Timeline to collapse

Francesco Cerini[1], Dylan Z Childs[2], and Christopher F Clements[1]

[1]School of Biological Sciences, University of Bristol
[2]School of Biosciences, University of Sheffield

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3   Francesco Cerini [1,*], Dylan Z. Childs[2], Christopher F. Clements[1]

4   1 School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, UK

5   2 School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK.

6   **emails** - Francesco Cerini: francesco.cerini@bristol.ac.uk *corresponding author

7   Dylan Childs: d.childs@sheffield.ac.uk

8   Christopher F. Clements: c.clements@bristol.ac.uk

Abstract

Contemporary rates of biodiversity decline emphasize the need for reliable ecological forecasting, but current methods vary in their ability to predict the declines of real-world populations. Acknowledging that stressors effects start at the individual level, and that it is the sum of these individual-level effects that drives populations to collapse, shifts the focus of predictive ecology away from using predominantly abundance data. Doing so opens new opportunities to develop predictive frameworks that utilize increasingly available multi-dimensional data, which have previously been overlooked for ecological forecasting. Here, we propose that stressed populations will exhibit a predictable sequence of observable changes through time: (i) changes in individuals' behaviour will occur as the first sign of increasing stress, followed by (ii) changes in fitness related morphological traits, (iii) shifts in the dynamics (e.g. birth rates) of populations, and finally (iv) abundance declines. We discuss how monitoring the sequential appearance of these signals may allow us to discern whether a population is increasingly at risk of collapse, or is adapting in the face of environmental change, providing a conceptual framework to develop new forecasting methods which combine multidimensional (e.g. behaviour, morphology, abundance) data.

1. INTRODUCTION

Extinction rates over the last century have been estimated to be higher than at any point in recent history, with human activity identified as the predominant driver of this "sixth mass extinction" (Ceballos et al., 2015). In addition to its positive effects on human wellbeing and culture (Dereniowska & Meinard, 2021), biodiversity underpins the stability and resilience of ecological systems on which humanity relies for food, fresh water, and clean air (Maron et al., 2017). At the root of human-induced extinctions are a suite of stressors - stimuli creating a physiologically demanding or life-threatening situation for an organism - such as habitat loss, pollution, overharvesting, and climatic change (Taborsky et al., 2021; Tilman et al., 2017). Such stressors can drive declines and erode a population's ability to recover in the face of disturbances, increasing the probability of population collapse (van de Leemput et al., 2018). Indeed, multi-faceted pressures can be self-reinforcing, driving rapid collapses – the so-called extinction vortex (Fagan & Holmes, 2005; N. F. Williams et al., 2021). Consequently, we are at a critical point for ecosystem management where, to preserve biodiversity and eco-system services, we need to reliably detect not only what systems are being most impacted by anthropogenic stressors, but which are most at risk of collapse (Clements & Ozgul, 2018).

This need has driven the development of predictive methods that aim to infer the risk of population collapse, ranging from classical Population Viability Analyses (PVA, Shaffer 1991) to more recently developed Early Warning Signals (EWS, (Clements & Ozgul, 2018; Scheffer et al., 2009; Shaffer, 1991). However, the diffi-cultly of surveying wild populations, together with economic limitations (T. A. Gardner et al., 2008), often results in noisy and short time series which can detrimentally affect the accuracy of such predictive tools (Clements et al., 2015; Coulson et al., 2001; Patterson et al., 2021). Most importantly, these methods have neglected other potentially powerful diagnostic features that theory and evidence suggest should be impacted by increasing environmental pressures and thus could act as additional indicators of approaching collapse. In fact, the final decline of a population to extinction is a manifestation of a host of changes to the structure and dynamics of that population. Such changes occur first at the individual level, and then – when a high enough proportion of the population exhibit similar changes – affect the dynamics of that population.

An individuals' physiology is the key mechanism through which organisms detect and respond to environmental change; for example stress hormone production is the initial trigger of phenotypic change (Lawton, 1991). Whilst using such physiological measures as tools to identify at risk populations certainly has merit (Ames et al., 2020), collecting data to achieve this requires tracking physiological parameters across multiple individuals of populations, an intrusive and resource-intensive task. Rather, focusing on the easily detectable downstream effects of these physiological changes provides individual-based data on the effects of stressors. These downstream effects could include changes in the behaviour of individuals (Berger-Tal et al., 2011), their morphologies, and/or life history traits (Baruah et al., 2019), alongside traditional abundance-based measures of extinction risk (Dakos et al., 2012). Gathering such multivariate information has historically been highly challenging in the natural world, but recent technological advancements in data-collection methods provide the opportunity to generate high throughput information on these multiple features of populations with a relatively low cost-benefit ratio (Thompson, 2013; Ward et al., 2017). However, what is still missing is a conceptual framework that explicitly shows how such multidimensional data are related to each other, and how they can be used to holistically understand the mechanisms driving populations to collapse.

1.1. Conceptual framework

The effect of increasing stressor intensity on a population propagates from the individual to the population level via a successive series of responses (here referred to as "signals of stress"). We refer to "stress" as the process whereby an organism reacts to stressors (Taborsky et al. 2021). The individual-level responses necessarily take place (and are observable) over smaller time scales than population-level signals; an individuals' behaviour or morphology can change during their lifespan, while the effect of stressors on the population abundance trends will be observable (except in face of an unpredictable extreme mortality event such as a wildfire) after one or more generations. This individual-to-population approach allows us to use individual stress responses as early indicators of change in population conditions, and to measure the impacts of the stressors in multiple dimensions simultaneously. Such an approach expands on recent work in the field of EWS, which consider abundance based EWS and shifts in the mean body size of the population simultaneously, leading to an increase of the overall predictive power (Clements et al. 2017, Burant *et al.* 2021). However, these approaches ignore the fact that such signals are not necessarily expected to change concurrently,

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but rather may occur sequentially as individuals' plasticity buffer them against negative environmental conditions. Considering this temporal aspect in the occurrence of individual-to-population level stress responses offers the opportunity to develop new forecasting tools which make use of increasingly available data.

To underpin the future development of forecasting tools, we present a conceptual framework – the "timeline to collapse" – which outlines a multidimensional approach to predict population decline and extinction. Supported by case studies on the effect of environmental stressors on different features of individuals (see Box1, 2, 3), we show how signals of increasing stress propagate from the individual to populational level and occur in a predictable temporal sequence (i.e. the timeline to collapse). We discuss how the "timeline" of responses provides a template to corroborate whether a population is at risk of collapse or is adapting to new conditions; we explore how this framework can provide novel ways to leverage data to understand how individuals and populations buffer themselves in the face of environmental change. Finally, we discuss how to implement the timeline concept to predict the fate of real-world populations.

