

1 **Tracking fitness in marine vertebrates: a review of current knowledge and**
2 **opportunities for future research.**

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21 **Abstract**

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

41
42 **Keywords:** Electronic tracking, telemetry, biologging, electronic sensors, behaviour, life history,
43 reproduction, survival, mortality, migration, non-breeding.

44

44 **Introduction**

45 Researchers have long been intrigued by animal movements, and have employed
46 electronic tracking in order to observe and understand such behaviour. Electronic tracking
47 involves the use of various technologies that either transmit (biotelemetry; Cooke et al. 2004a) or
48 log (i.e. biologging; Block 2005, Rutz and Hays 2007) information about an animal's position,
49 parameters from their surrounding environment (e.g. pressure, temperature) or state (e.g. activity
50 level, heart rate, body temperature). There are currently many types of biotelemetry and
51 biologging devices available for use in marine animal tracking studies (see reviews by Arnold
52 and Dewar 2001, Burger and Shaffer 2008, Godley et al. 2008, Wakefield et al. 2009, Cooke et
53 al. 2012, Wilson and Vandenberg 2012). Historically, most (but certainly not all) studies have
54 used such tools in a very descriptive way (e.g. characterizing movements and other at-sea
55 activities, or habitat use), without any consideration of the direct links to survival, growth and
56 body condition, population processes, or other components of an individual's life-history, let
57 alone its overall fitness.

58 Although fitness can be defined in many ways, there is general consensus regarding its
59 essence (reviewed in Barker 2009). Orr (2009) elegantly states that “fitness involves the ability of
60 organisms or, more rarely, populations or species, to survive and reproduce in the environment in
61 which they find themselves. It is the more ‘fit’ individuals that are able to survive and reproduce
62 to contribute most genes to the next generation”. Endler (1986) considered fitness to be a
63 measure of the degree to which there is a consistent relationship between a given trait and
64 survival, although he also noted that confusion often abounds regarding the difference between
65 fitness and adaptation. There is much philosophical debate regarding fitness (e.g. Mills and
66 Beatty 1979, Schaffer 1981, Sober 2001), and it is undoubtedly very difficult to measure
67 accurately in the wild, particularly for long-lived animals (Kozlowski 1993) such that researchers
68 usually rely on quantifying components of fitness that serve as proxies or surrogates (McGraw
69 and Caswell 1996, Irschick 2003). Consider the vast marine realm, which is generally
70 inhospitable to humans, but through which many other vertebrates roam freely. For many such
71 species we know little about their natural history, let alone the key determinants of their
72 individual fitness. Consider the challenges in determining the number of offspring produced by a
73 swordfish, whose gametes are expelled into the water column, and of which only a tiny
74 proportion will be fertilized and survive. Even for an ovoviviparous fish such as a tiger shark, it
75 would be exceedingly difficult to determine how many offspring that a single female produced
76 over her lifetime. Contrast that with, say, a terrestrial mammal like a black bear where it is
77 comparatively easy to quantify lifetime reproductive success of a sow and even to track the
78 survival and fitness of her offspring (Elowe and Dodge 1989). It is not surprising that we know
79 so little about the fitness of most marine vertebrates, especially those that spend the majority of
80 their time sub-surface. Seabirds and some marine mammals that come to shore at breeding
81 colonies, and some fish species that return to distinct spawning grounds (e.g. Pacific salmon,
82 *Oncorhynchus spp.*) do provide some unique opportunities to assess fitness of marine animals.
83 With the advent of electronic tagging one would presume that it is finally possible to track fitness
84 of marine vertebrates; however, have we actually made any progress in doing so?

85 In this review, our aim is to briefly summarize the current state of electronic tracking
86 studies focused on marine vertebrates, and to highlight the ways in which electronic tags have
87 been used to inform our knowledge of life-history and fitness-related processes. Specifically, we
88 highlight studies that combine electronic tracking, multiple sensor data, and, in some cases, other
89 scientific disciplines, to quantify variation in behaviour; to relate individual variation in

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

98 Although our focus is on electronic tracking, we have framed this within the domain of
99 evolutionary ecology and life-history by highlighting studies that use other disciplines to identify
100 the organismal traits and environmental conditions that most contribute to variation in lifetime
101 fitness. Since the advent of the research field in the early 1960s, the majority of animal tracking
102 studies have been largely descriptive, reporting patterns of movement without any discernable
103 links to fitness-related processes. Recently, however, an increasing number of tracking studies
104 have adopted an individual-based approach to this topic, where differences in fitness-related traits
105 are measured and the underlying causes of such variation identified. For the purposes of this
106 paper, it is necessary to define what we mean by fitness-related traits, processes, and endpoints.
107 Adopting ideas from the vast literature on fitness (Barker 2009, see also above), we define this as
108 any trait that can contribute to individual variation in lifetime fitness. Relevant fitness traits
109 include growth, timing of migration, breeding decisions, timing of reproduction, egg and clutch
110 size, foraging success, parental care, hatching and breeding success, overall fecundity and
111 survival (or mortality). These can be grouped into four general fitness-related categories, which
112 we discuss below: 1) foraging dynamics, energetics, and growth, 2) migration and other non-
113 breeding season activities, 3) mortality, and 4) reproduction.

114

115 **Tracking fitness: context and examples**

116 *Foraging, energetics, and growth*

117 In order to maximize fitness, animals must possess efficient mechanisms for energy
118 acquisition and expenditure (Kleiber 1975). The transfer of energy between an animal and its
119 environment is challenging to study in controlled laboratory settings; thus, attempting to quantify
120 energy budgets within the logistical constraints that apply to research on free-ranging animals is
121 even more challenging (Nagy et al. 1999). Nevertheless, telemetric and biologging approaches,
122 often in combination with oceanographic sampling and other techniques (e.g. doubly-labeled
123 water), have provided important insights into the processes that govern energy gain and use in
124 different habitats, particularly during foraging (Wilson et al. 2002, Goldbogen et al. 2006, Aoki et
125 al. 2012, Simon et al. 2012, Shepard et al. 2013). Energetically efficient foraging strategies are
126 essential for supporting metabolism, somatic growth, and parental investment. This requires a
127 low cost of transport for locomotion and feeding, as well as a high rate of energy (= resource)
128 acquisition. The interaction of these processes, and the properties of the physical environment,
129 determine the energetic efficiency of foraging. Therefore, investigating foraging behaviour of
130 free-ranging animals under natural conditions is a fundamental step towards understanding
131 energy flux between organisms and their environment (e.g. Weimerskirch et al. 2000, Shaffer et
132 al. 2003).

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

151 Travel speed is one of the most important parameters related to energy expenditure, but it
152 is also one of the most difficult to measure in free-swimming animals. Methods used to estimate
153 swimming speed of tagged animals have included a rotating propeller (Tanaka et al. 2001), a
154 flexible paddle wheel (Shepard et al. 2008a), vector resolution from depth rate and animal
155 orientation (Miller et al. 2004a, Simon et al. 2012), and flow noise (Burgess et al. 1998,
156 Goldbogen et al. 2006). Drag increases exponentially with speed and therefore greater speeds
157 require disproportionately more power output (energy use per unit time) (Vogel 1994). It follows
158 that animals will predictably choose cost efficient locomotor strategies and low speed for long
159 distance travel in order to minimize cost of transport (energy use per unit distance) (Williams
160 1999). Laboratory experiments with swimming animals showed that speed increased with body
161 size, a phenomenon explained post hoc by one theoretical framework (Bejan and Marden 2006).
162 Initial tag studies from free-ranging aquatic vertebrates showed that swimming speed was largely
163 independent of body size (Block et al. 1992, Sato et al. 2007), demonstrating that free-ranging
164 animals may exhibit different behaviours and locomotor performance to those expected from
165 laboratory studies. A subsequent analysis using comparative phylogenetic methods demonstrated
166 a significant, but very small increase in swimming speed (up to 2.5 m s^{-1}) with body size in
167 breath-hold divers (Watanabe et al. 2011). Although steady swimming speeds were between 0.5 -
168 2.5 m s^{-1} across a wide body size range, the largest animals exhibited the greatest speeds and thus
169 were able to cover greater distances while minimizing the cost of transport (Watanabe et al.
170 2011).

171 Because aquatic animals must navigate a complex three-dimensional environment, they
172 integrate their choice of swimming speed with a wide variety of behavioural strategies to ensure
173 successful locomotor and foraging performance. The combination of time-depth recorders
174 (TDRs) with accelerometers and video systems has uncovered specific mechanisms used by
175 animals to minimize energy costs. The most basic of these strategies is to employ gliding, either
176 in the form of burst-and-coast swimming (Videler and Weihs 1982, Williams 2001, Watanuki et
177 al. 2003, Sato et al. 2013), or gliding during the descent or ascent phase of a dive (Williams et al.
178 2000, Gleiss et al. 2011a, Gleiss et al. 2011b). The ability to distinguish active swimming strokes

179 from periods of gliding using accelerometer signals is important, given that mechanical work is
180 dependent on energy expenditure. Acceleration metrics related to periods of stroke-propelled
181 swimming, such as overall dynamic body acceleration (ODBA) and minimum specific
182 acceleration (MSA), have been developed to investigate both the fundamental mechanics and the
183 energetic cost of different behaviours (Gleiss et al. 2011c, Simon et al. 2012). The incorporation
184 of these and related kinematic parameters into mechanical models of swimming has the potential
185 to quantify multi-dimensional energy landscapes (power envelopes or energetic niches) that
186 define the amount of power required for various behaviours under different environmental
187 conditions (Wilson et al. 2011, Wilson et al. 2012, Shepard et al. 2013, Wilson et al. 2014). Of
188 course, detailed calibrations are required to generate relationships between acceleration profiles
189 and energetic costs (e.g. this Theme Section- Wright et al. 2014). Although possible to do so in
190 the lab, such calibrations are difficult in the field, especially for large animals. However, as the
191 number of studies linking metabolic rates to dynamic acceleration metrics increases, allometric
192 trends in different movement styles may be revealed, from which species-specific metrics could
193 be derived.

194 In addition to energy expenditure, tracking techniques have enabled researchers to
195 quantify foraging behaviours and identify specific feeding events. Changes in speed, orientation,
196 and acceleration have been used to infer prey capture attempts in a wide variety of animals
197 (Wilson et al. 2002, Goldbogen et al. 2006, Aoki et al. 2012, Simon et al. 2012, Naito et al.
198 2013). This indirect approach is greatly enhanced by complimentary data, such as simultaneous
199 video footage (Goldbogen et al. 2013, Watanabe and Takahashi 2013) or acoustics that quantify
200 echolocation clicks (Miller et al. 2004b, Watwood et al. 2006). Other direct measures of feeding
201 involve stomach temperature logging or telemetry in endotherms, which monitors rapid drops in
202 temperature upon prey capture and ingestion (Weimerskirch et al. 1994, Catry et al. 2004,
203 Sepulveda et al. 2004, Kuhn et al. 2009). The ability to quantify feeding performance, and the
204 concomitant estimation of energy expenditure during foraging, allows for an assessment of
205 foraging efficiency (Costa et al. 1989, Gremillet 1997, Williams and Yeates 2004, Goldbogen et
206 al. 2011). Ultimately, the efficiency of foraging determines the ability of an animal to extract
207 energy from the environment for a given prey density, resulting in its own mass gain or loss, and
208 that of any dependent offspring. Some of the largest marine endotherms, exemplified by the
209 largest baleen whales, rely on lipid stores acquired during extensive feeding bouts in summer
210 months that then must fuel large scale migrations across ocean basins to breeding grounds
211 (Goldbogen et al. 2011, Costa et al. 2012, Christiansen et al. 2013). Long term tag studies have
212 been able to track these changes in body condition in some large marine vertebrates, which are
213 manifested as changes in buoyancy, by quantifying changes in drift rate during glides (Thums et
214 al. 2011, Del Raye et al. 2013, Thums et al. 2013). Through simulation, this approach
215 (quantifying drift rates and migratory behaviour) has now been extended to estimate long term
216 changes in vital rates, fitness, and eventually population-level effects from perturbations in the
217 environment (e.g. this Theme Section- New et al. 2014). For ectotherms, even basic measures of
218 temperature (environment or body) have the potential to provide unprecedented information on
219 animal energetics (e.g. this Theme Section- Drenner et al. 2014).

