

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

INTRODUCTION: REVIEW

Tracking fitness in marine vertebrates: current knowledge and opportunities for future research

Glenn T. Crossin^{1,*}, Steven J. Cooke², Jeremy A. Goldbogen³, Richard A. Phillips⁴

¹Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada

²Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, Ontario K1S 5B6, Canada

³Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, California 93950, USA

⁴British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, Cambridgeshire CB3 0ET, UK

ABSTRACT: For more than 60 yr, electronic tags (including acoustic transmitters, archival loggers, and satellite tags) have been applied to free-ranging marine vertebrates to track their behaviour and characterize their spatial ecology. However, only recently have researchers begun using electronic tags to elucidate the processes that relate directly to fitness, i.e. the ability of organisms to survive and reproduce. We briefly review the history of tracking studies focused on marine vertebrates and then provide a general overview of studies that have used tracking to address fitness-related questions. Although many studies have used at-sea movement and activity data to better understand feeding ecology, physiology, and energetics, there is growing interest in the coupling of electronic tracking techniques with other disciplines to resolve the mechanisms underlying individual fitness, or more precisely the proxies thereof (survival, timing of reproduction, foraging success, etc.). We categorized studies into 4 general fitness-related areas: (1) foraging dynamics, energetics, and growth; (2) migration and other non-breeding season activities; (3) survival; and (4) reproduction. Despite recent advances in tracking technologies, which include multi-sensor loggers, tri-axial accelerometers, and miniaturized geopositioning systems, etc., very few studies on wild marine vertebrates truly measure individual fitness or proxies thereof. There is thus a need to design experimental, multi-disciplinary, and longitudinal studies that use genetics, individual-based modeling, and other techniques in an effort to resolve the mechanisms responsible for individual variation in fitness in marine vertebrates.

KEY WORDS: Electronic tracking · Telemetry · Biologging · Electronic sensors · Behaviour · Life history · Reproduction · Survival · Mortality · Migration · Non-breeding

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Researchers have long employed electronic tracking to observe and understand animal movements. Electronic tracking involves the use of various technologies that either transmit (biotelemetry; Cooke et al. 2004a) or log (i.e. biologging; Block 2005, Rutz & Hays 2009) information about an animal's position, its physiological state (e.g. activity level, heart rate,

body temperature) and parameters from the surrounding environment (e.g. pressure, temperature). There are currently many types of biotelemetry and biologging devices available for use in marine animal tracking studies (see reviews by Arnold & Dewar 2001, Burger & Shaffer 2008, Godley et al. 2008, Wakefield et al. 2009, Cooke et al. 2012, Wilson & Vandenberg 2012). Historically, most studies have used such tools in a very descriptive way (e.g. char-

acterizing movements and other at-sea activities, or habitat use), without any consideration of the direct links to survival, growth and body condition, population processes, or other components of an individual's life history, and overall fitness.

Although fitness can be defined in many ways, there is general consensus regarding its essence (reviewed in Barker 2009). Orr (2009) elegantly states that 'fitness involves the ability of organisms—or, more rarely, of populations or species—to survive and reproduce in the environment in which they find themselves' (p. 531). The more 'fit' individuals are those who survive to reproduce, thus passing along genes to the next generation. Endler (1986) considered fitness to be a measure of the degree to which there is a consistent relationship between a given trait and survival, although he also noted that confusion often abounds regarding the difference between fitness and adaptation. There is much debate regarding fitness (e.g. Mills & Beatty 1979, Schaffer 1981, Sober 2001), which is very difficult to measure accurately in the wild, particularly for long-lived animals (Kozłowski 1993), such that researchers usually rely on quantifying components of fitness that serve as proxies or surrogates (McGraw & Caswell 1996, Irschick 2003). We know little about the natural history of many marine vertebrates (especially those that spend the majority of their time sub-surface), let alone the key determinants of their individual fitness. Quantifying lifetime reproductive success (and even tracking the survival and fitness of offspring) for a terrestrial mammal such as a black bear is comparatively easy (Elowe & Dodge 1989). The same undertaking for marine vertebrates is very challenging because of external fertilization, low fertilization and survival rates, and difficulties in catching, tagging and tracking individuals. Seabirds and some marine mammals that come to shore at breeding colonies, as well as fish species that return to distinct spawning grounds (e.g. Pacific salmon *Oncorhynchus* spp.), provide some unique opportunities to assess fitness of marine animals. With the advent of electronic tagging, one would presume that it is finally possible to track fitness of marine vertebrates; however, have we actually made any progress in doing so?

In this review, we briefly summarize the current state of electronic tracking studies focused on marine vertebrates, and to highlight the ways in which electronic tags have been used to inform our knowledge of life history and fitness-related processes. Specifically, we highlight studies that combine electronic tracking, multiple sensor data, and, in some cases, other scientific disciplines, to quantify varia-

tion in behaviour; to relate individual variation in behaviour to variation in relevant fitness-related traits; and to identify the endogenous or exogenous factors that mediate individual variation in those traits through correlational and experimental approaches. We promote the thesis that an understanding of fitness-related processes in free-ranging marine animals must use electronic tracking in tandem with other physiological, hormonal, energetic, metabolic, genetic, or environmental disciplines, thus providing insights into the regulatory mechanisms that lead to variation in fitness endpoints. Although our review focuses on vertebrates, similar techniques have also been applied to marine invertebrates (e.g. Hays et al. 2012).

Since the advent of telemetry research in the early 1960s, the majority of animal tracking studies have been largely descriptive, reporting patterns of movement without any discernible links to fitness-related processes. Recently, however, an increasing number of tracking studies have adopted an individual-based approach, where differences in fitness-related traits are measured and the underlying causes of such variation are identified (see Fig. 1 for examples from this Theme Section). For the purposes of this paper, it is necessary to define what we mean by fitness-related traits. Adopting ideas from the vast literature on fitness (Barker 2009; see also above), we define a fitness-related trait as any trait that can contribute to individual variation in lifetime fitness. Relevant fitness traits include growth, timing of migration, breeding decisions, timing of reproduction, egg and clutch size, foraging success, parental care, hatching and breeding success, overall fecundity, and survival (or mortality). These can be grouped into 4 general fitness-related categories, which we discuss in the following section: (1) foraging dynamics, energetics, and growth; (2) migration and other non-breeding season activities; (3) mortality; and (4) reproduction.

TRACKING FITNESS: CONTEXT AND EXAMPLES

Foraging, energetics, and growth

In order to maximize fitness, animals must possess efficient mechanisms for energy acquisition and expenditure (Kleiber 1975). The transfer of energy between an animal and its environment is challenging to study in controlled laboratory settings; attempting to quantify energy budgets within the logistical constraints that apply to research on free-ranging animals is even more challenging (Nagy



Fig. 1. Examples of tracking applications from this Theme Section: (a) great hammerhead shark *Sphyrna mokarran* with a satellite tag attached to its dorsal fin (see Gallagher et al. 2014); (b) black legged kittiwake *Rissa tridactyla* bearing a geolocation logger on a leg band (see Schultner et al. 2014); (c) southern elephant seal *Mirounga leonina* fitted with a satellite transmitter (see New et al. 2014); and (d) emperor penguin *Aptenodytes forsteri* bearing a digital electrocardiogram and time-depth recorder to monitor oxygen regulation during deep dives (see A. K. Wright et al. 2014). Photo credits: (a) Evan D'Alessandro, (b) Tycho Anker-Nilssen, (c) Mark Hindell, (d) Paul Ponganis

et al. 1999). Nevertheless, telemetric and biologging approaches, often in combination with oceanographic sampling and other techniques (e.g. doubly-labeled water), have provided important insights into the processes that govern energy gain and use in different habitats, particularly during foraging (Wilson et al. 2002, Goldbogen et al. 2006, Aoki et al. 2012, Simon et al. 2012, Shepard et al. 2013).

Energetically efficient foraging strategies are essential for supporting metabolism, somatic growth, and parental investment. This requires a low cost of transport for locomotion and feeding, as well as a high rate of energy (= resource) acquisition. The interaction of these processes and the properties of the physical environment determine the energetic efficiency of foraging. Therefore, investigating for-

aging behaviour of free-ranging animals under natural conditions is a fundamental step towards understanding energy flux between organisms and their environment (e.g. Weimerskirch et al. 2000, Shaffer et al. 2003).

A major focus of tracking studies is to elevate the mechanics of animal locomotion across a wide range of temporal and spatial scales, from excursions across ocean basins (see next subsection) to an individual stroke of a fluke or fin. At the smallest scale, the advent of accelerometers and magnetometers in animal-borne tags has revealed important information about the kinematics of fine-scale movement and provided powerful proxies for movement-based energy expenditure (e.g. Halsey et al. 2011). The combination of multiple sensor modalities allows for several key locomotor parameters to be quantified, such as speed, stroke frequency, and body orientation. Long time-series data sets can generate ethograms of animal behaviour (Yoda et al. 2001, Sakamoto et al. 2009, Shamoun-Baranes et al. 2012), fine-scale automated positioning systems (e.g. Bunt & Kingsford 2014, Heupel & Simpfendorfer 2014, McLean et al. 2014, all in this volume), or daily diaries (Wilson et al. 2008), which describe behavioural states (i.e. feeding, mating, resting, or transit) as a function of location, depth, or time of day (Friedlaender et al. 2009, Whitney et al. 2010, Goldbogen et al. 2013, Watanabe & Takahashi 2013). These approaches aim to quantify key kinematic and physiological parameters that elucidate the energy budgets of animals in relation to foraging performance, growth, and reproduction. Because of the logistical and technological constraints, many early studies focusing on these parameters involved the use of large archival tags attached to relatively large aquatic vertebrates such as marine mammals, seabirds, and fish.

