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Review

Scaling from individual physiological measures to population-level demographic change: Case studies and future directions for conservation management

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ABSTRACT

Loss of biodiversity is a leading conservation issue and, accordingly, a central topic in ecological research is to predict how organisms respond to natural and anthropogenic environmental stressors. Proactive conservation science involves management strategies that rely on early identification and monitoring of threats before demographic instability is reached and may provide a more cost- and time-effective method for managing risks in an increasingly uncertain world. Using physiological measurements to predict organismal responses to environmental perturbations has historically been uncommon in the wild, despite the promise they hold as a tool to support management decisions. We provide an overview of interdisciplinary research that investigates environmental variation in conjunction with physiological processes to understand, and potentially predict, population-level demographic responses, which we refer to as Environment-Physiology-Demography, or EPD, studies. Using four EPD case studies (common murre, Cape mountain zebra, *Daphnia magna*, and common lizard) of the 29 we discovered during our literature review, we demonstrate how physiological biomarkers can be used as indicators of population change and/or stability to aid resource managers in the decision-making process. Of the 29 EPD studies we found, 72% were successful in connecting physiology to both an environmental and demographic change. Further, we outline geographic, taxonomic, and physiological biases observed across EPD studies, and the importance of considering the context-dependency of physiological traits when linking them to environmental variation and demographic processes. We encourage researchers to consider the EPD approach when investigating if and how the responses of individuals to environmental stressors translate into population-level consequences.

1. Introduction

With biodiversity declining at a quickening pace (Butchart et al., 2010), there is an increasing need to efficiently identify and act on conservation concerns. Early detection of demographic instability is critical to halting biodiversity loss, as declines can become more rapid at small population sizes due to genetic and spatial mechanisms (Peery et al., 2012). Proactive conservation approaches focus on identifying populations that are more susceptible to threats before they reach critical levels and are generally more cost effective and successful than reactive strategies (Drechsler et al., 2011). As a result, identifying tools that recognize individuals or populations experiencing negative consequences caused by environmental change would be highly valuable in conservation monitoring scenarios. Although several mechanistic tools exist (e.g. genetics, behaviour, physiology), environmental stressors such as direct anthropogenic disturbances, habitat alteration, and pollution often have a rapid physiological effect on individuals before a population decline is evident (Wikelski and Cooke, 2006; Ellis et al., 2012). As part of a broader contribution to conservation science, the discipline of conservation physiology aims to use physiological indicators to predict how natural and anthropogenic stressors may translate into changes in population demographics (e.g. declines), and how practitioners can use these tools to better manage wildlife populations. A variety of physiological traits have been proposed as potential conservation monitoring biomarkers, including metrics of stress physiology, immune function, cardiorespiratory physiology, toxicology,

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and reproductive physiology (Cooke et al., 2013a; Madliger et al., 2018).

There are several characteristics which make physiological biomarkers potentially valuable in population monitoring. First, physiology is highly sensitive, often changing rapidly to allow organisms to respond to environmental alteration. For example, Jimeno et al. (2018) recorded a change in metabolic rate in zebra finches (*Taeniopygia guttata*) within minutes of an experimental manipulation of noise level (human and natural predator sounds). Accordingly, physiological changes are predicted to occur well in advance of demographic changes (Ellis et al., 2012), affording conservation managers additional time to proactively design and implement strategies. Second, variation in physiology can often be related to the components of fitness (e.g. reproductive success, inter-annual survival) that drive population persistence. A recent meta-analysis of phylogenetic patterns revealed that both baseline and stress-induced measures of glucocorticoids (i.e. "stress" hormones) are negatively correlated with reproductive success across taxa (Schoenle et al., 2019). Indeed, one of the main applications physiology can have in conservation science is reflecting the disturbances that ultimately lead to decreased fitness through mechanisms such as compromises to immune function, reduced energy acquisition or utilization, or endocrine dysfunction (Busch and Hayward, 2009; Cooke and O'Connor, 2010; Cooke et al., 2013a; Madliger and Love, 2015). Third, physiological traits can provide an objective measure of an organism's perspective of its environment, therefore eliminating the bias that may come with interpreting environmental change from a human perspective (Busch and Hayward, 2009; Cooke et al., 2013b; Wilson et al., 2015). For example, using heart rate measures obtained from GPS-collared brown bears (*Ursus arctos*), Støen et al. (2015) mapped seasonal "landscapes of fear" associated with increased human presence and activity.

While there is much work outlining the potential of physiology to predict population-level change, studies that simultaneously link environmental change, physiology, and population-level dynamics (hereafter termed Environment-Physiology-Demography, or EPD, studies) have been relatively limited. For example, Beehner and Bergman (2017) reviewed 140 studies measuring stress (i.e. glucocorticoid) physiology in non-human primates and did not uncover a single study that simultaneously measured environmental quality, glucocorticoid levels, and fitness. This is most likely due to several interacting factors, including the necessity of multidisciplinary expertise and the time and budgetary commitment required to collect longitudinal datasets capable of estimating population changes. However, such studies are necessary to confirm that individual measures of physiology can indeed be scaled to the level of populations and subsequently applied as a monitoring tool for conservation science and management. Here, to investigate prevalence of the EPD approach and the role it could play in conservation science, we identify studies in the primary literature that simultaneously measured: (1) environmental quality or change in an environmental variable, (2) levels of a physiological trait, and (3) a change in population demographics (i.e. a change in population size or abundance). Research using noninvasive tools (no physical capture or handling of an animal), nonlethal tools (animals experience capture or restraint for sample collection), and lethal tools (sampling necessitates animal sacrifice) were included (Baker and Johanos, 2002; Pauli et al., 2009). Studies using lethal methods were included, in particular, if the research was directed towards understanding potential biomarkers for conservation-focused physiological assessments.

We constrained our coverage to animal taxa, but acknowledge that a similar investigation in plants is worthwhile yet beyond our scope and expertise. We defined physiology broadly and similarly to Cooke et al. (2013a) to include functional and mechanistic responses at all scales. While we did not consider body mass or size-corrected body mass as physiological traits, we did include more specific metrics of condition (e.g. total fat content) and growth rate. In addition, we specifically focused on changes at the population level for our demographic metric, rather than proxies or components of fitness measured at the individual level, as these may not always be an accurate indication of how a population will change as a whole. We acknowledge there is a vast array of physiological traits at the disposal of ecologists and conservation scientists (see Madliger et al., 2018), and that they vary in their response time to environmental perturbations. Some physiological traits may require days to weeks for a response to be measurable, while other traits can change in the minutes to hours following an environmental perturbation. As we believe the variation in integrating environmental quality over different time scales to be a strength of the conservation physiology toolbox, we have considered all physiological traits to warrant investigation as conservation monitoring biomarkers.

