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Transient demographic approaches can drastically expand the toolbox of coral reef science

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Abstract

Coral communities are threatened by an increasing plethora of abiotic and biotic disturbances. Preventing the ensuing loss of coral coverage and diversity calls for a mechanistic understanding of resilience across coral species and populations that is currently lacking in coral reef science. Assessments into the dynamics of coral populations typically focus on their long-term (*i.e. asymptotic*) characteristics, tacitly assuming stable environments in which populations can attain their long-term characteristics. Instead, we argue that greater focus is needed on investigating the *transient* (*i.e.* short-term) dynamics of coral populations to describe and predict their characteristics and trajectories within unstable environments. Applying transient demographic approaches to the evaluation and forecasting of the responses of coral populations to disturbance holds promise for expediting our capacity to predict and manage the resilience of coral populations, species, and communities.

Keywords:

Asymptotic dynamics, Population dynamics, Reef Conservation, Resilience, Short-term characteristics.

Introduction

46

47 Coral populations are sensitive to a range of biotic and abiotic pressures (Riegl 2020), many of

48 which will be exacerbated by future climatic change and human exploitation (Wolff et al. 2018;

49 Riegl and Glynn 2020). The future resilience of coral populations subsequently comprises their

50 capacity for enduring, and recovering from, this increased disturbance (Holling 1973).

51 Accordingly, a resilience-orientated focus is becoming commonplace in reef management

52 (Mcleod et al. 2019; McLeod et al. 2021), although this requires the ability for anticipating the

53 responses of coral populations to varying biotic and abiotic regimes (Lam et al. 2020).

54 Appropriately, state-structured demographic models are being increasingly utilised for

55 quantifying the mechanisms supporting or preventing the persistence and revival of disturbed

56 coral communities (e.g. Kayal et al. 2018; Cant et al. 2021). Indeed, understanding how

57 patterns in the survival, size, and reproduction of individual colonies influences population-

58 level characteristics is paramount for effectively managing conservation resources (Riegl et al.

59 2018; Pisapia et al. 2020). However, the contemporary application of state-structured

60 demographic approaches to ascertain the viability of coral populations does not reflect our need

61 to evaluate their resilience.

62 Structured population approaches examine how variation at the level of individuals

63 translates to population-level attributes (Caswell 2001). The state of individuals (typically their

64 size, age, or developmental stage [Caswell 2001]) arbitrates their survival and reproduction,

65 which in turn shape the responses of their population to local biotic and abiotic conditions

66 (Benton et al. 2006). Within natural populations, the diversity of individual-level

67 characteristics can be expressed through the state-structured vital rates of survival, progression

68 (growth & development), retrogression (shrinkage [Salguero-Gómez and Casper 2010] &

69 rejuvenation [Salguero-Gómez et al. 2013]), and reproduction (Metcalf and Pavard 2007).

70 Patterns across these vital rates, and their response to changing population structures,

71 subsequently underpin the characteristics of populations and define their capacity for tolerating

72 various environments (Boyce et al. 2006; Ehrlén et al. 2016). Equally, combined with an

73 explicit consideration for the interaction between multiple populations, structured population

74 analyses also facilitate the exploration of community recovery (Kayal et al. 2018) and

75 coexistence (Adler et al. 2010). Evaluating the vital rates and structure of numerous

76 populations, and their association with abiotic regimes, has thus proven instrumental in

77 calculating the extinction risk of highly threatened populations (Mace et al. 2008), and the

78 management, and conservation of natural communities (Morris and Doak 2002; Jongejans et

79 al. 2008).

80 With many coral communities facing imminent reassembly and population collapse,

81 the demand for an improved understanding of coral population dynamics has never been greater

82 (Edmunds and Riegl 2020). Although limited, the application of demographic theory within

83 coral research is not a novel concept (Edmunds et al. 2014). Veritably, there is a growing

84 appreciation for how the size structure of coral populations influences their dynamics and

85 endurance, with recent appeals for demographic approaches to be concentrated towards

86 gauging the resilience of coral communities (Dietzel et al. 2020; Pisapia et al. 2020; Cant et al.