Travel speed is one of the most important parameters related to energy expenditure, but it is also one of the most difficult to measure in free-swimming animals. Methods used to estimate swimming speed of tagged animals have included a rotating propeller (Tanaka et al. 2001), a flexible paddle wheel (Shepard et al. 2008a), vector resolution from depth rate and animal orientation (Miller et al. 2004a, Simon et al. 2012), and flow noise (Burgess et al. 1998, Goldbogen et al. 2006). Drag increases exponentially with speed and therefore greater speeds require disproportionately more power output (energy use per unit time) (Vogel 1994). It follows that animals will predictably choose cost-efficient locomotor strategies and low speed for long-distance travel to minimize the cost of transport (energy use per unit distance)

(Williams 1999). Laboratory experiments with swimming animals showed that speed increased with body size, a phenomenon explained post hoc by one theoretical framework (Bejan & Marden 2006). Initial tag studies from free-ranging aquatic vertebrates showed that swimming speed was largely independent of body size (Block et al. 1992, Sato et al. 2007), demonstrating that free-ranging animals may exhibit behaviours and locomotor performance different to those expected from laboratory studies. A subsequent analysis using comparative phylogenetic methods demonstrated a significant, but very small increase in swimming speed (up to 2.5 m s^{-1}) with body size in breath-hold divers (Watanabe et al. 2011). Although steady swimming speeds were between 0.5 and 2.5 m s^{-1} across a wide range in body size, the largest animals exhibited the greatest speeds and thus were able to cover greater distances while minimizing the cost of transport (Watanabe et al. 2011).

Because aquatic animals must navigate a complex 3-dimensional environment, they integrate their choice of swimming speed with a wide variety of behavioural strategies to ensure successful locomotor and foraging performance. The combination of time-depth recorders with accelerometers and video systems has uncovered specific mechanisms used by animals to minimize energy costs. The most basic of these strategies is to employ gliding, either in the form of burst-and-coast swimming (Videler & Weihs 1982, Williams 2001, Watanuki et al. 2003, Sato et al. 2013) or gliding during the descent or ascent phase of a dive (Williams et al. 2000, Gleiss et al. 2011a,b). The ability to distinguish active swimming strokes from periods of gliding using accelerometer signals is important, given that mechanical work is dependent on energy expenditure. Acceleration metrics related to periods of stroke-propelled swimming, such as overall dynamic body acceleration and minimum specific acceleration, have been developed to investigate both the fundamental mechanics and the energetic cost of different behaviours (Gleiss et al. 2011c, Simon et al. 2012). The incorporation of these and related kinematic parameters into mechanical models of swimming has the potential to quantify multi-dimensional energy landscapes (power envelopes or energetic niches) that define the amount of power required for various behaviours under different environmental conditions (Wilson et al. 2011, 2012, Shepard et al. 2013, Wilson et al. 2014, this volume). Detailed calibrations are required to generate relationships between acceleration profiles and energetic costs (e.g. S. Wright et al. 2014, this volume). Such calibrations

are difficult in the field, especially for large animals. However, as the number of studies linking metabolic rates to dynamic acceleration metrics increases, allometric trends in different movement styles may be revealed, from which species-specific metrics could be derived.

Tracking techniques have also enabled researchers to quantify foraging behaviours and identify specific feeding events. Changes in speed, orientation, and acceleration have been used to infer prey capture attempts in a wide variety of animals (Wilson et al. 2002, Goldbogen et al. 2006, Aoki et al. 2012, Simon et al. 2012, Naito et al. 2013). This indirect approach is greatly enhanced by complimentary data, such as simultaneous video footage (Goldbogen et al. 2013, Watanabe & Takahashi 2013) or acoustics that quantify echolocation clicks (Miller et al. 2004b, Watwood et al. 2006). Other direct measures of feeding involve stomach temperature logging or telemetry in endotherms, which monitors rapid drops in temperature upon prey capture and ingestion (Weimerskirch et al. 1994, Catry et al. 2004, Sepulveda et al. 2004, Kuhn et al. 2009). The ability to quantify feeding performance, and the concomitant estimation of energy expenditure during foraging, allows for an assessment of foraging efficiency (Costa et al. 1989, Gremillet 1997, Williams & Yeates 2004, Goldbogen et al. 2011). Ultimately, the efficiency of foraging determines the ability of an animal to extract energy from the environment for a given prey density, resulting in its own mass gain or loss, and that of any dependent offspring. Some of the largest marine endotherms, exemplified by the largest baleen whales, rely on lipid stores acquired during extensive feeding bouts in summer months that then must fuel large-scale migrations across ocean basins to breeding grounds (Goldbogen et al. 2011, Costa et al. 2012, Christiansen et al. 2013). Long-term tagging studies have been able to track these changes in body condition, which are manifested as changes in buoyancy, in some large marine vertebrates by quantifying changes in drift rate during glides (Thums et al. 2011, 2013, Del Raye et al. 2013). Through simulation, this approach (quantifying drift rates and migratory behaviour) has now been extended to estimate long-term changes in vital rates, fitness, and eventually population-level effects from perturbations in the environment (e.g. New et al. 2014, this volume). For ectotherms, even basic measures of temperature (environment or body) have the potential to provide unprecedented information on animal energetics (e.g. Drenner et al. 2014, this volume).

Migration and other activities during the non-breeding season

Until recently, relatively little was known about the non-breeding season movements of animals, and even less about the fitness consequences. Yet, the decisions animals make during this time affect the recovery of body condition, accumulation of fat and protein stores in advance of breeding, and hence their survival and subsequent fitness (Dingle 1996). The advent of new tracking technologies has revolutionized the field. Archival devices with long battery lives and low power consumption, particularly geolocators, have provided insights into the non-breeding activities of many marine predators, particularly seabirds, pinnipeds, and sea turtles. In seabirds for example, extraordinary circumpolar or trans-equatorial migrations have been described, wherein unexpectedly high levels of inter-individual variability in habitat use and preference have been observed (Croxall et al. 2005, Shaffer et al. 2006, Nathan et al. 2008, Rayner et al. 2011). Because of electronic tracking, these studies have allowed researchers to speculate on the implications of non-breeding movements for niche partitioning, population genetic structure, and speciation.

As technology has improved, there has also been a burgeoning of studies that combine geographic locations of migrants obtained using satellite telemetry or geolocation, with recording of dives, saltwater immersion (distinguishing time on the water versus in flight), internal temperature (indicating prey ingestion), dynamic acceleration, heart rate, or other aspects of behaviour. Concurrent use of multiple sensors has provided insights into differences in behaviour between daylight, twilight, and darkness; inferred reliance on nocturnal prey and the importance of lunar phase; influence of photoperiod on timing of migration; constraints associated with low light levels in the polar winter; effects of region, year, sex, status, etc.; and intra- and inter-specific foraging niche specialisation and resource partitioning (Green et al. 2005, Hays et al. 2006, Shepard et al. 2006, Bestley et al. 2008, Mackley et al. 2010, Pinet et al. 2011). Novel analytical methods have identified behavioural modes, for example diel patterns in travel rates of leatherback turtles *Dermochelys coriacea* using ARGOS tracks (Jonsen et al. 2006), the switch from directed movement to residency in elephant seals *Mirounga leonina* (Bestley et al. 2013), or between transiting, foraging, migration or breeding behaviour in great white sharks *Carcharodon carcharias* using relatively low temporal resolution data on position,

temperature, and daily time-at-depth histograms from pop-up archival transmitting tags (Jorgensen et al. 2012). Studies have also examined how age-specific changes in spatial patterns in threatened species can increase their risk of predation, fisheries harvest, or bycatch (Sims et al. 2005, Bailleul et al. 2007, Bestley et al. 2010, Lea et al. 2010, Mackley et al. 2011, Freeman et al. 2013).

Multi-sensor studies are especially pertinent where the insights into feeding ecology can be related to trade-offs in time and energy, the key currencies that underlie overall fitness. Direct measurement is possible with heart rate loggers, which can provide instantaneous estimates of energy expenditure associated with different activities. When used in conjunction with internal temperature sensors (which can be used to infer animal ingestion), heart rate loggers can provide information about foraging success and overall energy budget (Green et al. 2009, White et al. 2013). As an alternative, overall dynamic body acceleration can provide a useful proxy for energy expenditure. Likewise, energetic trade-offs can be investigated by incorporating indirect approaches to estimating body condition or composition (see previous sub-section). Energy cost of different activities or environments can be compared using a lower-tech approach; for example, analysis of temperature data from geolocators provides insights into the importance of heat loss while floating or swimming, which can be a major energetic consideration, particularly for seabirds (Richman & Lovvorn 2011, Garthe et al. 2012). In this Theme Section, Wilson et al. (2014) use tri-axial accelerometers to infer optimal swimming speeds of sockeye salmon *Oncorhynchus nerka* during both marine and freshwater homing migrations.