Our study presents a detailed cross-section of our findings as a series of four case studies that were chosen to illustrate the diversity of taxa, physiological traits, geographic areas, and conservation concerns that have been addressed by the EPD approach. Only studies which measured a biomarker, environmental variable, and demographic response in a population occurring in the wild or in a laboratory setting were included, excluding studies which modelled any of the three EPD components. We do, however, provide a discussion about the use of modelling in EPD research. For each case study, we provide an overview of the background and conservation issue for the study organism and review how environmental quality, physiology, and population change were linked. Following these examples, we outline the overall success of the EPD methodology and the implications of our results, including a discussion of geographic, taxonomic, and physiological biases, the need for species-specific investigations, and the context-dependency of physiological traits.

2. Case studies linking environment, physiology, and demography (EPD)

We conducted a comprehensive literature review up until February 2019 of English, primary academic literature (no review papers or gray material) using Web of Science Core Collection. To identify potential EPD studies, our search string included three sets of terms: 1) environmental terms (e.g. "habitat quality"); 2) physiological terms (e.g. "glucocorticoid"); 3) demographic terms (e.g. "population decline"). We manually excluded Web of Science Core Collection categories irrelevant to our search, such as those pertaining to medicine, human physiology, microbiology, geology, mathematics, physics, etc. The full search string can be viewed in the Supplementary Material (Appendix A1). In total, our search yielded 3810 articles. After sorting the results by relevance, we visually inspected the titles and abstracts of results until no articles fulfilling our search criteria were discovered. This process resulted in a total of 1500 search results that potentially used the EPD methodology. We individually screened results manually to confirm whether a study employed the full EPD methodology including identification of an environmental stressor, measurement of a physiological marker, and an associated change in population-level demographics. In total, we found 29 studies that were representative of the EPD methodology (Table 1). Below, we present four case studies as examples of how the EPD approach can potentially be valuable for conservation managers.

2.1. Baseline glucocorticoids link food stress and population decline in common murre in the circumpolar Arctic

2.1.1. Background

The common murre (*Uria aalge*) is a seabird adapted to the cool coastal waters of the Northern Hemisphere. One of the most abundant seabirds within its range, the common murre nests in large colonies on cliffs and rocky islands and feeds on a variety of marine organisms, with fish, cephalopods, and crustaceans making up most of its diet (Ainley et al., 2002). The distribution and abundance of seabirds has been shown to correlate with prey abundance (Hunt et al., 1996), so changes

Table 1

Summary of studies linking environmental quality, physiology, and demography (EPD) in animals. Physiological subdisciplines categorized as per Madliger et al. (2018).

Organism	Taxa	Geographic location	Environmental variable	Physiological metric (direction of response)	Physiological subdiscipline (s)	Demographic response (direction of response)	Reference
Green-eyed treefrog (*Litoria genimaculatta*)	Amphibian	Northern Queensland, Australia	Rainfall	Total fat-body mass (decreasing)	Bioenergetics and nutritional physiology	Population abundance (decrease)	Richards and Alford (2005)
Eastern yellow robin (*Eopsaltria australis*)[a]	Bird	Brigalow Belt South Bioregion, Queensland, Australia	Woodland extent	Heterophil to lymphocyte ratio (increasing)	Stress physiology	Extirpation risk (no effect)	Cosgrove et al. (2017)
12 Fynbos-resident bird species (Passeriformes)	Bird	Fynbos biome, South Africa	Temperature	Evaporative water loss (increasing), resting metabolic rate (no effect), body temperature (no effect)	Bioenergetics and nutritional physiology	Population abundance (decreasing)	Milne et al. (2015)
Common murre (*Uria aalge*)	Bird	Cook Inlet, Gulf of Alaska, USA	Food abundance	Glucocorticoids - plasma corticosterone (increasing)	Stress physiology	Population abundance (decreasing)	Kitaysky et al. (2007)
South polar skua (*Catharact maccormicki*)	Bird	Adélie Land, Antarctica	Persistent organic pollutants (POPs) in blood (environmental proxy)	Glucocorticoids - plasma corticosterone, (increasing), prolactin (no effect)	Stress physiology; reproductive physiology	Population growth rate (decreasing)	Goutte et al. (2018)
Wandering albatross (*Diomedea exulans*)	Bird	Possession Island, southwestern Indian Ocean	Age and sex	Plasma oxidative stress (increasing), plasma haptoglobin (increasing)	Stress physiology	4-year population-level survival rate (no effect), reproductive performance (decreasing)	Costantini et al. (2015)
Four fish species (*Pimephales promelas*, *Margariscus margarita*, *Catostomus commersonii*, *Salvelinus namaycush*)[a]	Fish	Ontario, Canada	Environmental estrogens	Vitellogenin (VTG) induction (increasing), histopathological damage (increasing)	Reproductive physiology	Population abundance (decreasing)	Palace et al. (2009)
White grunt (*Haemulon plumierii*)[a]	Fish	Bight of Old Robinson, Abaco, Bahamas	Seagrass cover	Growth rate proxy - RNA:DNA (no effect)	Bioenergetics and nutritional physiology; genetics	Population abundance (increasing)	Yeager et al. (2012)
Four fish species (*Scartichthys viridis*, *Graus nigra*, *Auchenionchus microcirrhis*, *Girella laevifrons*)	Fish	Coastal waters off central Chile	El Niño and La Niña events	Somatic growth rates (decreasing)	Bioenergetics and nutritional physiology	Population abundance (decreasing)	Hernandez-Miranda and Ojeda (2006)
Baltic clam (*Macoma balthica*)	Invertebrate	Gulf of Finland, northern Baltic Sea	Hypoxia	Catalase (no effect), glutathione reductase (increasing), glutathione S-transferase (no effect), acetylcholinesterase enzyme (decreasing)	Enzyme activity	Population abundance (decreasing)	Villnäs et al. (2019)
Daphnia magna	Invertebrate	Laboratory	Organophospha-te pesticide concentration	Cholinesterase activity (decreasing)	Enzyme activity	Population growth rate (decreasing)	Duquesne and Küster (2010)
Daphnia pulex	Invertebrate	Storrs Pond, New Hampshire, USA	Toxicity of arsenic	Heat shock protein - 83 mRNA (increasing)	Stress physiology	Population abundance (decreasing)	Chen et al. (1999)
Glanville fritillary butterfly (*Melitaea cinxia*)	Invertebrate	Åland Islands, Finland	Temperature	Serpin-1 (increasing), vitellin-degrading protease precursor (increasing), phosphoglucose isomerase (increasing)	Enzyme activity; genetics	Population abundance (increasing)	Saastamoinen et al. (2013)
Grasshopper (*Chorthippus albonemus*)	Invertebrate	Inner Mongolia, China	Livestock grazing	Transcriptome activity: *betA* and *CHDH* genes, genes involved in serine-type peptidase activity and development, adaptive genes (increasing), genes involved in ribosomal processes (decreasing)	Genetics	Population abundance (increasing)	Qin et al. (2017)
Rotifer (*Brachionuscalyciflorus*)	Invertebrate	Laboratory (Wuhan, China)	Toxicity of cyanobacterial blooms	Reactive oxygen species (increasing), malondialdehyde (increasing), glutathione (increasing), superoxide dismutase activity (decreasing), catalase activity (decreasing), mRNA expression of MnSOD, CuZnSOD, and CAT (decreasing)	Stress physiology	Population growth rate (decreasing)	Liang et al. (2017)
Two coral species (*Agaricia agaricites*, *Agaricia tenuifolia*)	Invertebrate	South-central Belize	Ocean warming	Heat shock protein expression (increasing)	Stress physiology	Population abundance (increasing)	Robbart et al. (2004)