2. THE TIMELINE TO COLLAPSE

Individuals in a population, whilst experiencing similar unfavourable abiotic or biotic conditions (e.g. resource scarcity, pollution), can respond to this pressures in different ways, primarily through shifts in behaviour and/or morphological and life history traits. Behaviours, by their nature, are plastic and subject to rapid changes in the face of novel stimuli (Tuomainen & Candolin, 2011). Regardless of whether highly plastic behaviours are sufficient to maintain fitness in the presence of stressors (Mazza et al., 2020) or prove maladaptive (Hendry et al., 2008), they represent the earliest easily observable individual-level responses to sub-optimal environmental conditions (Figure 1B, Box 1). If behavioural shifts cannot maintain optimal conditions for growth and reproduction, an individual will start to change morphologically as it loses condition (e.g. through decreases in body mass, Figure 1C) or as it expresses morphological adaptation/defences. Thus, morphological traits (e.g. mass, antipredatory features, symmetry, Box 2) provide a secondary response to environmental stressors via plastic or adaptive physiology-driven changes (both intra and inter-generational). As with behavioural changes, morphological shifts can buffer an individual against some environmental pressure but cannot do so indefinitely in the presence continuously changing conditions. Thus, such morphological shifts can be concurrent with or

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followed by decreases in reproduction (i.e. life history traits adjustments) and increases in mortality rates. Declines in reproductive rates represent some of the last stages of adaptive plasticity in life history, where resources are reallocated from reproduction to maintain the survival of the individual whilst allowing for the possible exploitation of improved future conditions (Fleming et al., 2016). Such life history traits modifications, whilst not as readily measurable as morphological or behaviour change, will have significant and detectable effects on population abundances observable over longer (>1 generation) time frames. These may not necessarily lead to immediate population declines but can manifest as a loss of resilience potentially triggering EWS. Indeed, decreases in reproductive success and increases in mortality may induce population abundance declines and subsequent rebounds (e.g. due to density dependant reproduction, Figure 1D). If these changes drive the system toward a tipping point (Mallela & Hastings, 2021), this phase of the timeline may result in a significant temporal trend in one or more statistical moments of population abundance (Dakos et al., 2012), with indicators such as variance, autocorrelation, density ratio, and skewness acting as warning signals of collapse (Clements & Ozgul, 2018). Such EWS have been criticised because of their high false positive rates (Burthe et al., 2016), but observing them in the context of the timeline to collapse – i.e. after having already detected changes in behaviours and traits – provides additional evidence to suggest such signals are true positives. In fact, these slowly occurring life history changes inducing EWS represents the ultimate signals a population may show before a continuous decline in abundance. If environmental stressors still increase after these signals – and if individuals cannot move\migrate – the populations death rate will increase and abundance will continuously decline (Figure 1D). At this point, a population may be "committed to extinction", where genetic factors (e.g. inbreeding, Vucetich & Waite 1999) and demographic constraints (e.g. Allee effect (Kramer & Drake, 2010) may mutually reinforce one another to rapidly propel it to extinction (Fagan & Holmes, 2005).

We define the "timeline to collapse" such temporal sequence of observable signals, starting with rapid behavioural responses to stressors, followed by morphological shifts, changes in life history that shapes abundance dynamics, and then by continuous declines in the abundance of a population until extinction (Figure 1).

This temporal pattern of signals will necessarily develop at time scales relevant to the study organism, i.e. lifespans and generations rather than absolute time periods. For small invertebrates, behavioural shifts may be

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observable over hours (e.g., *Daphnia* depth shifts, Oram & Spitze 2013), while changes in abundance may happen over days. For larger vertebrates, shifts in morphology may take place over months (e.g., Steller sea lions weight loss, Trites & Donnelly 2003) whilst EWS occurrence and subsequent abundance declines may occur over years. Regardless of the direction of the shifts and the stressor's nature, we expect the temporal sequence in the typology of signals (behavioural, morphological, abundance; Figure 1) to remain broadly consistent.

2.1. Framework boundaries and scope

The timeline to collapse concept builds upon work in a number of different research areas, including behavioural ecology, physiology and predictive ecology, and the recent suite of work on EWS (Baruah et al., 2019; Clements et al., 2017). However, whilst EWS are a feature of the framework, we do not propose to apply critical slowing down theory to all signals of stress in the timeline, nor to try predicting when shifts in behaviour, traits, or measures of population variability will occur. Rather, our focus is describing the succession in time of different responses and how together these might be used to infer approaching population collapse. We consider the timeline to collapse as a framework aiming to (i) to holistically consider multiple, often overlooked, types of data as tools for predictive ecology, and (ii) discriminate populations tending toward extinction from those simply adapting in the face of change. In fact, analysing both behaviour and morphology offers the opportunity to discern between a population where behavioural plasticity is sufficient to lessen the effects of stressors (maintain fitness) from a population where behavioural plasticity alone is insufficient to maintain fitness, leading to changes in morphological traits and the subsequent timeline steps (Figure 1). It is the temporal sequence of signals across all facets which together represent a comprehensive signature of the effects of increasing stressors intensity on a population, and thus whether collapse is approaching.

2.2. Framework details

The timeline to collapse concept assumes continuously increasing stressor intensity – be that biotic or abiotic – taking place over multiple generations (Figure 1A) such that a population is able to respond, rather than sudden step-shifts in a stressor which may eradicate a population in the absence of any indicators (Clements & Ozgul, 2018). When visualising the timeline, we identify the time points when the population's average

169   values of a given behaviour or trait change significantly from the values observed under stable conditions (T_{Bs}

170   and T_{Ms} points, Figure 1), and the time points when the plastic limits of change in the behaviour and morphol-

171   ogy are reached (T_{Be} and T_{Me}, Figure 1). Although such points may visually resemble "tipping points", applying

172   EWS theory to anticipate them is inappropriate, as there is currently no theory which suggests that behavioural

173   or trait metrics (which are not expected to pass through a tipping point) should show the critical slowing down

174   phenomenon required for EWS to be present (Dakos et al., 2018).

