatial and temporal reach beyond ship-based observations and autonomous satellite-linked oceanographic sensors such as Argo floats (Figure 1d).

The data from the animal-borne instrumentation are stored in the MEOP-CTD database, which is publicly accessible through the MEOP data portal (http://meop.net). The database currently contains 529,373 profiles, 75% of which are freely available (Table 1). Private data can be accessed upon request. The database comprises profiles of temperature and practical salinity as a function of pressure, located in space and time (Box 1). Some profiles also incorporate fluorescence or dissolved oxygen.

Various tools have been developed to increase accessibility; for example, the MEOP-CTD database is directly available on the Ocean Data View web page (https://odv.awi.de/data/ocean/meop-ctd-marine-mammals-database). The database is also included in major oceanographic databases, including the World Ocean Database (WOD) distributed by the National Oceanographic Data Centre (NODC) and the Coriolis Ocean Dataset for Reanalysis (CORA, Cabanes et al., 2013). The MEOP consortium is associated with the Global Ocean Observing System (GOOS), the Partnership for Observation of the Global Oceans (POGO), and the Integrated Marine Observing System (IMOS), and it is
developing connections with the Joint WMO-IOC Technical Commission for Oceanography and Marine Meteorology (JCOMM) to achieve better coordination with other marine observing capabilities.

THE SCIENCE

Instrumented animals have become an essential source of temperature (e.g., Figure 2a), salinity, and fluorescence profiles, particularly for the polar oceans. To date, approximately 100 peer-reviewed papers have been published using MEOP data; they describe the work of biological and physical oceanography communities studying both polar regions as well as some temperate areas (see http://meop.net for a list of publications). These studies are often at the interface between ecology and physical oceanography—illustrating the contributions and originality of the MEOP approach.

Biological Oceanography

MEOP data have been used for biological studies incorporating a range of topics including foraging ecology, physiology, multi-predator tracking, and animal responses to oceanographic conditions. The data have been particularly useful for examining the foraging ecology of southern elephant seals (Mirounga leonina) in relation to oceanographic conditions (e.g., McIntyre et al., 2011; Labrousse et al., 2015; Hindell et al., 2016). For example, Hindell et al. (2016) used a large MEOP data set to link foraging behavior and habitat structure in time and space for southern elephant seals. One finding from this study is that while Antarctic shelf waters are prime habitat for both sexes, female seals tend to move northward as the sea ice advances (Figure 2b), whereas male seals are less affected by sea ice. It has also been shown that elephant seals interact with mesoscale eddies in Circumpolar Antarctic frontal regions to optimize their foraging strategy (Cotté et al., 2015).

CTD-SRDLs have also been useful for investigating the influence of environmental conditions on the foraging ecology of other species, such as Weddell seals (Leptonychotes weddellii; Boehme et al., 2016), crabeater seals (Lobodon carcinophaga; Costa et al., 2010), harbor seals (Phoca vitulina; Blanchet et al., 2015), hooded seals (Cystophora cristata; Andersen et al., 2013), and Australian sea lions (Neophoca cinerea; Lowther et al., 2013). More sophisticated models of foraging behavior that include both horizontal and vertical dimensions have been tested for southern elephant, Weddell, Antarctic fur (Arctocephalus gazella), and crabeater seals (Bestley et al., 2015).

Reptilian species such as olive ridley (Lepidochelys olivacea) and green (Chelonia mydas) turtles (Chambault et al., 2015, 2016) have also been equipped with CTD-SRDLs. In a study investigating how the foraging behavior of olive ridley turtles is driven by oceanographic and biological conditions, Chambault et al. (2016) revealed a number of interesting findings such as the vital role played by the thermocline on the foraging behavior of this species.

Physical Oceanography

Animal-derived data have enabled significant insights into physical oceanography, and many studies have shown that animal-deployed SRDLs significantly improved the coverage of regions poorly sampled by traditional methods. Roquet et al. (2013) found that using seal-derived data to constrain a model simulation of the ocean substantially modified the estimated surface mixed-layer properties and circulation patterns in the Southern Ocean. The seal data improved the agreement of the model simulation with independent satellite observations of sea ice concentration. Marine animal-derived data complement data from other in situ sources, such as Argo floats and ship-based measurements. Grist et al. (2011) used Argo and marine mammal profiles to produce a 1° gridded data set (“ATLAS”) that reveals distinctive boundary current-related temperature minima in the Labrador Sea and at the east Greenland coast. Isachsen et al. (2014) used data collected by instrumented hooded seals as well as Argo floats to reveal increased temperature and salinity conditions over much of the Nordic Seas. Merged Argo and animal-borne data have also been used to characterize several sectors of the Antarctic Circumpolar Current (e.g., Boehme et al., 2008; Charrassin et al., 2008; Roquet et al., 2009).