(*continued on next page*)

Table 1 (*continued*)

Organism	Taxa	Geographic location	Environmental variable	Physiological metric (direction of response)	Physiological subdiscipline (s)	Demographic response (direction of response)	Reference
Red colobus monkeys (*Procolobus rufomitratus*)[a]	Mammal	Kibale National Park, Uganda	Food availability and quality	Glucocorticoids - faecal corticosterone (increasing)	Stress physiology	Population abundance (no effect)	Chapman et al. (2015)
Elk (*Cervus elaphus*) and wolf (*Canis lupus*)[a]	Mammal	Yellowstone National Park (elk + wolves), Voyageurs and Isle Royale national parks (wolves), USA	Snowmobile traffic	Glucocorticoids - faecal corticosterone (increasing)	Stress physiology	Population abundance (no effect)	Creel et al. (2002)
White-tailed deer (*Odocoileus virginia*)[a]	Mammal	Eastern Rio Grande Plains of south Texas, USA	Agricultural root plowing	Blood serum urea nitrogen (no effect), urinary urea nitrogen and creatinine (no effect), faecal and rumen nitrogen (no effect)	Bioenergetics and nutritional physiology	Population abundance (no effect)	Ruthven et al. (1994)
Asian elephant (*Elephas maximus*)	Mammal	Myanmar	Climate (temperature and rainfall)	Glucocorticoids - faecal corticosterone (increasing)	Stress physiology	Population abundance (decreasing)	Mumby et al. (2015)
Black howler (*Alouatta pigra*)	Mammal	Southern Belize, Central America	Hurricane	Glucocorticoids - faecal corticosterone (increasing)	Stress physiology	Population abundance (decreasing)	Behie and Pavelka (2013)
Cape mountain zebra (*Equus zebra zebra*)	Mammal	Cape Town, South Africa	Forage quality	Glucocorticoids - faecal corticosterone (increasing), androgens - faecal testosterone (increasing)	Stress physiology; reproductive physiology	Population growth rate (decreasing)	Lea et al. (2018)
Common voles (*Microtus arvalis*)	Mammal	León province, Spain	Agricultural land cover	Glucocorticoids - faecal corticosterone (increasing)	Stress physiology	Population abundance (increasing)	Navarro-Castilla et al. (2014)
Red deer (*Cervus elaphus*)	Mammal	Iberian Peninsula	Diet quality	Faecal nitrogen content (increasing) and kidney fat index (increasing)	Bioenergetics and nutritional physiology	Population abundance (increasing)	Santos et al. (2018)
Ringed seal (*Pusa hispida*)	Mammal	Hudson's Bay, Canada	Sea ice dynamics	Body condition (decreasing), glucocorticoids - blubber corticosterone (increasing)	Bioenergetics and nutritional physiology; stress physiology	Population abundance (decreasing)	Ferguson et al. (2017)
Tree dtella (*Gehyra variegata*)[a]	Reptile	Kinchenga National Park, New South Wales, Australia	Temperature and rainfall	Body condition (decreasing), growth (decreasing)	Bioenergetics and nutritional physiology	Population abundance (no effect)	Grimm-Seyfarth et al. (2018)
Common lizard (*Zootoca vivipa*)[a]	Reptile	Massif Central Mountains, France	Thermal condition	Glucocorticoids - plasma corticosterone (decreasing)	Stress physiology	Extinction risk (no effect)	Dupoué et al. (2018)
Common lizard (*Zootoca vivipara*)	Reptile	Massif Central Mountains, France	Ambient temperature	Telomere length (decreasing)	Stress physiology; genetics	Extinction risk (increasing)	Dupoué et al. (2017)
Galapagos marine iguana (*Amblyrhynchus cristatus*)	Reptile	Galapagos Islands	Famine events	Glucocorticoids - plasma corticosterone (increasing)	Stress physiology	Population abundance (decreasing)	Romero and Wikelski (2001)

[a] Indicates EPD studies that did not find a relationship between all three variables.

to marine ecosystems are expected to affect seabirds like the common murre. As with other species of birds, the main glucocorticoid in common murres is corticosterone, a hormone involved in the energetic and behavioural response to stressors and workload (Astheimer et al., 1992; Sims and Holberton, 2000). While increased corticosterone may be beneficial in the short-term as an acute response to cope with a stressor (Sims and Holberton, 2000), chronically elevated levels (elevated baseline corticosterone) caused by chronic stress may result in negative long-term fitness effects as individuals must alter behaviour to invest resources towards coping with the stressor rather than for reproductive activities (Bonier et al., 2009a; Bonier et al., 2009b). Further, immunosuppressive properties of glucocorticoids (Auphan et al., 1995; El-Lethey et al., 2003) may leave an individual more susceptible to being immunocompromised and thereby further reduce survival or the ability to reproduce successfully.

2.1.2. Conservation issue

Populations of marine predators in the north Pacific are declining (Hunt and Byrd, 1999). Several studies have hypothesized that the reduced fitness in marine predators is linked to food-related stress during breeding (Merrick et al., 1987; Hunt, 1999), but few studies have shown direct evidence of this relationship. This link is important to identify because it provides a mechanism for population declines, potentially allowing conservation managers to determine the underlying cause and therefore target management strategies appropriately. Further, as fish stocks are indeed declining world-wide (Myers and Worm, 2003), understanding the consequences of these declines is important for conservation scientists and those invested in preserving the world's biodiversity.

2.1.3. Links among environment, physiology, and demography

Kitaysky et al. (2007) aimed to test the hypothesis that food-related stress would result in reduced fitness in common murres inhabiting two colonies in Alaska. To do so, their study measured both baseline and acute levels of corticosterone at a colony with a decreasing population and at a colony with an increasing population to determine if variation in physiology related to changes in food abundance, fecundity, and individual survival. The authors demonstrated that food abundance, a measure of fish abundance in the waters surrounding the colonies at three time scales (current 2 weeks, current month, and previous month), had a significant negative correlation with both baseline (all time scales) and acute (previous month) corticosterone levels. This correlation demonstrates a possible link between an environmental change (food abundance) and a physiological change (corticosterone levels). Their findings also showed a negative correlation between baseline corticosterone levels and measures of fecundity, namely hatching success, fledging success, and reproductive success. The link between baseline corticosterone and measures of fecundity illustrates how a change in physiology may link to a change in population fitness. Indeed, the authors confirmed that the colony with a declining population of common murre showed a significant negative correlation between baseline corticosterone and survival of individual birds. Overall, the work by Kitaysky et al. (2007) suggests that corticosterone secretion (a physiological change) is a mechanism which links an environmental change (degraded food stocks) to a demographic change (decreased fitness and population decline) in the common murre.

