

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

INTRODUCTION: REVIEW

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

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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

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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 & Vandenabeele 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 biologing 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 (Westerberg 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.

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