220

221 *Migration and other activities during the nonbreeding season*

222 The techniques highlighted in the previous section have been applied to a diverse range of
223 marine vertebrates during the nonbreeding season. This is a key life-history phase, when animals

224 are no longer constrained by breeding duties to return to a central place nor accommodate the
225 slow movements of dependent young, and so can engage in long-distance, energetically-
226 demanding migrations. Until recently, relatively little was known about these movements, and
227 even less about the fitness consequences. Yet, the decisions they make during this time affect the
228 recovery of body condition, and accumulation of fat and protein stores in advance of breeding,
229 and hence their survival and subsequent fitness (Dingle 1996). The advent of new technologies
230 has revolutionised the field; archival devices with long battery lives and low power consumption,
231 particularly geolocators (which record light levels that can then be used to infer latitudes and
232 longitudes), have now been deployed on numerous predators, particularly seabirds, pinnipeds and
233 sea turtles that are land-based during breeding and can be recaptured for device recovery in
234 subsequent years. Such studies have highlighted extraordinary circumpolar or trans-equatorial
235 migrations, shown unexpectedly high levels of variability among individuals, and examined
236 habitat use or preference in detail, demonstrating intra- and inter-specific spatial and temporal
237 segregation with implications for niche partitioning, population genetic structure and, ultimately,
238 speciation (Croxall et al. 2005, Shaffer et al. 2006, Nathan et al. 2008, Rayner et al. 2011). The
239 availability of detailed information on individual trajectories has led to a burgeoning in the study
240 of movement ecology, which seeks to understand the causes and consequences of individual
241 movement, often in a complex mathematical framework (Schick et al. 2008).

242 As technology has improved, there has also been a burgeoning of studies that combine
243 geographic locations of migrants obtained using satellite-telemetry or geolocation, with recording
244 of dives, saltwater immersion (distinguishing time on the water vs. in flight), internal temperature
245 (indicating prey ingestion), dynamic acceleration, heart rate or other aspects of behaviour. These
246 have tested a wide range of ecological hypotheses; concurrent use of multiple sensors has
247 provided insights into differences in behaviour between daylight, twilight and darkness; inferred
248 reliance on nocturnal prey and the importance of lunar phase; influence of photoperiod on timing
249 of migration; constraints associated with low light levels in the polar winter; effects of region,
250 year, sex, status etc.; and intra- and inter-specific foraging niche specialisation and resource
251 partitioning (Green et al. 2005, Hays et al. 2006, Shepard et al. 2006, Bestley et al. 2008,
252 Mackley et al. 2010, Pinet et al. 2011). Novel analytical methods have identified behavioural
253 modes, for example diel patterns in travel rates of leatherback turtles *Dermochelys coriacea* using
254 ARGOS tracks (Jonsen et al. 2006), the switch from directed movement to residency in elephant
255 seals *Mirounga leonina* (Bestley et al. 2013), or between transiting, foraging, migration or
256 breeding behaviour in great white sharks *Carcharodon carcharias* using relatively low temporal
257 resolution data on position, temperature and daily time-at-depth histograms from pop-up archival
258 transmitting tags (Jorgensen et al. 2012). Studies have also detected ontogenetic changes in
259 activity patterns or mapped events so that the location of particular behaviours can be related to
260 conservation issues, highlighting spatial differences in susceptibility of threatened species to
261 predation, targeted harvesting or bycatch in fisheries (Sims et al. 2005, Bailleul et al. 2007,
262 Bestley et al. 2010, Lea et al. 2010, Mackley et al. 2011, Freeman et al. 2013).

263 Multi-sensor studies are especially pertinent where the insights into feeding ecology can
264 be related to trade-offs in time and energy, the key currencies that underlie overall fitness. Direct
265 measurement is possible with heart rate loggers, which with calibration provide instantaneous
266 estimates of energy expenditure associated with different activities of migrants, and in
267 conjunction with estimation of prey ingestion from internal temperature sensors, allow the
268 calculation of foraging success and overall energy budgets (Green et al. 2009, White et al. 2013).
269 As an alternative, overall dynamic body acceleration (ODBA) can provide a useful proxy for
270 energy expenditure, and energetic trade-offs can also be investigated by incorporating indirect

271 approaches to estimating body condition or composition (see previous section). Energy cost of
272 different activities or environments can be compared using a lower-tech approach; for example,
273 analysis of temperature data from geolocators would provide insights into the importance of heat
274 loss while floating or swimming, which can be a major energetic consideration, particularly for
275 seabirds (Richman & Lovvorn 2011, Garthe et al. 2012). In this Theme Section, Wilson et al.
276 (2014) use tri-axial accelerometers to infer optimal swimming speeds of sockeye salmon
277 (*Oncorhynchus nerka*) during both marine and freshwater homing migrations.

278 Another useful approach for examining fitness consequences of migration is to combine
279 conventional tracking with forensic methods of diet determination, because the quantity and
280 quality of prey consumed during the nonbreeding or the immediate pre-breeding period affects
281 adult condition and the resources that can be devoted to egg formation in birds, or to foetal
282 development in viviparous animals. Thus geocator and satellite-tracking data have been
283 integrated with stable isotope analysis of tissues synthesised during the nonbreeding period (e.g.
284 feathers, whiskers and baleen), to infer trophic level, carbon source and potentially prey type,
285 foraging overlap and segregation (Phillips et al. 2009, Suryan and Fischer 2010, Young et al.
286 2010, Bentaleb et al. 2011, Thiebot et al. 2012). There is considerable scope to extend such
287 approaches to the study of carryover effects; stable isotope analyses suggested that the estimated
288 proportion of energetically-rich copepods consumed in the prebreeding period influenced timing
289 of breeding and egg volume in female Cassin's auklets *Ptychoramphus aleuticus*, although there
290 was no effect on males (Sorensen et al. 2009), and trophic level during the nonbreeding period
291 was correlated positively with egg mass in Atlantic puffins *Fratercula arctica* (Kouwenberg et al.
292 2013).

293 Despite the technological advances, researchers rarely addressed the direct consequences
294 of individual migration strategies for survival or breeding success in the following summer, nor
295 whether carryover effects from breeding might affect the subsequent migration. This has changed
296 recently, with several observational or experimental studies demonstrating an effect of previous
297 breeding outcome on migration patterns, typically manifested during the immediate post-breeding
298 period rather than on the return journey to the colony (Bogdanova et al. 2011, Catry et al. 2011,
299 2013) (e.g. this Theme Section- Schultner et al. 2014). There is also some evidence for carryover
300 effects from the nonbreeding to subsequent breeding season, affecting the decision to defer
301 breeding, laying date, egg dimorphism or size, or breeding success, and in some cases this has
302 been related to adult body condition or hormone levels (Daunt et al. 2006, Crossin et al. 2010,
303 Crossin et al. 2012a, Crossin et al. 2013a, Crossin et al. 2013b, Kouwenberg et al. 2013). In this
304 context, analysis of hormones may be particularly informative, as stressors activate the
305 hypothalamic-pituitary-adrenal cortex (HPA) which responds by increasing circulating levels of
306 glucocorticoid hormones (CORT) that trigger physiological and behavioural responses promoting
307 survival in the face of environmental change (Bokony et al. 2009). In addition to effects on
308 nutritional status and hormone levels, differences in migration strategy may influence exposure to
309 pollutants (e.g. mercury, persistent organic pollutants and hydrocarbons), with possible endocrine
310 disruption and other impacts on breeding deferral, fecundity or survival (Ragland et al. 2011,
311 Montevecchi et al. 2012, Leat et al. 2013, Tartu et al. 2013). Carryover effects may also occur
312 across important life-history transitions (e.g., during smoltification) as documented for sea trout
313 (*Salmo trutta*) implanted with PIT tags and exposed to exogenous cortisol manipulation (e.g. this
314 Theme Section- Midwood et al. 2014).

315 Finally, an improved understanding of migration patterns and the potential or measured
316 energetic and fitness consequences is increasingly important in an era of rapid global change, as
317 the combined impact of anthropogenic threats (e.g. changing climate, bycatch, overfishing,

318 invasive predators and oil pollution) is unprecedented (Shillinger et al. 2008, Barbraud et al.
319 2012, Hazen et al. 2013, Maxwell et al. 2013). In some cases there is a need to study the
320 effectiveness of management interventions such as captive breeding, including to evaluate the
321 behaviour of released animals relative to wild individuals (Westerberg et al. 2014). For some
322 species, considerable effort has been directed at modelling future habitat requirements and
323 availability, and at relating survival prospects to foraging constraints associated with reduced
324 light levels during the temperate or polar winter (Green et al. 2005, Daunt et al. 2006, McIntyre et
325 al. 2011, Hazen et al. 2013, White et al. 2013). However, for most migrants, accurate projection
326 of demographic responses to environmental change will rest on future tracking studies that enable
327 the prediction of nonbreeding distribution based on habitat availability and preference, the
328 modelling of energetic trade-offs, and links between these components and individual fitness.
329 Even basic knowledge of the factors that influence habitat use and movement of wild marine
330 vertebrates is lacking for most species, and for some discrete life stages (e.g. the dispersal of
331 marine juveniles and ontogeny of migration are not well studied because of limitations relating to
332 small size and the often long interval to first breeding; recent attempts to fill this knowledge gap
333 include Hays et al. 2010, Gutowsky et al. 2013). Studies that use high-resolution positioning data
334 combined with sophisticated modeling and model selection procedures (e.g. this Theme Section-
335 Heupel and Simpfendorfer 2014) have much potential for unraveling the energetic and life-
336 history drivers of spatial and movement ecology.