2.2. Faecal glucocorticoids and androgens predict population decline in Cape mountain zebras of South Africa

2.2.1. Background

Cape mountain zebra (*Equus zebra zebra*) are found in thicket and grassland habitats located primarily in the Cape Floristic Region of the Eastern and Western Cape provinces of South Africa. The Mediterranean climate in this region is known for high biodiversity and a high number of endemic species (Cowling and Holmes, 1992; Boshoff et al., 2016). Many grass species grow abundantly in the region and are the Cape mountain zebra's primary food source (Penzhorn, 1988). Populations of Cape mountain zebra occur across high-quality and low-quality habitats varying in the abundance and quality of grass (Lea et al., 2016). As outlined in the case study above, glucocorticoids have been proposed as potentially valuable biomarkers of stress and fitness as they can fluctuate in response to environmental conditions and changes to social environments (Busch and Hayward, 2009; Mehta and Josephs, 2010). In particular, faecal glucocorticoids represent an integrated noninvasive metric of physiological stress over a species-specific duration, often 6–24 h (Palme, 2005; Sheriff et al., 2011). A recent meta-analysis indicated that faecal glucocorticoids consistently increase under periods of human disturbance (Dantzer et al., 2014).

The female defence polygyny social structure of the Cape mountain zebra consists of breeding group populations with a single stallion, a maximum of five unrelated mares and their offspring, and excess stallions that form bachelor groups (Penzhorn, 1979; Linklater, 2000). Androgens are a steroid hormone associated with secondary sexual characteristic development (Foradori et al., 2008) that influence social behaviours related to breeding, dominance, and aggression (Mehta and Josephs, 2010). High levels of androgens may also reduce fitness through immune suppression, reduced parental care, aggression towards mating partners and offspring, and overall high energetic costs (Wingfield et al., 2001; Miles et al., 2007). Thus, it is expected that androgen levels indicate the physiological effects of sexual behaviour and social conditions for Cape mountain zebra populations (Mehta and Josephs, 2010; Lea et al., 2018).

2.2.2. Conservation issue

Cape mountain zebra populations, listed as vulnerable by IUCN (Novellie, 2008), have been declining for decades and are the focus of many conservation projects due to extremely low population numbers. Active conservation has helped the population rebound from a severe bottleneck of 80 individuals to approximately 5000 individuals (Hrabar and Kerley, 2015). Yet, there are numerous conservation management challenges because the subspecies is managed as a metapopulation of 75 isolated populations. Models linking breeding site selection and population dynamics demonstrate that population density and growth rates are lower in low quality habitat, driven by lower survival and reproduction rates (Pulliam and Danielson, 1991). Populations with lower densities and growth rates may require more active conservation measures like consistent translocation of individuals from populations in high quality habitat (Pulliam, 1988). As a result, predicting population trends may provide insight for implementation of active conservation measures to avoid a population crash.

2.2.3. Links among environment, physiology, and demography

Lea et al. (2018) measured faecal glucocorticoid hormones and faecal androgens to estimate chronic stress and male reproductive status in Cape mountain zebras. Glucocorticoids were used to measure stress in response to changes in environmental conditions, and androgens were assessed to measure secondary sexual characteristics, such as intrasexual competition and sex ratio skew (Wingfield et al., 2001; Miles et al., 2007; Busch and Hayward, 2009). Together, the measurement of faecal glucocorticoids and androgens represent chronic exposure of circulating hormone levels experienced during the gut passage time (Dantzer et al., 2014) and provide an approximation of overall population health (Lea et al., 2018). Lea et al. (2018) found that faecal glucocorticoids were highest prior to the summer rainfall and elevated in habitats with lower grass abundance. Additionally, faecal androgens were found to be positively associated with higher male sex ratios and negatively associated with female fecundity. Finally, faecal glucocorticoids were negatively associated with population growth rates. A chronic increase in glucocorticoids leads to a diversion of energy away from reproduction commonly causing lower population growth (McEwen and Wingfield, 2003), thus, populations with chronically higher glucocorticoid production often display population declines (Lea et al., 2018). The authors illustrate the use of integrating multiple physiological subdisciplines (see Table 1; Madliger et al., 2018) in EPD research: glucocorticoid (stress physiology) and androgen (reproductive physiology) levels provided a link between physiology, environmental conditions, and population-level fitness. Populations with high glucocorticoid levels may be declining and, as a result, may require active translocation of individuals from healthy populations to improve population growth. The authors illustrate how noninvasive monitoring through faecal hormones has promise as a surrogate for direct population monitoring.

2.3. Cholinesterase enzyme activity as a biomarker of deleterious organophosphates in Daphnia magna in lentic freshwater systems

2.3.1. Background

Daphnia magna is a small freshwater crustacean that has long been used in laboratory studies as a model organism for ecotoxicology (Guilhermino et al., 1996; Petrie et al., 2015) and in water quality monitoring efforts (Storey et al., 2011). Being particularly sensitive to organophosphate pollution from insecticide application, *D. magna* is a useful model species for studying lethal and sub-lethal effects of a variety of toxicants across levels of biological organization (Duquesne and Küster, 2010). *Daphnia* spp. play an important role in aquatic food webs, as predators of microorganisms (e.g. algae) and as a significant food source for many small fishes (Duquesne and Küster, 2010). Monitoring environmental toxicant concentrations in *Daphnia* spp. using sublethal endpoints can provide valuable insight into the health of both *Daphnia* spp. populations and the ecosystems in which they are found.

The inhibition of cholinesterase (ChE) enzymes interferes with proper neuron function, leading to both sublethal effects and potentially death (particularly in invertebrates that are often exposed to ChE inhibitors in the form of agricultural insecticides; Kristoff et al., 2010). Specifically, ChE inhibition consists of the removal of the neurotransmitters acetylcholine (ACh) or butyrylcholine (BCh) at nerve synapses, leading to ACh/BCh build-up and uncontrollable firing of the afflicted neuron (Fulton and Key, 2001). Organophosphate pesticides, having entered freshwater systems from sources like agricultural runoff, target and inhibit ChE (Duquesne, 2006) and force the affected organism to synthesize new cholinesterases. The inhibition of ChE activity is a sensitive physiological endpoint (Duquesne, 2006) that can be reliably detected in *D. magna*, and therefore used to measure sublethal effects of organophosphate exposure in this species.

2.3.2. Conservation issue

Toxic organic pollutants frequently enter aquatic systems through agricultural runoff and industrial and urban pollution, with a panoply of potential adverse impacts on wildlife and ecosystem health (Baldwin et al., 2016). In addition to providing insight into human pollutant output through water quality monitoring and analytical chemistry, toxicological studies on ubiquitous model organisms or particularly sensitive species can make significant contributions to the way humans monitor and mitigate the ecological consequences of such pollution by examining lethal and sublethal effects of known toxicants on wildlife. As one specific example, understanding the sublethal effects of toxicants (e.g. organophosphates, a common class of pesticide used in agriculture) on *D. magna* can be used to link levels of contamination to population-level effects, with implications for ecosystem health and environmental monitoring (Farré and Barceló, 2003).

