

Rapid-response recorders reveal interplay between marine physics and seabird behaviour

F. Daunt^{1,*}, G. Peters², B. Scott³, D. Grémillet², S. Wanless¹

¹Natural Environment Research Council (NERC) Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BW, United Kingdom

²Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France

³University of Aberdeen, Department of Zoology, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom

ABSTRACT: In the marine environment, the distribution of primary producers and higher trophic levels is strongly dictated by the physical characteristics of the water column. Typically, life concentrates in regions where there are strong horizontal or vertical gradients in temperature or density ('frontal regions'). Top predators, such as diving mammals and birds, target fronts and their associated high biomass of prey. Until now, the study of the interaction between diving predators and the physical environment has been hindered by the lack of adequate instrumentation. The response times of the available animal-borne temperature–depth recorders have been too slow to accurately measure the external environment where the animals are foraging. This limitation has been overcome by the development of a lightweight, rapidly responding temperature–depth logger. The instrument was successfully deployed on 2 diving seabird species (the common guillemot *Uria aalge* and the European shag *Phalacrocorax [Stictocarbo] aristotelis*) in the North Sea. A method for correcting temperature data for the time lag in the response of the temperature sensor is presented. The findings show the potential of this technology in 2 important ways: in providing unparalleled information on the interaction between predators and the marine environment, and as a low-cost method of obtaining high-quality oceanographic data.

KEY WORDS: Diving endotherms · Common guillemot · European shag · Predator–prey · Oceanography · Tidal currents · Thermocline · Data logger

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INTRODUCTION

It has long been recognised that temperature plays a critical role in marine ecosystem function (Atkins 1928, Wüst 1935). In coastal temperate regions, variations in vertical water temperature gradients are caused by the interaction of seasonal and diurnal cycles of solar irradiation, seasonal wind patterns, monthly and daily cycles of the tide and bathymetry (Mann & Lazier 1996). These variables create a predictable ocean structure consisting of regions of mixed, stratified and frontal temperature and/or salinity gradients. The tim-

ing of formation and location of the different regions of stratification are key drivers of the temporal and spatial distribution of primary production and associated higher trophic level biomass, with marine life typically concentrated at frontal regions (Pingree et al. 1975, Boyd & Arnbohm 1991, Franks 1992, Russell et al. 1999). Unpredictable weather patterns, operating at a variety of temporal scales from a few days (e.g. storms) to years (e.g. North Atlantic Oscillation), may disrupt ocean temperature structure and thus can also have a significant impact on biological processes (Mann & Lazier 1996).

Links between these oceanographic features and the behavioural patterns of marine top predators have long been suspected (Ainley & Jacobs 1981, Hunt & Schneider 1987), but remain poorly understood. Attaching solid-state recorders to free-living animals allows us to measure directly the interaction between marine predators and ocean temperature. This technology also provides a low-cost means of obtaining oceanographic data over a variety of temporal and spatial scales (Boyd 1997, Wilson et al. 2002). The principal techniques for measuring ocean temperature have important limitations: ship-based studies are very expensive and replication is rarely affordable, resulting in a lack of temporal resolution (Longhurst 1998); mooring data provide good resolution through time, but are highly localised (Kinzig 1999); thermal sensor satellites only measure the top few tenths of a millimetre of the water column, have a poor horizontal resolution and are affected by clouds (Minster 1997).

Until now, suitable animal-borne temperature-loggers have had slow response times and have been unable to record temperature change accurately (McCafferty et al. 1999, Campagna et al. 2000, Koudil et al. 2000, Boehlert et al. 2001, Boyd et al. 2001, Watanuki et al. 2001, Charrassin et al. 2002; cf. Wilson et al. 2002 for discussion). Whilst these authors have improved their data using a variety of modelling techniques, here we describe an instrument that records accurately the temperature-depth profile of animals' foraging dives, with a precision that brings us substantially nearer to that of ship-based equipment.