337

338 *Mortality*

339 Beyond being an important phenomenon in population dynamics (Beverton and Holt
340 1957), mortality is of direct relevance to fitness given that once an animal is dead, its fitness is
341 zero. However, from a fitness perspective, the timing of mortality is perhaps the most relevant
342 aspect. Mortality prior to maturation or (successful) reproduction would clearly yield zero
343 lifetime fitness, while mortality after some degree of reproductive success could mean that some
344 level of fitness had been obtained, depending on the life-history of a given species, adult age,
345 condition, etc. Mortality is obviously a natural phenomenon, and indeed can be exceedingly high
346 (e.g. early life stages of most fishes and sea turtles), but can also be mediated directly (e.g.
347 hunting, harvest) and indirectly (e.g. disease, change in ecosystem structure) by human activities.
348 While a simple concept, mortality was rather difficult to measure directly in marine vertebrates
349 until the advent of electronic tagging techniques (Pollock et al. 2004). In some species with
350 strong fidelity to a breeding (e.g. marine mammals, seabirds, Pacific salmon) or foraging site
351 (e.g. some sharks), it may be relatively easy to quantify mortality using band returns or resights,
352 yet that approach provides little insight into the location, timing or mechanism underlying
353 mortality. Although tracking can be used to infer mortality, other issues including tag failure,
354 shedding or loss (Hays et al. 2007), predation (such that the tag is removed by another animal;
355 Cooke and Philipp 2004), poor detection efficiency of receivers (Melnichuk 2012), and the
356 difficulty of differentiating mortality from emigration (Yergey et al. 2012) can make it difficult to
357 know with certainty. Some efforts have been put into the development of mortality sensors (see
358 Cooke et al. 2004a) but they have yet to be used widely. Additionally, studies have documented
359 tagging impacts on animals, which can include effects on, among other things, mortality. Many
360 studies aim to minimize tagging effects, and will sometimes use controlled holding studies or
361 other pilot studies in an effort to identify optimal size and mass of devices, effects on movement
362 and agility, and best physical position on the body for placement. Addressing these issues prior to

363 tagging are important for both scientific, and, increasingly, ethical reasons (see reviews by
364 Ropert-Coudert and Wilson 2005, Cooke et al 2011).

365 Documenting the level of natural or anthropogenic mortality is a common goal of marine
366 vertebrate tracking studies, particularly those involving devices that transmit information. Heupel
367 and Simpfendorfer (2002) studied mortality levels of young blacktip sharks (*Carcharhinus*
368 *limbatus*) using acoustic telemetry coupled with modeling. Notably, all natural and fishing
369 mortality occurred within the first 15 weeks of the study while animals remained on nursery
370 grounds, revealing a period of vulnerability. Given the intense management efforts focused on
371 Pacific salmon, there have been numerous studies identifying the magnitude and location of
372 mortality for out-migrating smolts (Melnychuk et al. 2007, Brown et al. 2013, Romer et al. 2013,
373 and Rechisky et al. 2014, Brosnan et al. 2014 in this Theme Section) and returning adults (e.g.
374 Cooke et al. 2006a, Crossin et al. 2007, Crossin et al. 2009) in coastal waters and freshwater.
375 Some of those studies have contrasted the survival of hatchery and wild fish (e.g. Johnson et al.
376 2010, Moore et al. 2012, Aarestrup et al. 2014 - this Theme Section) to inform management.
377 Another management application has involved use of acoustic telemetry to estimate natural
378 mortality of lingcod (*Ophiodon elongatus*) in a marine reserve and evaluate reserve effectiveness
379 (Starr et al. 2005). Although tracking studies focused on mortality are dominated by those on
380 fish, there are examples from other taxa. For example, Reid et al. (1995) quantified mortality of
381 radio-tagged manatees (*Trichechus manatus latirostris*) in Florida estuaries, and several studies
382 have quantified mortality of sea turtles (reviewed in Godley et al. 2008). Indeed, although not
383 always a stated objective, nearly every tracking study reports some basic information on
384 mortality (Hart and Hyrenbech 2009).

385 Beyond documenting natural mortality, there has been much effort directed at
386 documenting bycatch mortality in commercial fisheries or catch-and-release mortality from
387 recreational fisheries, although only recently have these commonly involved electronic tracking
388 (Donaldson et al. 2008, Maxwell et al. 2013). Given that mortality is often cryptic, tracking
389 studies provide one of the few means to objectively assess mortality. Hays et al. (2003) published
390 one of the first studies to use satellite telemetry to quantify bycatch mortality in marine turtles;
391 data that can be incorporated into population and management models (Chaloupka et al. 2004).
392 The earliest catch-and-release study using acoustic telemetry to assess mortality in a recreational
393 marine fishery revealed mortality was of Atlantic sailfish (*Istiophorus albicans*) and revealed
394 mortality that would have otherwise been undetected (Jolley et al. 1979). Studies on bonefish
395 (*Albula vulpes*) post-release mortality in shallow tidal creeks using acoustic telemetry revealed
396 that predator density had a major impact on survival (Cooke and Philipp 2004), whereas for
397 Atlantic bluefin tuna (*Thunnus thynnus*) studied with PSAT tags (pop-up satellite archival tags) in
398 the Gulf of St. Lawrence, little post-release mortality was observed (Stokesbury et al. 2011). In
399 one study PSAT tags were used to contrast mortality of striped marlin (*Kajikia audax*) captured
400 and released using different hook types (Domeier et al. 2003). Beyond simply documenting
401 mortality, the goal of much of the fisheries interaction research is to develop strategies to reduce
402 mortality (McClellan et al. 2009).

403 Electronic tags, either alone or in combination with other techniques such as blood
404 sampling to assess physiological status, are able to elucidate the details of mortality (Cooke et al.
405 2008). For example, using a non-lethal biopsy approach on fish tagged with radio and acoustic
406 transmitters (see Cooke et al. 2005 for approach), Miller et al. (2011) revealed genomic
407 signatures that predicted migratory failure (i.e. mortality) of Pacific salmon destined for
408 spawning grounds. Cooke et al. (2006) and Crossin et al. (2009) used similar approaches to

409 associate more traditional physiological measures (e.g. stress and reproductive hormones, ions,
410 metabolites) with mortality of sockeye salmon at the ocean-to-river transition. Such mechanistic
411 studies of mortality are still rare in marine vertebrates. Gallagher et al. (2014, this Theme
412 Section) adopted a different approach to study the consequences of fisheries interactions for
413 several shark species; satellite tags were used to assess post-release mortality levels, and blood
414 samples and reflex indicators collected in parallel from other sharks at time of capture provided
415 the context in which to interpret mortality patterns.

416

417 *Reproduction*

418 When an animal reproduces, one of its first considerations is where and when to breed.
419 Electronic tracking has been used to identify and characterize reproductive locales for a number
420 of marine species. For example, satellite telemetry was used in a threatened sea-duck species, the
421 Stellar's eider (*Polysticta stelleri*), to identify population-specific breeding areas across Arctic
422 regions, which had hitherto been unknown (Petersen et al. 2006). This information was useful for
423 differentiating breeding characteristics of Atlantic and Pacific populations, and suggested
424 evolutionary and ecological factors influencing their distributions. In a different study, acoustic
425 and radio telemetry were coupled with egg drift sampling and histological analyses to
426 characterize the marine-to-freshwater movements and spawning locations of endangered Gulf
427 sturgeon (*Acipenser oxyrinchus desotoi*) (Fox et al. 2000). This study provided new insights into
428 the different spawning schedules of males and females, with important implications for
429 conservation and management. For many pelagic marine species, however, and especially fish,
430 knowledge of breeding or spawning locations is sparse or unavailable due in part to the obvious
431 difficulty of observing these events (e.g. the coelacanth, *Latimeria menadoensis*). Satellite
432 telemetry has been used with some success to identify spawning activity in wide-ranging bluefin
433 tunas (*Thunnus thynnus*) (Lutcavage et al. 1999, Block et al. 2001, Teo et al. 2007, Lutcavage et
434 al. 2012). In Atlantic bluefin tuna, for example, tagging revealed areas in the North Atlantic as
435 important spawning areas, which dispelled long-held ideas that the Gulf of Mexico was the
436 principal breeding area (Lutcavage et al. 1999). Similarly, in shortnose sturgeon (*Acipenser
437 brevirostrum*), acoustic telemetry arrays revealed new breeding habitats for individuals that could
438 not spawn in historical locations within a fragmented river system, and were thus forced to move
439 across marine areas to new river systems (Zydlowski et al. 2011). In loggerhead turtles (*Caretta
440 caretta*), identification and use of breeding areas within established marine protected areas in the
441 eastern Mediterranean Sea, as well as in Baja California, were determined using GPS loggers and
442 ARGOS transmitters (Peckham et al. 2007, Schofield et al. 2009). These studies provided data
443 and recommendations for guiding conservation policy at both local and regional scales. Although
444 not they are not marine species per se, the spawning locations of female muskellunge (*Esox
445 masquinongy*) and northern pike (*Esox lucius*) were identified via oviduct tagging (Pierce 2004,
446 Pierce et al. 2007). In this method, acoustic transmitters are inserted into the oviducts of mature
447 female fish, which are then expelled along with eggs when the fish spawns, thus allowing
448 researchers to track the movement to, and activity on, precise spawning sites. For the first time
449 oviduct tagging was used to identify the spawning sites of a pelagic fish, the European perch
450 *Perca fluviatilis*, in the Baltic sea (Skovrind et al. 2013). Other studies have used electronic
451 tracking to identify not only breeding site location, but also site fidelity (i.e. philopatry), for a
452 variety of marine taxa including bonefish (Humston et al. 2005), loggerhead turtles and green
453 turtles (*Chelonia mydas*) (Limpus et al. 1992; Broderick et al. 2007; Tucker 2010), ringed seals
454 (*Phoca hispida*; Kelly et al. 2010), harbour seals (*Phoca vitulina*; Van Parijs et al. 2000), King

455 eiders (*Somateria spectabilis*; Phillips and Powell 2006), nurse sharks (*Ginglymostoma cirratum*,
456 Pratt and Carrier 2001), bluefin tuna (Teo et al. 2007), red tilefish (*Branchiostegus japonicus*;
457 Mitamura et al. 2005), and Atlantic cod (*Gadus morhau*; Robichaud and Rose 2001). Despite the
458 innate programming for philopatry in some species, navigating to natal breeding locations is
459 nevertheless a massive challenge. Ueda (2014, this Theme Section) conducted a series of
460 experiments to manipulate the endocrine and sensory physiology systems of Pacific salmon and
461 reveal the mechanisms by which adult salmon are able to successfully home to natal spawning
462 grounds. In many cases, information on breeding location, multi-year habitat use and breeding
463 site fidelity provided vital information with direct application to management and conservation.