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176   Nevertheless, a stress induced increase in the variance of these metrics - among individuals and through time

177   - may be expected, together with changes in the mean. When stressor intensity starts to increase, individual

178   responses will vary based on, for example, personality and past experience for behaviours (Dingemanse et al.,

179   2010), or genetic pre-disposition for more or less plasticity in morphological traits (e.g. due to intrinsic inter-

180   individual variability, Tanner & Dowd 2019). Such differential personality-and-physiology-based stress re-

181   sponses would lead to an increase in the variability around mean changes in behaviours or morphologies (Fig-

182   ure 1). However, selection will over time homogenize these around the new (optimum) behaviour/trait values

183   that allow individuals to survive, or around the physiological limits (i.e. low variance around the new mean of

184   individuals, Figure 1). Although such patterns in the variance provide additional metrics to monitor (Patrick et

185   al., 2021), they are less likely to contain information about the risk of population collapse; rather, we propose

186   such information lays in the temporal sequence of the different signals.

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188   Whilst the initiation time points of behavioural, morphological, and abundance shifts (T_{Bs}, T_{Ms} and T_{As}, Figure

189   1) are expected to be sequential, the time intervals over which such shifts occur (I_B, I_M and I_A, Figure 1) may

190   overlap. Indeed, changing a behaviour above a given threshold may require the use of energy reserves which

191   triggers changes in morphological traits. For example, for a seabird population (Figure 1), increasing foraging

192   distance may be the first response to decreasing food availability. Acquisition of additional resources derived

193   from flying further distances to feed may be sufficient to compensate for this additional effort outside the

194   breeding season. However, if the food is needed to feed chicks (Fayet et al. 2021), some of these resources

195   will be allocated to the offspring and the individual will either i) fail to fully replenish their energy stores (e.g.

196   start to lose weight) or ii) decrease feeding rate to offspring to ensure they have the energy needed to cope with

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197 the extended foraging distance (Fayet et al., 2021). This will result in observing flight distance increasing

198 together with declines in the body weight of adults (overlap among I_B and I_M, Figure 1), offspring, or both.

199 However, in other scenarios we may observe a clear temporal distinction between signals time intervals (i.e.

200 no overlap among I_B and I_M). For instance, in the presence of an invasive predator, a prey can go through an

201 initial fast and discrete behavioural change (e.g., a shift in microhabitat use, Pierce 1988), followed by a me-

202 dium speed response (e.g., change in body size due to different conditions in the new microhabitat, (Leibold

203 & Tessier, 1991)), without any overlap between these two signals.

204

205 **3. ECOLOGICAL INSIGHTS**

206 Whilst the temporal order of signals provides information on a population's future, *post hoc* analysis of be-

207 havioural and morphological shifts offer a means to characterise the stress responses of populations. We sug-

208 gest that the change in the mean values of behaviours or morphological traits between pre-stress (stable) con-

209 ditions and the onset of the next signal of stress (e.g. from when behaviours start to change to when body traits

210 start to change) represents an "intrinsic stressor buffering capacity": a measure of the ability of a behaviour or

211 trait's plasticity to ameliorate stress pressure. Defining B_s and M_s as the mean values of a monitored behav-

212 ioural metric and morphological trait during stable conditions, and B_x and M_x their respective values at the

213 onset of the next buffering signal/level (Figure 1, Point 1 and 2) we could extract quantifiable ranges of vari-

214 ation (ΔB for behaviour and ΔM for morphological trait, Figure 1).

215

216 From this framework, ΔB and ΔM could be calculated for traits that can undergo continuous shifts and com-

217 pared among different species and populations. For instance, nematodes and rotifers show extreme plasticity

218 in morphology (reductions of up to one-third of original body size (Rebecchi et al., 2020)) to cope with long

219 periods of environmental pressure (e.g. exsiccation of habitat). The resulting high value of ΔM would reflect

220 the large amount of pressure they can buffer by changing morphology before the eventual occurrence of abun-

221 dance signals in the population. In contrast, e.g. amphibian species with limited drought resistance would dis-

222 play much lower ΔM in comparison. Such plasticity proxies may be compared among different species to

223 indicate which biological/ecological traits (group living vs solitary animals, bigger vs smaller dimensions,

224 specialist vs generalist etc.) lead to species more resistant to stressors. Additionally, average ΔB and ΔM may

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225 vary among populations of the same species, due to difference in biogeographic history and genetic structure

226 (e.g. allelic heterozygosity (Hansson & Westerberg, 2002)), which may provide information on how such fac-

227 tors shape capacity to cope with stress. Such changes will likely occur in multiple behaviours or traits simul-

228 taneously in order to cope with increasingly stressful conditions, and thus measuring behaviours or traits in

229 multiple dimensions (e.g. social interactions, distance foraging occurs over, time spent inside burrow, etc.)

230 would allow plasticity in multi-dimensions to be quantified, and tools such as those employed in the analysis

231 of functional diversity could be readily applied to these data (Mammola et al., 2021).

232

4. KEY QUESTIONS

234 The timeline to collapse provides a conceptual framework to synthesize multiple types of data to help infer the

235 future dynamics of ecological systems. However, applying this to real-world populations requires identifying

236 appropriate data to monitor (behaviours, traits, abundances), measuring baselines against which change can be

237 quantified, and developing statistical tools to holistically consider these data simultaneously to provide robust

238 detections of increasing stress and possible forecasting techniques. Below we consider some of the key ques-

239 tions required to turn the conceptual timeline framework into an appliable pipeline for monitoring and conser-

240 vation management.

241

4.1. How to select and acquire the data that are more indicative of stress?

243 Some behaviours and morphological signals may provide general indicators of increasing stressors' intensity

244 (e.g. increased dispersal for vagile species), but selecting signals which are relevant to the taxa of interest

245 remains key (McClanahan et al., 2020). Expert knowledge can aid in this (Reside et al., 2019), identifying

246 behaviours and traits that are most likely to change given the nature of the stressor or, when the identity of the

247 stressors is unknown, can provide general indicators of an individual's condition. Ideally, behaviours and mor-

248 phology measure that are easily collectable thought automated and non-invasive means are to be preferable.

249 Many cutting-edge data collection tools can get frequent measures of such multivariate data needed to build

250 accurate timeseries. For example, GPS tracking, biologging, acoustic monitoring, and photographic analysis

251 are now able to extract data on behaviours and morphological traits, providing invaluable information even

252 from a subset of the population, (Desjonquères et al., 2020; Sequeira et al., 2021; Shimada et al., 2021; H. J.