Another useful approach for examining fitness consequences of migration is to combine conventional tracking with forensic methods of diet determination. The quantity and quality of prey consumed during the non-breeding or the immediate pre-breeding period affects adult condition and the resources that can be devoted to egg formation in birds, or to fetal development in viviparous animals. Thus, geocator and satellite-tracking data have been integrated with stable isotope analysis of tissues synthesized during the non-breeding period (e.g. feathers, whiskers, and baleen) to infer trophic level, carbon source, prey type, foraging overlap, and segregation (Phillips et al. 2009, Suryan & Fischer 2010, Young et al. 2010, Bentaleb et al. 2011, Thiebot et al. 2012). Such approaches can be extended to the study of carryover effects: stable isotope analyses suggested that the estimated proportion of energetically rich cope-

pods consumed in the pre-breeding period influenced timing of breeding and egg volume in female Cassin's auklets *Ptychoramphus aleuticus* (Sorensen et al. 2009), and trophic level during the non-breeding period was correlated positively with egg mass in Atlantic puffins *Fratercula arctica* (Kouwenberg et al. 2013).

Despite the technological advances, researchers rarely addressed the direct consequences of individual migration strategies for survival or breeding success in the following summer, nor whether carryover effects from breeding might affect the subsequent migration. This has changed recently, especially in seabird research, with several observational or experimental studies demonstrating an effect of previous breeding outcome on migration patterns, particularly during the immediate post-breeding period rather than on the return journey to breeding areas (Bogdanova et al. 2011, Catry et al. 2011, 2013, Schultner et al. 2014, this volume). There is also some evidence for carryover effects from the non-breeding to subsequent breeding season, affecting the decision to defer breeding, laying date, egg dimorphism or size, or breeding success, and in some cases this has been related to adult body condition or hormone levels (Daunt et al. 2006, Crossin et al. 2010, 2012a, 2013a,b, Kouwenberg et al. 2013). Hormonal (e.g. endocrine) analyses can be particularly informative in this context, especially when attempting to understand the mechanisms (physiological, environmental) responsible for variation in behaviour, survival, and breeding output (Bókony et al. 2009). When used in combination with electronic tracking, hormonal manipulations are an especially powerful means for identifying the physiological mediators of carryover effects and links between life-history stages (e.g. Midwood et al. 2014, this volume). Carryover effects can also be linked to pollutants (e.g. mercury, persistent organic pollutants, hydrocarbons), with variation in migration strategy affecting exposure and resulting in potential endocrine disruption and negative impacts on various aspects of reproduction or survival (Ragland et al. 2011, Montevecchi et al. 2012, Leat et al. 2013, Tartu et al. 2013).

An improved understanding of migration patterns and the potential or measured energetic and fitness consequences is increasingly important, as the combined impact of anthropogenic threats (e.g. changing climate, bycatch, overfishing, invasive predators, and oil pollution) is unprecedented (Shillinger et al. 2008, Barbraud et al. 2012, Hazen et al. 2013, Maxwell et al. 2013). With respect to many threatened or endangered species conservation efforts, the effectiveness

of captive breeding programs needs evaluation, which includes the behavioural (e.g. telemetric) monitoring of released individuals relative to wild ones (Westenberg et al. 2014, this volume). For some species, considerable effort has been directed at modelling future habitat requirements and availability, and at relating survival prospects to foraging constraints associated with reduced light levels during the temperate or polar winter (Green et al. 2005, Daunt et al. 2006, McIntyre et al. 2011, Hazen et al. 2013, White et al. 2013). However, for most migrants, accurate projection of demographic responses to environmental change will rest on future tracking studies that enable the prediction of non-breeding distribution based on habitat availability and preference, the modelling of energetic trade-offs, and links between these components and individual fitness. Even basic knowledge of the factors that influence habitat use and movement of wild marine vertebrates is lacking for most species, and for some discrete life stages (e.g. the dispersal of marine juveniles and ontogeny of migration are not well studied because of limitations relating to small size and the often long interval to first breeding; recent attempts to fill this knowledge gap include Hays et al. 2010, Gutowsky et al. 2013). Studies that use high-resolution positioning data combined with sophisticated modeling and model selection procedures (e.g. Heupel & Simpfendorfer 2014) have much potential for unraveling the energetic and life-history drivers of spatial and movement ecology.

Mortality

Beyond being an important phenomenon in population dynamics (Beverton & Holt 1957), mortality is of direct relevance to fitness given that once an animal is dead, its fitness is zero. However, from a fitness perspective, the timing of mortality is perhaps the most relevant aspect. Mortality prior to maturation or (successful) reproduction would clearly yield zero lifetime fitness, while mortality after some degree of reproductive success could mean that some level of fitness had been obtained, depending on the life history of a given species, adult age, condition, etc. Mortality is obviously a natural phenomenon and can be exceedingly high (e.g. early life stages of most fishes and sea turtles), but can also be mediated directly (e.g. hunting, harvest) and indirectly (e.g. disease, change in ecosystem structure) by human activities. While a simple concept, mortality was rather difficult to measure directly in marine vertebrates

until the advent of electronic tagging techniques (Pollock et al. 2004). In some species with strong fidelity to a breeding (e.g. marine mammals, seabirds, Pacific salmon) or foraging site (e.g. some sharks), it may be relatively easy to quantify mortality using band returns or resights, yet that approach provides little insight into the location, timing, or mechanism underlying mortality. Although tracking can be used to infer mortality, other issues including tag failure, shedding or loss (Hays et al. 2007), predation (such that the tag is removed by another animal; Cooke & Philipp 2004), poor detection efficiency of receivers (Melnychuk 2012), and the difficulty of differentiating mortality from emigration (Yergey et al. 2012) can make it difficult to determine with certainty. Some efforts have been put into the development of mortality sensors (see Cooke et al. 2004a), but they have yet to be used widely. Additionally, tagging itself may affect animal mortality. Many studies aim to minimize tagging effects and will sometimes use controlled holding studies or other pilot studies in an effort to identify optimal size and mass of devices, effects on movement and agility, and best location on the body for placement. Addressing these issues prior to tagging is important for both scientific and ethical reasons (see reviews by Ropert-Coudert & Wilson 2005, Cooke et al. 2011).

Documenting mortality is a common goal in many marine vertebrate tracking studies. For example, Heupel & Simpfendorfer (2002) studied mortality levels of young blacktip sharks *Carcharhinus limbatus* using acoustic telemetry coupled with modelling. Notably, all natural and fishing mortality occurred within the first 15 wk of the study while animals remained on nursery grounds, revealing a period of vulnerability. Given the intense management efforts focused on Pacific salmon, there have been numerous studies identifying the magnitude and location of mortality for out-migrating smolts (Melnychuk et al. 2007, Brown et al. 2013, Romer et al. 2013; Rechisky et al. 2014, Brosnan et al. 2014, both this volume) and returning adults (e.g. Cooke et al. 2006a, Crossin et al. 2007, 2009) in coastal waters and freshwater. Some of those studies have contrasted the survival of hatchery and wild fish (e.g. Johnson et al. 2010, Moore et al. 2012, Aarestrup et al. 2014, this volume) to inform management. Another management application has involved the use of acoustic telemetry to estimate natural mortality of lingcod *Ophiodon elongatus* in a marine reserve and evaluate reserve effectiveness (Starr et al. 2005). Although tracking studies focused on mortality are dominated by those on fish, there are examples from other taxa: Reid et al. (1995)

quantified mortality of radio-tagged manatees *Trichechus manatus latirostris* in Florida estuaries, and several studies have quantified mortality of sea turtles (reviewed in Godley et al. 2008). Indeed, although not always a stated objective, nearly every tracking study reports some basic information on mortality (Hart & Hyrenbach 2009).

Electronic tracking has increasingly been used to document bycatch mortality in commercial fisheries or catch-and-release mortality from recreational fisheries (Donaldson et al. 2008, Maxwell et al. 2013). Given that mortality is usually difficult to observe in the marine environment, tracking studies provide one of the few means to objectively assess this aspect. Hays et al. (2003) published one of the first studies to use satellite telemetry to quantify bycatch mortality in marine turtles; such data can be incorporated into population and management models (Chaloupka et al. 2004). The earliest catch-and-release study using acoustic telemetry to assess mortality in a recreational marine fishery was of Atlantic sailfish *Istiophorus albicans* and revealed mortality that would have been undetected with other methods (Jolley et al. 1979). A study on post-release mortality in bonefish *Albula vulpes* in shallow tidal creeks using acoustic telemetry revealed that predator density had a major impact on survival (Cooke & Philipp 2004), whereas for Atlantic bluefin tuna *Thunnus thynnus* studied with pop-up satellite archival tags in the Gulf of St. Lawrence, little post-release mortality was observed (Stokesbury et al. 2011). In one study, pop-up satellite archival tags were used to contrast mortality of striped marlin *Kajikia audax* captured and released using different hook types (Domeier et al. 2003). Beyond simply documenting mortality, the goal of much of the fisheries interaction research is to develop strategies to reduce mortality (McClellan et al. 2009).