464 Once animals reach breeding areas, the timing of reproduction accounts for a large
465 proportion of the total variance in lifetime fitness. For nearly all animals, breeding is usually
466 restricted to a window of opportunity that is timed to match seasonal availability of food
467 resources. Variation in timing can result in reproductive isolation (allochrony), which in turn
468 leads to selection for adaptive reproductive phenotypes and provides a mechanism for adaptive
469 radiation (Hendry and Day 2007). Despite the abundance of papers that examine reproductive
470 timing in wild animals, examples where telemetry or bio-logging techniques are used to
471 characterize variation in these events are few, presumably because reproduction is often very
472 predictable and for many species relatively easy to observe. There are nevertheless a few
473 examples. Clear differences in male and female loggerhead turtle arrival at a marine protected
474 area breeding site showed a clear bimodal distribution (e.g. protandry); these GPS tracks directly
475 aid the conservation and management of this species (Schofield et al. 2013). Radio telemetry was
476 used to identify the timing of reproduction by populations of chinook salmon (*Oncorhynchus*
477 *tshawytscha*) in the Kenai River of Alaska (Burger et al. 1985). The authors speculated how
478 variation in spawning times might influence the fitness of individuals, but did not directly
479 measure any such endpoints. Differences in the timing of reproduction by male and female
480 spotted seatrout (*Cynoscion nebulosus*) have also been described via acoustic telemetry
481 (Lowerre-Barbieri et al. 2013). Goutte et al. (2014, this Theme Section) examined the links
482 between breeding phenology of black-legged kittiwakes (*Rissa tridactyla*) and levels of the stress
483 hormone, corticosterone (cort); although baseline cort levels were correlated with trip duration
484 and destination during the pre-laying period, the decision to breed, and laying date, were
485 influenced not by cort but by individual body condition, suggesting that the proximate
486 mechanisms underlying timing of breeding are complex.

487 Electronic tracking has been used frequently to study reproductive activity and behaviour,
488 especially in fish where courtship and spawning behaviour is often difficult to observe. Acoustic
489 telemetry arrays have identified broad-scale movement patterns in deep shelf environments as
490 evidence of spawning aggregation in bonefish and linked these movement and spatial patterns to
491 specific moon phases (Danylchuk et al. 2011). At a smaller scale, egg-laying behaviour and
492 reproductive timing was characterized in female small spotted catsharks (*Scyliorhinus canicula*)
493 via time-depth telemetry and the tracking of vertical movements that are known to correspond to
494 egg laying (Wearmouth et al. 2012). Similarly, recent studies in nurse shark (*Ginglymostoma*
495 *cirratum*) used 3-dimensional accelerometry to differentiate mating from other peripheral
496 behaviours (resting, swimming, etc.) (Whitney et al. 2010). Attempts to quantify energetic costs
497 of breeding and courtship behaviour involved electromyogram telemetry (EMG), most frequently
498 in Pacific salmon where muscle contraction and tailbeat frequency relationships yielded estimate
499 of energy expenditure (Healey et al. 2003, Hruska et al. 2007). These studies allow activity
500 budgets to be estimated, as well as the costs of various behaviours related to courtship, nest

501 construction, and defense. The energetics of parental care have been examined in centrarchid
502 fishes using combinations of radio-telemetry, underwater videography and direct observation.
503 These studies demonstrated a diversity of species-specific parental care strategies that ranged in
504 duration and intensity, and offered insights into their evolution (Cooke et al. 2006b). Attempts to
505 quantify diversity and costs of very fine scale behaviours have used biotelemetry of heart rate
506 (e.g. electrocardiogram, ECG; Lucas et al. 1991), tail-beat frequency (Ross et al. 1981), and
507 EMG (Cooke et al. 2004b). ECG and EMG are invasive techniques requiring surgical
508 implantations; however, the alternative is to use accelerometry (Wilson et al. 2007, Shepard et al.
509 2008b), which has great potential to reveal the costs of behaviour in the context of reproduction.

510 There have been recent attempts to identify physiological mechanisms of parental care in
511 marine vertebrates by using experimental manipulation in tandem with electronic tracking. Using
512 time-depth recorders, physiological sampling, and exogenous corticosterone implants in female
513 macaroni penguins (*Eudyptes chrysolophus*), variation in baseline corticosterone was identified
514 as a key predictor of parental foraging behaviour and chick growth (Crossin et al. 2012b). Cottin
515 et al. (2014, this Theme Section) took a similar approach in their study of parental care in Adélie
516 penguins (*Pygoscelis adeliae*), wherein males were similarly implanted with exogenous
517 corticosterone and foraging behaviour and chick growth monitored. This study highlights how the
518 hormonal control of foraging and parental care can differ among species (e.g. macaroni penguins)
519 and between sexes. It also highlights how experimental manipulation of hormonal state and
520 tracking can be combined to address life-history questions. Cottin et al. (2013) also used this
521 approach when they manipulated prolactin levels in male Adélie penguins and found an effect on
522 parental foraging behaviour but without an ultimate fitness effect on chick growth. Generally, the
523 physiological mechanisms governing parental care, particularly from an endocrine perspective,
524 are fairly well known, especially for birds and some freshwater fishes (e.g. the sunfishes,
525 Centrarchidae; Cooke et al. 2006b). Studies of marine fishes and marine mammals, where it is
526 difficult to observe parental behaviour, will benefit from tracking techniques.

527

528 **Future opportunities: moving beyond fitness proxies?**

529 Despite the realization that physiological systems are important mediators of life-history
530 variation (Ricklefs and Wikelski 2002), the physiological basis of most life-history trade-offs
531 remains unknown. Experimental studies using physiological sampling and electronic tracking
532 techniques like those described above will allow us to move beyond an understanding of simple
533 performance-related traits (e.g. locomotion, maximum sustainable metabolic rates, etc.) and
534 towards an understanding of the key mechanisms underlying life-history variation and fitness
535 related events. Indeed, the many studies that we have highlighted in this brief review use
536 electronic tagging to some extent to characterize fitness proxies, thus allowing inferences about
537 true fitness. However, there are virtually no electronic tagging studies where true fitness is
538 measured directly. There are certainly numerous technical challenges that exist given the inherent
539 challenges in working on marine vertebrates, many of which are mobile within a vast open
540 environment. Moving beyond individual fitness proxies might require advances in three
541 interrelated areas:

- 542 1. Advanced sensor development: We can only presume that tracking devices will
543 continue to get smaller and lighter, with greater battery life and memory capacity that
544 would allow researchers to track individuals across life-history stages. The
545 development of sensors that allow estimations of reproductive output (or

546 reproductive state, e.g. reproductive hormone levels) and survival would facilitate
547 this aim. At present, it is in many cases impossible to determine the link between say
548 winter or non-breeding movements and survival, particularly for pelagic species.
549 Identifying the time and location of mortality events would allow researchers to
550 address direct fitness questions. Similarly, sensors that can estimate or quantify
551 reproductive output (e.g. number of eggs expelled during spawning events) as well
552 as the timing and location of such events would similarly expand our understanding
553 the factors influencing individual variation in reproductive output. However, the
554 creation of smaller and more advanced tags is only one aspect; the very real problem
555 of long-term tag attachment, with minimal tag effects, must be addressed, especially
556 for long-term studies.

557 2. Long-term, repeated measures studies: There are many inherent difficulties in
558 designing and maintaining the long-term, longitudinal studies that span the full life
559 cycles of study animals. This type of study is nonexistent for most marine
560 vertebrates, but could be possible as new tracking and sensor technologies become
561 available. Such long-term studies, wherein fitness components can be monitored in
562 individual animals, across multiple life-history stages, would yield insights to the
563 working of fitness like that done for great tits (*Parus major*), studies for a 39 year
564 period in their natural environment (McCleery et al. 2004). Attempts to gain broader
565 spatial coverage would also facilitate this, and the newly established ICARUS
566 Initiative is a notable example, working to establish a global, remote sensing
567 platform for scientists tracking small organisms over large spatial scales
568 (icarusinitiative.org). Finally, for marine studies that span ocean basins and
569 jurisdictional boundaries, data-sharing may become necessary and more common
570 allows, thus facilitating researcher efforts by groups addressing similar questions
571 (e.g. Bailey et al. 2012).

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

585
586 To conclude, there is continued need for creativity as researchers push the frontiers
587 of technology and biology to study wild marine vertebrates in their natural environment.
588 Twenty years ago one could only dream of studies that attempt to explain variation in fitness
589 among individuals – constrained by technology and forced to select “ideal model systems”
590 that were convenient and tractable. Today, tracking fitness in a wide range of marine

591 vertebrate taxa is possible and with that comes the opportunity to unlock fascinating secrets
592 of marine life. Additional innovation is needed as we strive to move from what at best are
593 “marginal” fitness proxies to truly measuring (and tracking!) fitness in wild marine
594 vertebrates.

595
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601
602 **Figure Legends**

603 Figure 1: Electronic tracking, biologging, and other techniques have much promise for gaining
604 insights on fitness-related events and processes in a variety of marine vertebrate taxa. Four
605 studies assembled in this theme section highlight the use of electronic tracking and biologging
606 techniques to advance our understanding of the factors affecting fitness in four principal life-
607 history stages that we reviewed. Panel A shows a great hammerhead shark, *Sphyrna mokarran*,
608 with a satellite tag attached to its dorsal fin. Using both tracking and physiological sampling
609 techniques, this study examined the effects simulated catch-and-release angling stress on
610 subsequent patterns of behaviour and survival (Gallagher et al. 2014). Panel B shows a black
611 legged kittiwake, *Rissa tridactyla*, bearing a geolocation loggers on a leg band. Geolocators and
612 endocrine manipulations were used to examine nonbreeding distributions in the North Atlantic
613 and migratory carryover effects on reproduction (Schultner et al. 2014). Panel C shows a
614 Southern elephant seal, *Mirounga leonina*, fitted with satellite transmitter. This study reveals
615 links between environmental change and fitness by examining how short-term (seasonal) shifts in
616 marine behaviour affect long-term patterns of reproduction and survival (New et al. 2014). Panel
617 D shows an emperor penguin (*Aptenodytes forsteri*) bearing a digital electrocardiogram (ECG)
618 and time depth recorder to monitor oxygen regulation during deep dives (Wright et al. 2014).
619 Photo credits: Evan D’Alessandro (A), Tycho Anker-Nilssen (B), Mark Hindell (C), Paul
620 Ponganis (D).

