

COMMENTARY

From physiology to physics: are we recognizing the flexibility of biologging tools?

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ABSTRACT

The remote measurement of data from free-ranging animals has been termed ‘biologging’ and in recent years this relatively small set of tools has been instrumental in addressing remarkably diverse questions – from ‘how will tuna respond to climate change?’ to ‘why are whales big?’. While a single biologging dataset can have the potential to test hypotheses spanning physiology, ecology, evolution and theoretical physics, explicit illustrations of this flexibility are scarce and this has arguably hindered the full realization of the power of biologging tools. Here we present a small set of examples from studies that have collected data on two parameters widespread in biologging research (depth and acceleration), but that have interpreted their data in the context of extremely diverse phenomena: from tests of biomechanical and diving-optimality models to identifications of feeding events, Lévy flight foraging strategies and expanding oxygen minimum zones. We use these examples to highlight the remarkable flexibility of biologging tools, and identify several mechanisms that may enhance the scope and dissemination of future biologging research programs.

KEY WORDS: Acoustic telemetry, Energetics, Hypoxia, Logger, Penguin, Scaling, Seal, Shark, Stroke frequency, Temperature

Introduction

The collective term ‘biologging’ has been coined to describe a process by which researchers gain information (typically position, behavior, movement or physiological status) from an animal remotely (see Glossary). Its value with aquatic animals has been highlighted repeatedly (Cooke et al., 2004; Metcalfe et al., 2012; Rutz and Hays, 2009), and in recent years, the diversity of biologging applications has expanded dramatically. In contrast, the suite of parameters recorded by biologging devices has expanded at a much slower pace. While temperature, pressure (depth), heart rate, location and acceleration have been measured in aquatic animals for decades, recent studies have seen these few parameters address remarkably diverse phenomena (Fig. 1). The same type of device that is used to estimate an animal’s daily energy budget [e.g. accelerometers (Halsey et al., 2009)] is also used to help explain why diving mammals attain larger sizes than fish (e.g. Watanabe et al., 2011). An instrument that reveals preferences for dissolved oxygen levels [e.g. a depth sensor (Stramma et al., 2012)] also provides evidence of Lévy flight foraging strategies (e.g. Humphries et al., 2010).

The advantages and disadvantages of using a specific biologging sensor for addressing a particular problem have been thoroughly considered, and are reviewed elsewhere [e.g. in the context of ecology (Cooke et al., 2004), energy expenditure (Halsey et al., 2008) and conservation physiology (Metcalfe et al., 2012)]. Less well recognized, however (or perhaps simply less well documented), is how the collection of a dataset on a single biologging parameter can potentially facilitate insights spanning physiology, ecology, evolution and theoretical physics. While hypothesis-driven research is often argued as the most powerful (Kell and Oliver, 2004; Underwood, 1997), where novel observations are made with difficult-to-study species, the potential for multiple, diverse (and often *post hoc*) discoveries can be significant, but explicit illustrations of this potential are scarce. Undoubtedly, this research gap contributed to a perceived ‘under-utilization’ of biologging in the aquatic sciences (Cooke et al., 2004), and is a potential hindrance to maximizing the power of biologging science.

This paper represents an argument for the flexibility of biologging tools. While the general message is transferable to terrestrial systems, we focus on examples drawn from the aquatic literature. Largely, this choice is due to the marine bias in historical and contemporary development of biologging science (Rutz and Hays, 2009). We identify a series of studies that collected data on two parameters widespread in biologging research (acceleration and depth; often with similar device specifications and attachment methods) but that interpreted these data in the context of extremely diverse phenomena. Regardless of whether the flexibility of biologging tools is fully acknowledged by the scientific community, the aim of this paper is to provide an explicit illustration of this flexibility; to stimulate the broader adoption of multidisciplinary biologging research; and to present a framework for overcoming some of the key barriers to interpreting biologging datasets across diverse scientific fields.

Biologging tools are flexible: an illustration

Here we present a set of studies that collected similar biologging data, but that analyzed or interpreted these data in vastly different ways. Acceleration and depth examples were chosen for three reasons: (1) these sensors produce some of the more flexible (in terms of diverse analyses) biologging data; (2) their collection is becoming increasingly widespread in the aquatic sciences; and (3) many interpretations of acceleration data are made within the context of relative water depth, and vice versa. Each of these examples measured either depth or acceleration (or both) in free-ranging aquatic animals, and these data were central to testing each specific hypothesis.