87 2021; Lachs et al. 2021). However, prevailing knowledge of coral population dynamics centres

88 around isolated patterns in colony survival, changes in size, or recruitment, and long-term

89 (*asymptotic*) population characteristics. Quantifying the asymptotic characteristics of various

90 populations presents a valuable comparative tool for exploring abiotic tolerances (Beissinger

91 and Westphal 1998). Yet, to achieve their asymptotic dynamics, populations typically require

92 stable conditions, which seldom occur naturally, and are becoming increasingly unlikely given

93 current climate projections (Hastings et al. 2018; Francis et al. 2021). Consequently, a focus

94 towards exploring the asymptotic characteristics of populations limits our appreciation of their

95   dynamics within natural environments (Ezard et al. 2010), and will inhibit our capacity to

96   accurately predict the future condition of global coral assemblages.

97   Cyclic abiotic and biotic disturbances (e.g. seasonality in temperature or resource

98   availability) ensure that natural environments rarely exist at a stable equilibrium (Williams et

99   al. 2011). The perpetual instability generated by regular disturbances ensures that natural

100   populations rarely attain their asymptotic trajectories (Hastings 2001; Hastings et al. 2018).

101   Instead, the short-term or *transient* characteristics of populations, which reflect their dynamics

102   within non-equilibrate environments, play a fundamental role in the assembly of biological

103   communities (Hastings 2004). With the transient dynamics of populations defining their

104   performance following disturbance, these characteristics also represent quantifiable measures

105   of population resilience (Capdevila et al. 2020). Globally, coral communities are being exposed

106   to increasingly recurrent disturbance events (Hughes et al. 2018), with various species shifting

107   their distributions poleward or establishing populations within marginal habitats (Beger et al.

108   2014; Camp et al. 2018; Vergés et al. 2019). Here, we discuss why enhancing our capacity for

109   anticipating the future resilience of coral communities requires an understanding of the

110   transient dynamics in their constituent populations.

111   **Transient *versus* asymptotic population dynamics**

112   Population dynamics characterise and define the trajectories of populations according to the

113   individual-level allocation of resources towards survival, changes in size (or the state of

114   interest), and reproduction (Box 1). Any population can be structured according to the

115   distribution of its individuals across some state variable, be that age, size, developmental stage,

116   or a combination. The transition of individuals across state classes is, in turn, mediated by

117   selection gradients that emerge from the state-specific patterns of survival and reproduction

118   (Groenendael et al. 1988; van Tienderen 2000). In state-structured demography, patterns across

Box 1: Scaling from individuals to communities.

Following individual corals over time facilitates the calculation of vital rate patterns relating to colony survival, size, and reproduction, and how they govern the characteristics of populations and their wider community interactions (Fig. I). As corals mature and grow, they experience changes in their resource demands, with the capacity of corals for continually meeting these changing demands subsequently influencing their ability to maintain their somatic condition and tolerate local biotic and abiotic stressors (Hughes 1984). The repeated survey of individual colonies allows for documenting how the size of individuals regulates their survival, development, and reproductive contribution over time, and how this is shaped by changing environmental conditions. Condensing these temporal observations from across multiple tagged colonies then allows population ecologists to explore how individual-level vital rates underpin the dynamics of populations.