MATERIALS AND METHODS

Instrumentation. The PreciTD (Earth & Ocean Tech.) is a 2 Mbyte multichannel data logger with a 12 bit A/D converter that allows internal temperature, exter-

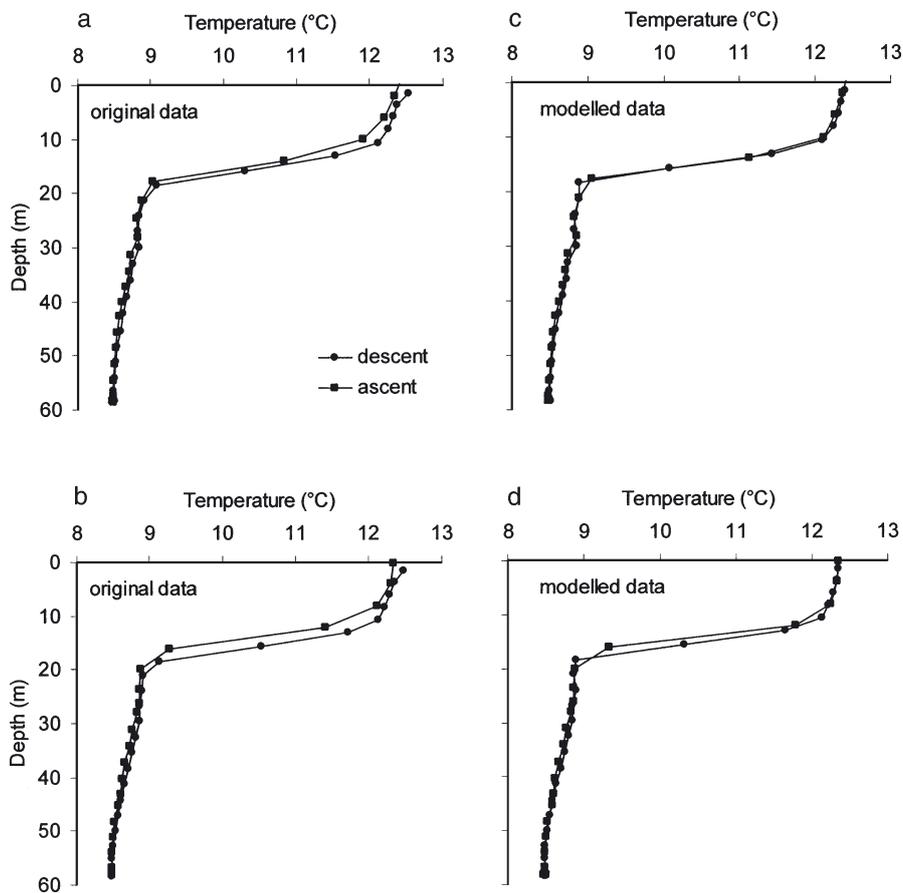


Fig. 1. *Uria aalge*. (a) Temperature–depth profile of single dive by a common guillemot measured by a PreciTD logger with descent and ascent phases shown separately; (b) second example from same bird. High performance of the logger is evident from the raw data. However, the effects of the time lag in temperature due to the response time of the logger and the swimming speed of the bird are apparent during the period of rapid temperature change, for example as the bird travels through the thermocline. The 2 examples illustrate extremes of discrepancy between the descent and ascent profiles found in our data. (c,d) Modelled temperature for dives in (a) and (b) respectively

nal temperature and pressure to be sampled at programmable intervals. The hydrodynamically shaped housing protects the external sensor in a groove, facilitating the water to flow freely across the sensor during submerged measurements. Temperature resolution is ca. 0.005 K (measurement uncertainty is 0.03 K, range 0 to 20°C); pressure resolution is 5 to 6 mbar \approx 6 cm water column (measurement uncertainty 20 mbar, range 0 to 20 bar above atm = 0 to 200 m). For each device, a traceable calibration of temperature and pressure was performed, and an analysis of errors was carried out according to the root-sum-squares method in order to assess maximum measurement uncertainty. The logger dimensions are: length 80 mm, diameter 19 mm, max height 22 mm; total operational mass is 22.5 to 22.9 g.