253 Williams et al., 2020, (Supplementary Material Table S1)).

254

4.2. How can we define baselines?

256 A quantitative and/or qualitative definition of "normal" values for the identified behavioural, morphological,

257 and abundance indicators is needed to pinpoint the moment in time when stress responses start (T_{Bs}, T_{Ms}, T_{As},

258 Figure 1). Defining such values in wild populations ideally requires long term monitoring data (Wauchope et

259 al., 2021) on the multiple facets of a population under non-stressed conditions. Alternatively, a comparative

260 approach between populations experiencing different levels of stressors intensity could provide baseline values

261 such as along a stress gradient (Ingram et al., 2021) – a space-for-time substitution (Keith *et al.* 2018, Fayet et

262 al. 2021). Nevertheless, populations in different conditions - that suit a space-for-time substitution - as well as

263 long-term monitoring data are rare and could be case-specific. In such situations, can ecological theory help

264 us to set more general baseline expectations? Possible approaches could lie within, for example, Dynamic

265 Energy Budget models (Baas et al. 2018). Such models can be parameterized with standard life-cycle data –

266 obtainable over short periods of time (e.g. body length, growth rate, maximum reproduction rate, etc.) - to

267 derive quantitative parameters describing the studied organism's energetics. Doing this with data from popu-

268 lations in stable conditions could represent a viable baseline distribution from which one can compare observed

269 changes in energetics parameters (Lika et al., 2011). Likewise, mechanistic trait-driver models derived by

270 Metabolic Scaling Theory can link the traits frequency distributions to individual performance and growth

271 rates predictions. One could try to calculate the traits distribution characteristics of a population in non-stressed

272 condition (e.g. constant positive growth rate) to build a baseline, whereby a variation in such traits distribution

273 (e.g. individuals starting to lose biomass) could be used to predict individual performance and how this will

274 scale up to influence demography of populations (Enquist et al., 2015).

275

4.3. How can we handle the multivariate data to better forecast populations future?

277 Regardless of how a baseline is defined, the big challenge ahead in the timeline application is understanding

278 how to compare multivariate estimates to observed changes in behaviours, traits, and abundances and how to

279 use these signals to improve population collapse forecasting. Using normalisation and summation of multiple

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280 signals to improve predictive power has previously been done (e.g. combining morphology data with abun-

281 dance EWS (Clements et al., 2017; Drake & Griffen, 2010)), but it might not be scalable to the full timeline

282 data pool given the long-time interval that can separate behavioural signals from abundance EWS. New ap-

283 proaches may lie within the more recent multivariate time series modelling (Wei, 2018) that could allow one

284 to fit the timeline data (i.e. parallel time series of behaviour, traits, and abundance) while taking into account

285 the inter-dependencies between them (e.g. how behaviour can influence morphology and vice versa). For in-

286 stance, Multivariate Autoregressive State Space models (Holmes et al., 2012) can use information on historical

287 trajectories of multiple variables to forecast future values while accounting for multiple sources of uncertainty

288 (Zhu et al., 2018). Alternatively, deep learning networks such as recurrent neural and temporal convolutional

289 neural networks (Bury et al., 2021; Lai et al., 2018; Lara-Benítez et al., 2021) could provide an obvious but

290 more powerful approach to forecast future trends or changes in such variables (Guo et al., 2020), though these

291 tools will require large amounts of data to train the models, which are only feasibly collected through auto-

292 mated means.

293

294 **5. CAVEATS**

295 The timeline to collapse concept necessarily makes assumptions about how stressors will impact populations.

296 The main assumption is that stressors will increase over time (Figure 1), allowing populations to respond

297 gradually to increases in environmental pressure. However, as with EWS and PVA, sudden and/or catastrophic

298 "pulse" disturbances (drought, storms, fires etc.) may lead to significant changes in the abundance or distribu-

299 tion of a population without any warning. Moreover, even in cases of the assumed "ramped" disturbance, the

300 mutable nature of biological systems may create situations where the sequence of signals may be different (e.g.

301 body traits shift occurs first, triggering then behavioural shift (Burant et al., 2021). Fully applying the frame-

302 work requires studying species that show plastic and quantifiable behaviours and morphological traits, where

303 gathering data is easy at the individual level, and thus it may not be fully applicable to sessile organisms (e.g.

304 Anthozoa), obligate parasite species, or plants and fungi. Nevertheless, we believe that in such cases a partial

305 application of the timeline concept (e.g., monitoring morphological traits and abundance data) will improve

306 the predictive horizon of eventual collapses compared to considering only abundance. Finally, although in this

307 piece we decided to focus on more immediately observable traits shifts, we acknowledge that for animal taxa

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308 that undergo seasonal activity cycles, as well as for non-animal species, changes in phenology can be consid-

309 ered as other potential signals to include in the timeline framework. Phenological shifts are well known to be

310 induced by e.g. climate change (Menzel et al., 2020; Samplonius et al., 2018) but are often observed over long

311 time periods (e.g. birds earlier arrival to breeding sites occurred over 20 years (Koleček et al., 2020).

312

6. CONCLUSION and Future directions

314 Considering how anthropogenic stressors impact populations via changes in individual-level features provides

315 a key step forward in predicting population extinction. Doing so has allowed us to develop a conceptual frame-

316 work where the temporal aspect of stress signals can act as a corroborative tool to infer risk of population

317 collapse. The next steps to assessing the potential of this framework is to obtain complete and accurate datasets

318 covering the full suite of timeline components (see Box 3) for populations driven to collapse by increasing

319 stress. A *post hoc* analysis of the multivariate dynamics of such collapses would guide in understanding the

320 best approaches to use to forecast future ones. Experimental data from study models (e.g. micro-mesocosms

321 populations (Altermatt et al., 2015; Beermann et al., 2018; Clements & Ozgul, 2016)) would be of invaluable

322 help in this, whereby one could implement different disturbance scenarios (Jacquet & Altermatt, 2020) while

323 accurately collecting the multidimensional data. Nevertheless, the literature groundings of the timeline idea

324 already provide a conceptual model for the development of monitoring programs covering a broader spectrum

325 of data than is typically considered by resource managers. Such a holistic view of how the behaviours, mor-

326 phological features, and dynamics of populations change as they become increasingly stressed offers hope of

327 a step-shift in the accuracy of methods to predict population declines, helping in the urgent fight against bio-

328 diversity loss.