2.3.3. Links among environment, physiology, and demography

Concentrations of the organophosphate paraoxon-methyl at $1.0\,\mu g\,L^{-1}$ significantly inhibited ChE activity in *D. magna*, increased swimming velocity, and decreased filtration activity (i.e. food consumption). At increased paraoxon-methyl concentrations ($\geq 1.5\,\mu g\,L^{-1}$) the overall increase in energy expenditure from synthesizing new ChE enzymes and higher swimming velocities, along with the reduced energy intake from decreased filtration activity, was linked to poorer growth, development, and reproductive performance detectable at the population level (Duquesne and Küster, 2010). Previous toxicological work with *D. magna* showed a decrease in population growth rate following exposure to sublethal concentrations of organophosphates (Duquesne, 2006). The relationship between concentration and severity of symptoms appears to be divisible into several ranges: at lower concentrations (approximately $< 1.0\,\mu g\,L^{-1}$) the sublethal effects are mild enough to be overcome by *D. magna;* at moderate concentrations (between approximately 1.0 and $1.5\,\mu g\,L^{-1}$) sublethal effects are elicited with visible impacts on individuals and (in the long-term) populations; and, at high concentrations lethal effects are observed (Duquesne, 2006; Duquesne and Küster, 2010). To maximize the efficacy of long-term monitoring of organophosphates with *D. magna*, conservationists working in contaminated aquatic systems should seek out the primary sources of organophosphates and work with land managers to minimize new contaminant inflow. Biomonitoring of *D. magna* can play a critical role in assessing the effectiveness of such initiatives.

2.4. Telomere length predicts climate change-induced extinction risk in common lizards of the Massif Central region, France

2.4.1. Background

The common lizard (*Zootoca vivipara*) is a small, cold-adapted, ground-dwelling lacertid widely distributed across Eurasia. Ectothermic species such as the common lizard are generally incapable of internally regulating body temperature, and thus must rely on their surrounding thermal environment to achieve optimal body temperature (Angilletta and Angilletta, 2009). To do so, ectotherms often behaviourally thermoregulate (e.g. basking or seeking shade) to optimize performance and fitness (Clusella-Trullas et al., 2011; Huey et al., 2012). Mountain populations of the common lizard recently went extinct at low altitudes in the southern region of their European range, likely as a result of climate change-induced warmer and drier weather (Sinervo et al., 2010; Le Galliard et al., 2012). The common lizard is a particularly interesting species to study from a synergistic climate change-physiology perspective as (1) range-restricted species, like mountain species, have experienced some of the most extreme range contractions caused by recent climate change (Parmesan, 2006), and (2) ectothermic species may be more susceptible to decline as their basic physiological functions like locomotion, growth, and reproduction are strongly influenced by their surrounding thermal environment (Deutsch et al., 2008).

In ecological systems, a tipping point is a catastrophic bifurcation which will drive a system towards an alternate state from which it cannot return directly to its former state (Scheffer et al., 2012; Donohue et al., 2016). In deteriorating environments, tipping points historically precede populations collapses. Identifying early warning signals before the catastrophic collapse of a population may aid in successful environmental management (Dai et al., 2012). Telomere length analysis has been suggested as one such early warning signal. Telomeres are the repetitive non-coding DNA sequences and protein complexes that cap the end of eukaryotic chromosomes (Blackburn, 1991) and their attrition (i.e. shortening) is thought to play a central role in cell deterioration with advancing age (Heidinger et al., 2012), accelerating after repeated exposure to chronic life stress (e.g. environmental stressors; Monaghan and Haussmann, 2006; Horn et al., 2010). As telomere length reflects biological age (in contrast to chronological age), and thus reproductive status and capability, the inclusion of this biomarker into predictive conservation science could dramatically enhance recovery plans of wild populations (Nakagawa et al., 2004; Barrett et al., 2013; Breuner et al., 2013).

2.4.2. Conservation issue

The natural compensatory responses of species to environmental change are limited: relocate to more favourable conditions (i.e. spatial distribution shift) or adjust to new environments via evolutionary adaptation, or behavioural or physiological plasticity (Scheffers et al., 2016). Failure to redistribute or adjust results in demographic collapse and extinction (Sinervo et al., 2010). Current research suggests that while extinction risks from climate change are species- and population-specific and can vary considerably, they are expected to accelerate for every degree rise in global temperatures (Thomas et al., 2004; Urban, 2015). It is therefore paramount to enhance our understanding of climate change impacts on ecological processes at an individual and population scale to conserve global biodiversity (Martin and Watson, 2016; Scheffers et al., 2016).

2.4.3. *Links among environment, physiology, and demography*

Dupoué et al. (2017) used a 10-year (2005–2015) dataset from ten natural populations of common lizards at different altitudes to determine if telomere length could be used as a biomarker to measure demographic responses to warmer temperatures. Relative common lizard abundances significantly decreased over the study period in low-altitude populations with warmer ambient temperatures. As predicted, a non-linear relationship was indeed found between telomere length and population extinction risk with shorter telomeres in populations facing highest risks of extinction (lowest altitudes, highest minimal daily temperatures, negative changes in relative abundance; see Supplementary Table S1 in Dupoué et al., 2017). Dupoué et al. (2017) therefore identified a physiological parameter, telomere length, as a reliable early warning signal to assess the stability of a wild population and provide a useful tool for future studies investigating climate change impacts on extinction risk from the individual to population scale.

3. Discussion

3.1. *Overall success of EPD methodology*

We identified 29 studies that utilized the EPD approach (Table 1). Of these, 8 were unable to link the three EPD metrics together. Our results were encouraging regarding the potential for incorporating a variety of physiological mechanisms into population monitoring and predictive/proactive conservation across a diversity of taxa. We acknowledge that there could be some publication bias, with studies finding negative results potentially less likely to be published, and we urge scientists to add such investigations to the literature as they are important for determining the value of mechanistic approaches for conservation science. Indeed, the 8 studies we identified that were unable to connect EPD metrics offer insight into specific scenarios where difficulties may arise.