Diving adaptations

Biologging has been fundamental to identifying adaptations to submergence in diving animals and, along with heart rate, depth and acceleration data have arguably facilitated the greatest insights. Bi-

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Glossary

Aquatic animal

For the purpose of this commentary, we consider an animal that undertakes any activity in water as 'aquatic'. In part, this is because many of the advances in biologging have occurred with subjects that spend only part of their life in aquatic habitats (e.g. diving birds, turtles, etc.).

Biologging

This term was first proposed by Boyd et al. [as 'bio-logging' (Boyd et al., 2004)], and refers to the practice of logging and relaying physical and/or biological data using animal-attached tags (Hooker et al., 2007; Rutz and Hays, 2009). Biologging devices can either store (e.g. archival loggers) or transmit (e.g. acoustic transmitters) measured data, but for this commentary we use the term to encompass all forms of data retrieval.

Accelerometer

Accelerometer devices can be loggers or transmitters that record whole-animal or partial body acceleration. Animal movement is generally achieved through muscle contraction, which leads to body and/or limb acceleration. Accordingly, acceleration has been used as a proxy for quantifying movement since at least 1963 (Cavagna et al., 1963), and has emerged as a powerful metric for identifying activity patterns in broad aquatic taxa within the past decade or so (e.g. Yoda et al., 1999). When attached to animals, accelerometers can record acceleration in one, two or three spatial axes simultaneously and at high sampling frequencies. For loggers, the accelerometer device generally must be retrieved to acquire data (Houghton et al., 2009; Watanabe et al., 2012), whereas transmitters require remote detection of acceleration data summaries by receivers (Payne et al., 2011; Payne et al., 2013). This represents a major trade-off: loggers will provide data at far greater resolution, but need to be retrieved and are generally larger; transmitters are often smaller and do not need to be retrieved, but provide summaries of acceleration measurements rather than raw values. Accelerometer devices are often equipped with auxiliary sensors such as pressure (depth) or temperature.

axial accelerometer loggers fitted to the carapace of hawksbill turtles, *Eretmochelys imbricata*, revealed an inverse relationship between dive duration and activity that was consistent with selection for increased diving durations (Okuyama et al., 2012). The acceleration data were also used to show that the pre-dive volume of air inhaled by the turtles strongly influenced diving duration. Macaroni penguins, *Eudyptes chrysolophus*, fitted with acceleration and depth loggers (on the medial section of the back) exhibited steep body angles during ascent and descent phases of dives with long bottom periods, but shallow angles when little or no time was spent near the bottom (Sato et al., 2004). This pattern was suggested as a mechanism to increase the chance of revisiting profitable patches of prey (Sato et al., 2004) – a hypothesis supported by ascent/descent angles during feeding versus non-feeding dives in Adelie penguins, which were determined by integrating depth loggers and swimming speed sensors (Robert-Coudert et al., 2001).

Oxygen that is collected at the surface by diving animals should be carefully allocated to allow for efficient foraging under water, and because energy use increases drastically with swimming speed, it seems intuitive that diving animals in particular should tend to travel at speeds that minimize the cost of transport (Boyd et al., 1995; Gallon et al., 2007). In a phylogenetically informed meta-analysis drawing on depth and acceleration data, Watanabe and colleagues (Watanabe et al., 2011) provided the strongest evidence to date (Ruxton, 2011) of optimal diving strategies in air-breathers. Oxygen stores increase more rapidly with body size than does metabolic rate or the costs of swimming (Halsey et al., 2006), so large divers can stay submerged longer than small ones. Because large divers also swim faster (Watanabe et al., 2011), these considerations point to an

explanation of why air-breathing divers such as pinnipeds and whales attain larger body sizes than most fish species. Interestingly, the largest of divers (including blue, fin and humpback whales) exhibit shorter dive durations than expected for their size (Croll et al., 2001), and acceleration and depth tag data helped identify lunge-feeding costs as a major factor limiting these dives (Goldbogen et al., 2011).