The logger has a temperature-response time $T_{0.9}$ (i.e. time to reach 90% ΔT , following a sudden temperature change) of ca. 1.8 s. The response characteristic of a typical sensor follows an exponential decay function of the form

$$R(t) = 1 - e^{-b_s t} \quad (1)$$

where R is the time-dependent response (expressed as a relative proportion of ΔT), b_s is the sensor-specific constant (1.3 s^{-1} for a PreciTD) and t the time in s. This enables the sensor to stabilize to within 0.1 K of the new temperature within 3 to 5 s during field applications, where sudden temperature changes never exceed 20°C.

Field deployment on marine birds. We attached the device to 9 common guillemots *Uria aalge* and 4 European shags *Phalacrocorax (Stictocarbo) aristotelis* on the Isle of May, SE Scotland ($56^\circ 11' \text{ N}$, $02^\circ 33' \text{ W}$), on 23 to 27 June 2001. Breeding adults with chicks were caught at the nest site using a nylon noose (common guillemot) or crook (European shag) attached to the end of a bamboo pole. A PreciTD was attached to the back of the common guillemots or the underside of the tail of the European shags using Tesa tape (Beiersdorf). Temperature and depth were recorded every 2 s. The loggers were retrieved on the birds' return from a foraging trip, $1.31 \pm 1.48 \text{ SD}$ days later. Programming and downloading was achieved using a standard terminal program (e.g. MS Hyperterminal).

Data analysis: logger performance. Due to the response function of the temperature sensor, there is a time lag between true temperature and temperature measured by the instrument (cf. UNESCO 1988). This led to a difference in the temperature profiles of the descent and ascent cast recordings, dependent on the travelling speed of the animals through the water column (common guillemots mean descent [$\pm \text{SD}$] = $1.32 \pm 0.07 \text{ m s}^{-1}$, ascent = $1.21 \pm 0.11 \text{ m s}^{-1}$; European shags descent = $1.23 \pm 0.19 \text{ m s}^{-1}$, ascent = $1.65 \pm 0.07 \text{ m s}^{-1}$;

analysis using Multitrace, Jensen Software Systems). Therefore, to provide a truer reflection of the temperature-depth profiles of the birds, a model was devised to estimate true temperature from the measured data, taking into account the time lag of the temperature sensor (Appendix 1).

Data analysis: field data. For each bird, data were taken from 1 complete bout (i.e. cluster of dives; Sibly et al. 1990). Number of dives per bout ranged from 8 to 146 (mean = $58 \pm 51 \text{ SD}$) for common guillemots and 12 to 28 (mean = 21 ± 7) for European shags. The mean temperature in each 1 m depth band was derived for each bout using both ascent and descent profiles. The profiles, thermocline depths and minimum and maximum foraging depths were calculated by taking the mean of the mean bout values.

RESULTS AND DISCUSSION

Two separate common guillemot dives are shown in Fig. 1a and b respectively. The temperature model significantly improved our estimate of true water temperature in all cases (Fig. 1c,d). The performance of the PreciTD represents a significant improvement on other current devices (Fig. 2), and brings us considerably closer to CTD performance, e.g. Valeport 602: $T_{0.9}$ = ca. 1.5 s (www.valeport.com); Falmouth Scientific Excell Micro CTD: $T_{0.9}$ = ca. 1.2 s (www.falmouth).