Ruthven et al. (1994), Creel et al. (2002), Palace et al. (2009), Yeager et al. (2012), Chapman et al. (2015), Cosgrove et al. (2017), Dupoué et al. (2018), and Grimm-Seyfarth et al. (2018) successfully measured environmental variables (e.g. fragmentation, human-induced disturbances, pollution), physiological metrics (e.g. estrogens, body condition, glucocorticoid levels), and demographic processes (e.g. extirpation risk, population abundance). However, when drawing conclusions from the EPD metrics that they measured, each study failed to link all three components together and determine a population-level effect. There does not appear to be a pattern in the type of physiological subdiscipline used within these unsuccessful EPD studies with four studies measuring stress physiology, three studies measuring bioenergetics and nutritional physiology, and one study measuring reproductive physiology. Quantifying parameters from these physiological subdisciplines could indicate that they are poor subdisciplines in understanding population-level changes; however, it is more likely that the study system itself in each case had confounding factors which resulted in lack of success. Indeed, two of the physiological subdisciplines, stress physiology and bioenergetics and nutritional physiology, were likewise the most abundant subdisciplines used throughout the 29 EPD studies (17/29 and 8/29, respectively). Two studies (Palace et al., 2009 and Yeager et al., 2012) were unsuccessful in linking population abundance change to environmental and physiological metrics, and the remaining six studies were unable to detect a demographic change, potentially because the environmental and/or physiological metrics chosen were unsuitable for that particular study. The 8 studies each acknowledged limitations of their research and discussed the importance of considering confounding factors (e.g. behavioural adaptations to stressors, seasonal and annual changes in distributions, the biomarker chosen, and several others like health, food availability, age, sex, reproductive history, and life cycle stage). Furthermore, some studies (Ruthven et al., 1994; Yeager et al., 2012; Cosgrove et al., 2017; Grimm-Seyfarth et al., 2018) suggest that demographic processes may have been better explained by multiple metrics of physiology, indicating a need to sometimes measure a suite of physiological traits, rather than relying on a single metric to represent the effect of complex environmental stressors on demographics (Madliger and Love, 2014). No taxonomic bias was observed, as these unsuccessful EPD studies included birds, mammals, fishes, and reptiles.

As an alternate avenue to assess potential causes of a failed EPD linkage, we can compare two studies that used the same biomarker in similar species, with one successfully connecting EPD metrics (Behie and Pavelka, 2013: black howler monkeys [*Alouatta pigra*]), and one that did not (Chapman et al., 2015: red colobus monkeys [*Procolobus rufomitratus*]). Both EPD studies evaluated how changes in food availability and quality could influence glucocorticoid levels and subsequently affect population demographics of monkey species. Behie and Pavelka (2013) found that, due to Hurricane Iris, black howler monkeys in southern Belize were forced to forage on less nutritional food (e.g. foliage compared to fruit) resulting in post-hurricane-increased glucocorticoid levels and negatively correlating with population density (i.e. population decline). Behie and Pavelka (2013) therefore conducted successful EPD research by linking increased glucocorticoid levels to nutritional stress with consequential population declines. Chapman et al. (2015) likewise assessed changes in food availability and quality for a monkey species but was not able to link EPD metrics together. They investigated diet of the red colobus monkey within a protected area in Uganda to determine if nutritional decreases in fragmented habitats influenced population demographics. Red colobus monkeys residing in degraded forest fragments where diet was poor showed stress levels more than twice those in unfragmented forest areas, with consumption of a low-quality diet in one month resulting in higher glucocorticoid levels in the subsequent month. However, despite apparent reduced diet quality and increased stress levels, red colobus monkey populations remained stable. The authors note that increases in group size and behavioural flexibility may have supported red colobus monkey population stability, suggesting that it may be necessary to monitor social and behavioural responses to understand how changes in environmental quality might influence demography. It is additionally possible that the nature of the environmental disturbance could be driving the ability to establish an EPD linkage: the black howler monkey population underwent decline as a result of an unexpected, intense change in food quality due to a hurricane, whereas the red colobus monkey population remained stable even in poor-diet habitats that had been slowly degraded over decades.

Overall, failure to connect EPD metrics may occur if the environmental change is cyclical (e.g. seasonal variation) or the change is not severe enough to elicit a physiological response (i.e. if the environmental change does not constitute a stressor). This was likely the case in Cosgrove et al. (2017), where woodland extent within a 500-m radius was not correlated with heterophil:lymphocyte ratio, an indication of chronic stress, in eastern yellow robins (*Eopsaltria australis*). The authors speculate that habitat fragmentation may not have been as important as total habitat loss for robin persistence, and it is therefore also possible that the environmental variable measured may not have adequately captured the total habitat change robins were facing across the landscape. Lack of an EPD connection may also occur if organisms are able to compensate for physiological changes associated with an environmental disturbance. Creel et al. (2002) found that faecal glucocorticoid levels were elevated in both elk (*Cervus elaphus*) and wolves (*Canis lupus*) in North American national parks in response to snowmobile activity, but they did not observe any concomitant changes in population demographics. They suggest that elk and wolf populations compensate for the physiological effects of increased snowmobile activity and propose that the large snowmobile tracks left in snow may even have benefited wolves by making travel across the landscape easier. Finally, Palace et al. (2009), Cosgrove et al. (2017), and Dupoué et al. (2018) discuss the importance of understanding and accounting for life history aspects of a given species, as well as spatial distribution, and the underlying physiological role of the biomarker of interest when conducting EPD research. In cases such as these, it may be useful to implement an approach which measures several variables per EPD metric, as mentioned above.

3.2. Geographic, taxonomic, and physiological biases

Since EPD studies are part of the broader conservation literature, it is worth considering whether they are influenced by the same biases that affect conservation science as a whole. Biases in the geographic distribution of available scientific literature and effective conservation action exist on multiple spatial scales and may represent imbalances on the level of biogeographic realms (e.g. palearctic, [Jenkins and Joppa, 2009]), biomes (e.g. tundra, [Lawler et al., 2006]), or countries (influenced by socioeconomic development, politics, etc. [Kark et al., 2009; Martin et al., 2012]). Protected status is more likely to be assigned within ecoregions and habitat types that are less accessible and thus less likely to be exploited by humans (Joppa and Pfaff, 2009), and the proportion of terrestrial ecology studies undertaken in protected areas is disproportionately high (Martin et al., 2012). Therefore, it is plausible that there exist important relationships between the amount or proportion of protected area within a given geographic area, the quantity of available conservation research within such an area, and the usefulness of such research to conservation managers. The majority of EPD studies found appear to be concentrated in relatively affluent, English-speaking areas (Fig. 1). Additionally, we found few marine EPD studies, possibly due to difficult accessibility to study sites and safe acquisition of samples (e.g. in-water capture of animals, increased risk of inducing barotrauma in deep-water species).

There also exists considerable variation in the feasibility of using different physiological metrics (particularly nonlethal metrics) to assess individual fitness and population-level effects across species. For example, glucocorticoids in mammals and birds can be measured noninvasively through faecal glucocorticoid analysis (e.g. Dantzer et al., 2016) or more invasively through blood sampling (e.g. Richardson et al., 2018), but the former is not feasible in fish and the latter is not always possible (nonlethally) in insects. The relative prevalence of lethal/nonlethal/noninvasive sampling appears subject to biases in taxonomy and physiological metrics. Lethal sampling is generally considered more "acceptable" in invertebrates than vertebrates (McCravy, 2018) even when nonlethal alternatives are available (e.g. Lecq et al., 2015). Although conservation work often involves at-risk species and lethal sampling would therefore be inappropriate, we did not limit our findings to exclude lethal methods. In particular, the lethal *D. magna* case study was selected as it is unique in that the EPD aspect did not concern the conservation of the species but instead focused on toxicology and applications to environmental monitoring with implications for larger groups of species/ecosystem health.