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Figure captions:

Figure 1. Theoretical example of a timeline to collapse. We posit a population of seabirds inhabiting an area

where prey resources (e.g. fish stocks) begin a continuous decline (A). The curves in panels B and C represent

respectively the average values of a behavioural and morphological trait calculated from a pool of individuals

in the population through time, and the coloured shaded areas show the variance around the mean. The red

curve in panel D shows the abundance of the population. First a shift is observed in the behaviour (time point

T_{Bs}), where the average foraging distance increases (together with the variance) compared to the average meas-

ured during stable conditions B_s (B). The foraging distance increase until it reaches a physiological limit (time

point T_{Be}), defining the time interval I_B where a continuous change is observable. After, or during I_B, we ob-

serve a decrease in average body size (with increase in the variance) compared to that measured during stable

conditions M_s (C), at time T_{Ms}. The body size will change until its physiological limit (T_{Me}), defining the time

interval where such continuous change is observable (I_M). Later, the abundance trend of population will show

alterations in the pre-decline indicators such as Early Warning Signals, that will start to be observable at time

point T_{As}, and will last until T_{Ae}, defining the time interval I_A. Subsequently, the continuous decreases to ex-

tinction (D) will begin at time point T_{Es}, and will end with the extinction of the population at time T_{Ee}, lasting

the time interval I_E. The first occurrence of the signals projected on the lower Time axes shows the sequence

in the category of observable signals of stress starting at the individuals' level (B, C) and propagating to the

population level (D), defining the Timeline to Collapse. The small black dotted lines project the starting point

of the shifts in morphological traits and abundance dynamics on the behaviour (point 1) and morphological

trait (point 2) curves. Projected on the vertical axis, those points identify B_x and M_x: the values of behavioural

and morphological metrics at the time of the onset of the next signal along the timeline. The interval of change

(brackets) from the average values defines the intrinsic stress buffering capacities of that behaviour (ΔB) and
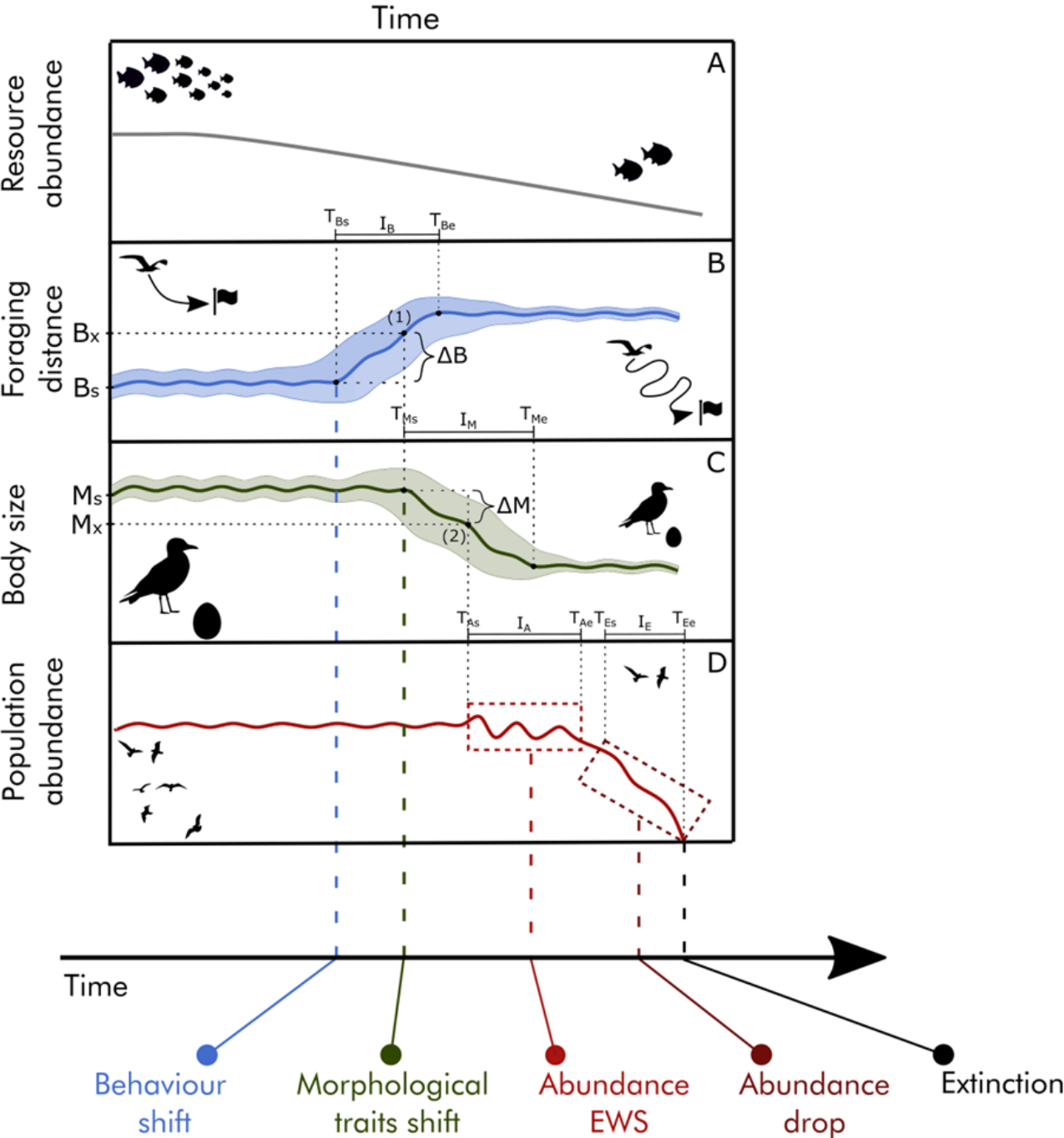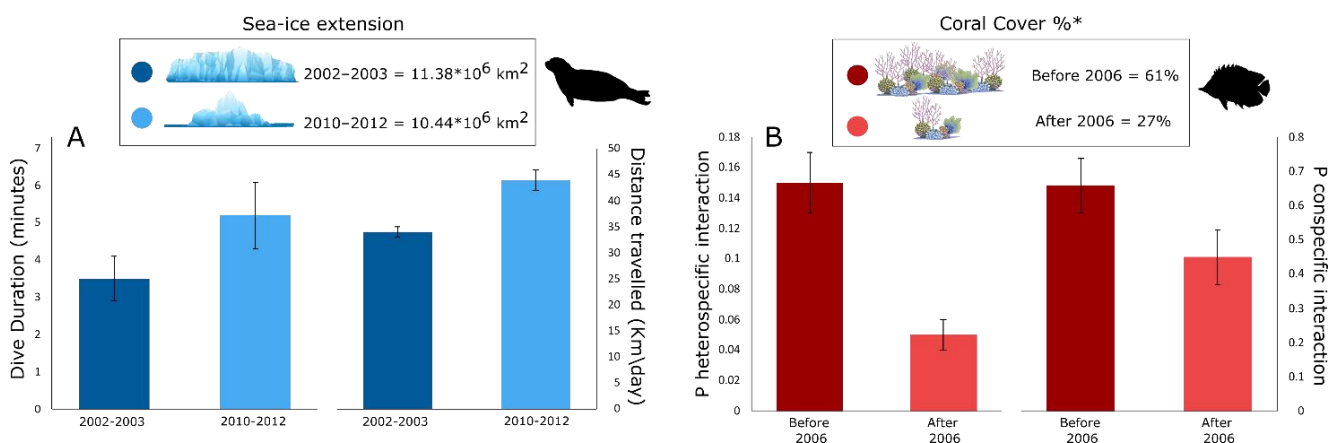
morphological trait (ΔM).