621

621 **References**

- 622 Aarestrup K, Baktoft H, Koed A, del Villar D, Thorstad EB (2014) Comparison of riverine and
623 early marine migraton behaviour and survival of wild and hatchery-reared sea trout (*Salmo*
624 *trutta*) smolts. Mar Ecol Prog Ser 000:000-000
- 625 Aoki K, Amano M, Mori K, Kouroggi A, Kubodera T, Miyazaki N (2012) Active hunting by
626 deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. Mar Ecol
627 Prog Ser 444:289-322
- 628 Arnold G, Dewar H (2001) Electronic tags in marine fisheries research: a 30-year perspective. In:
629 Sibert J, Nielsen J (eds). Methods and Technologies in Fish Biology and Fisheries, Vol 1.
630 Academic Press, Dordrecht, The Netherlands. p 7-64
- 631 Bailey H, Fossette S, Bograd SJ, Shillinger GL, Swithenbank AM, Georges J-Y, Gaspar P,
632 Strömberg KHP, Paladino FV, Spotila JR, Block BA, Hays GC (2012) Movement patterns for
633 a critically endangered species, the leatherback turtle (*Dermochelys coriacea*), linked to
634 foraging success and population status. PLoS One 7:e36401
- 635 Bailleul F, Charrassin JB, Monestiez P, Roquet F, Biuw M, Guinet C (2007) Successful foraging
636 zones of southern elephant seals from the Kerguelen Islands in relation to oceanographic
637 conditions. Phil Trans R Soc Lond B 362:2169-2181
- 638 Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H (2012) Effects of
639 climate change and fisheries bycatch on Southern Ocean seabirds: a review. Mar Ecol Prog
640 Ser 454:285-307
- 641 Barker JSF (2009) Defining fitness in natural and domesticated populations. In: Adaptation and
642 Fitness in Animal Populations. van der Werf J et al. (eds). Springer-Verlag, Heidelberg, p 3-14
- 643 Bentaleb I, Martin C, Vrac M, Mate B, Mayzaud P, Siret D, de Stephanis R, Guinet C (2011)
644 Foraging ecology of Mediterranean fin whales in a changing environment elucidated by
645 satellite tracking and baleen plate stable isotopes. Mar Ecol Prog Ser 438:285-302
- 646 Bestley S, Patterson TA, Hindell MA, Gunn JS (2008) Feeding ecology of wild migratory tunas
647 revealed by archival tag records of visceral warming. J Anim Ecol 77:1223-1233
- 648 Bestley S, Patterson TA, Hindell MA, Gunn JS (2010) Predicting feeding success in a migratory
649 predator: integrating telemetry, environment, and modeling techniques. Ecology 91:2373-2384
- 650 Bestley S, Jonsen ID, Hindell MA, Guinet C, Charrassin JB (2013) Integrative modelling of
651 animal movement: incorporating in situ habitat and behavioural information for a migratory
652 marine predator. Proc R Soc B 280:000-000
- 653 Bejan A, Marden JH (2006) Unifying constructal theory for scale effects in running, swimming
654 and flying. Journal of Experimental Biology 209:238-248
- 655 Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. Ministry of
656 Agriculture, Fisheries and Food, London
- 657 Block BA (2005) Physiological ecology in the 21st century: advancements in biologging science.
658 Integr Comp Biol 45:305-320
- 659 Block BA, Booth D, Carey FG (1992) Direct measurement of swimming speeds and depth of
660 blue marlin. J Exp Biol 166:267-284.

661 Block BA, Dewar H, Blackwell S, Williams T, Farwell CJ, Prince ED, Boustany A, Teo SLH,
662 Seitz A, Fudge D, Walli A (2001) Electronic tags reveal migratory movements, depth
663 preferences and thermal biology of Atlantic bluefin tuna. *Science* 293:1310-1314

664 Bogdanova MI, Daunt F, Newell M, Phillips RA, Harris MP, Wanless S (2011) Seasonal
665 interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding
666 performance and winter distribution. *Proc R Soc B* 278:2412-2418

667 Bokony V, Lendvai AZ, Liker A, Angelier F, Wingfield JC, Chastel O (2009) Stress response
668 and the value of reproduction: are birds prudent parents? *Amer Nat* 173:589-598

669 Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of
670 sea turtles. *Proc R Soc B* 274:1533-1539

671 Brosnan IG, Welch DW, Rechisky ER, Porter AD (2014) Evaluating the influence of
672 environmental factors on yearling Chinook salmon survival in the Columbia River plume
673 (USA). *Mar Ecol Prog Ser* 000:000-000

674 Brown RS, Oldenburg EW, Seaburg A, Cook KV, Skalski JR, Eppard MB, Deters
675 KA (2013) Survival of seaward-migrating PIT and acoustic-tagged juvenile chinook salmon in
676 the Snake and Columbia rivers: an evaluation of length-specific tagging effects. *Animal*
677 *Biotelemetry* 1:000-000 doi:10.1186/2050-3385-1-8

678 Bunt CM, Kingsford M.J. (2014) Movement, habitat utilization and behaviour of coral trout,
679 *Plectropomus leopardus*, during and after the reproductive period on the southern Great
680 Barrier Reef. *Mar Ecol Prog Ser* 000:000-000

681 Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research
682 and conservation of seabirds. *Auk* 125:253-64

683 Burger CV, Wilmot RL, Wangaard DB (1985) Comparison of spawning areas and times for two
684 runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. *Can J Fish*
685 *Aquat Sci* 42:693-700

686 Catry P, Phillips RA, Phalan B, Silk JRD, Croxall JP (2004) Foraging strategies of grey-headed
687 albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events.
688 *Mar Ecol Prog Ser* 280:261-273

689 Catry P, Dias MP, Phillips RA, Granadeiro JP (2011) Different Means to the Same End: Long-
690 Distance Migrant Seabirds from Two Colonies Differ in Behaviour, Despite Common
691 Wintering Grounds. *PLoS One* 6

692 Catry P, Dias MP, Phillips RA, Granadeiro JP (2013) Carry-over effects from breeding modulate
693 the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94:1230-
694 1235

695 Chaloupka M, Parker D, Balazs G (2004). Tracking turtles to their death- reply to Hays et al. *Mar*
696 *Ecol Prog Ser* 283:301-302

697 Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D (2013) Minke whales maximise
698 energy storage on their feeding grounds. *J Exp Biol* 216:427-436

699 Cooke SJ, Philipp DP (2004) Behaviour and mortality of caught-and-released bonefish (*Albula*
700 *spp.*) in Bahamian waters with implications for a sustainable recreational fishery. *Biol*
701 *Cons* 118:599-607

- 702 Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004a) Biotelemetry: a
703 mechanistic approach to ecology. *Trends in Ecology and Evolution* 19:334-343.
- 704 Cooke SJ, Thorstad E, Hinch SG (2004b) Activity and energetics of free-swimming fish: insights
705 from electromyogram telemetry. *Fish Fisheries* 5:21-52
- 706 Cooke SJ, Crossin GT, Patterson D, English K, Hinch SG, Young JL, Alexander R, Healey MC,
707 Van Der Kraak G, Farrell AP (2005) Coupling non-invasive physiological and energetic
708 assessments with telemetry to understand inter-individual variation in behaviour and
709 survivorship of sockeye salmon: development and validation of a technique. *J Fish Biol*
710 67:1342-1358
- 711 Cooke SJ, Hinch SG, Crossin GT, Patterson DA, English KK, Healey MC, Shrimpton JM, Van
712 Der Kraak G, Farrell AP (2006a) Mechanistic basis of individual mortality in Pacific salmon
713 during spawning migrations. *Ecology* 87:1575-1586
- 714 Cooke SJ, Philipp DP, Wahl DH, Weatherhead PJ (2006b) Energetics of parental care in six
715 syntopic centrarchid fishes. *Oecologia* 148:235-249
- 716 Cooke SJ, Hinch SG, Farrell AP, Patterson DA, Miller-Saunders K, Welch DW, Donaldson MR,
717 Hanson KC, Crossin GT, Olsson I, Cooperman MS, Mathes MT, Hruska KA, Wagner GN,
718 Thomson R, Hourston R, English KK, Larsson S, Shrimpton JM, Van Der Kraak G (2008)
719 Developing a mechanistic understanding of fish migrations by linking telemetry with
720 physiology, behaviour, genomics and experimental biology: an interdisciplinary case study on
721 adult Fraser River sockeye salmon. *Fisheries* 33: 321-338
- 722 Cooke SJ, Woodley CM, Eppard MB, Brown RS, Nielsen JL (2011) Advancing the surgical
723 implantation of electronic tags in fish: a gap analysis and research agenda based on a review of
724 trends in intracoelomic tagging effects studies. *Rev Fish Biol Fisheries* 21:127-151
- 725 Cooke SJ, Hinch SG, Lucas MC, Lutcavage M (2012) Biotelemetry and biologging. In: Zale AV,
726 Parrish DL, Sutton TM (eds). *American Fisheries Society*, Bethesda, MD, p 819-860
- 727 Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of Antarctic Fur Seals in relation to
728 changes in prey availability. *Ecology* 70:596-606
- 729 Costa DP, Breed GA, Robinson PW (2012) New insights into pelagic migrations: implications
730 for ecology and conservation. *Ann Rev Ecol Evol Syst* 43:73-96
- 731 Cottin M, Chastel O, Kato A, Debin M, Takahashi A, Ropert-Coudert Y, Raclot T (2013)
732 Decreasing prolactin levels lead to a lower diving effort but do not affect breeding success in
733 Adélie penguins. *Horm Behav* 000:000-000
- 734 Cottin M et al. (2014) Corticosterone administration leads to a transient alteration of foraging
735 behaviour and complexity in a diving seabird. *Mar Ecol Prog Ser* 000:000-000
- 736 Crossin GT, Hinch SG, Cooke SJ, Welch DW, Batten SD, Patterson DA, Van Der Kraak G,
737 Shrimpton JM, Farrell AP (2007) Behaviour and physiology of sockeye salmon homing
738 through coastal waters to a natal river. *Mar Biol* 152:905-918
- 739 Crossin GT, Hinch SG, Cooke SJ, Cooperman MS, Patterson DA, Welch DW, Hanson KC,
740 Olsson I, English KK, Farrell AP (2009) Mechanisms influencing the timing and success of
741 reproductive migration in a capital breeding, semelparous fish species: the sockeye salmon.
742 *Physiol Biochem Zool* 82:635-652

- 743 Crossin GT, Trathan PN, Phillips RA, Dawson A, Le Bouard F, Williams TD (2010) A carryover
744 effect of migration underlies individual variation in reproductive readiness and extreme egg
745 size dimorphism in macaroni penguins. *Amer Nat* 176:357-366
- 746 Crossin GT, Phillips RA, Trathan PN, Fox DS, Dawson A, Wynne-Edwards KE, Williams TD
747 (2012a) Migratory carryover effects and endocrinological correlates of reproductive decisions
748 and reproductive success in female albatrosses. *Gen Comp Endocrinol* 176:151-157
- 749 Crossin GT, Trathan PN, Phillips RA, Gorman KB, Dawson A, Sakamoto KQ, Williams TD
750 (2012b) Corticosterone predicts foraging behaviour and parental care in macaroni penguins.
751 *Amer Nat* 180:E31-41
- 752 Crossin GT, Phillips RA, Lattin CR, Romero LM, Williams TD (2013a) Corticosterone mediated
753 costs of reproduction link current to future breeding. *Gen Comp Endocrinol* 193:112-120
- 754 Crossin GT, Phillips RA, Wynne-Edwards KA, Williams TD (2013b) Post-migratory body
755 condition and ovarian steroid production predict breeding decisions by female gray-headed
756 albatrosses. *Physiol Biochem Zool* 000:000-000
- 757 Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR (2005) Global circumnavigations:
758 tracking year-round ranges of non-breeding albatrosses. *Science* 307:249-250
- 759 Danylchuk, AJ. Cooke SJ, Goldberg TL, Suski CD, Murchie KJ, Danylchuk SE, Shultz AD,
760 Haak CR, Brooks EJ, Koppelman JB, Phillip DP (2011) Aggregations and offshore
761 movements as indicators of spawning activity of bonefish (*Albula vulpes*) in The Bahamas.
762 *Mar Biol* 158:1981-1999
- 763 Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter
764 foraging and breeding phenology in a temperate seabird. *Behav Ecol Sociobiol* 59:381-388
- 765 Del Raye G, Jorgensen SJ, Krumhansl K, Ezcurra JM, Block BA (2013) Travelling light: white
766 sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale
767 migration. *Proc R Soc B* 280:000-000
- 768 Dingle H (1996) *Migration: The Biology of Life on the Move*. Oxford University Press, Oxford
- 769 Domeier ML, Dewar H, Nasby-Lucas N (2003) Mortality rate of striped marlin (*Tetrapturus*
770 *audax*) caught with recreational tackle. *Mar Fresh Res* 54:435-445
- 771 Donaldson MR, Arlinghaus R, Hanson KC, Cooke SJ (2008) Enhancing catch-and-release
772 science with biotelemetry. *Fish Fisheries* 9:79-105
- 773 Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG (2012) A synthesis of
774 tagging studies examining the behaviour and survival of anadromous salmonids in marine
775 environments. *PLoS One* 7:e31311
- 776 Drenner SM, Hinch SG, Martins EG, Robichaud D, Thompson LA, Patterson DA, Cooke SJ,
777 Thomson RE (2014) Variable thermal experience and diel thermal patterns of homing sockeye
778 salmon in coastal marine waters. *Mar Ecol Prog Ser* 000:000-000
- 779 Elowe KD, Dodge WE (1989) Factors affecting black bear reproductive success and cub survival.
780 *J Wildlife Manag* 53:962-968
- 781 Endler JA (1986) *Natural Selection in the Wild*. Princeton Univ. Press, Princeton. NJ.