The selection for increased body mass coupled with the need to spend extended periods at the surface make diving animals good subjects for biologging (they are large enough to carry devices, and deployment is often easier than for permanently submerged animals), and unsurprisingly, most findings have been interpreted in the context of oxygen allocation. However, the same parameters often collected for diving adaptation studies have also addressed questions of how animals move, with both diving and non-diving animals used to test predictions about how physics should govern locomotion.

Biomechanics

Earlier theoretical models predicted that geometrically similar animals should swim at the same speed, with stroke ('tail-beat') frequencies proportional to body mass^{-0.33} (e.g. Hill, 1950). However, acceleration and depth loggers externally attached to a variety of seabirds, pinnipeds and cetaceans (Sato et al., 2010; Watanabe et al., 2011) revealed that swimming speeds did increase with mass (swimming speed ~mass^{0.08}), and that the decrease in stroke frequency with body mass was not consistent with the theoretical models (Sato et al., 2010). These data stimulated considerations of basal metabolic rate, drag, pitch angles and depth, and these helped to explain the discrepancy (Sato et al., 2010). In a later study that examined variation in the mass–stroke frequency relationship, Watanabe et al. (Watanabe et al., 2012) used accelerometer loggers fitted to the dorsal surface of Greenland sharks, *Somniosus microcephalus*, to show that the stroke frequency and burst acceleration of this species is lower than predicted by their size, which is probably driven by cold temperatures. This highlighted an apparent paradox, because Greenland sharks are known to actively predate much faster-swimming, endothermic seals (Watanabe et al., 2012). Arctic seals avoid polar bear predation by sleeping in surface waters, and this behavior may make them vulnerable to shark predation (Watanabe et al., 2012).

Lunge feeding in baleen whales has been identified as the largest biomechanical event on earth (Potvin, 2009) and, as mentioned previously, severely limits their diving durations. Two-axis accelerometers and depth loggers (attached to the dorsal surface) were combined with hydrodynamic modeling to quantify the mechanical work of lunge feeding in free-ranging blue whales, and it was found that despite the huge energetic costs of this behavior, the foraging efficiency of blue whales can be an order of magnitude higher than for other marine mammals (Goldbogen et al., 2011).

A combination of acceleration and depth loggers have also revealed that the patterns of undulating flight (intermittent patterns of powered locomotion and gliding) commonly identified in flying birds is also present in several species of shark and pinniped (Gleiss et al., 2011; Nakamura et al., 2011). An early theoretical study proposed that such intermittent locomotion could afford energetic savings (Weihs, 1973), but recent considerations of data from acceleration and depth loggers deployed on pinnipeds suggest that these savings may be marginal (Davis and Weihs, 2007; Miller et al., 2012; Sato et al., 2013).

The resolution of data used in these examinations of how animals move are often very similar to those that analyze and interpret