Electronic tags, either alone or in combination with other techniques such as blood sampling to assess physiological status, are able to elucidate the details of mortality (Cooke et al. 2008). For example, using a non-lethal biopsy approach on fish tagged with radio and acoustic transmitters (see Cooke et al. 2005 for methods), Miller et al. (2011) revealed genomic signatures that predicted migratory failure (i.e. mortality) of Pacific salmon destined for spawning grounds. Cooke et al. (2006a) and Crossin et al. (2009) used similar approaches to associate more traditional physiological measures (e.g. stress and reproductive hormones, ions, metabolites) with mortality of sockeye salmon at the ocean-to-river transition. Such mechanistic studies of mortality are still rare in marine vertebrates. Gallagher et al. (2014, this volume)

adopted a different approach to study the consequences of fisheries interactions for several shark species: satellite tags were used to assess post-release mortality levels, and blood samples and reflex indicators collected in parallel from other sharks at time of capture provided the context in which to interpret mortality patterns.

Reproduction

When an animal reproduces, one of its first considerations is where and when to breed. Electronic tracking has been used to identify and characterize reproductive locales for a number of marine species. For example, satellite telemetry was used in a threatened sea-duck species, the Stellar's eider *Polysticta stelleri*, to identify population-specific breeding areas across Arctic regions, which had hitherto been unknown (Petersen et al. 2006). This information was useful for differentiating breeding characteristics of Atlantic and Pacific populations, and suggested evolutionary and ecological factors influencing their distributions. In a different study, acoustic and radio telemetry were coupled with egg drift sampling and histological analyses to characterize the marine-to-freshwater movements and spawning locations of endangered Gulf sturgeon *Acipenser oxyrinchus desotoi* (Fox et al. 2000).

For many pelagic marine species, however, and especially fish (e.g. the coelacanth *Latimeria menadoensis*), knowledge of breeding or spawning locations is sparse or unavailable due in part to the obvious difficulty of observing these events. Satellite telemetry has been used with some success to identify spawning activity in wide-ranging bluefin tunas *Thunnus thynnus* (Lutcavage et al. 1999, 2012, Block et al. 2001, Teo et al. 2007). In Atlantic bluefin tuna, for example, tagging revealed areas in the North Atlantic as important spawning areas, which dispelled long-held ideas that the Gulf of Mexico was the principal breeding area (Lutcavage et al. 1999). Similarly, in shortnose sturgeon *Acipenser brevirostrum*, acoustic telemetry arrays revealed new breeding habitats for individuals that could not spawn in historical locations within a fragmented river system, and were thus forced to move across marine areas to new river systems (Zydlewski et al. 2011). In loggerhead turtles *Caretta caretta*, identification and use of breeding areas within established marine protected areas in the eastern Mediterranean Sea, as well as in Baja California, were determined using GPS loggers and ARGOS transmitters (Peck-

ham et al. 2007, Schofield et al. 2009). These studies provided data and recommendations for guiding conservation policy at both local and regional scales.

Although they are not marine species per se, the spawning locations of female muskellunge *Esox masquinongy* and northern pike *Esox lucius* were identified via oviduct tagging (Pierce 2004, Pierce et al. 2007). With this method, acoustic transmitters are inserted into the oviducts of mature female fish and then expelled along with eggs when the fish spawn, thus allowing researchers to track the movement to, and activity at, precise spawning sites. The first application of this method to pelagic/marine fish was for the European perch *Perca fluviatilis* in the Baltic Sea (Skovrind et al. 2013). Other studies have used electronic tracking to identify not only breeding site location, but also site fidelity (i.e. philopatry), for a variety of marine taxa including bonefish (Humston et al. 2005), loggerhead turtles and green turtles *Chelonia mydas* (Limpus et al. 1992, Broderick et al. 2007, Tucker 2010), ringed seals *Phoca hispida* (Kelly et al. 2010), harbour seals *Phoca vitulina* (Van Parijs et al. 2000), king eiders *Somateria spectabilis* (Phillips & Powell 2006), nurse sharks *Ginglymostoma cirratum* (Pratt & Carrier 2001), bluefin tuna (Teo et al. 2007), red tilefish *Branchiostegus japonicus* (Miyamura et al. 2005), and Atlantic cod *Gadus morhua* (Robichaud & Rose 2001). Despite the innate programming for philopatry in some species, navigating to natal breeding locations is nevertheless a massive challenge. Ueda (2014, this volume) conducted a series of experiments to manipulate the endocrine and sensory physiology systems of Pacific salmon and reveal the mechanisms by which adult salmon are able to successfully home to natal spawning grounds. In many cases, information on breeding location, multi-year habitat use, and breeding site fidelity provided vital information with direct application to management and conservation.

Once animals reach breeding areas, the timing of reproduction accounts for a large proportion of the total variance in lifetime fitness. For nearly all animals, breeding is usually restricted to a window of opportunity that is timed to match seasonal availability of food resources. Variation in timing can result in reproductive isolation (allochrony), which in turn leads to selection for adaptive reproductive phenotypes and provides a mechanism for adaptive radiation (Hendry & Day 2005).

Telemetry or biologging techniques are still only rarely used to examine reproductive timing in wild animals, presumably because reproduction is often very predictable and for many species is relatively

easy to observe. For example, differences in male and female loggerhead turtle arrival at a marine protected area breeding site showed a clear bimodal distribution (e.g. protandry); these GPS tracks directly aid the conservation and management of this species (Schofield et al. 2013). Radio telemetry was used to identify the timing of reproduction by populations of Chinook salmon *Oncorhynchus tshawytscha* in the Kenai River of Alaska (Burger et al. 1985). The authors speculated how variation in spawning times might influence the fitness of individuals, but did not directly measure any such endpoints. Differences in the timing of reproduction by male and female spotted seatrout *Cynoscion nebulosus* have also been described via acoustic telemetry (Lowerre-Barbieri et al. 2013). Goutte et al. (2014, this volume) examined the links between breeding phenology of black-legged kittiwakes *Rissa tridactyla* and levels of the stress hormone corticosterone: although baseline corticosterone levels were correlated with trip duration and destination during the pre-laying period, the decision to breed and laying date were influenced not by corticosterone but by individual body condition, suggesting that the proximate mechanisms underlying timing of breeding are complex.

Electronic tracking has been used frequently to study reproductive activity and behaviour, especially in fish where courtship and spawning behaviour is often difficult to observe. Acoustic telemetry arrays have identified broad-scale movement patterns in deep shelf environments as evidence of spawning aggregation in bonefish and linked these movement and spatial patterns to specific moon phases (Danylchuk et al. 2011). At a smaller scale, egg-laying behaviour and reproductive timing was characterized in female small spotted catsharks *Scyliorhinus canicula* via time-depth telemetry and the tracking of vertical movements that are known to correspond to egg laying (Wearmouth et al. 2013). Similarly, a recent study in nurse sharks *Ginglymostoma cirratum* used 3-dimensional accelerometry to differentiate mating from other peripheral behaviours (resting, swimming, etc.) (Whitney et al. 2010). Attempts to quantify energetic costs of breeding and courtship behaviour involved electromyogram (EMG) telemetry, most frequently in Pacific salmon, where muscle contraction and tailbeat frequency relationships yielded estimates of energy expenditure (Healey et al. 2003, Hruska et al. 2007). These studies allow estimation of activity budgets, as well as the costs of various behaviours related to courtship, nest construction, and defense. The energetics of parental care have been examined in centrarchid fishes using combinations of radio telemetry,

underwater videography, and direct observation, which highlight the diversity of adaptive tactics and strategies (Cooke et al. 2006b). Attempts to quantify diversity and costs of very fine-scale behaviours have used biotelemetry of heart rate (e.g. electrocardiogram [ECG]; Lucas et al. 1991), tail-beat frequency (Ross et al. 1981), and EMG (Cooke et al. 2004b). ECG and EMG are invasive techniques requiring surgical implantations; the alternative is to use accelerometry (Wilson et al. 2008, Shepard et al. 2008b), which has great potential to reveal the costs of behaviour in the context of reproduction.

There have been recent attempts to identify physiological mechanisms of parental care in marine vertebrates using experimental manipulation in tandem with electronic tracking. Using time-depth recorders, physiological sampling, and exogenous corticosterone implants in female macaroni penguins *Eudyptes chrysolophus*, variation in baseline corticosterone was identified as a key predictor of parental foraging behaviour and chick growth (Crossin et al. 2012b). Cottin et al. (2014a, this volume) took a similar approach in their study of parental care in Adélie penguins *Pygoscelis adeliae*, wherein males were similarly implanted with exogenous corticosterone, and foraging behaviour and chick growth were monitored. Their study highlights how the hormonal control of foraging and parental care can differ among species (e.g. compared to macaroni penguins) and between sexes. It also highlights how experimental manipulation of hormonal state and tracking can be combined to address life-history questions. Cottin et al. (2014b) also used this approach when they manipulated prolactin levels in male Adélie penguins and found an effect on parental foraging behaviour but without an ultimate fitness effect on chick growth. Generally, the physiological mechanisms governing parental care, particularly from an endocrine perspective, are fairly well known, especially for birds and some freshwater fishes (e.g. the sunfishes, Centrarchidae; Cooke et al. 2006b). Studies of marine fishes and marine mammals, where it is difficult to observe parental behaviour, will benefit from tracking techniques.