Crucially, state-structured demographic approaches enable the quantification of the relationship between abiotic conditions and population-level characteristics. Such an understanding is necessary if ecologists are to accurately predict the impact of recurrent disturbances and simulate populations under varying climate scenarios. Similarly, by understanding interactions across the dynamics of various co-occurring populations, and their differential responses to changing conditions, ecologists can better understand the mechanisms driving coexistence (Adler et al. 2010), and predict the transition of coral communities amidst changing climatic conditions (Hughes 1996; Kayal et al. 2018; Cant et al. 2021). Indeed, although more time consuming, demographic approaches transcend the correlative techniques previously used for evaluating the viability of coral populations and communities, and for predicting their resilience to future climatic stressors (Edmunds et al. 2014; Edmunds and Riegl 2020).
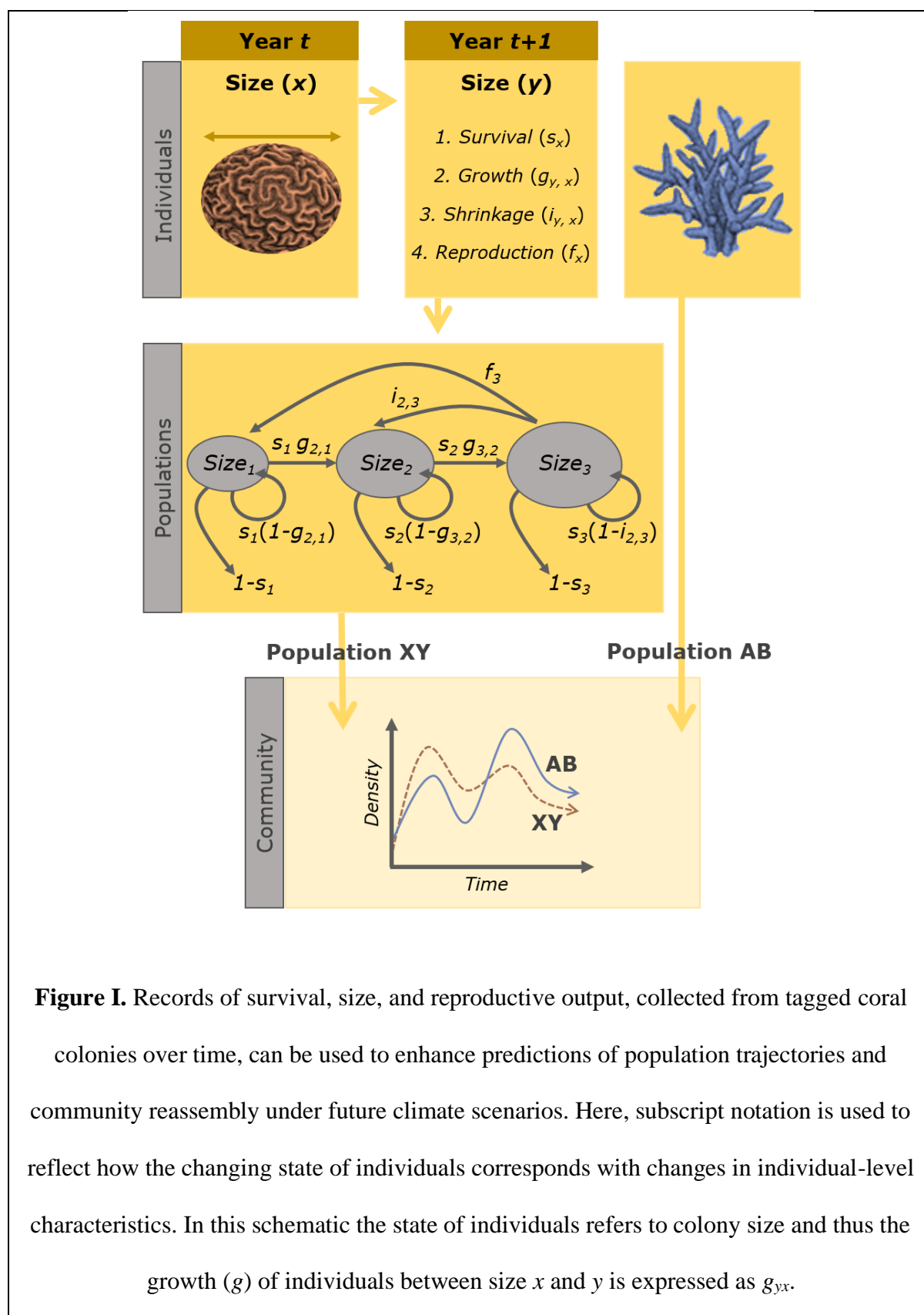
Figure I. Records of survival, size, and reproductive output, collected from tagged coral colonies over time, can be used to enhance predictions of population trajectories and community reassembly under future climate scenarios. Here, subscript notation is used to reflect how the changing state of individuals corresponds with changes in individual-level characteristics. In this schematic the state of individuals refers to colony size and thus the growth (g) of individuals between size x and y is expressed as g_{yx}.