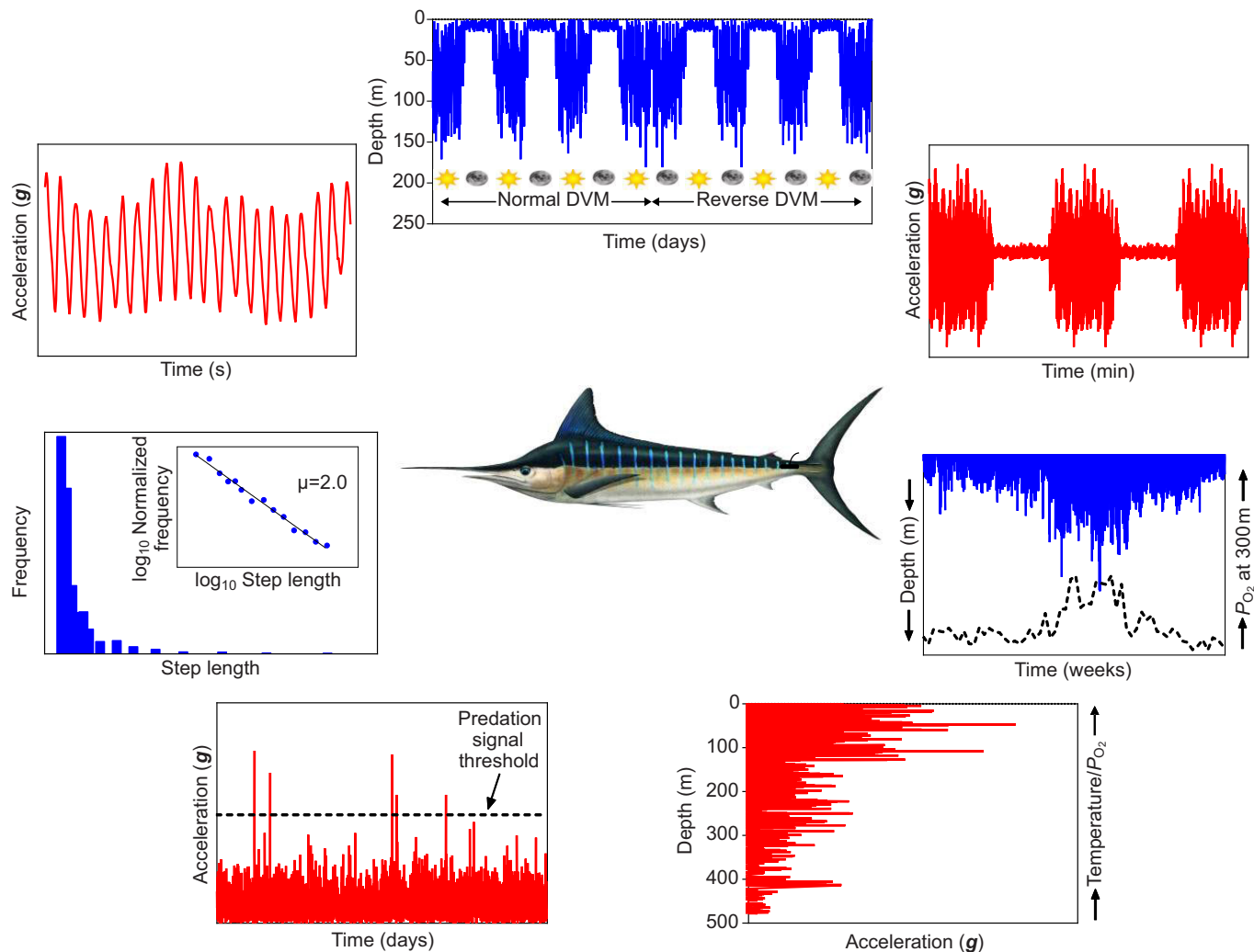


Fig. 1. Flexible tools. A conceptual illustration of the diverse objectives that can be addressed by an animal-borne acceleration (red data) and depth (blue data) logging device. Clockwise from top: a switch in diel vertical migration (DVM) pattern (e.g. Payne et al., 2013; Sims et al., 2005); evidence for intermittent locomotion (e.g. Gleiss et al., 2011); oxygen-driven vertical habitat selection (e.g. Stramma et al., 2012); reduced locomotory function in low oxygen/temperature habitats (e.g. Gilly et al., 2012); identification of predation frequency (e.g. Kokubun et al., 2011; Watanabe and Takahashi, 2013); changes in vertical position consistent with Lévy flight foraging (e.g. Sims et al., 2008); and quantification of stroke frequencies (e.g. Sato et al., 2010).

acceleration and depth data in the context of why they move, with identification of feeding events or foraging strategies common pursuits.

Feeding and foraging

While central to ecology, monitoring the foraging strategies of animals is logistically challenging, particularly in aquatic habitats. Recently, however, acceleration and depth data have facilitated exciting observations of both searching for food and feeding.