We found a bias towards terrestrial and freshwater work, and additionally EPD studies were not evenly distributed across taxonomic groups. Taxonomic biases in conservation science are well-documented, with disproportionate representation of charismatic species and higher-level taxa (primarily vertebrates and especially mammals; Donaldson et al., 2016). The EPD studies in Table 1 are predominantly focused on vertebrates, with a large proportion (31%) investigating mammalian species. The studied species within a given taxonomic group were fairly diverse, and most species would not be described as charismatic (e.g. vole, Baltic clam, common murre) relative to species that are most often stereotyped as being charismatic in conservation science (e.g. polar bears, pandas, large sharks). Also, convenient laboratory model species such as *Daphnia* spp. were not overrepresented in EPD studies featuring invertebrate species.

A high proportion of the examined EPD studies relied on tools in the physiological subdiscipline of stress physiology (17/29), with 11 of the 29 studies using glucocorticoids as their physiological metric. Although four of the 17 stress physiology studies did incorporate other subdisciplines (bioenergetics and nutritional physiology, reproductive physiology, and genetics), metrics like sex hormones, metabolites, enzyme activity, gene expression, and telomere length were less represented. Following stress physiology, 8 EPD studies examined bioenergetics and nutritional physiology metrics. Most EPD studies chose one physiological subdiscipline to use as their physiological proxy; however, 6 studies took a combined approach and included multiple disciplines (see Table 1 for a detailed account of the physiological metric and subdisciplines examined in each study). While the vast utility of glucocorticoids and stress-related biomarkers are appreciated, there is a large, diverse body of physiological metrics suitable for EPD studies (Madliger et al., 2018) and it would be encouraging to see greater investigation of other metrics to determine their usefulness as

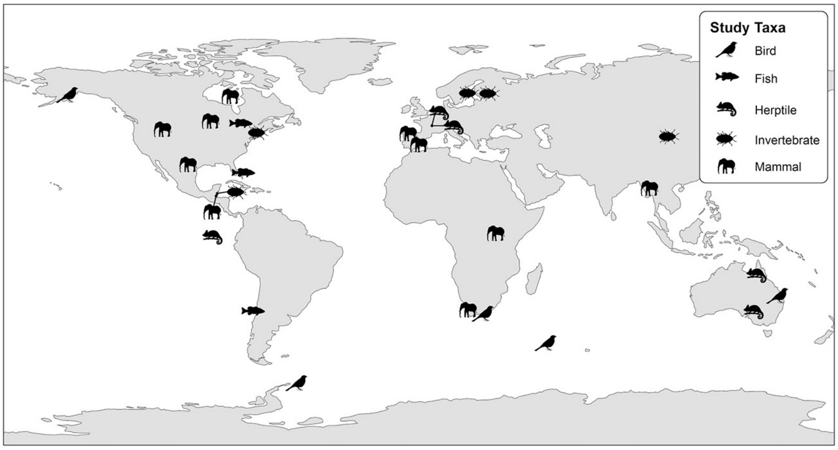

Fig. 1. Taxonomic and geographic diversity of studies attempting to link environmental quality, physiology, and demography (EPD) in wild animal populations. Note that only studies focusing on wild animal populations have been included (the three laboratory studies have been excluded; refer to Table 1).

predictive conservation biomarkers given that glucocorticoids have such diverse functions (MacDougall-Shackleton et al., 2019).

3.3. The need for species-specific investigations

Although demonstrating links from environmental change to a fitness outcome in a given species is encouraging for the broad-scale application of this conservation technique, there is ample evidence that supports the need to independently establish these links on a per-species or even a per-population basis. Some studies which have examined multiple species or multiple populations of the same species have found contradictory effects of an environmental variable on physiology and fitness. For example, Kleist et al. (2018) tested if anthropogenic noise from compressors at oil and gas well pads would result in fitness consequences for populations of mountain bluebird (*Sialia currucoides*), western bluebird (*Sialia mexicana*), and ash-throated flycatcher (*Myiarchus cinerascens*). Some results were as expected and consistent across species; for example, noise negatively correlated with baseline glucocorticoid levels in adult females of all three species. The effect of noise on hatching success was not as straightforward. Agreeing with the authors' hypothesis, noise negatively correlated with hatching success in western bluebirds; however, noise also showed a weak positive correlation with hatching success in ash-throated flycatchers, and there was no clear effect in mountain bluebirds. Given that the methodology and study system were standardized across species for this study, the results demonstrate the need to independently test species as results from even closely related organisms may not be the same.

Care must also be taken when applying findings across different populations of the same species, as demonstrated by the first case study (Kitaysky et al., 2007). The authors showed the contrasting effect of food stress on fitness in the common murre across two different colonies: while increased corticosterone levels directly correlated with decreased individual survival in a colony with a declining population, the same could not be said for individuals from an increasing colony as persistence was independent of foraging conditions and corticosterone secretion during reproduction. To ensure effective conservation management decisions, it is important that physiology-based strategies are tailored for both the target species and population. Only through further EPD investigations will we fully understand whether findings in one scenario are transferable to others.

3.4. Context-dependent physiological traits

Many physiological traits are context dependent, and this should be taken into consideration when attempting to integrate conservation physiology into an adaptive management strategy. Individual measures of physiology fluctuate due to natural changes throughout the life cycle, including reproductive status (Kitaysky et al., 2007), season (Mumby et al., 2015), and age (Grava et al., 2013). Hormone levels, in particular androgens and estrogens, are typically dependent on sex and reproductive status (Lea et al., 2018; Barrington, 2019), and in some species, stressors can have a greater effect on one sex compared to the other (Grava et al., 2013; Dantzer et al., 2014). Complex interactions between the local environment and life history strategy and/or stage, or even social status, can impact how stressors will affect an individual's fitness (Schoenle et al., 2018). It is essential that researchers account for these natural fluctuations to confirm that a physiological response is related to the disturbance in question, and not extenuating factors (Dantzer et al., 2014; Madliger and Love, 2014).

The method by which a physiological metric is measured must also be considered. As defined by Pauli et al. (2009), “noninvasive sampling techniques are either unperceived by an animal subject or are perceived by an animal but do not elicit a chronic-stress response or a reduction in fitness.” Noninvasive sampling techniques, like faecal collection, are less stressful to sensitive populations and may better represent an animal's stress levels over longer time periods (Dantzer et al., 2014). However, noninvasive techniques are not always appropriate or possible. It is generally accepted that nonlethal techniques which require capture of an animal, for blood or tissue collection, also offer a realistic baseline measure of stress if sample collection occurs within the first 2–3 min of the animal being captured (Romero and Reed, 2005; Lawrence et al., 2018). Overall, it is imperative to have a detailed understanding of a species' life history to control for underlying biological characteristics, reproductive status, season, and social factors to appropriately make use of physiological measures for conservation management.