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120   these multiple vital rates can subsequently be condensed into a population projection matrix

121   (A), with each matrix element (a_{ij}) expressing the expected transition of individuals into state

122   class i from state class j during the time interval t to $t+1$, or the per-capita a/sexual contributions

123   of state j individuals into state class i during that same interval (Caswell 2001). This population

124   matrix can then be used to project the size of a population (N, number of individuals) over time,

125   using the change in its state structure (**n**):

$$N_{t+1} = \sum \mathbf{n}_{t+1} = \sum A\mathbf{n}_t. \tag{1}$$

126

127   Within a stable environment, the state structure of a population is expected to converge towards

128   an equilibrium state (Caswell 2001). At equilibrium, the size of a population is then expected

129   to change at a constant rate over time, termed its asymptotic population growth rate (λ, Caswell

130   2001). The value of λ, for any state-structured population, is equal to the dominant eigenvalue

131   of its corresponding population matrix A. Estimates of λ represent the proportional change in

132   the size of populations over time, and exist on a non-negative scale reflecting population

133   growth ($\lambda > 1$), decline ($\lambda < 1$), or stasis ($\lambda = 1$).

134   Crucially, though, with populations rarely exposed to stable conditions or equilibria,

135   deterministic estimates of λ are unlikely to represent a true reflection of a population's

136   trajectory (Boyce 1992; Beissinger and Westphal 1998). To achieve their asymptotic growth

137   rate populations require a stable population structure, at which their vital rate patterns will

138   maintain a consistent distribution of individuals across state classes over time (Caswell 2001).

139   Yet, for their stable structure to manifest, populations typically require time in a constant

140   environment to allow the state distribution of individuals to convergence towards equilibrium,

141   without displacement by local disturbances (Fig 1; Bierzychudek 1999). Additionally, the vital

142   rate patterns used in constructing population projection matrices are themselves not consistent,

143   and contingent on the environmental conditions in which they are observed (Benton and Grant

144 1996; Boyce et al. 2006). Equally, as populations change in size their dynamics are subject to

145 density–dependant processes that regulate their trajectories within shared environments (Engen

146 et al. 1998; Lande et al. 2003). Thus the dynamics of populations can be expected to vary over

147 time as environmental conditions change (Tuljapurkar and Orzack 1980; Tuljapurkar 1989).
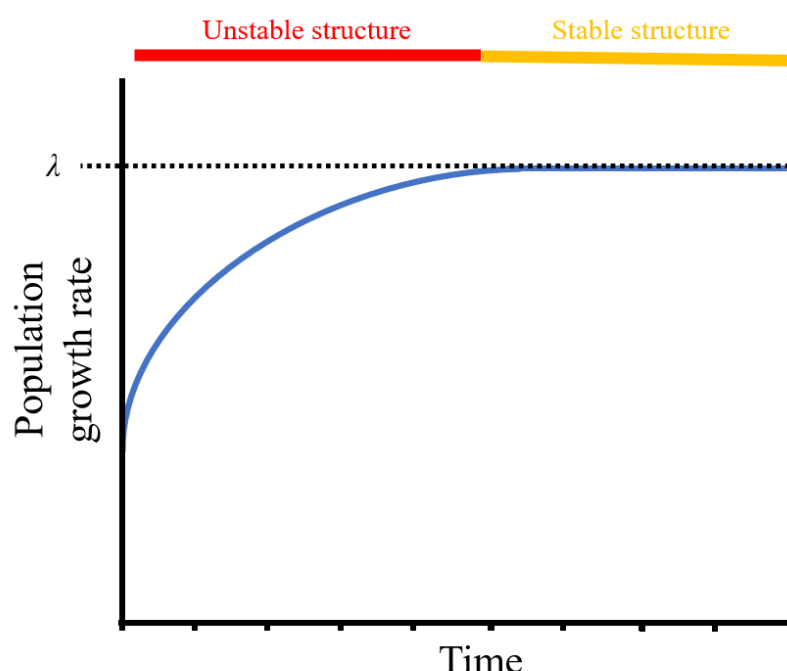

148 **Figure 1.** At stationary equilibrium, populations are expected to change size at a constant

149 rate, termed their asymptotic growth rate (λ). However, to display asymptotic characteristics,

150 populations need a stable state structure and so require time at equilibrium to enable the

151 development of this stable structure. In the absence of a stable state structure, populations

152 will display varying growth rates as they converge towards asymptotic expectations, even

153 within equilibrate environments. Note that, although in this schematic the populations growth

154 rate is increasing towards its asymptotic trajectory, estimates of λ can also reflect asymptotic

155 decline.