- 782 Freeman R, Dean B, Kirk H, Leonard K, Phillips RA, Perrins CM, Guilford T (2013) Predictive
783 ethoinformatics reveals the complex migratory behaviour of a pelagic seabird, the Manx
784 Shearwater. *J Roy Soc Inter* 6:279
- 785 Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN, Ware C, Weinrich MT, Hurst T, Wiley D
786 (2009) Diel changes in humpback whale *Megaptera novaeangliae* feeding behaviour in
787 response to sand lance *Ammodytes spp.* behaviour and distribution. *Mar Ecol Prog Ser* 395:91-
788 100
- 789 Gallagher AJ, Serafy JE, Cooke SJ, Hammerschlag N (2014) Physiological stress response, reflex
790 impairment, and survival of five sympatric shark species following experimental capture and
791 release. *Mar Ecol Prog Ser* 000:000-000
- 792 Garthe S, Ludynia K, Huppopp O, Kubetzki U, Meraz JF, Furness RW (2012) Energy budgets
793 reveal equal benefits of varied migration strategies in northern gannets. *Mar Biol* 159:1907-
794 1915
- 795 Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE, Norman B, Hays GC, Quintana F, Grundy E,
796 Campagna C, Trites AW, Block BA, Wilson RP (2011a) Convergent evolution in locomotory
797 patterns of flying and swimming animals. *Nature Comm* 2:352.
- 798 Gleiss AC, Norman B, Wilson RP (2011b) Moved by that sinking feeling: variable diving
799 geometry underlies movement strategies in whale sharks. *Funct Ecol* 25:595-607
- 800 Gleiss AC, Wilson RP, Shepard ELC (2011c) Making overall dynamic body acceleration work:
801 on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol Evol* 2:23-33
- 802 Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ
803 (2008) Satellite tracking of sea turtles: where have we been and where do we go next. *Endan*
804 *Species Res* 4:3-22
- 805 Goldbogen JA, Calambokidis J, Shadwick RE, Oleson EM, McDonald MA, Hildebrand JA
806 (2006) Kinematics of foraging dives and lunge-feeding in fin whales. *J Exp Biol* 209:1231-
807 1244.
- 808 Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011)
809 Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence
810 on krill density. *J Exp Biol* 214:131-146
- 811 Goldbogen JA, Calambokidis J, Friedlaender AS, Francis J, DeRuiter SL, Stimpert AK, Falcone
812 E, Southall BL (2013) Underwater acrobatics by the world's largest predator: 360 degrees
813 rolling manoeuvres by lunge-feeding blue whales. *Biol Lett* 9:000-000.
- 814 Goutte A,
- 815 Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during
816 year-round foraging in macaroni penguins. *Mar Ecol Prog Ser* 296:183-196
- 817 Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of
818 parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the
819 macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529-538
- 820 Gremillet D (1997) Catch per unit effort, foraging efficiency, and parental investment in breeding
821 great cormorants (*Phalacrocorax carbo carbo*). *ICES J Mar Sci* 54:635-644

822 Gutowsky SE, Tremblay Y, Kappes MA, Flint EN, Klavitter J, Laniawe L, Costa DP, Naughton
823 MB, Romano MD, Shaffer SA (2013) Divergent post-breeding distribution and habitat
824 associations of fledgling and adult black-footed albatrosses *Phoebastria nigripes* in the Northe
825 Pacific. Ibis 000:000-000 doi: 10.1111/ibis12119

826 Halsey LG, Shepard ELC, Wilson RP (2011) Assessing the development and application of the
827 accelerometry technique for estimating energy expenditure. Comp Biochem Physiol A
828 158:305-314

829 Hays GC, Broderick AC, Godley BJ, Luschi P, Nichols WJ (2003) Satellite telemetry suggests
830 high levels of fishing-induced mortality in marine turtles. Mar Ecol Prog Ser 262:305-309

831 Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags
832 deployed on marine animals stop transmitting? J Exp Mar Biol Ecol 349:52-60

833 Hays GC, Hobson VJ, Metcalfe JD, Righton D, Sims DW (2006) Flexible foraging movements
834 of leatherback turtles across the north Atlantic Ocean. Ecology 87:2647-2656

835 Hays GC, Fossette S, Katselidis KA, Mariani P, Schofield G (2010) Ontogenetic development of
836 migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. J Roy Soc
837 Interface 7:1319-1327

838 Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries
839 NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Lévy searches: jellyfish can
840 search the water column like fish. Proc R Soc B 279:465-473

841 Hart KM, Hyrenbach KD (2009) Satellite telemetry of marine megavertebrates: the coming of
842 age of an experimental science. Endan Species Res 10:9-20

843 Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne
844 JP, Costa DP, Crowder LB, Block BA (2013) Predicted habitat shifts of Pacific top predators
845 in a changing climate. Nature Climate Change 3:234-238

846 Healey MC, Lake R, Hinch SG. 2003. Energy expenditures during reproduction by sockeye
847 salmon (*Oncorhynchus nerka*). Behaviour 140:161-182

848 Hendry AP, and Day T. 2005. Population structure attributable to reproductive time: isolation by
849 time and adaptation by time. Molec Ecol 14:901-916

850 Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks,
851 *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fish Aquat
852 Sci 59:624-632

853 Heupel MR, Simpfendorfer CA (2014) Importance of environmental and biological drivers in the
854 presence and space use of a reef- associated shark. Mar Ecol Prog Ser 000:000-000

855 Hruska KA, Hinch SG, Healey MC, Farrell AP (2007) Electromyogram telemetry, nondestructive
856 physiological biopsy, and genetic markers: linking recent techniques with behavioural
857 observations for the study of reproductive success in sockeye salmon mating systems. Amer
858 Fish Soc Symp 54:17-29

859 Humston R, Ault JS, Larkin MF, Luo J. 2005. Movements and site fidelity of the bonefish *Albula*
860 *vulpes* in the northern Florida Keys determined by acoustic telemetry. Mar Ecol Prog Ser 291:
861 237-248

862 Irschick DJ 2003. Measuring performance in nature: implications for studies of fitness within
863 populations. *Integ Comp Biol* 433:396-407

864 Johnson SL, Power JH, Wilson DR, Ray J (2010) A comparison of the survival and migratory
865 behaviour of hatchery-reared and naturally reared steelhead smolts in the Alsea River and
866 estuary, Oregon, using acoustic telemetry. *N Amer J Fish Manag* 30:55-71

867 Jonsen ID, Myers RA, James MC (2006) Robust hierarchical state-space models reveal diel
868 variation in travel rates of migrating leatherback turtles. *J Anim Ecol* 75:1046-1057

869 Jolley J, John W, Irby J, Edwin W (1979) Survival of tagged and released Atlantic sailfish
870 (*Istiophorus platypterus*: Istiophoridae) determined with acoustical telemetry. *Bull Mar*
871 *Sci* 29:155-169

872 Jorgensen SJ, Arnoldi NS, Estess EE, Chapple TK, Ruckert M, Anderson SD, Block BA (2012)
873 Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon*
874 *carcharias*) migration and offshore behaviour. *PLoS One* 7:e47819

875 Kelly BP, Badajos OH, Kunnasranta M, Moran JR, Martinez-Bakker M, Wartzok D, Boveng P
876 (2010) Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biol*
877 33:1095-1109

878 Kleiber M (1975) The fire of life: an introduction to animal energetics. Kreiger, Huntington, NY.
879 p 453

880 Kouwenberg AL, Hipfner JM, McKay DW, Storey AE (2013) Corticosterone and stable isotopes
881 in feathers predict egg size in Atlantic puffins *Fratercula arctica*. *Ibis* 155:413-418

882 Kozlowski J (1993) Measuring fitness in life history studies. *Trends Ecol Evol* 8:84-85

883 Kuhn CE, Crocker DE, Tremblay Y, Costa DP (2009) Time to eat: measurements of feeding
884 behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *J*
885 *Anim Ecol* 78:513-523

886 Lea MA, Johnson D, Melin S, Ream R, Gelatt T (2010) Diving ontogeny and lunar responses in a
887 highly migratory mammal, the northern fur seal *Callorhinus ursinus*. *Mar Ecol Prog Ser*
888 419:233-247

889 Leat EHK, Bourgeon S, Magnusdottir E, Gabrielsen GW, Grecian WJ, Hanssen SA, Olafsdottir
890 K, Petersen A, Phillips RA, Strøm H, Ellis S, Fisk AT, Bustnes JO, Furness RW, Borgå K
891 (2013) Influence of wintering area on persistent organic pollutants in a breeding migratory
892 seabird. *Mar Ecol Prog Ser* 491:277-293

893 Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of
894 green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern
895 Australian rookeries. *Wildlife Res* 19:347-358

896 Lowerre-Barbieri SK, Walters S, Bickford J, Cooper W, Muller R (2013) Site fidelity and
897 reproductive timing at a spotted seatrout spawning aggregation site: individual versus
898 population scale behaviour. *Mar Ecol Prog Ser* 481:181-197

899 Lucas MC, Priede IG, Armstrong JD, Gindy ANZ, De Vera L (1991) Direct measurements of
900 metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of
901 heart rate telemetry. *J Fish Biol* 39:325-345