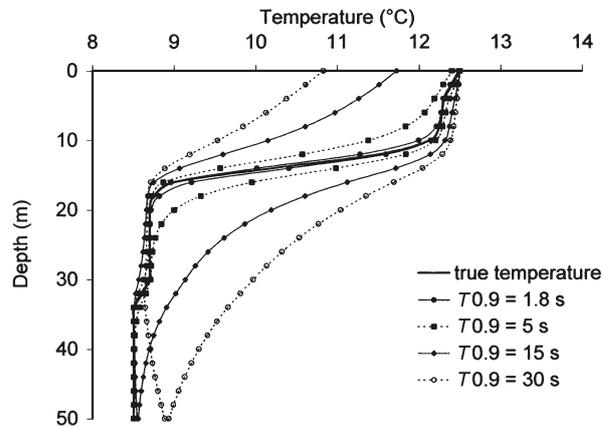


Fig. 2. Comparison between performance of PreciTD and loggers with a slower temperature response time ($T_{0.9}$, the time to reach 90% of the change in temperature). Hypothetical temperature–depth profile corresponding to that experienced by common guillemots in this study was subjected to a series of negative exponential models with varying values of the sensor-specific constant b_s (see Eq. 1). With the exception of the PreciTD, the examples of b_s illustrated do not describe particular instruments, but span the range of response times currently available. No other logger has achieved better than $T_{0.9} = 5 \text{ s}$. The speed of the loggers through the water column was set at 1 m s^{-1} , to match the typical speed of CTD casts. Descent (lower) and ascent (upper) profiles are shown in each case

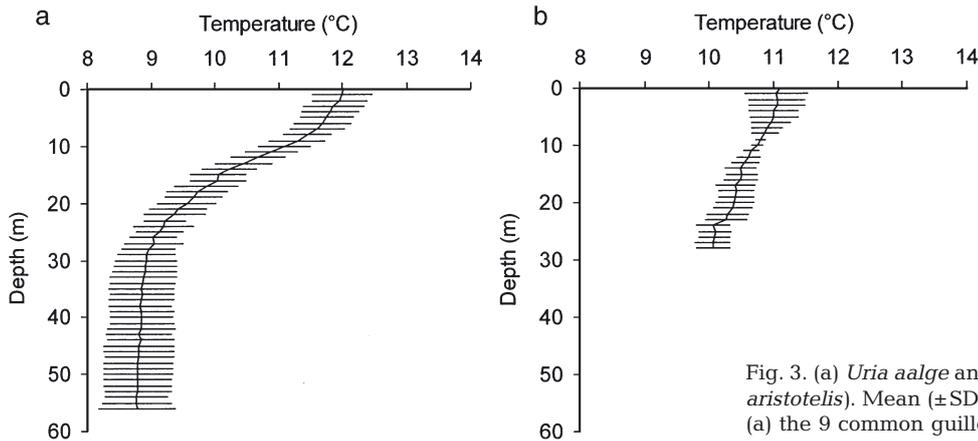


Fig. 3. (a) *Uria aalge* and (b) *Phalacrocorax (Stictocarbo) aristotelis*. Mean (\pm SD) temperature–depth profiles for (a) the 9 common guillemots and (b) 4 European shags

com); SAIV (Sagstad & Iverson Engineering) SD204: T0.9 = ca. 0.5 s (www.saivas.com).

The development of this fast-response logger is important in 2 ways: (1) It provides accurate information on the favoured habitats of foraging divers. By comparing these data with the availability of the different water types (e.g. stratified, mixed, frontal) within the animals' foraging range, we can test whether they are selecting areas with specific vertical temperature gradients that typically support high levels of primary production. The 2 species in this study utilised highly contrasting water types (Fig. 3). The common guillemots were foraging in stratified water (mean \pm SD sea-surface temperature = $12.0 \pm 0.5^\circ\text{C}$, bottom temperature = $8.8 \pm 0.5^\circ\text{C}$; thermocline depth: top = 7.9 ± 2.7 m, bottom = 21.1 ± 5.9 m) over a broad depth range (minimum foraging depth = 14.4 ± 17.5 m, maximum foraging depth = 52.9 ± 6.8 m). European shags were diving in water with no strong thermocline (sea-surface temperature = $11.1 \pm 0.5^\circ\text{C}$, bottom temperature = $10.3 \pm 0.4^\circ\text{C}$), and were making much shallower dives within a narrower depth band (minimum foraging depth = 17.8 ± 8.4 m, maximum foraging depth = 25.8 ± 4.3 m). (2) Attaching the PreciTD logger to a diving predator provides a cost-effective method of monitoring temporal changes in the marine environment (Boyd 1997, Wilson et al. 2002). For example, variations in thermocline depth due to internal waves driven by tidal currents (Mann & Lazier 1996) are detected when a predator dives continuously in the same location (Fig. 4). Work is ongoing that will couple accurate locational information (Weimerskirch et al. 2002) with temperature–depth data, enabling us to collect physical data through space and time in the areas where the birds are operating. These data will greatly supplement physical data collected using traditional platforms, in particular in areas that are poorly covered by vessels, moorings or satellites (Charrassin et al. 2002).