156

157 Recurrent perturbations prevent populations from acquiring, or preserving, a stable

158 state structure (Bierzychudek 1999; Williams et al. 2011). Instead, environments persist within

159   a non-equilibrate condition maintaining populations within a transient state during which their

160   trajectories can radically differ from asymptotic expectations (Stott et al. 2010, 2011; Hastings

161   et al. 2018). Accordingly, anticipating the future condition and endurance of populations

162   requires an awareness for their transient characteristics (Box 2; Ezard et al. 2010). Moreover,

163   with the transient characteristics of populations reflecting their response to disturbance and

164   instability, they represent quantifiable measures of population resilience (Capdevila et al.

165   2020). Transient shifts in the state structure of populations can elevate (*amplification*) or

166   diminish (*attenuation*) their growth rates relative to asymptotic projections (Townley et al.

167   2007). Equally, for populations existing in a transient state, there is a natural tendency for their

168   state structure to converge towards a stable structure (Caswell 2001). Intuitively, with

169   population resilience comprised of the attributes of *resistance* (the ability to withstand

170   disturbances), *compensation* (the ability to benefit from disturbances) and *recovery* (the speed

171   and ability to reattain stability), the transient characteristics of populations resemble these

172   features of resilience (Hodgson et al. 2015; Capdevila et al. 2020).

Box 2: Measuring transient population characteristics.

Within natural environments, abiotic and biotic perturbations generate constant shifts within the state structure of populations ensuring they persist within a transient state, rather than converging towards equilibrium (Hastings et al. 2018). Within this transient state, the growth rate of populations can differ dramatically from their asymptotic trajectories, with populations undergoing *amplification* (increases in growth rate) or *attenuation* (declines in growth rate), which can subsequently influence the viability of a population in the longer-term (Fig. II). Accordingly, it is necessary to explore the transient characteristics of populations to gain insights into their responses to disturbance, and therefore better

understand their resilience (Ezard et al. 2010; Capdevila et al. 2020). Evaluating the transient dynamics of populations is made possible through the calculation of transient indices from population projection matrices (Stott et al. 2011). These measures include population *reactivity* ($\overline{\rho}$) and *first-timestep attenuation* ($\underline{\rho}$) which describe the increase or decline in a populations growth rate within one time interval of a perturbation, relative to λ (Stott et al. 2011). Equally, the measures of *maximal amplification* ($\overline{\rho}_{max}$) and *maximal attenuation* ($\underline{\rho}_{max}$) can be used to evaluate the maximum amplification or attenuation expected in the growth rate of populations, relative to λ (Townley et al. 2007; Townley and Hodgson 2008).
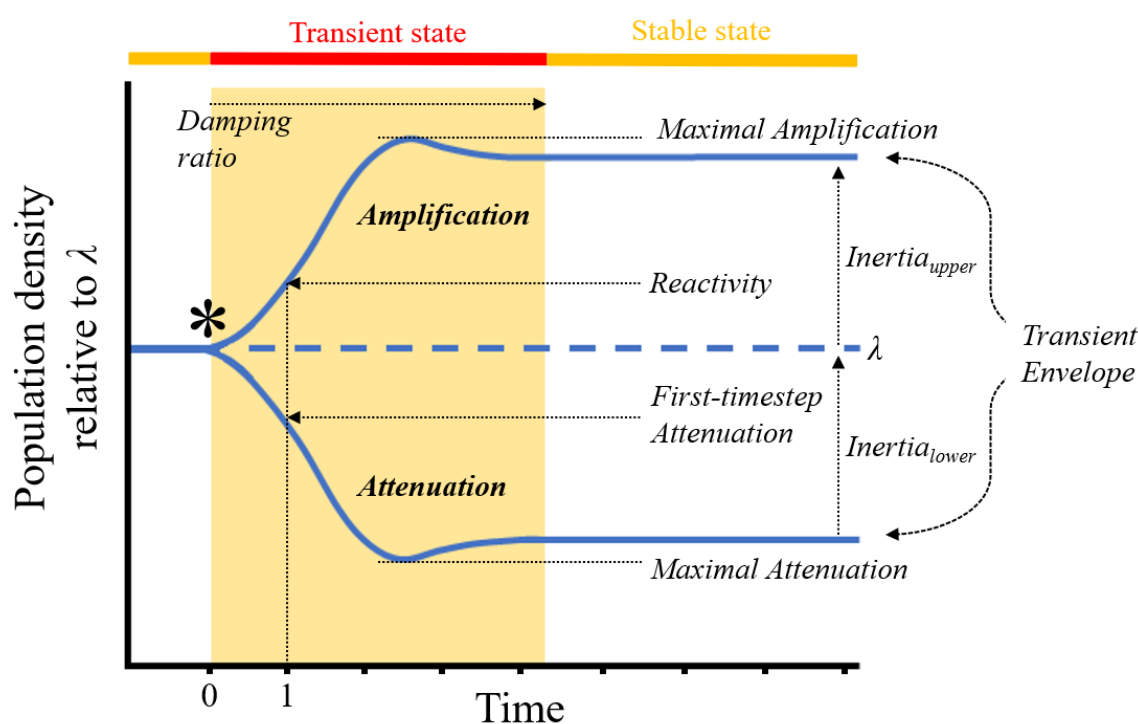