FUTURE OPPORTUNITIES: MOVING BEYOND FITNESS PROXIES

Despite the realization that physiological systems are important mediators of life-history variation (Ricklefs & Wikelski 2002), the physiological basis of most life-history trade-offs remains unknown. Experimental studies using physiological sampling and

electronic tracking techniques like those described in the present review will allow us to move beyond an understanding of simple performance-related traits (e.g. locomotion and maximum sustainable metabolic rates) and towards an understanding of the key mechanisms underlying life-history variation and fitness-related events. Indeed, the many studies that we have highlighted in this review use electronic tagging to some extent to characterize fitness proxies, thus allowing inferences about true fitness. However, there are virtually no electronic tagging studies where true fitness is measured directly. Moving beyond individual fitness proxies might require advances in 3 interrelated areas, described in this section.

Advanced sensor development

Tracking devices will likely continue to become smaller and lighter, with greater battery life and memory capacity that would allow researchers to track individuals across life-history stages. The development of sensors that allow estimations of reproductive output (or reproductive state, e.g. reproductive hormone levels) and survival would facilitate this aim. For example, at present, it is often impossible to determine the link between winter or non-breeding movements and survival, particularly for pelagic species. Identifying the time and location of mortality events would allow researchers to address direct fitness questions. Similarly, sensors that can estimate or quantify reproductive output (e.g. number of eggs expelled during spawning events) as well as the timing and location of such events would similarly expand our understanding of the factors influencing individual variation in reproductive output. However, the creation of smaller and more advanced tags is only one aspect; the problem of prolonged tag attachment, with minimal tag effects, must be addressed, especially for long-term studies.

Long-term, repeated-measures studies

There are many inherent difficulties in designing and maintaining the long-term, longitudinal studies that span the full life cycles of study animals. This type of study is nonexistent for most marine vertebrates, but could be possible as new tracking and sensor technologies become available. Such long-term studies, wherein fitness components can be monitored in individual animals across multiple life-

history stages would yield insights into the mechanisms underlying fitness, such as the 39 yr study of great tits *Parus major* in their natural environment (McCleery et al. 2004). Attempts to gain broader spatial coverage would also facilitate this, and the newly established ICARUS Initiative is a notable example, working to establish a global, remote sensing platform for scientists tracking small organisms over large spatial scales (icarusinitiative.org). Finally, for marine studies that span ocean basins and jurisdictional boundaries, data-sharing may become necessary and more common, thus facilitating research efforts by groups addressing similar questions (e.g. Bailey et al. 2012).

Genomic integration

Genomic techniques in which gene expression is described in free-ranging animals at key life-history stages or transitions are proving to be a powerful means for resolving the many physiological processes that underlie variation in fitness, especially when coupled with electronic tracking techniques. The best example of this at present is by Miller et al. (2011), who identified the key physiological processes that predicted the failure of sockeye salmon during migration. In these fish, the fitness result of a failed migration is clear—zero fitness. A recent review of molecular genetics in seabird studies highlights the value of these approaches in understanding their ecology, evolution, and conservation (Taylor & Friesen 2012). When used in the context of long-term, repeated-measures tracking studies, genomic integration and molecular genetic approaches to tracking studies will help resolve the trade-offs and constraints that individuals face at various times during their lifetime.

To conclude, there is continued need for creativity as researchers push the frontiers of technology and biology to study wild marine vertebrates in their natural environment. Twenty years ago, one could only dream of studies that attempted to explain variation in fitness among individuals—researchers were constrained by technology and forced to select ‘ideal model systems’ that were convenient and tractable. Today, tracking fitness in a wide range of marine vertebrate taxa is possible and with that comes the opportunity to unlock fascinating secrets of marine life. Additional innovation is needed as we strive to move from what at best are ‘marginal’ fitness proxies to truly measuring (and tracking) fitness in wild marine vertebrates.

Acknowledgements. We thank the authors who contributed to the Theme Section on ‘Tracking fitness in marine vertebrates’. We also thank the talented editorial and production staff at Inter-Research for facilitating this synthesis. G.T.C. and S.J.C. are supported by the Ocean Tracking Network of Canada. S.J.C. is also supported by the Canada Research Chairs Program, National Sciences and Engineering Research Council of Canada, and the Bonefish and Tarpon Trust.

LITERATURE CITED

- Aarestrup K, Baktoft H, Koed A, del Villar-Guerra D, Thorstad EB (2014) Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts. *Mar Ecol Prog Ser* 496:197–206
- Aoki K, Amano M, Mori K, Kourogi A, Kubodera T, Miyazaki N (2012) Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. *Mar Ecol Prog Ser* 444:289–301
- Arnold G, Dewar H (2001) Electronic tags in marine fisheries research: a 30-year perspective. In: Sibert J, Nielsen J (eds) *Methods and technologies in fish biology and fisheries*, Vol 1. Academic Press, Dordrecht, p 7–64
- Bailey H, Fossette S, Bograd SJ, Shillinger GL and others (2012) Movement patterns for a critically endangered species, the leatherback turtle (*Derموchelys coriacea*), linked to foraging success and population status. *PLoS ONE* 7:e36401
- Bailleul F, Charrassin JB, Monestiez P, Roquet F, Biuw M, Guinet C (2007) Successful foraging zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic conditions. *Philos Trans R Soc Lond B* 362: 2169–2181
- Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H (2012) Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Mar Ecol Prog Ser* 454:285–307
- Barker JSF (2009) Defining fitness in natural and domesticated populations. In: van der Werf J, Graser HU, Frankham R, Gondro C (eds) *Adaptation and fitness in animal populations*. Springer, Heidelberg, p 3–14
- Bejan A, Marden JH (2006) Unifying constructal theory for scale effects in running, swimming and flying. *J Exp Biol* 209:238–248
- Bentaleb I, Martin C, Vrac M, Mate B and others (2011) Foraging ecology of Mediterranean fin whales in a changing environment elucidated by satellite tracking and baleen plate stable isotopes. *Mar Ecol Prog Ser* 438:285–302
- Bestley S, Patterson TA, Hindell MA, Gunn JS (2008) Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *J Anim Ecol* 77: 1223–1233
- Bestley S, Patterson TA, Hindell MA, Gunn JS (2010) Predicting feeding success in a migratory predator: integrating telemetry, environment, and modeling techniques. *Ecology* 91:2373–2384
- Bestley S, Jonsen ID, Hindell MA, Guinet C, Charrassin JB (2013) Integrative modelling of animal movement: incorporating *in situ* habitat and behavioural information for a migratory marine predator. *Proc Biol Sci* 280:20122262, doi:10.1098/rspb.20122262
- Beverton RJH, Holt SJ (1957) On the dynamics of exploited