Figure 1.

BOX 1. Overview of behavioural signals

725 Behavioural changes are amongst the most rapid changes that individuals can perform to cope with sub-optimal

726 conditions (Greggor et al., 2016). Broadly, behaviours comprise movement and habitat use, foraging activities,

727 reproductive and social behaviours (Berger-Tal et al., 2011). All these categories of behaviour can be modified

728 by stressors; many studies show variation in e.g. foraging activity and dispersal of individuals in response to

729 declining resource availability (Couvillon et al., 2014; Fayet et al., 2021), climatic change (Gauzens et al.,

730 2021; Hamilton et al., 2015; Holt & Jørgensen, 2015), and invasive species (Lenda et al., 2013). Indeed,

731 changes in the movement patterns can be amongst the first observable signals of increasing stress, as individ-

732 uals seek to minimise the impacts of, say, declining food availability by moving to new foraging areas or by

733 reducing activity levels (depressing metabolism, Trites & Donnelly 2003). For instance, on Svalbard (Nor-

734 way), a population of ringed seals suffered a major reduction in sea-ice level resulting in fewer areas where

735 the seals could feed intensively. Subsequent monitoring of movement patterns showed that seals swam greater

736 distances and dived for longer periods (Box 1 Figure A, bars indicate standard error; data adapted from Ham-

737 ilton et al. 2015). Spatial movement constitutes perhaps the most easily observed and measurable signal of

738 increasing stress for vagile species, as data can often be captured remotely e.g. via GPS tracking or remote

739 camera monitoring, techniques which bridge taxa (vertebrate and invertebrates, Hertel et al. 2019, Tini et al.

740 2018) and realms (marine and terrestrial , Shimada et al. 2021).

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744 In addition to movement patterns, individuals may react to stressors by altering rates of intra - and - interspe-

745 cific interactions, including effects observed in social and communicative behaviours (Kunc & Schmidt,
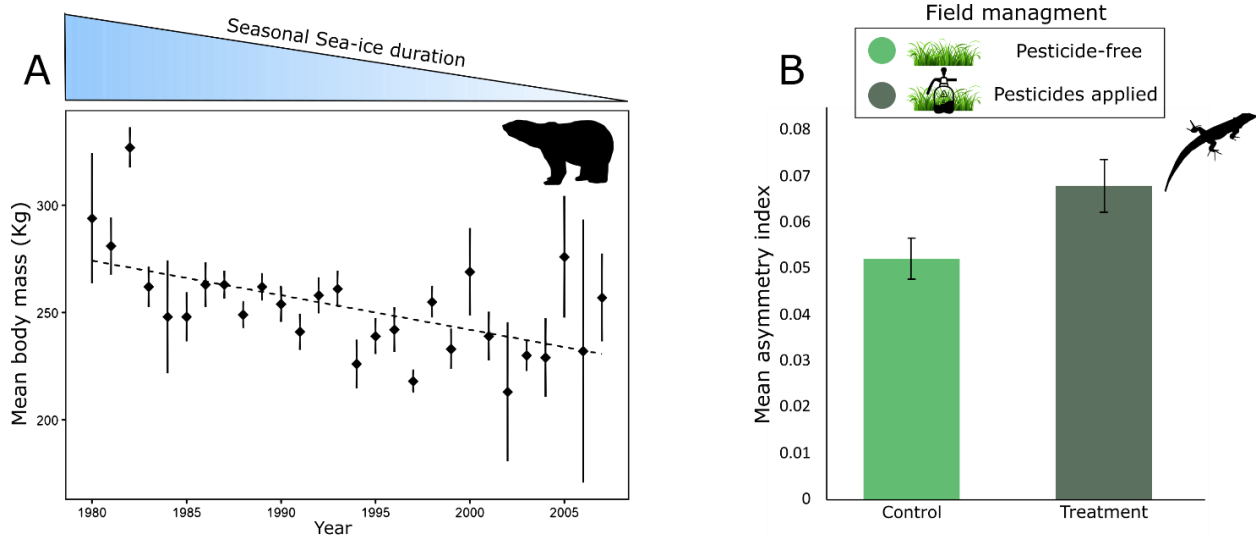
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2021). Resource scarcity may lead individuals to allocate energy to essential activities (e.g. foraging), decreasing actions not linked to survival, such as the engagement in territorial defence. Such a response was seen in multiple species of central Indo-Pacific corallivorous butterfly fishes (*Chetodon* spp., Keith et al. 2018) in the aftermath of a bleaching event in 2016 which led to a reduction in corals. Observations suggested that the probability of both heterospecific and conspecific aggressive encounters decreased significantly (Box 1 Figure B, Bars are 95% confidence intervals; data adapted from Keith et al. 2018) as nutritional deficits increased the relative energetic cost of resource defence behaviour (Keith et al. 2018). Similarly, acoustically active insects and amphibians may change the acoustic properties of the mating signals in response to temperature change (Singh et al. 2020). Moreover, anthropogenic noise can induce reductions in whistles and echolocation click rates of social cetaceans (Pellegrini et al., 2021).