Animal search patterns are a key component of optimal foraging theory, and 'Lévy flights' have probably received the most attention. Lévy flights are a category of random-walk consisting of a series of short 'step lengths' (distances between successive turns) connected by longer step lengths (Bartumeus et al., 2005), with step lengths drawn from a probability distribution with a power-law tail (Sims et al., 2008). Theory suggests they represent an optimal foraging strategy where prey is sparsely and randomly distributed (Bartumeus et al., 2005), and biologging data have recently been used to test whether animal search patterns are consistent with these theoretical predictions (see Sims et al., 2007). Depth loggers attached to a

variety of teleosts, sharks, turtles, penguins and seals were used to examine vertical step lengths, and the frequency distributions of these were similar to the Lévy flight theoretical optimum, with prey distributions also displaying Lévy-like fractal patterns (Sims et al., 2008). A subsequent study took this further, using depth-loggers to show that some predatory fish (blue shark, *Prionace glauca*, and bigeye tuna, *Thunnus obesus*) switch from movements approximating Lévy flights to Brownian motion (considered sufficient for locating abundant prey) when moving from less-productive to prey-rich habitats, respectively (Humphries et al., 2010).

While Lévy flights are not evidence of feeding per se, accelerometer loggers attached to feeding apparatus have recently been used to directly identify feeding events, and this represents an exciting new avenue for biologging research. While in fish this method has been limited to captive animals [i.e. common carp, *Cyprinus carpio* (Makiguchi et al., 2012)], head-mounted tri-axial accelerometer and depth loggers attached to free-ranging Antarctic penguins proved a successful means of measuring prey encounter rates, with active head movements coinciding with prey encounters

(calibrated by images recorded by bird-borne cameras) in almost 90% of samples (Kokubun et al., 2011). In another free-ranging penguin study (Watanabe and Takahashi, 2013), head- and body-mounted accelerometer and depth sensors enabled the identification of individual prey-capture events, and predation frequency distributions were shown to follow a power-law model consistent with the Lévy flight strategies mentioned previously.

These examples highlight the potential of biologging tools for simultaneously identifying fundamental ecological parameters: searching for energy, acquiring it, and linking this with prey distributions. While the flow of energy between trophic levels undoubtedly underpins many behaviors, fluctuations in abiotic factors (e.g. changes in light, temperature and tidal flow) also strongly influence the movement and activity of animals, and the same acceleration and depth datasets that are used to evaluate foraging and feeding strategies can potentially be interpreted in the context of these abiotic fluctuations.

Diel rhythm plasticity

Diel rhythms (any rhythmic pattern of behavior or activity that operates at a frequency close to 24 h) are ubiquitous in nature, having been observed in organisms ranging from unicellular cyanobacteria to mammals, and are considered to confer an adaptive advantage (Yerushalmi and Green, 2009). Because a synchronization of endogenous (circadian) rhythms and activity rhythms generally increases fitness (Yerushalmi and Green, 2009), reversal of a diel activity rhythm is likely to indicate strong selective pressures, and acceleration and depth data are increasingly used to identify these switches.

Depth loggers attached to the dorsal fin of basking sharks, *Cetorhinus maximus*, revealed a reversal of diel vertical migration (DVM) that was associated with different thermal habitats (Sims et al., 2005). It was suggested that the variable habitats drove a shift in zooplankton behavior, and that this in turn influenced basking shark behavior (Sims et al., 2005). A similar interpretation was made for leatherback turtles, with plastic DVM (revealed through depth loggers) likely associated with changing distributions of zooplankton (Hays et al., 2006). While normal and reverse DVM is the dominant rhythm in basking shark behavior, depth loggers have also shown that tidal rhythms influence vertical migrations in this species, again a likely reflection of shifting zooplankton fields (Shepard et al., 2006). Acceleration and depth transmitters implanted into yellowfin bream, *Acanthopagrus australis*, found that normally diurnal bream consistently switched to a nocturnal lifestyle in the days following rainfall, and this was interpreted in the context of a potential shift in energetic status (Payne et al., 2013). In a test of the effects of ecotourism on natural behavior, depth loggers were attached to the caudal peduncle of free-ranging whitetip reef sharks, *Triaenodon obesus*, at a popular recreational dive site (Fitzpatrick et al., 2011). The normally nocturnal sharks were stimulated into diurnal activity by the presence of dive boats, with drastic changes in depth distributions seen before and after the arrival of dive operators.

Examples in this section illustrate how biologging can be used to identify rhythmic exogenous factors (i.e. light level, tides, etc.) that drive animal behavior, and also factors that cause variability in these behaviors. Activity rhythm research, by definition, treats time as the independent variable. As with variation through time, the distribution and behavior of animals is also strongly influenced by spatial variation in environmental conditions, and examining acceleration and depth data in this context is becoming an increasingly important pursuit.