The complement of studies we found that established an EPD link used a variety of traits that deal with diverse aspects of physiological functioning including immune function, reproductive and other endocrine responses, energetics (e.g. growth and body condition), oxidative status, etc. As we acknowledged in the introduction, there is variation among different types of physiological metrics in terms of how quickly they reflect changes in environmental conditions, with some traits more sensitive or responsive over shorter timescales than others. However, we did not observe any patterns in the integration time of the physiological traits in relation to whether they were successful at establishing an EPD link. Successful examples included traits that could change over the course of hours (e.g. faecal glucocorticoids, oxidative stress) as well as metrics that may take days or longer to be altered (e.g. vitellogenin, body condition, growth). We believe this illustrates that no physiological metric should be overlooked, but we recognize that snapshots of physiological function may not always be sufficient to understand whole organism response to stressors. Certainly, there may be cases where within-individual changes in physiology may need to be monitored (rather than randomly sampled across time) to fully understand whether a given environmental change translates into costs to fitness (Dantzer et al., 2014; Madliger and Love, 2015; Madliger and Love, 2016). Additionally, given that a change in a specific physiological trait does not necessarily signal that an environmental disturbance will have a lasting negative consequence for an organism, it is highly important to validate the level (i.e. threshold) at which a physiological trait will signal a decline in fitness, and whether these patterns then translate into demographic changes.

3.5. Modelling EPD

Ecological models are increasingly recognized as important tools for predicting the impacts of climate and land-use changes on populations (Millspaugh and Thompson, 2011). Modelling has traditionally attempted to link changes in environmental quality to demographic processes, such as population growth and distribution, but more recently physiology-based models have gained popularity (Evans et al., 2015). For example, Fordham et al. (2013) demonstrated how the addition of physiological metrics to correlative ecological niche models helped improve predictions of abundance and range shifts in response to climate change in two commercially important marine species, blacklip abalone (*Haliotis rubra*) and greenlip abalone (*Haliotis laevigata*). While earlier models predicted that these species would benefit from warmer ocean temperatures, the inclusion of physiological measurements instead revealed that blacklip and greenlip abalone would undergo population declines and range contractions, respectively. Although ecological models that explicitly take an EPD approach are currently limited in the literature, we advocate for their development as they improve our understanding of species responses to changing environments and promote predictive conservation science.

Physiology-based models may also be useful in modelling parts of the EPD approach by supplementing empirical experiments with simulated effects on population and demography (Evans et al., 2015). Energy budget models (e.g. dynamic energy budgets) and individual-based models (or agent-based models) are two examples of models used to simulate some or all links between environment, physiology, and demography that could be specifically useful in in EPD studies (Huse and Ellingsen, 2008; Chen et al., 2012). Chen et al. (2012) implemented a dynamic energy budget model to investigate impacts of environmentally pulsed copper exposure on population dynamics of tilapia (*Oreochromis mossambicus*) using available empirical data. Their estimated median population growth decreased significantly under pulsed copper activities due to changes in adult survival and larval survival and growth functions. Their study concluded that metal exposure could have negative impacts of physiological responses and thus population stability. In another modelling example, Huse and Ellingsen (2008) used an individual-based model to predict capelin (*Mallotus villosus*) distributions and population dynamics under global warming scenarios using biophysical ocean models and food availability data. Their simulations predicted spawning and distribution shifts associated with warming, providing valuable reproductive and range data for managers and stakeholders. Future EPD studies could use individual-based models in a similar way to simulate population dynamics and predict demography.

An exhaustive coverage of current physiology-based models is beyond the scope of our study, but Jørgensen et al. (2012), Evans et al. (2015), and Koenigstein et al. (2016) discuss examples of models that may be used for this technique. The recent review by Evans et al. (2015) suggests that mechanistic models need to be developed with parameterized physiological information as a means of improving model predictions and may also present an opportunity for physiologists to contribute more towards climate change research and the field of conservation physiology. We encourage ecological modellers, conservation physiologists, and resource managers to work collaboratively to create the best-informed models and advance the field of predictive conservation science.

3.6. Conclusions and future directions

During our comprehensive literature search, we commonly found studies that discovered a correlation between an environmental metric and a physiological marker, or that linked variation in physiology to proxies of individual fitness. Future research may consider investigating the number of studies which linked two of the three EPD metrics together; for example, research which linked physiological parameters to demographic processes, but did not mention or was unable to identify underlying environmental drivers of change. This type of investigation would likely be well-suited to being explored on a trait-by-trait basis. To date, the component of EPD methodology lacking in most research is the demography aspect, most likely due to the limited resources or multidisciplinary expertise necessary to conduct longitudinal research capable of determining population-level results. Clutton-Brock and Sheldon (2010) and Lindenmayer and Likens (2018) detail potential reasons why long-term studies may fail or are ineffective, and are therefore more difficult to achieve, with factors including difficulty in maintaining uninterrupted funding and key personnel. Further, unforeseen difficulties can impede successful long-term research like major human or natural disturbances. However, the monitoring of at-risk populations is essential in effective proactive conservation science, and in the long term is often more cost-effective than rescuing imperiled populations (Drechsler et al., 2011). With respect to the EPD method, biomarkers must be validated as useful in predicting demographic responses to environmental stressors, and consequently, studies must monitor populations after physiological responses are measured. This validation is especially important as some populations may adapt to changes so that increased responses to stress no longer have a negative effect on populations (Wingfield and Sapolsky, 2003), or populations may even benefit from perceived disturbances (e.g. yellow-bellied marmots; Ozgul et al., 2010). The EPD case studies we examined illustrate the potential to scale an individual physiological response to a population-level demographic change, a commonly cited barrier to on-the-ground application of conservation physiology techniques (Cooke and O'Connor, 2010).

We recognize that the field of EPD research is relatively new; however, its goals and applications may prove useful for informing how to conserve and protect biodiversity. Integrated EPD studies can generate meaningful data to support animal conservation and management actions synergistically. Further, the EPD approach can be used to evaluate the impact of a variety of changing environmental conditions on demographic factors and we therefore contend that there is a need to better link eco-physiological data with population-level resource management. As the majority of research in the fields of conservation science and conservation physiology have mainly focused on mammals and higher vertebrates (Lennox and Cooke, 2014; Donaldson et al., 2016) with a number of taxa-specific sampling methods (McCravy, 2018), we suggest future research to investigate underrepresented taxa (e.g. amphibians) and nonlethal methods for lower vertebrates and invertebrates. It is also vital for the scientific community to place efforts towards the development of interdisciplinary predictive models that specifically incorporate EPD methodology. Despite the important considerations we touched on above, we argue that EPD research can provide unique and important information to solve conservation problems. Where seemingly simpler techniques such as direct population modelling are logistically difficult (e.g. Cape mountain zebra; Lea et al., 2018), EPD can potentially be more cost-effective. Where other techniques have failed to point to key threats due to latent population responses, EPD offers a tool that can help managers to act proactively, before windows of opportunity begin to close.

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Declaration of competing interest

The authors declare no conflict of interest including any financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, their work.

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