The direction of change in behavioural metrics (foraging distance, prevalence of an interaction type, duration in time of given actions etc.) will vary depending on a species' environmental tolerance, trophic level, and stressor type. Whilst a lack of resources may trigger increases in movement, the arrival of an invasive predator may induce a prey species to reduce movement (to reduce encounter rates) or to shift microhabitat use toward a more shelter-oriented strategy (McMahan & Grabowski 2019). Environmental stressors may also increase the variance in behavioural metrics, e.g. poor environmental conditions enhanced the variability of foraging trip duration in young albatrosses (Patrick et al., 2021). Previous experience may also play a critical role in determining an individual's response to stressors. For instance, compared to naïve individuals, fishes with previous experience of predation events showed stronger antipredator behaviours (e.g. decreasing swimming activity) when they were represented with the chemical cues of the predator (Vilhunen et al., 2005). Likewise, the evolutionary history of a population can shape an individuals' capacity to react to environmental pressure; lizard species performed antipredatory behaviours in response to a new predatory snake if the lizards evolved with other snake species which share similar predatory features (shape, chemical cues etc.) with the introduced predator (Ortega et al., 2017). Consequently, a population's ecological and biogeographical history must be considered when identifying behavioural signals of stress.

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BOX 2. Overview of morphological signals

To mitigate the effects of increasing stressors intensity individuals can respond to maximize survival and reproductive output through changes in morphological and fitness-related life history traits (Fox et al., 2019). Such changes are driven by hormone responses, metabolic adjustments and resource re-allocation, and can include reductions in body mass, decreases in growth, shifts in reproductive schedules, and antipredatory morphological trait expression. Here we focus on morphological shifts as they are more easily observable and measurable compared to fitness related life history traits. For example, morphological features can be measured remotely through photographic analysis, while measuring reproductive outputs or patterns of sexual maturity requires strict monitoring with particular time periods (e.g. breeding seasons).

Environmental stressors substantially affect morphological trait distributions, both prior to or concurrent with shifts in the demography and dynamics of a population (Baruah et al., 2019; Pigeon et al., 2017). The reduction in body size due to sub-optimal food consumption is a general response to resources scarcity (Trites & Donnelly 2003). In numerous taxa, body size reduction is also directly and indirectly induced by climatic change and habitat fragmentation (J. L. Gardner et al., 2011; Lomolino & Perault, 2007; Sheridan & Bickford, 2011; Thoral et al., 2021). For instance, a population of polar bears from the Western Hudson Bay (Canada) was monitored between 1979-2004 during a period where sea-ice cover showed an overall trend toward earlier sea-ice breakup induced by climate change (Stirling & Derocher, 2012). The study found significant declines in mean adult female polar bear mass during this period (Box 2 Figure A, bars indicate standard error, dashed line indicates fit of linear regression [r=-0.549, p<0.01]; data adapted from Stirling & Derocher, 2012) which strongly correlated with the progressively earlier dates of sea ice breakup. The pattern was likely driven by changes in their hunting behaviour as bears prematurely abandoned seals hunting zones and were forced to fast for progressively longer periods.

Figure with panels A and B. Panel A: scatter plot of Mean body mass (Kg) versus Year (1980–2005) with a declining dashed trend line, topped by a "Seasonal Sea-ice duration" gradient triangle and a polar bear silhouette. Panel B: bar chart of Mean asymmetry index for Control (Pesticide-free) and Treatment (Pesticides applied) under "Field managment", with a lizard silhouette.

Body size is a key trait that directly affects thermoregulation and rates of energy intake and utilization (J. L. Gardner et al., 2011), and has recently been suggested as a possible measure of population stability (Clements & Ozgul, 2016b). In fact, changes in body size of diatoms algae preceded a regime shift in a lake ecosystem (Spanbauer et al., 2016), and experimental populations exhibit the same pattern, showing that – when resources decrease – declines in average body size precede declines in population size (Baruah et al., 2019). In situations where longitudinal measures of body size/mass are available, change in individual growth rates could be used as a potentially more accurate stress signal, since growth rate will respond more rapidly compared to measures of mean body size. Indeed, Bjorndal et al. (2017) reported a decrease in the growth rate of individuals of three sea turtle species in response to climatic stressors and anthropogenic degradation of their foraging areas.

Reductions in size is the most likely outcome of stress, although some stressors may lead to other patterns of change. For instance, environmental pressures can lead to a decrease in defensive morphological traits: e.g. UV light exposure in pregnant individuals of a freshwater cladoceran induced the reduction of antipredator spines in their offspring, and subsequently increased predation risk for new-borns (Eshun-Wilson et al., 2020). Conversely, the novel pressure that an invasive predator puts on a native population can trigger increases in predator induced-defences (Zhang et al. 2017). Chemical pollutants can affect body symmetry, with pesticides used in hazelnut orchards leading to increased fluctuating asymmetry in morphological traits linked to intra-specific interactions (i.e. femoral pores, Box 2 Figure B, bars indicate standard error, data adapted from Sim-bula et al. 2021) in lacertids. Indeed, increasing fluctuating asymmetry has been suggested as an indicator of

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815   loss of genetic variation prior to extinction (Leary & Allendorf, 1989). This suite of responses, including (but

816   not limited to) declining body mass/size, expression of chemical induced antipredatory features, and asym-

817   metry in meristic features will generally occur over (relative to the organism's lifespan) longer time periods

818   than rapid behavioural changes, but may still occur within the life span of an individual (i.e. ≤ 1 generation),