Interacting with oceanography

Particularly in an era of anthropogenic climate change, understanding how aquatic animals respond to variation in the physical environment has been a major goal of marine scientists. Near-future predictions of decreased oceanic pH, increased temperature and expanding oxygen minimum zones (OMZs) have driven an explosion of studies aimed at improving our ability to predict physiological and behavioral responses of aquatic animals to these stressors. Among these, biologging approaches have been central to identifying how contemporary oceanographic conditions drive patterns in the distribution and behavior of a suite of aquatic animals.

Because oxygen partial pressures and temperature generally decrease with water depth, the 'high-performance' (Brill, 1996) physiology of billfish and tunas is thought to strongly influence their depth distribution, and biologging depth data have provided crucial insights into habitat preferences of this group of animals. Depth loggers attached to southern bluefin tuna, *Thunnus maccoyii*, showed that they actively adjust their vertical distribution in line with variation in ocean temperature and light levels, effectively reducing exposure to major fluctuations in both parameters (Patterson et al., 2008). *Thunnus maccoyii* is classified as Critically Endangered (Collette et al., 2011), and these temperature-preference data have been integrated into spatial management of the species (Hobday et al., 2010). Fish with high routine metabolic rates are generally considered to be relatively intolerant of low-oxygen habitats (Seibel, 2011), and depth loggers attached to Atlantic blue marlin, *Makaira nigricans*, have revealed not only that they have a preference for highly oxygenated surface waters, but also that they exhibit more-frequent forays into deeper water when the OMZ is farther from the surface (Stramma et al., 2012). This perceived 'intolerance' of low-oxygen water has been used to predict responses in the distribution of these fish to future expanding OMZs, and these predictions are generally bleak (Stramma et al., 2012). In contrast, despite high routine metabolic rates (Rosa and Seibel, 2010), depth loggers have shown that jumbo squid, *Dosidicus gigas*, undergo frequent DVMs into severe oxygen-minimum zones (Gilly et al., 2006). Accelerometer and depth loggers attached to free-ranging *D. gigas* recently revealed that locomotor function and vertical velocities are suppressed significantly in the OMZ (Gilly et al., 2012), which is consistent with laboratory findings of a significant capacity for metabolic suppression under hypoxic conditions in the same species (Rosa and Seibel, 2010). Accelerometer data from loggers attached to little penguins, *Eudyptula minor*, were examined in the context of thermocline presence, with higher foraging efficiencies (estimated from the frequency and amplitude of flipper beatings) coinciding with more pronounced thermal stratification (Pelletier et al., 2012). A similar interaction with thermocline depth was found for thick-billed murre, *Uria lomvia*, with accelerometer and depth loggers used to suggest that the birds respond to variable prey distributions that are driven by the thermal structure of water masses (Takahashi et al., 2008).

Arguably one of the more topical of biologging applications, depth and acceleration loggers are providing crucial insights into how physical oceanography (temperature and oxygen in particular) shapes the distribution and behavior of a range of aquatic animals (Rutz and Hays, 2009). These data are already being used to underpin management strategies for a number of commercially important fisheries (e.g. Hobday et al., 2010), and given the changes to oceanic conditions that are predicted in coming decades, interpreting biologging data in this context is likely to become increasingly important.

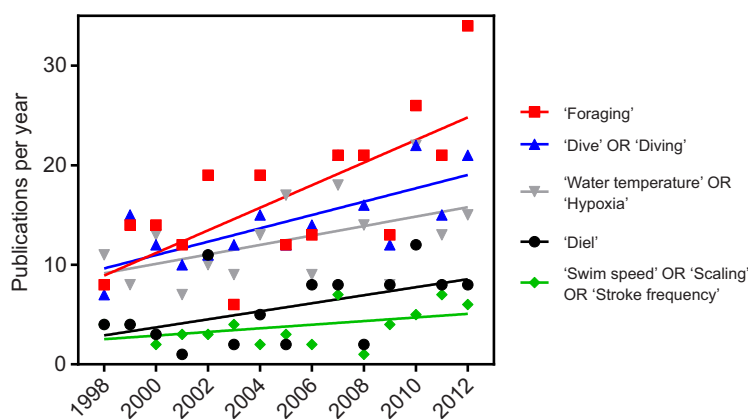


Fig. 2. Bias in biologging dissemination. A title, abstract or key words primary literature search was conducted with the following search terms: [fish OR seal OR penguin OR shark OR turtle OR whale] AND [logger OR transmitter] AND [each term listed in the key]. Source: Scopus.