- 902 Lutcavage ME, Brill RW, Skomal GB, Chase BC, Howey PW (1999) Results of a pop-up
 903 satellite tagging of spawning class fish in the Gulf of Maine: do North Atlantic bluefin tuna
 904 spawn in the mid-Atlantic? *Can J Fish Aquat Sci* 56:173-177
- 905 Lutcavage ME, Galuardi B, Lam TCH (2012) Predicting potential Atlantic spawning grounds of
 906 western Atlantic bluefin tuna based on electronic tagging results, 2002-2011. ICCAT
 907 SCRS/2012/157, 7 pp
- 908 Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Fox AD, Furness RW (2010)
 909 Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar Ecol Prog*
 910 *Ser* 406:291-303
- 911 Mackley EK, Phillips RA, Silk JRD, Wakefield ED, Afanasyev V, Furness RW (2011) At-sea
 912 activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis*
 913 from South Georgia. *Mar Biol* 158:429-438
- 914 Maxwell SM, Hazen EL, Bograd SJ, Halpern BS, Breed GA, Nickel B, Teutschel NM, Benson S,
 915 Bailey H, Kappes MA, Kuhn C, Weise MJ, Mate B, Shaffer SA, Hassrick J, Henry RW, Irvine
 916 L, McDonald BI, Robinson PW, Block BA, Costa DP (2013) Cumulative human impacts on
 917 marine predators. *Nature Comm* 000:000-000
- 918 McCleery RH, Pettifor RA, Armbruster P, Meyer K, Sheldon BC, Perrins CM (2004)
 919 Components of variance underlying fitness in a natural population of the great tit *Parus major*.
 920 *Amer Nat* 164:E62-E72
- 921 McClellan CM, Read AJ, Price BA, Cluse WM, Godfrey MH (2009) Using telemetry to mitigate
 922 the bycatch of long-lived marine vertebrates. *Ecol App* 19:1660-1671
- 923 McGraw JB, Caswell H (1996) Estimation of individual fitness from life-history data. *Amer Nat*
 924 147:47-64.
- 925 McIntyre T, Anson IJ, Bornemann H, Plotz J, Tosh CA, Bester MN (2011) Elephant seal dive
 926 behaviour is influenced by ocean temperature: implications for climate change impacts on an
 927 ocean predator. *Mar Ecol Prog Ser* 441:257-272
- 928 McLean MF, Simpfendorfer CA, Heupel MR, Dadswell MJ, Stokesbury MJW (2014) Diversity
 929 of behavioural patterns displayed by a summer feeding aggregation of Atlantic sturgeon in the
 930 intertidal region of Minas Basin, Bay of Fundy, Canada. *Mar Ecol Prog Ser* 000:000-000
- 931 Melnychuk MC (2012) Detection efficiency in telemetry studies: definitions and evaluation
 932 methods. In: Adams N, Beeman J, Eiler J (eds) *Telemetry Techniques: A User Guide for*
 933 *Fisheries Research*. American Fisheries Society Books, Bethesda, MD. p 339-357
- 934 Melnychuk MC, Welch DW, Walters CJ, Christensen V (2007) Riverine and early ocean
 935 migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the
 936 Cheakamus River, British Columbia. *Hydrobiologia* 582:55-65
- 937 Midwood JD, Larsen MH, Boel M, Jepsen N, Aarestrup K, Cooke SJ (2014) Does cortisol
 938 manipulation influence outmigration behaviour, survival and growth of sea trout? A field-test
 939 of carryover effects in wild fish. *Mar Ecol Prog Ser* 00:000-000
- 940 Miller KM, Li S, Kaukinen KH, Ginther N, Hammill E, Curtis JMR, Patterson DA, Sierocinski
 941 T, Donnison L, Pavlidis P, Hinch SG, Hruska KA, Cooke SJ, English KK, Farrell AP (2011)
 942 Genomic signatures predict migration and spawning failure in wild Canadian salmon. *Science*
 943 331:214-217

- 944 Miller PJO, Johnson MP, Tyack PL, Terray EA (2004a) Swimming gaits, passive drag and
945 buoyancy of diving sperm whales *Physeter macrocephalus*. *J Exp Biol* 207:1953-1967
- 946 Miller PJO, Johnson MP, Tyack PL (2004b) Sperm whale behaviour indicates the use of
947 echolocation click buzzes 'creaks' in prey capture. *Proc R Soc B* 271:2239-2247
- 948 Mills S, Beatty J (1979) The propensity interpretation of fitness. *Phil Sci* 46:263-286
- 949 Mitamura H, Arai N, Mitsunaga Y, Yokota T, Takeuchi H, Tsuzaki T, Itani M (2005) Directed
950 movements and diel burrow fidelity patterns of red tilefish *Branchiostegus japonicus*
951 determined using ultrasonic telemetry. *Fisheries Sci* 71:491-498
- 952 Moore M, Berejikian BA, Tezak EP (2012) Variation in the early marine survival and behaviour
953 of natural and hatchery-reared Hood Canal steelhead. *PLoS One* 7:e49645
- 954 Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds.
955 *Ann Rev Nutrit* 19:247-277
- 956 Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A (2013) Unravelling the
957 mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct Ecol*
958 000:000-000 doi: 10.1111/1365-2435.12083
- 959 Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) Movement
960 ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA*
961 105:19052-19059
- 962 New LF, Clark JS, Costa DP, Fleishman E, Hindell MA, Klanjšček T, Lusseau D, Kraus S,
963 McMahon CR, Robinson PW, Schick RS, Schwarz LK, Simmons SE, Thomas L, Tyack P,
964 Harwood J (2014) Using short-term measures of behaviour to estimate long-term fitness of
965 Southern elephant seals. *Mar Ecol Prog Ser* 000:000-000
- 966 Orr HA (2009) Fitness and its role in evolutionary genetics. *Nat Rev Genet* 10:531-539
- 967 Peckham S, Maldonado DD, Walli A, Ruiz G, Crowder L, Nichols W (2007) Small-scale
968 fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS One* 2:e1041
- 969 Petersen MR, Bustnes JO, Systad GH (2006) Breeding and moulting locations and migration
970 patterns of the Atlantic population of Steller's eiders *Polysticta stelleri* as determined from
971 satellite telemetry. *J Avian Biol* 37:58-68
- 972 Phillips LM, Powell AN (2006) Evidence for wing molt and breeding site fidelity in King eiders.
973 *Waterbirds* 29:148-153
- 974 Phillips RA, Bearhop S, McGill R, Dawson DA (2009) Stable isotopes reveal individual variation
975 in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding
976 period. *Oecologia* 160:795-806
- 977 Pierce RB (2004) Oviduct insertion of radio transmitters as a means of locating northern pike
978 spawning habitat. *North American J Fisher Manag* 24:244-248
- 979 Pierce RB, Younk JA, Tomcko CM (2007) Expulsion of miniature radio transmitters along with
980 eggs of muskellunge and northern pike—a new method for locating critical spawning habitat.
981 *Environ Biol Fishes* 79:99-109
- 982 Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011) Celestial moderation of tropical seabird
983 behaviour. *PLoS One* 6

- 984 Pollock KH, Jiang H, Hightower JE (2004) Combining radio-telemetry and fisheries tagging
985 models to estimate fishing and natural mortality rates. *Trans Amer Fish Soc* 133:639-648
- 986 Pratt HL, Carrier JC (2001) A review of elasmobranch reproductive behaviour with a case study
987 on the nurse shark, *Ginglymostoma cirratum*. *Environ Biol Fishes* 60:157-188
- 988 Ragland JM, Arendt MD, Kucklick JR, Keller JM (2011) Persistent organic pollutants in blood
989 plasma of satellite-tracked adult male loggerhead sea turtles (*Caretta caretta*). *Environ Toxic*
990 *Chem* 30:1549-1556
- 991 Rayner MJ, Hauber ME, Steeves TE, Lawrence HA, Thompson DR, Sagar PM, Bury SJ, Landers
992 TJ, Phillips RA, Ranjard L, Shaffer SA (2011) Contemporary and historical separation of
993 transequatorial migration between genetically distinct seabird populations. *Nat Commun*
994 2:1330
- 995 Rechisky ER, Welch DW, Porter AD, Hess J, Narum S (2014) Testing for delayed mortality
996 effects in the early marine life history of Columbia River yearling chinook salmon. *Mar Ecol*
997 *Prog Ser* 000:000-000
- 998 Richman SE, Lovvorn JR (2011) Effects of air and water temperatures on resting metabolism of
999 auklets and other diving birds. *Physiol Biochem Zool* 84:316-332
- 1000 Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. *Trends Ecol Evol* 17:462-468
- 1001 Reid JP, Bonde RK, O'Shea TJ (1995) Reproduction and mortality of radio-tagged and
1002 recognizable manatees on the Atlantic coast of Florida. In: *Population Biology of the Florida*
1003 *Manatee*, p 171-191
- 1004 Robichaud D, Rose GA (2001) Multiyear homing of Atlantic cod to a spawning ground. *Can J*
1005 *Fish Aquat Sci* 58:2325-2329
- 1006 Romer JD, Leblanc CA, Clements S, Ferguson JA, Kent ML, Noakes D, Schreck CB (2013)
1007 Survival and behaviour of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in
1008 Oregon, USA. *Environ Biol Fish* 96:849-863
- 1009 Ropert-Coudert Y, Wilson PR (2005) Trends and perspectives in animal-attached remote sensing.
1010 *Front Ecol Environ* 3:437-444
- 1011 Ross LG, Watts W, Young AH (1981) An ultrasonic biotelemetry system for the continuous
1012 monitoring of tail-beat rate from free-swimming fish. *J Fish Biol* 18:479-490
- 1013 Rutz C, Hays GC (2009) New frontiers in biologging science. *Biol Lett* 5:289-292
- 1014 Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can
1015 Ethograms Be Automatically Generated Using Body Acceleration Data from Free-Ranging
1016 Birds? *PLoS One* 4:000-000
- 1017 Sato K, Watanuki Y, Takahashi A, Miller PJO, Tanaka H, Kawabe R, Ponganis PJ, Handrich Y,
1018 Akamatsu T, Watanabe Y, Mitani Y, Costa DP, Bost CA, Aoki K, Amano M, Trathan P,
1019 Shapiro A, Naito Y (2007) Stroke frequency, but not swimming speed, is related to body size
1020 in free-ranging seabirds, pinnipeds and cetaceans. *Proc R Soc B* 274:471-477
- 1021 Sato K, Aoki K, Watanabe YY, Miller PJO (2013) Neutral buoyancy is optimal to minimize the
1022 cost of transport in horizontally swimming seals. *Sci Rep* 3
- 1023 Schaffer WM (1981) On reproductive value and fitness. *Ecology* 62:1683-1685