Figure II. Various measures exist for quantifying the transient characteristics of populations, and how the short-term responses of populations following a disturbance (*) will modify their trajectories relative to asymptotic expectations.

> The *damping ratio* (ρ) of a population defines the rate at which at population will converge back to a stable equilibrium following a perturbation to its stable structure (Caswell 2001). Finally, *upper* & *lower population inertia* (*Inertia$_{upper}$* & *Inertia$_{lower}$* respectively) can be used to explore the extent to which the transient characteristics of populations influence their long-term trajectories, also known as a populations *transient envelope* (*TE*) (Koons et al. 2005; Stott et al. 2011).

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174   Evaluating the transient characteristics of populations, and therefore their demographic

175 resilience, is possible through the calculation of transient measures readily accessible from

176 population projection matrices (Box 2; see Stott et al. [2011] for a detailed review). Briefly,

177 measures of *reactivity* ($\overline{\rho}$) and *first-timestep attenuation* ($\underline{\rho}$) reflect the initial behaviour in a

178 population's growth rate following a perturbation, with the *damping ratio* (ρ) describing the

179 rate at which a population is expected to reacquire a stable state structure (Caswell 2001; Stott

180 et al. 2011). Alternatively, estimates of *maximal amplification* ($\overline{\rho}_{max}$), *maximal attenuation*

181 ($\underline{\rho}_{max}$), and *population inertia* (*Inertia$_x$*) illustrate the magnitude by which the growth rate of

182 a population can be expected to fluctuate, and the influence of this short-term variation on the

183 population's long-term trajectory (Koons et al. 2005; Townley et al. 2007; Stott et al. 2011).

184 Furthermore, with population projection matrices providing a link between each transient

185 characteristic and a population's vital rates, sensitivity analyses can be applied to evaluate the

186 mechanistic drivers underlying the short-term characteristics of populations (Stott 2016;

187 Caswell 2019). Overall, transient demographic approaches present an effective tool for

188 explicitly evaluating the resilience of natural populations (Capdevila et al. 2020), and have

189 proven instrumental in our understanding of the establishment of populations within new and

190 variable environments (Iles et al. 2016; McDonald et al. 2016, 2017; Jelbert et al. 2019).

Coral population dynamics: Current knowledge

To examine the advancement of state-structured population approaches within coral research, we conducted a review of the relevant ecological literature. Specifically, we searched for the term coral* AND demograph* across the titles, abstracts, and keywords of research literature within the SCOPUS database. We applied our search across all indexed peer-reviewed journals published between 1960 and 2020, inclusive. This search initially returned 781 studies, from which we retained all studies that explicitly measured or quantified state-structured patterns in the survival, size transitions (including shrinkage via partial mortality or fission), and/or reproduction (e.g. fecundity) of coral colonies. We also retained studies measuring larval settlement rates, as the recruitment of early life stage individuals is a key demographic aspect within coral communities (Adjeroud et al. 2017). Following this refinement, we retained a total of 145 studies (~19% of our original search), which we then categorised according to whether they involved the presentation of (i) asymptotic dynamics/simulations, (ii) transient characteristics, or (iii) an assessment of vital rate patterns only.