- fish populations. Ministry of Agriculture, Fisheries and Food, London
- Block BA (2005) Physiological ecology in the 21st century: advancements in biologging science. *Integr Comp Biol* 45:305–320
- Block BA, Booth D, Carey FG (1992) Direct measurement of swimming speeds and depth of blue marlin. *J Exp Biol* 166:267–284
- Block BA, Dewar H, Blackwell S, Williams T and others (2001) Electronic tags reveal migratory movements, depth preferences and thermal biology of Atlantic bluefin tuna. *Science* 293:1310–1314
- Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. *Proc Biol Sci* 278:2412–2418
- Bókony V, Lendvai AZ, Liker A, Angelier F, Wingfield JC, Chastel O (2009) Stress response and the value of reproduction: are birds prudent parents? *Am Nat* 173:589–598
- Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. *Proc Biol Sci* 274:1533–1538
- Brosnan IG, Welch DW, Rechisky EL, Porter AD (2014) Evaluating the influence of environmental factors on yearling Chinook salmon survival in the Columbia River plume (USA). *Mar Ecol Prog Ser* 496:181–196
- Brown RS, Oldenburg EW, Seaburg A, Cook KV, Skalski JR, Eppard MB, Deters KA (2013) Survival of seaward-migrating PIT and acoustic-tagged juvenile Chinook salmon in the Snake and Columbia Rivers: an evaluation of length-specific tagging effects. *Anim Biotelem* 1:8, doi:10.1186/2050-3385-1-8
- Bunt CM, Kingsford MJ (2014) Movement, habitat utilization and behaviour of coral trout *Plectropomus leopardus* during and after the reproductive period on the southern Great Barrier Reef. *Mar Ecol Prog Ser* 496:33–45
- Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. *Auk* 125:253–264
- Burger CV, Wilmot RL, Wangaard DB (1985) Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. *Can J Fish Aquat Sci* 42:693–700
- Burgess WC, Tyack PL, Le Boeuf BJ, Costa DP (1998) A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep-Sea Res II* 45:1327–1351
- Catry P, Phillips RA, Phalan B, Silk JRD, Croxall JP (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar Ecol Prog Ser* 280:261–273
- Catry P, Dias MP, Phillips RA, Granadeiro JP (2011) Different means to the same end: long-distance migrant seabirds from two colonies differ in behaviour, despite common wintering grounds. *PLoS ONE* 6:e26079
- Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94:1230–1235
- Chaloupka M, Parker D, Balazs G (2004) Tracking turtles to their death—reply to Hays et al. *Mar Ecol Prog Ser* 283: 301–302
- Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D (2013) Minke whales maximise energy storage on their feeding grounds. *J Exp Biol* 216:427–436
- Cooke SJ, Philipp DP (2004) Behaviour and mortality of caught-and-released bonefish (*Albula* spp.) in Bahamian waters with implications for a sustainable recreational fishery. *Biol Conserv* 118:599–607
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004a) Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* 19:334–343
- Cooke SJ, Thorstad E, Hinch SG (2004b) Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish Fish* 5:21–52
- Cooke SJ, Crossin GT, Patterson D, English K and others (2005) Coupling non-invasive physiological and energetic assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *J Fish Biol* 67:1342–1358
- Cooke SJ, Hinch SG, Crossin GT, Patterson DA and others (2006a) Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. *Ecology* 87: 1575–1586
- Cooke SJ, Philipp DP, Wahl DH, Weatherhead PJ (2006b) Energetics of parental care in six syntopic centrarchid fishes. *Oecologia* 148:235–249
- Cooke SJ, Hinch SG, Farrell AP, Patterson DA and others (2008) Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behaviour, genomics and experimental biology: an interdisciplinary case study on adult Fraser River sockeye salmon. *Fisheries* 33:321–338
- Cooke SJ, Woodley CM, Eppard MB, Brown RS, Nielsen JL (2011) Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Rev Fish Biol Fish* 21:127–151
- Cooke SJ, Hinch SG, Lucas MC, Lutcavage M (2012) Biotelemetry and biologging. In: Zale AV, Parrish DL, Sutton TM (eds) *Fisheries techniques*, 3rd edn. American Fisheries Society, Bethesda, MD, p 819–860
- Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70:596–606
- Costa DP, Breed GA, Robinson PW (2012) New insights into pelagic migrations: implications for ecology and conservation. *Annu Rev Ecol Evol Syst* 43:73–96
- Cottin M, MacIntosh AJJ, Kato A, Takahashi A, Debin M, Raclot T, Ropert-Coudert Y (2014a) Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. *Mar Ecol Prog Ser* 496:249–262
- Cottin M, Chastel O, Kato A, Debin M, Takahashi A, Ropert-Coudert Y, Raclot T (2014b) Decreasing prolactin levels lead to a lower diving effort but do not affect breeding success in Adélie penguins. *Horm Behav* 65:134–141
- Crossin GT, Hinch SG, Cooke SJ, Welch DW and others (2007) Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. *Mar Biol* 152:905–918
- Crossin GT, Hinch SG, Cooke SJ, Cooperman MS and others (2009) Mechanisms influencing the timing and success of reproductive migration in a capital breeding, semelparous fish species: the sockeye salmon. *Physiol Biochem Zool* 82:635–652
- Crossin GT, Trathan PN, Phillips RA, Dawson A, Le Bouard F, Williams TD (2010) A carryover effect of migration

- underlies individual variation in reproductive readiness and extreme egg size dimorphism in macaroni penguins. *Am Nat* 176:357–366
- Crossin GT, Phillips RA, Trathan PN, Fox DS, Dawson A, Wynne-Edwards KE, Williams TD (2012a) Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. *Gen Comp Endocrinol* 176:151–157
- Crossin GT, Trathan PN, Phillips RA, Gorman KB, Dawson A, Sakamoto KQ, Williams TD (2012b) Corticosterone predicts foraging behaviour and parental care in macaroni penguins. *Am Nat* 180:E31–E41
- Crossin GT, Phillips RA, Lattin CR, Romero LM, Williams TD (2013a) Corticosterone mediated costs of reproduction link current to future breeding. *Gen Comp Endocrinol* 193:112–120
- Crossin GT, Phillips RA, Wynne-Edwards KA, Williams TD (2013b) Postmigratory body condition and ovarian steroid production predict breeding decisions by female gray-headed albatrosses. *Physiol Biochem Zool* 86:761–768
- Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR (2005) Global circumnavigations: tracking year-round ranges of non-breeding albatrosses. *Science* 307:249–250
- Danylchuk AJ, Cooke SJ, Goldberg TL, Suski CD and others (2011) Aggregations and offshore movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas. *Mar Biol* 158:1981–1999
- Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behav Ecol Sociobiol* 59:381–388
- Del Raye G, Jorgensen SJ, Krumhansl K, Ezcurra JM, Block BA (2013) Travelling light: white sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale migration. *Proc R Soc B* 280:20130836, doi:10.1098/rspb.2013.0836
- Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, Oxford
- Domeier ML, Dewar H, Nasby-Lucas N (2003) Mortality rate of striped marlin (*Tetrapturus audax*) caught with recreational tackle. *Mar Freshw Res* 54:435–445
- Donaldson MR, Arlinghaus R, Hanson KC, Cooke SJ (2008) Enhancing catch-and-release science with biotelemetry. *Fish Fish* 9:79–105
- Drenner SM, Hinch SG, Martins EG, Robichaud D and others (2014) Variable thermal experience and diel thermal patterns of homing sockeye salmon in coastal marine waters. *Mar Ecol Prog Ser* 496:109–124
- Elowe KD, Dodge WE (1989) Factors affecting black bear reproductive success and cub survival. *J Wildl Manag* 53:962–968
- Endler JA (1986) Natural selection in the wild. Princeton University Press, Princeton, NJ
- Fox DA, Hightower JE, Parauka FM (2000) Gulf sturgeon spawning migration and habitat in the Choctawhatchee River system, Alabama-Florida. *Trans Am Fish Soc* 129: 811–826
- Freeman R, Dean B, Kirk H, Leonard K, Phillips RA, Perrins CM, Guilford T (2013) Predictive ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx shearwater. *J R Soc Interface* 10:2013279, doi: 10.1098/rsif.2013.0279
- Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN and others (2009) Diel changes in humpback whale *Megaptera novaeangliae* feeding behaviour in response to sand lance *Ammodytes* spp. behavior and distribution. *Mar Ecol Prog Ser* 395:91–100
- Gallagher AJ, Serafy JE, Cooke SJ, Hammerschlag N (2014) Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Mar Ecol Prog Ser* 496: 207–218
- Garthe S, Ludynia K, Huppopp O, Kubetzki U, Meraz JF, Furness RW (2012) Energy budgets reveal equal benefits of varied migration strategies in northern gannets. *Mar Biol* 159:1907–1915
- Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE and others (2011a) Convergent evolution in locomotory patterns of flying and swimming animals. *Nat Commun* 2:352
- Gleiss AC, Norman B, Wilson RP (2011b) Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Funct Ecol* 25: 595–607
- Gleiss AC, Wilson RP, Shepard ELC (2011c) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol Evol* 2:23–33
- Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang Species Res* 4:3–22
- Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA (2006) Kinematics of foraging dives and lunge-feeding in fin whales. *J Exp Biol* 209:1231–1244
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214: 131–146
- Goldbogen JA, Calambokidis J, Friedlaender AS, Francis J, DeRuiter SL, Stimpert AK, Falcone E, Southall BL (2013) Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge-feeding blue whales. *Biol Lett* 9:20120986, doi:10.1098/rsbl.2012.0986
- Goutte A, Angelier F, Bech C, Clément-Chastel C and others (2014) Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes. *Mar Ecol Prog Ser* 496:233–247
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during year-round foraging in macaroni penguins. *Mar Ecol Prog Ser* 296:183–196
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538
- Gremillet D (1997) Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES J Mar Sci* 54:635–644
- Gutowsky SE, Tremblay Y, Kappes MA, Flint EN and others (2013) Divergent post-breeding distribution and habitat associations of fledgling and adult black-footed albatrosses *Phoebastria nigripes* in the North Pacific. *Ibis* 156: 60–72
- Halsey LG, Shepard ELC, Wilson RP (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comp Biochem Physiol A* 158:305–314