Conclusions: semantic antics and horses for courses?

In their seminal paper describing the metabolic theory of ecology, J. H. Brown and colleagues argued that organismal metabolic rates control ecological processes at all levels of organization, and represent a tangible link among life span, growth rates, competition and predation, and tropho-dynamics (Brown et al., 2004). All of the studies cited in the present commentary were fundamentally concerned with the acquisition or expenditure of energy, and as Brown and colleagues explain, this is central to all biophysical processes. As such, categorizing the main theme of a biologging study relies on a degree of semantics: lunge-feeding in baleen whales could be interpreted in the context of biomechanics or as an adaptation to diving; and vertical migrations in basking sharks are an example of a diel rhythm and, equally, a foraging strategy. The context within which biologging data are interpreted may largely reflect personal, research-program or institutional bias, and the past decade has seen large thematic disparities (approaching an order of magnitude; Fig. 2) in how we disseminate biologging data. Certainly some datasets will have less potential for diverse analysis or interpretation than others, but simply increasing the scope of keyword selection may be one of the most efficient ways to broaden the disciplinary significance of a given biologging study.

Several practical factors are likely to hinder multidisciplinary biologging approaches to some degree. Becoming familiarized with diverse analytical concepts and tools is an obvious example [e.g. truncated versus synthetic power law distributions for identifying Lévy flight foraging, phylogenetically informed statistics (PIS) for diving optimality models and biomechanics, generalized linear mixed modeling (GLMM) for oceanographic interactions]; however, these are increasingly well developed and documented (Burnham and Anderson, 2002; Garland et al., 2005; Rutz and Hays, 2009; Sims et al., 2008), and can often be undertaken with freely available software (e.g. the PDAP Package for PIS, R for GLMM).

Perhaps then, the most significant barrier is one of interest. A climate change scientist using biologging to determine whether tuna have a preference for warm, highly oxygenated surface water may not be interested in also determining whether they forage optimally (Lévy flights) or are more active during the day than at night. Similarly, a researcher testing diving optimality models might not care whether their tagged seals forage more above the thermocline than below.

Will this change? While we hope that our illustration of flexibility stimulates some multi-disciplinary considerations among biologging scientists, a powerful attribute of future biologging research may lie in the sharing of data. The potential for diverse interpretations of a biologging dataset will be more easily identified by the biologging

community as a whole than the collectors of the data independently, and perhaps this is the key to greater exploitation of biologging tools. Several aquatic biologging data-sharing networks are already in operation (e.g. the Ocean Tracking Network Global Data Warehouse: <http://oceantrackingnetwork.org/about/data>; Pacific Ocean Shelf Tracking Project: <http://www.postprogram.org/>; and Australian Animal Tagging and Monitoring System: <http://aatams.emii.org.au/aatams/>), and while their general aim is to integrate data acquisition across multi-institutional monitoring stations, they also represent a powerful tool for stimulating multidisciplinary biologging collaborations. Through the sharing of details on study species, sensor type and tagging location (often several years prior to publication), other members of these networks have the opportunity to open dialogue with researchers from other fields, and we believe these discussions have the potential to significantly enhance the exploitation of biologging datasets. With many journals encouraging (and often mandating) the public archiving of scientific data, such collaborations will hopefully become increasingly common.

Ultimately, the first step is to recognize that biologging data can have multidisciplinary relevance. Regardless of whether this is already acknowledged by the biologging community in general, we hope this paper contributes not just to the adoption of biologging research, but also to the broader dissemination of a given biologging program.

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Competing interests

The authors declare no competing financial interests.

Author contributions

N.L.P. and J.M.S. conceived the study. N.L.P., M.D.T., Y.Y.W. and J.M.S. drafted and edited the manuscript.

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