- 1024 Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN,
1025 McClellan CM, Clark JS (2008) Understanding movement data and movement processes:
1026 current and emerging directions. *Ecol Lett* 11:1338-1350
- 1027 Schofield G, Lilley MKS, Bishop CM, Brown P, Katselidis KA, Dimopoulis P, Pantis JD, Hays
1028 GC (2009) Conservation hotspots: implications of intense spatial area use by breeding male
1029 and female loggerheads at the Mediterranean's largest rookery. *Endan Spec Res* 10:191-202
- 1030 Schofield G, Scott R, Dimadi A, Fossette S, Katselidis KA, Koutsoubas D, Lilley MKS, Pantis
1031 JD, Karagouni AD, Hays GC (2013) Evidence-based marine protected area planning for a
1032 highly mobile endangered marine vertebrate. *Biol Cons* 161:101-109
- 1033 Schultner J, Moe B, Chastel O, Tartu S, Bech C, Kitaysky AS (2014) Experimental evidence for
1034 corticosterone as a mediator of carry-over effects between breeding and migration in the
1035 kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser* 000:000-000
- 1036 Sepulveda CA, Kohin S, Chan C, Vetter R, Graham JB (2004) Movement patterns, depth
1037 preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus*
1038 *oxyrinchus*, in the Southern California Bight. *Mar Biol* 145:191-199
- 1039 Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of
1040 reproduction in free-ranging albatrosses. *Funct Ecol* 17:66-74
- 1041 Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller H, Taylor
1042 GA, Foley DG, Block BA, Costa DP (2006) Migratory shearwaters integrate oceanic
1043 resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci USA*
1044 103:12799-12802
- 1045 Shamoun-Baranes J, Bom R, van Loon EE, Ens BJ, Oosterbeek K, Bouten W (2012) From sensor
1046 data to animal behaviour: an oystercatcher example. *PLoS One* 7:000-000.
- 1047 Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal
1048 rhythms in diving behaviour of pelagic sharks identified by signal processing of archival
1049 tagging data. *Mar Ecol Prog Ser* 328:205-213
- 1050 Shepard ELC, Wilson RP, Liebsch N, Quintana F, Laich AG, Lucke K (2008a) Flexible paddle
1051 sheds new light on speed: a novel method for the remote measurement of swim speed in
1052 aquatic animals. *Endan Species Res* 4:157-164
- 1053 Shepard ELC, Wilson RP, Quintana F, Gómez Laich A, Liebsh N, Albareda DA, Halsey LG,
1054 Gleiss A, Morgan DT, Myers AE, Newman C, Macdonald DW (2008b) Identification of
1055 animal movement patterns using tri-axial accelerometry. *Endan Spec Res* 10:47-60
- 1056 Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy
1057 landscapes shape animal movement ecology. *Amer Nat* 182:298-312
- 1058 Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, Gaspar P, Wallace BP,
1059 Spotila JR, Paladino FV, Piedra R, Eckert SA, Block BA (2008) Persistent leatherback turtle
1060 migrations present opportunities for conservation. *PloS Biol* 6:1408-1416
- 1061 Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water:
1062 behaviour and kinematics of humpback whale lunge feeding. *J Exp Biol* 215:3786-3798
- 1063 Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel
1064 vertical migration in the plankton-feeding basking shark. *J Anim Ecol* 74:755-761

- 1065 Skovrind M, Flindt Christensen EA, Carl H, Jacobsen L, Møller PR (2013). Marine spawning
1066 sites of perch *Perca fluviatilis* revealed by oviduct-inserted acoustic transmitters. *Aquat Biol*
1067 000:000-000
- 1068 Sober E (2001) The two faces of fitness. In: Singh RS et al. (eds) *Thinking About Evolution*.
1069 Cambridge University Press, Cambridge
- 1070 Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird:
1071 stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim*
1072 *Ecol* 78:460-467
- 1073 Starr RM, O'Connell V, Ralston S, Breaker L (2005) Use of acoustic tags to estimate natural
1074 mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a marine reserve. *Mar*
1075 *Tech Soc J* 39:19-30
- 1076 Stokesbury MJW, Neilson JD, Susko E, Cooke SJ. (2011) Estimating Mortality of Atlantic
1077 bluefin tuna (*Thunnus thynnus*) in an experimental recreational catch-and-release fishery. *Biol*
1078 *Cons* 144:2684-2691
- 1079 Suryan RM, Fischer KN (2010) Stable isotope analysis and satellite tracking reveal interspecific
1080 resource partitioning of nonbreeding albatrosses off Alaska. *Can J Zool* 88:299-305
- 1081 Tartu S, Goutte A, Bustamante P, Angelier F, Moe B, Clement-Chastel C, Bech C, Gabrielsen
1082 GW, Bustnes JO, Chastel O (2013) To breed or not to breed: endocrine response to mercury
1083 contamination by an Arctic seabird. *Biol Lett* 9:000-000 doi 10.1098/rsbl.2013.0317
- 1084 Teo SLH, Boustany A, Dewar H, Stokesbury MJW, Weng KC, Beemer S, Seitz AC, Farwell CJ,
1085 Prince ED, Block BA (2007) Annual migrations, diving behaviour, and thermal biology of
1086 Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. *Mar Biol*
1087 151:1-18
- 1088 Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of migrating
1089 adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *J*
1090 *Exp Biol* 204:3895-3904
- 1091 Taylor SA, Friesen VL (2012) Use of molecular genetics for understanding seabird evolution,
1092 ecology and conservation. *Mar Ecol Prog Ser* 451:285-304
- 1093 Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on
1094 wintering areas explained by population-scale foraging segregation in space or time. *Ecology*
1095 93:122-130
- 1096 Thums M, Bradshaw CJA, Hindell MA (2011) In situ measures of foraging success and prey
1097 encounter reveal marine habitat-dependent search strategies. *Ecology* 92:1258-1270
- 1098 Thums M, Bradshaw CJA, Sumner MD, Horsburgh JM, Hindell MA (2013) Depletion of deep
1099 marine food patches forces divers to give up early. *J Anim Ecol* 82:72-83
- 1100 Tucker AD (2010) Nest site fidelity and clutch frequency of loggerhead turtles are better
1101 elucidated by satellite telemetry than by nocturnal tagging efforts: implications for stock
1102 estimation. *J Exp Mar Biol Ecol* 383:48-55
- 1103 Ueda H (2014) Mechanisms of homing ability in Pacific salmon: insights from biotelemetry,
1104 endocrinology, and neurophysiology. *Mar Ecol Prog Ser* 000:000-000

- 1105 Van Parijs SM, Janik VM, Thompson PM (2000) Display-area size, tenure length, and site
1106 fidelity in the aquatically mating male harbour seal, *Phoca vitulina*. *Can J Zool* 78:2209-2217
- 1107 Videler JJ, Weihs D (1982) Energetic advantages of burst-and-coast swimming of fish at high
1108 speeds. *J Exp Biol* 97:169-178
- 1109 Vogel S (1994) *Life in Moving Fluids: The Physical Biology of Flow*. Princeton University
1110 Press, Princeton, NJ
- 1111 Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of
1112 pelagic seabirds using individual movement data: a review. *Mar Ecol Prog Ser* 391:165-182
- 1113 Watanabe YY, Sato K, Watanuki Y, Takahashi A, Mitani Y, Amano M, Aoki K, Narazaki T,
1114 Iwata T, Minamikawa S, Miyazaki N (2011) Scaling of swim speed in breath-hold divers. *J*
1115 *Anim Ecol* 80:57-68
- 1116 Watanabe YY, Takahashi A (2013) Linking animal-borne video to accelerometers reveals prey
1117 capture variability. *Proc Natl Acad Sci USA* 110:2199-2204
- 1118 Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-
1119 propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth.
1120 *Proc R Soc B* 270:483-488
- 1121 Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL (2006) Deep-diving foraging
1122 behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol* 75:814-825
- 1123 Wearmouth VJ, Southall EJ, Morritt D, Sims DW (2012) Identifying reproductive events using
1124 archival tags: egg-laying behaviour of the small spotted catshark *Scyliorhinus canicula*. *J Fish*
1125 *Biol* 82:96-110
- 1126 Weimerskirch H, Doncaster P, Cuénot-Chaillet F (1994) Pelagic seabirds and the marine
1127 environment: foraging patterns of wandering albatrosses in relation to prey availability and
1128 distribution. *Proc R Soc B* 255:91-97
- 1129 Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient?
1130 Optimal use of wind by flying albatrosses. *Proc R Soc B* 267:1869-1874
- 1131 Westerberg H, Sjöberg N, Lagenfelt I, Aarestrup K, Righton D (2014) Behaviour of stocked and
1132 naturally recruited European eels during migration. *Mar Ecol Prog Ser* 000:000-000
- 1133 White CR, Green JA, Martin GR, Butler PJ, Grémillet D (2013) Energetic constraints may limit
1134 the capacity of visually guided predators to respond to Arctic warming. *J Zool (Lond)*
1135 289:119-126
- 1136 Whitney NM, Pratt HL, Jr., Pratt TC, Carrier JC (2010) Identifying shark mating behaviour using
1137 three-dimensional acceleration loggers. *Endan Spec Res* 10:71-82
- 1138 Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to
1139 energetic optimization. *Phil Trans R Soc Lon B* 354:193-201
- 1140 Williams TM (2001) Intermittent swimming by mammals: a strategy for increasing energetic
1141 efficiency during diving. *Amer Zool* 41:166-176
- 1142 Williams TM, Davis RW, Fuiman LA, Francis J, Le Boeuf BL, Horning M, Calambokidis J,
1143 Croll DA (2000) Sink or swim: Strategies for cost-efficient diving by marine mammals.
1144 *Science* 288:133-136

- 1145 Williams TM, Yeates L (2004) The energetics of foraging in large mammals: a comparison of
1146 marine and terrestrial predators. *Internat Cong Ser* 1275:351-358
- 1147 Wilson RP, Vandenabeele S (2012) Technological innovation in archival tags used in seabird
1148 research. *Mar Ecol Prog Ser* 451:245-262
- 1149 Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine
1150 endotherms: the case for haste in penguins. *Anim Behav* 63:85-95
- 1151 Wilson RP, Shepard ELC, Liebsh N (2007) Prying into the intimate details of animal lives: use of
1152 a daily diary on animals. *Endan Spec Res* 4:123-137
- 1153 Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use
1154 of a daily diary on animals. *Endan Spec Res* 4:123-137
- 1155 Wilson RP, McMahon CR, Quintana F, Frere E, Scolaro A, Hays GC, Bradshaw CJA (2011) N-
1156 dimensional animal energetic niches clarify behavioural options in a variable marine
1157 environment. *J Exp Biol* 214:646-656
- 1158 Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the
1159 movement and distribution of foraging animals. *Proc R Soc B* 279:975-980
- 1160 Wilson SM, Hinch SG, Drenner SM, Martins EG, Furey NB, Patterson DA, Welch DW, Cooke
1161 SJ (2014) Coastal marine and in-river migration behaviour of adult sockeye salmon en route to
1162 spawning grounds. *Mar Ecol Prog Ser* 000:000-000
- 1163 Wright AK, Ponganis K, McDonald B, Ponganis P (2014) Heart rates of emperor penguins diving
1164 at sea: implications for oxygen store management. *Mar Ecol Prog Ser* 000:000-000
- 1165 Wright S, Metcalfe JD, Hetherington S, Wilson RP (2014) Estimating activity-specific energy
1166 expenditure in a teleost fish using accelerometer loggers. *Mar Ecol Prog Ser* 000:000-000
- 1167 Yergey ME, Grothues TM, Able KW, Crawford C, DeCristofer K (2012) Evaluating discard
1168 mortality of summer flounder (*Paralichthys dentatus*) in the commercial trawl fishery:
1169 developing acoustic telemetry techniques. *Fish Res* 115:72-81
- 1170 Yoda K, Naito Y, Sato K, Takahashi A, Nishikawa J, Ropert-Coudert Y, Kurita M, Le Maho Y
1171 (2001) A new technique for monitoring the behaviour of free-ranging Adélie penguins. *J Exp
1172 Biol* 204:685-690
- 1173 Young HS, McCauley DJ, Dirzo R, Dunbar RB, Shaffer SA (2010) Niche partitioning among and
1174 within sympatric tropical seabirds revealed by stable isotope analysis. *Mar Ecol Prog Ser*
1175 416:285-294
- 1176 Zydlewski GB, Kinnison MT, Dionne PE, Zydlewski J, Wippelhauser GS (2011) Shortnose
1177 sturgeon use small coastal rivers: the importance of habitat connectivity. *J Appl Ichthyol*
1178 27:41-44



Fig. 1