- Hart KM, Hyrenbach KD (2009) Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endang Species Res* 10:9–20
- Hays GC, Broderick AC, Godley BJ, Luschi P, Nichols WJ (2003) Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. *Mar Ecol Prog Ser* 262:305–309
- Hays GC, Hobson VJ, Metcalfe JD, Righton D, Sims DW (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87:2647–2656
- Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? *J Exp Mar Biol Ecol* 349:52–60
- Hays GC, Fossette S, Katselidis KA, Mariani P, Schofield G (2010) Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *J R Soc Interface* 7:1319–1327
- Hays GC, Bastian T, Doyle TK, Fossette S and others (2012) High activity and Lévy searches: jellyfish can search the water column like fish. *Proc Biol Sci* 279:465–473
- Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ and others (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nat Clim Change* 3:234–238
- Healey MC, Lake R, Hinch SG (2003) Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). *Behaviour* 140:161–182
- Hendry AP, Day T (2005) Population structure attributable to reproductive time: isolation by time and adaptation by time. *Mol Ecol* 14:901–916
- Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Can J Fish Aquat Sci* 59:624–632
- Heupel MR, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the presence and space use of a reef-associated shark. *Mar Ecol Prog Ser* 496:47–57
- Hruska KA, Hinch SG, Healey MC, Farrell AP (2007) Electromyogram telemetry, nondestructive physiological biopsy, and genetic markers: linking recent techniques with behavioural observations for the study of reproductive success in sockeye salmon mating systems. *Am Fish Soc Symp* 54:17–29
- Humston R, Ault JS, Larkin MF, Luo J (2005) Movements and site fidelity of the bonefish *Albula vulpes* in the northern Florida Keys determined by acoustic telemetry. *Mar Ecol Prog Ser* 291:237–248
- Irschick DJ (2003) Measuring performance in nature: implications for studies of fitness within populations. *Integr Comp Biol* 43:396–407
- Johnson SL, Power JH, Wilson DR, Ray J (2010) A comparison of the survival and migratory behaviour of hatchery-reared and naturally reared steelhead smolts in the Alsea River and estuary, Oregon, using acoustic telemetry. *N Am J Fish Manag* 30:55–71
- Jolley J, John W, Irby J, Edwin W (1979) Survival of tagged and released Atlantic sailfish (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. *Bull Mar Sci* 29:155–169
- Jonsen ID, Myers RA, James MC (2006) Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *J Anim Ecol* 75:1046–1057
- Jorgensen SJ, Arnoldi NS, Estess EE, Chapple TK, Ruckert M, Anderson SD, Block BA (2012) Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon carcharias*) migration and offshore behaviour. *PLoS ONE* 7:e47819
- Kelly BP, Badajos OH, Kunasranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P (2010) Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biol* 33:1095–1109
- Kleiber M (1975) *The fire of life: an introduction to animal energetics*. Kreiger, Huntington, NY
- Kouwenberg AL, Hipfner JM, McKay DW, Storey AE (2013) Corticosterone and stable isotopes in feathers predict egg size in Atlantic puffins *Fratercula arctica*. *Ibis* 155: 413–418
- Kozłowski J (1993) Measuring fitness in life history studies. *Trends Ecol Evol* 8:84–85
- Kuhn CE, Crocker DE, Tremblay Y, Costa DP (2009) Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *J Anim Ecol* 78:513–523
- Lea MA, Johnson D, Melin S, Ream R, Gelatt T (2010) Diving ontogeny and lunar responses in a highly migratory mammal, the northern fur seal *Callorhinus ursinus*. *Mar Ecol Prog Ser* 419:233–247
- Leat EHK, Bourgeon S, Magnusdottir E, Gabrielsen GW and others (2013) Influence of wintering area on persistent organic pollutants in a breeding migratory seabird. *Mar Ecol Prog Ser* 491:277–293
- Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl Res* 19:347–358
- Lowerre-Barbieri SK, Walters S, Bickford J, Cooper W, Muller R (2013) Site fidelity and reproductive timing at a spotted seatrout spawning aggregation site: individual versus population scale behavior. *Mar Ecol Prog Ser* 481: 181–197
- Lucas MC, Priede IG, Armstrong JD, Gindy ANZ, De Vera L (1991) Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. *J Fish Biol* 39:325–345
- Lutcavage ME, Brill RW, Skomal GB, Chase BC, Howey PW (1999) Results of a pop-up satellite tagging of spawning class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Can J Fish Aquat Sci* 56: 173–177
- Lutcavage ME, Galuardi B, Lam TCH (2012) Predicting potential Atlantic spawning grounds of western Atlantic bluefin tuna based on electronic tagging results, 2002–2011. *ICCAT SCRS/2012/157*
- Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Fox JW, Furness RW (2010) Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar Ecol Prog Ser* 406:291–303
- Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Furness RW (2011) At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia. *Mar Biol* 158: 429–438
- Maxwell SM, Hazen EL, Bograd SJ, Halpern BS and others (2013) Cumulative human impacts on marine predators. *Nature Comm* 4:2688, doi:10.1038/ncomms3688
- McCleery RH, Pettifor RA, Armbruster P, Meyer K, Sheldon BC, Perrins CM (2004) Components of variance underlying fitness in a natural population of the great tit *Parus major*. *Am Nat* 164:E62–E72
- McClellan CM, Read AJ, Price BA, Cluse WM, Godfrey MH

- (2009) Using telemetry to mitigate the bycatch of long-lived marine vertebrates. *Ecol Appl* 19:1660–1671
- McGraw JB, Caswell H (1996) Estimation of individual fitness from life-history data. *Am Nat* 147:47–64
- McIntyre T, Ansorge IJ, Bornemann H, Plötz J, Tosh CA, Bester MN (2011) Elephant seal dive behaviour is influenced by ocean temperature: implications for climate change impacts on an ocean predator. *Mar Ecol Prog Ser* 441:257–272
- McLean MF, Simpfendorfer CA, Heupel MR, Dadswell MJ, Stokesbury MJW (2014) Diversity of behavioural patterns displayed by a summer feeding aggregation of Atlantic sturgeon in the intertidal region of Minas Basin, Bay of Fundy, Canada. *Mar Ecol Prog Ser* 496:59–69
- Melnichuk MC (2012) Detection efficiency in telemetry studies: definitions and evaluation methods. In: Adams N, Beeman J, Eiler J (eds) *Telemetry techniques: a user guide for fisheries research*. American Fisheries Society Books, Bethesda, MD, p 339–357
- Melnichuk MC, Welch DW, Walters CJ, Christensen V (2007) Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. *Hydrobiologia* 582:55–65
- Midwood JD, Larsen MH, Boel M, Jepsen N, Aarestrup K, Cooke SJ (2014) Does cortisol manipulation influence outmigration behaviour, survival and growth of sea trout? A field-test of carryover effects in wild fish. *Mar Ecol Prog Ser* 496:135–144
- Miller KM, Li S, Kaukinen KH, Ginther N and others (2011) Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science* 331:214–217
- Miller PJO, Johnson MP, Tyack PL, Terray EA (2004a) Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J Exp Biol* 207:1953–1967
- Miller PJO, Johnson MP, Tyack PL (2004b) Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proc Biol Sci* 271:2239–2247
- Mills S, Beatty J (1979) The propensity interpretation of fitness. *Philos Sci* 46:263–286
- Mitamura H, Arai N, Mitsunaga Y, Yokota T, Takeuchi H, Tsuzaki T, Itani M (2005) Directed movements and diel burrow fidelity patterns of red tilefish *Branchiostegus japonicus* determined using ultrasonic telemetry. *Fish Sci* 71:491–498
- Moore M, Berejikian BA, Tezak EP (2012) Variation in the early marine survival and behaviour of natural and hatchery-reared Hood Canal steelhead. *PLoS ONE* 7:e49645
- Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annu Rev Nutr* 19:247–277
- Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct Ecol* 27:710–717
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) Movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* 105:19052–19059
- New LF, Clark JS, Costa DP, Fleishman E and others (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Mar Ecol Prog Ser* 496:99–108
- Orr HA (2009) Fitness and its role in evolutionary genetics. *Nat Rev Genet* 10:531–539
- Peckham SH, Diaz DM, Walli A, Ruiz G, Crowder LB, Nichols WJ (2007) Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS ONE* 2:e1041
- Petersen MR, Bustnes JO, Systad GH (2006) Breeding and moulting locations and migration patterns of the Atlantic population of Steller's eiders *Polysticta stelleri* as determined from satellite telemetry. *J Avian Biol* 37:58–68
- Phillips LM, Powell AN (2006) Evidence for wing molt and breeding site fidelity in king eiders. *Waterbirds* 29:148–153
- Phillips RA, Bearhop S, McGill R, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* 160:795–806
- Pierce RB (2004) Oviduct insertion of radio transmitters as a means of locating northern pike spawning habitat. *N Am J Fish Manag* 24:244–248
- Pierce RB, Younk JA, Tomcko CM (2007) Expulsion of miniature radio transmitters along with eggs of muskellunge and northern pike—a new method for locating critical spawning habitat. *Environ Biol Fishes* 79:99–109
- Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011) Celestial moderation of tropical seabird behaviour. *PLoS ONE* 6:e27662
- Pollock KH, Jiang H, Hightower JE (2004) Combining radio-telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Trans Am Fish Soc* 133:639–648
- Pratt HL Jr, Carrier JC (2001) A review of elasmobranch reproductive behaviour with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environ Biol Fishes* 60:157–188
- Ragland JM, Arendt MD, Kucklick JR, Keller JM (2011) Persistent organic pollutants in blood plasma of satellite-tracked adult male loggerhead sea turtles (*Caretta caretta*). *Environ Toxicol Chem* 30:1549–1556
- Rayner MJ, Hauber ME, Steeves TE, Lawrence HA and others (2011) Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. *Nat Commun* 2:332
- Rechisky EL, Welch DW, Porter AD, Hess JE, Narum SR (2014) Testing for delayed mortality effects in the early marine life history of Columbia River Basin yearling Chinook salmon. *Mar Ecol Prog Ser* 496:159–180
- Reid JP, Bonde RK, O'Shea TJ (1995) Reproduction and mortality of radio-tagged and recognizable manatees on the Atlantic coast of Florida. In: O'Shea TJ, Ackerman BB, Percival HF (eds) *Population biology of the Florida manatee*. Information and Technology Report 1. US Geological Survey, Washington, DC, p 171–191
- Richman SE, Lovvorn JR (2011) Effects of air and water temperatures on resting metabolism of auklets and other diving birds. *Physiol Biochem Zool* 84:316–332
- Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. *Trends Ecol Evol* 17:462–468
- Robichaud D, Rose GA (2001) Multiyear homing of Atlantic cod to a spawning ground. *Can J Fish Aquat Sci* 58:2325–2329
- Romer JD, Leblanc CA, Clements S, Ferguson JA, Kent ML, Noakes D, Schreck CB (2013) Survival and behaviour of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA. *Environ Biol Fishes* 96:849–863