Following the seminal work of Hughes and Jackson (1980), the application of state-structured demographic assessments has increased within coral research, with a particularly rapid growth in popularity since 2007 (Fig. 2). However, much of this research (97%) has focused on either exploring the asymptotic dynamics of coral populations (34%; 50 studies) or solely evaluating patterns across one or more of the vital rates of survival, changes in size, or reproduction (63%; 91 studies). Presently, the majority of knowledge regarding the dynamics of coral populations centres around their long-term trajectories. Thus, our current understanding regarding the dynamics of coral populations assumes that these populations will experience the stable environments necessary for achieving optimum population structures.
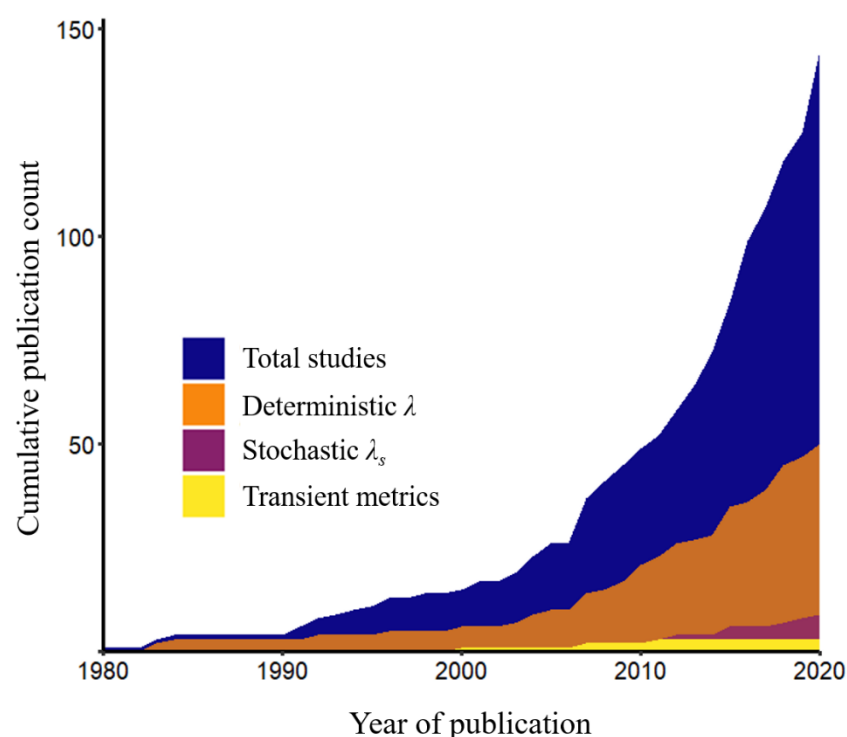
Figure 2. The cumulative number of studies that explicitly explore the state-structured demographics of coral populations as identified by our search for the term coral* AND demograph* across the peer-reviewed literature within the SCOPUS database. The colour scale differentiates between studies that focus on only investigating patterns in colony survival, growth, and/or reproduction, and those that utilised estimates of either deterministic population growth (λ), stochastic asymptotic characteristics (λ_s), or transient population characteristics, to evaluate the dynamics of coral populations.

A limited amount of previous research has considered the unpredictable nature of natural environments when evaluating the future trajectories of coral populations. Our search identified nine studies that either included estimates of stochastic population growth (λ_s; Lewontin and Cohen 1969) or explicitly parameterised the density-dependant regulation of vital rates within their population models (Fig. 2; see Linares et al. 2007; Linares and Doak

227   2010; Hernandez-Pacheco et al. 2011; Vardi et al. 2012; Bramanti et al. 2015; Mercado-Molina

228   et al. 2015; Kayal et al. 2018; Montero-Serra et al. 2019). Estimates of λ_s describe the average

229   periodic change in the size of a population over a series of successive time intervals (Engen

230   and Saether 1998). As such, this metric of population performance provides a more accurate

231   consideration of vital rate and environmental variation when evaluating future population

232   trajectories, compared to deterministic λ. However, with estimates of λ_s often derived using a

233   series of population sizes estimated over numerous time intervals or with initial inconsistent

234   estimates of population size omitted, λ_s is still fundamentally a long-term measure of population

235   viability (Ellner and Rees 2007). Consequently, this measure still neglects the short-term

236   characteristics of populations, and thus our capacity to fully anticipate the future dynamics of

237   coral populations remains restricted.

238   Whilst state-structured demographic approaches are being adopted within coral

239   research, our review of the literature demonstrates how prominently the assumption of stable

240   equilibria dominates our understanding of coral population dynamics. Subsequently, we lack

241   the understanding necessary for accurately projecting the future reassembly and persistence of

242   coral communities under increasingly recurrent disturbance regimes. Only three of the 145

243   studies in our literature search calculated measures of the transient characteristics of coral

244   populations (Fig. 2; see Hughes and Tanner 2000; Linares et al. 2007; Bruno et al. 2011).