Seal-derived data have played an instrumental role in furthering our understanding of Antarctic shelf circulation and the formation of Antarctic Bottom Water (AABW). In 2011, observations from seal-borne CTD-SRDLs were central to solving a 30+-year-old puzzle regarding AABW in the Weddell-Enderby Basin (Ohshima et al., 2013). Observations of very high salinity shelf water were linked to a new source of AABW off Cape Darnley, East Antarctica. Analyzing an additional two years of data, Williams et al. (2016) showed that Prydz Bay, situated just east of Cape Darnley, makes a secondary contribution to AABW (Figure 2c). However these authors observed that the production of dense shelf water was partly suppressed by melting of nearby ice shelves, revealing a potential vulnerability of AABW formation to increased ice shelf melt rates.

Using the maximum depth of benthic dives, seal-derived data have identified troughs in the continental shelf (Padman et al., 2010) that allowed intrusions of Circumpolar Deep Water (CDW) under

<table>
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<th>Tags</th>
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TABLE 1. Number of profiles, deployments, and tags currently in the MEOP CTD-SRDL database.
the Wilkins Ice Shelf, accelerating its collapse (Padman et al., 2012). In addition, Zhang et al. (2016) used seal-acquired observations to describe intrusions of warm but modified CDW into the continental shelf waters of the Bellingshausen Sea, with important implications for the stability of the West Antarctic Ice Sheet. Seal CTD-SRDLs have been an important data source for understanding the seasonal cycle of water flow in the vicinity of Greenland (Grist et al., 2014) and East Antarctica (Williams et al., 2011), and also for understanding Antarctic sea ice melting and formation (e.g., Charrassin et al., 2008; Meredith et al., 2011; Tamura et al., 2016).

Animal-borne loggers have also been used as “mooring” type instruments. For example, Meredith et al. (2011) used a >8-month time series of hydrographic properties in the vicinity of the South Orkney Islands collected by a southern elephant seal to illustrate the seasonal progression of upper-ocean water mass properties and stratification for the area, and found the difference between local (modeled) and regional (inferred) ice production to be significant. Merging seal-derived data with ship-based and Argo float observations, Pellichero et al. (2017) described the seasonal cycle of the ocean mixed-layer characteristics and the stability of the ocean mixed layer over the Southern Ocean, specifically under sea ice. Their results suggest that changes in regional sea ice distribution and annual duration, as currently observed, widely affect the buoyancy budget of the underlying mixed layer.

**FIGURE 2.** Examples of MEOP data applications. (a) Tracks of southern elephant seals moving south from the Kerguelen Islands to the Antarctic, with temperature profiles to depths of more than 1,000 m. *Image provided by Clive McMahon, Sydney Institute of Marine Science, Australia.* (b) Distribution of 229 adult female southern elephant seals tracked around Antarctica between 2004 and 2009 in four seasons defined as three-month periods: Postbreeding (November–January), Postmolt 1 (February–April), Postmolt 2 (May–July), Postmolt 3 (August–October). Area-restricted (i.e., feeding; red dots) and transit (black dots) modes are superimposed on two broad-scale habitats defined in the study, shelf (light blue) and deep ocean (dark blue). From Hindell et al. (2016) (c) Seal-derived data indicating dense shelf water (DSW) around Prydz Bay, Antarctica. Colored circles show the spatial distribution of bottom-of-dive salinity corresponding to DSW. Cyan and dark green contours show fast ice and polynya regions, respectively. Inverted triangles show the locations of bottom modified Shelf Water values from seal data post-September on the continental slope north of Cape Darnley, split into saline (>34.6) values west of 69°E (cyan) and fresher (<34.6) values east of 69°E (blue). Adapted from Williams et al. (2016)
CONCLUSION AND THE FUTURE

The addition of marine mammals to the global array of ocean profilers provides a powerful and cost-effective means for dramatically extending the ocean-observing system for both biological and physical oceanography communities. Animal-borne sensors provide almost circumpolar oceanographic sampling of the Southern Ocean, including extensive coverage during the polar winter, thereby filling an important blind spot in conventional coverage by satellites, ships, and Argo floats. These unique observations are a major component of the sustained contribution of ocean observations to the Global Ocean Observing System. Furthermore, MEOP data should improve the quality of projections provided by ocean climate models such as Mercator or the Southern Ocean State Estimate. Animal-derived observations extend the research community’s capability into regions of national and international significance by providing essential oceanographic data, for example, the continental slope and shelf regions around Antarctica.

Overall, the past decade of animal tagging demonstrates the component and feasibility of this approach for ocean observation. At the core of this success is a unique collaboration between biologists and physical oceanographers fostered by the MEOP consortium, one of the few examples of a truly multidisciplinary approach that has created great outputs for both communities. As the technology continues to improve rapidly, the prospective outcomes of these cross-disciplinary international efforts are particularly promising for advancing polar and coastal oceanographic research. 

SUPPLEMENTAL MATERIAL S1

A list of acknowledgments and contributors to the MEOP consortium is available online at https://doi.org/10.1371/journal.pone.0132686.

REFERENCES


Kovacs, K.M. 2013. The impact of animal plat-


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