- Ropert-Coudert Y, Wilson PR (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Environ* 3:437–444
- Ross LG, Watts W, Young AH (1981) An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. *J Fish Biol* 18:479–490
- Rutz C, Hays GC (2009) New frontiers in biologging science. *Biol Lett* 5:289–292
- Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS One* 4:e5479
- Sato K, Watanuki Y, Takahashi A, Miller PJO and others (2007) Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc Biol Sci* 274:471–477
- Sato K, Aoki K, Watanabe YY, Miller PJO (2013) Neutral buoyancy is optimal to minimize the cost of transport in horizontally swimming seals. *Sci Rep* 3:2205, doi:10.1038/srep02205
- Schaffer WM (1981) On reproductive value and fitness. *Ecology* 62:1683–1685
- Schofield G, Lilley MKS, Bishop CM, Brown P and others (2009) Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endang Species Res* 10:191–202
- Schofield G, Scott R, Dimadi A, Fossette S and others (2013) Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. *Biol Conserv* 161:101–109
- Schultner J, Moe B, Chastel O, Tartu S, Bech C, Kitaysky AS (2014) Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser* 496:125–133
- Sepulveda CA, Kohin S, Chan C, Vetter R, Graham JB (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Mar Biol* 145:191–199
- Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Funct Ecol* 17:66–74
- Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci USA* 103:12799–12802
- Shamoun-Baranes J, Bom R, van Loon EE, Ens BJ, Oosterbeek K, Bouten W (2012) From sensor data to animal behaviour: an oystercatcher example. *PLoS ONE* 7:e37997
- Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Mar Ecol Prog Ser* 328:205–213
- Shepard ELC, Wilson RP, Liebsch N, Quintana F, Laich AG, Lucke K (2008a) Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endang Species Res* 4:157–164
- Shepard ELC, Wilson RP, Quintana F, Gómez Laich A and others (2008b) Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* 10:47–60
- Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. *Am Nat* 182:298–312
- Shillinger GL, Palacios DM, Bailey H, Bograd SJ and others (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol* 6:e171
- Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water: behaviour and kinematics of humpback whale lunge feeding. *J Exp Biol* 215:3786–3798
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J Anim Ecol* 74:755–761
- Skovrind M, Christensen EAF, Carl H, Jacobsen L, Møller PR (2013) Marine spawning sites of perch *Perca fluviatilis* revealed by oviduct-inserted acoustic transmitters. *Aquat Biol* 19:201–206
- Sober E (2001) The two faces of fitness. In: Singh RS, Krimbas CB, Paul DB, Beatty J (eds) *Thinking about evolution: historical, philosophical, and political perspectives*, Vol 2. Cambridge University Press, Cambridge, p 309–321
- Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim Ecol* 78:460–467
- Starr RM, O'Connell V, Ralston S, Breaker L (2005) Use of acoustic tags to estimate natural mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a marine reserve. *Mar Technol Soc J* 39:19–30
- Stokesbury MJW, Neilson JD, Susko E, Cooke SJ (2011) Estimating mortality of Atlantic bluefin tuna (*Thunnus thynnus*) in an experimental recreational catch-and-release fishery. *Biol Conserv* 144:2684–2691
- Suryan RM, Fischer KN (2010) Stable isotope analysis and satellite tracking reveal interspecific resource partitioning of nonbreeding albatrosses off Alaska. *Can J Zool* 88:299–305
- Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *J Exp Biol* 204:3895–3904
- Tartu S, Goutte A, Bustamante P, Angelier F and others (2013) To breed or not to breed: endocrine response to mercury contamination by an Arctic seabird. *Biol Lett* 9:20130317, doi:10.1098/rsbl.2013.0317
- Taylor SA, Friesen VL (2012) Use of molecular genetics for understanding seabird evolution, ecology and conservation. *Mar Ecol Prog Ser* 451:285–304
- Teo SLH, Boustany A, Dewar H, Stokesbury MJW and others (2007) Annual migrations, diving behaviour, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Mar Biol* 151:1–18
- Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93:122–130
- Thums M, Bradshaw CJA, Hindell MA (2011) In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology* 92:1258–1270
- Thums M, Bradshaw CJA, Sumner MD, Horsburgh JM, Hindell MA (2013) Depletion of deep marine food patches forces divers to give up early. *J Anim Ecol* 82:72–83

- Tucker AD (2010) Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock estimation. *J Exp Mar Biol Ecol* 383:48–55
- Ueda H (2014) Homing ability and migration success in Pacific salmon: mechanistic insights from biotelemetry, endocrinology, and neurophysiology. *Mar Ecol Prog Ser* 496:219–232
- Van Parijs SM, Janik VM, Thompson PM (2000) Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*. *Can J Zool* 78:2209–2217
- Videler JJ, Weihs D (1982) Energetic advantages of burst-and-coast swimming of fish at high speeds. *J Exp Biol* 97:169–178
- Vogel S (1994) *Life in moving fluids: the physical biology of flow*. Princeton University Press, Princeton, NJ
- Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar Ecol Prog Ser* 391:165–182
- Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey capture variability. *Proc Natl Acad Sci USA* 110:2199–2204
- Watanabe YY, Sato K, Watanuki Y, Takahashi A and others (2011) Scaling of swim speed in breath-hold divers. *J Anim Ecol* 80:57–68
- Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc Biol Sci* 270:483–488
- Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL (2006) Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol* 75:814–825
- Wearmouth VJ, Southall EJ, Morrill D, Sims DW (2013) Identifying reproductive events using archival tags: egg-laying behaviour of the small spotted catshark *Scyliorhinus canicula*. *J Fish Biol* 82:96–110
- Weimerskirch H, Doncaster P, Cuénot-Chaillet F (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc Biol Sci* 255:91–97
- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc Biol Sci* 267:1869–1874
- Westerberg H, Sjöberg N, Lagenfelt I, Aarestrup K, Righton D (2014) Behaviour of stocked and naturally recruited European eels during migration. *Mar Ecol Prog Ser* 496:145–157
- White CR, Green JA, Martin GR, Butler PJ, Grémillet D (2013) Energetic constraints may limit the capacity of visually guided predators to respond to Arctic warming. *J Zool* 289:119–126
- Whitney NM, Pratt HL Jr, Pratt TC, Carrier JC (2010) Identifying shark mating behaviour using three-dimensional acceleration loggers. *Endang Species Res* 10:71–82
- Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philos Trans R Soc Lond B* 354:193–201
- Williams TM (2001) Intermittent swimming by mammals: a strategy for increasing energetic efficiency during diving. *Am Zool* 41:166–176
- Williams TM, Yeates L (2004) The energetics of foraging in large mammals: a comparison of marine and terrestrial predators. *Int Congr Ser* 1275:351–358
- Williams TM, Davis RW, Fuiman LA, Francis J and others (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* 288:133–136
- Wilson RP, Vandenabeele S (2012) Technological innovation in archival tags used in seabird research. *Mar Ecol Prog Ser* 451:245–262
- Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Anim Behav* 63:85–95
- Wilson RP, Shepard ELC, Liebsh N (2007) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang Species Res* 4:123–137
- Wilson RP, McMahon CR, Quintana F, Frere E, Scolaro A, Hays GC, Bradshaw CJA (2011) N-dimensional animal energetic niches clarify behavioural options in a variable marine environment. *J Exp Biol* 214:646–656
- Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc Biol Sci* 279:975–980
- Wilson SM, Hinch SG, Drenner SM, Martins EG and others (2014) Coastal marine and in-river migration behaviour of adult sockeye salmon en route to spawning grounds. *Mar Ecol Prog Ser* 496:71–84
- Wright AK, Ponganis K, McDonald BI, Ponganis PJ (2014) Heart rates of emperor penguins diving at sea: implications for oxygen store management. *Mar Ecol Prog Ser* 496:85–98
- Wright S, Metcalfe JD, Hetherington S, Wilson R (2014) Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. *Mar Ecol Prog Ser* 496:19–32
- Yergey ME, Grothues TM, Able KW, Crawford C, DeCristofer K (2012) Evaluating discard mortality of summer flounder (*Paralichthys dentatus*) in the commercial trawl fishery: developing acoustic telemetry techniques. *Fish Res* 115–116:72–81
- Yoda K, Naito Y, Sato K, Takahashi A and others (2001) A new technique for monitoring the behaviour of free-ranging Adélie penguins. *J Exp Biol* 204:685–690
- Young HS, McCauley DJ, Dirzo R, Dunbar RB, Shaffer SA (2010) Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis. *Mar Ecol Prog Ser* 416:285–294
- Zydlewski GB, Kinnison MT, Dionne PE, Zydlewski J, Wipplhauser GS (2011) Shortnose sturgeon use small coastal rivers: the importance of habitat connectivity. *J Appl Ichthyol* 27:41–44

Submitted: October 29, 2013; Accepted: December 11, 2013

Proofs received from author(s): January 20, 2014