819   or across multiple sequential generations (e.g. Clements et al. 2017).
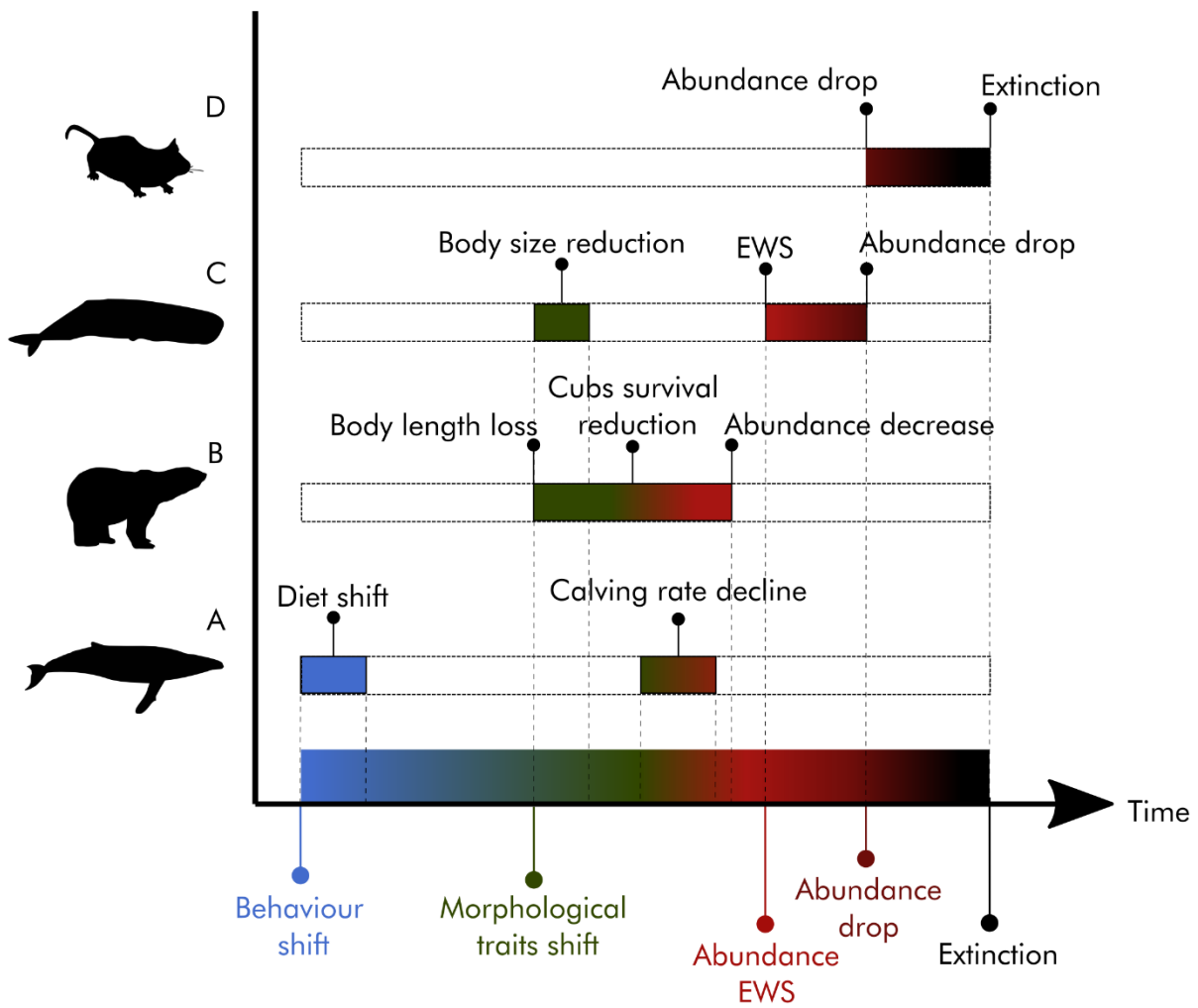
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BOX 3. Timeline fragments

In the timeline framework we highlighted the individual's and population's facets (behaviour, morphology and abundance) where stress induced change is more likely to occur and easier to measure in a monitoring perspective. This of course is a simplification of the whole spectrum (Box 3 Figure, horizontal axis) of stress responses – and thus potential signals – that can happen at the individuals and at the population level. In fact, when a high proportion of a population is similarly stressed, individual-level effects (behavioural and morphological changes) can propagate to alter the structure and dynamics of a population through changes in rates of birth, death, immigration, and emigration; all life history traits that can be altered before any abundance based Early Warning Signal (EWS) become detectable. Examples of phenotypic changes that shape an individual's life history traits (e.g. fecundity (Boggs & Ross, 1993)) with subsequent effects on fitness and population dynamics are numerous in the literature, and we can consider them as partial timeline to collapse where just some of expected signals where analysed or where the stressors are not increased enough yet. For instance, a study on the Gulf of St. Lawrence's (Québec, Canada) humpback whale population found a shift in diet (i.e. a behavioural change, Box 3 Figure A) caused by a decrease in resources (Gavrilchuk et al., 2014); years later, another study on the same population showed a subsequent decline in calving rates (e.g. life history adjustment, potentially leading to abundance EWS Box 3 Figure A). The author postulated that this signal could indicate that the population trends can be affected in the near future by the environmental change (Kershaw *et al.* 2021), i.e. possibly entering the EWS phase of the timeline.

Similarly, climatic change has impacted many polar bear populations particularly due to reduction in sea-ice availability. A study in the southern Beaufort Sea of Alaska population found first a body condition reduction (i.e. a morphological signal) and subsequently a decrease of reproductive rates and cubs survival (Rode et al., 2010) (Box 3 Figure B). The authors state that the low duration of the hunting ground (sea-ice platforms) induced a change in the feeding activity of the bears that triggered the loss of condition. Such change in behaviour, although postulated to happen, was not monitored for this population, otherwise this could have represented an almost complete timeline to collapse example. In fact, the abundance of the same population was monitored in a more recent paper that found a slight decrease compared to previous years estimates(Obbard et al., 2018). The decrease could indicate that the population is showing higher variance in the abundance

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849   estimates, and could be prone to show EWS of collapse, if recurrent monitoring would be carried on and if sea

850   ice keeps reducing.

851   Another example of partial timeline where EWS were detectable was given in the paper by Clements et. al

852   (Clements et al., 2017) where the historical collapse of, among others species, sperm whale populations was

853   found to be preceded by a change in body size and subsequent EWS (Box 3 Figure C). Finally, modern litera-

854   ture gives us also unfortunate examples of collapse until extinction due to anthropogenic stressors that were

855   recorded in recent times; the population of the Bramble Cay melomys was declared extinct in 2016, after a

856   continuous decline in the abundance estimates was observed in the scattered monitoring activities (Fulton,

857   2017). The oceanic inundation rate increase due to climate change is hypothesized to have driven a strong

858   habitat and resource reduction responsible for the Bramble Cay melomys decline. Likely, with monitoring

859   programs, some change in the movement pattern and in the condition of individuals would have been observed

860   before the ultimate collapse of this small rodents population. Despite such richness of partial examples, a

861   complete timeline to collapse is still to be observed; not surprisingly given the complexity of collecting and

862   analyse such multivariate data on a stressed population. Nevertheless, the current technological advancement

863   now allow us to collect such different kind of data in an automated way that suites the drawing of the timeline

864   to collapse.

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