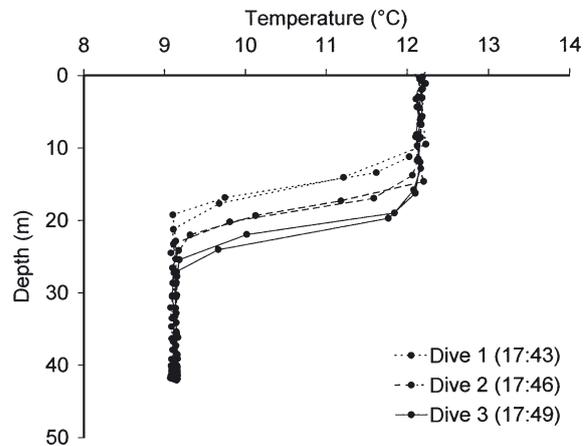


Fig. 4. Variation in thermocline depth over time at a fixed location measured by PreciTD logger. Three consecutive dives made by a common guillemot *Uria aalge* are shown (descent and ascent values for each dive). Sea-surface and bottom temperature were stable, but there were large oscillations in depth of thermocline due to internal waves caused by tidal currents (Mann & Lazier 1996). Time of day shown in parentheses

The development of the instrument described in this paper is an important step in the study of marine ecosystems. The significance of temperature in marine dynamics has been apparent for many decades (Atkins 1928, Wüst 1935), but collecting accurate data has consistently been limited by imprecise instrumentation or high cost. The wide use of small precision recorders in numerous diving vertebrate species with high temporal and spatial coverage will improve significantly our understanding of predator–prey dynamics and the effects of climate change (Aebischer et al. 1990, Reid et al. 1998, Ottersen et al. 2001, Thompson & Ollason 2001) and fishing activities (Hammond & Croxall 1988, Furness & Tasker 1997) on marine ecosystems.

Appendix 1. Temperature correction

An important parameter characterising the performance of a temperature sensor is its response time, the time needed to stabilise at a new temperature level following a sudden temperature change from one stable temperature to another. The response properties of a temperature sensor can be characterised by the time taken to reach a given percentage of any temperature difference ΔT (e.g. $T_{0.63}$, $T_{0.9}$).

The relative response of a sensor to any stepwise temperature change follows a typical exponential decay function of the form:

$$R(t) = 1 - e^{-b_s t} \quad (1)$$

where R is the response (relative, from 0 to $1 \Delta T$), b_s is the sensor-specific constant (1.3 s^{-1} for the PreciTD) and t = time (s). Thus, the measured temperature, T' , at time t (s) is dependent on the true temperature at that time, T_t , the measured temperature before the temperature change, T_0 ,

and the response function of the logger:

$$T' = T_0 - [(T_0 - T_t) \times (1 - e^{-b_s t})] \quad (2)$$

Eq. (2) can be rearranged to determine true temperature T_t from measured temperatures T' and T_0 :

$$T_t = T_0 - \frac{T_0 - T'}{1 - e^{-b_s t}} \quad (3)$$

Eq. (3) assumes stepwise temperature changes between adjacent readings such that the sensor is subjected to the new temperature for the whole of the duration of t . In reality, however, temperature changes gradually. Therefore, for a change from, for example, warmer to colder water, the logger is subjected to the warmer water for a longer period of time than the model suggests. To account for this, we adjusted b_s by a factor of 0.75 to achieve optimum results. Our criterion for good model performance was the match between descent and ascent phases of the dive

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