245   Alongside asymptotic population characteristics, these studies estimated population damping

246   ratios to outline the rate at which their focal populations would converge back to a stable state

247   structure following a perturbation. Yet, the damping ratio represents a dimensionless,

248   mathematical property of population projection matrices, and alone is of limited use to

249   population managers seeking to predict the short term responses of populations to disturbance

250   (Stott et al. 2011). Forecasting the resilience of coral populations is essential for the future

251   conservation of various reef communities (Roche et al. 2018; Lam et al. 2020). We have

252   illustrated here, however, that current approaches used in coral population ecology to evaluate

253   population growth rates do not constitute measures of population resilience. Our understanding

254   of coral population dynamics needs to be further expanded in order to meet our need for

255   quantifying the resilience, and responses, of coral communities to increasingly frequent

256   disturbances.

Transient dynamics and the resilience of coral communities

258   Exploring the transient characteristics of coral populations will enhance our understanding

259   regarding the future diversity, condition, and resilience, of coral communities. The frequency

260   of widespread thermal stress events is increasing across global coral communities, and soon

261   expected to exceed the recovery time required by most coral species (Hughes et al. 2018; Sully

262   et al. 2019). Presently, considerable value is placed on classifying coral species according to

263   their morphological and functional traits, with the subsequent categorisation of coral taxa

264   offering proxies for the vulnerability of various coral communities to said recurrent stress

265   events (Darling et al. 2012, 2019). Quantifying the relative affinities of different coral

266   populations for demographic recovery presents the opportunity for justifying these

267   assumptions; helping to distinguish the species and populations most vulnerable and or resilient

268   to projected recurrent disturbance regimes.

269   Intuitively, the amplification and attenuation characteristics of populations

270   simultaneously reflect their stability following a disturbance. However, recognising the

271   differential attributes of compensation and resistance in different populations is important for

272   managing the future condition of biological communities (Capdevila et al. 2020). Assessments

273   of coral communities following repeated disturbances have demonstrated divergent shifts in

274   species compositions (Adjeroud et al. 2009; Pratchett et al. 2011, 2020). With knowledge of

275   the capacity for various coral populations to undergo demographic amplification or for

276 avoiding demographic attenuation, we can begin to forecast and anticipate the reassembly of

277 coral communities, thereby improving the effectiveness of adaptive reef management.

278 Alternatively, a disturbance does not necessarily imply a negative impact, merely a change to

279 a system (Pickett and White 1985). Disturbances to the structure of populations can be brought

280 about by the cessation of a continuous pressure, changes in resource availability, or

281 establishment within a novel environment. The transient characteristics of populations offer

282 insights into their invasive potential (Iles et al. 2016), with the ability of natural populations

283 for undergoing demographic compensation underpinning their capacity for exploiting changes

284 within their local environments (Jelbert et al. 2019). Accordingly, comprehending and

285 quantifying demographic compensation within coral populations will aid predicting the

286 winners and losers in reef communities targeted by conservation initiatives, restoration

287 strategies, or climate induced range shifts. Assessing coral reef community resilience within

288 such a framework requires an increased focus on the temporal nature of resilience, a view that

289 would transcend current approaches of conducting single reef assessments to determine

290 resilience (Maynard et al. 2015; McLeod et al. 2021).

291 Complexities in the modelling approaches used to explore the dynamics of natural

292 populations have resulted in these techniques remaining largely overlooked within coral

293 research (Edmunds et al. 2014). Indeed, parametrising the demographic models needed to

294 quantify population characteristics requires considerable amounts of data (Ellner et al. 2002).

295 Although, despite the data demanding nature of state-structured demographic models, the

296 collection of the necessary data regarding the survival, transitions in size, fragmentation, and

297 recruitment, of individual coral colonies is possible alongside current reef monitoring efforts

298 (Edmunds and Riegl 2020). Furthermore, new techniques for analysing the demographic

299 characteristics of populations structured by a continuous state variable like size (Integral

300 Projection Models [IPMs; Easterling et al. 2000]) have reduced the data demands of

301   demographic assessments (Ramula et al. 2009). As a result, IPM frameworks are growing in

302   popularity throughout coral research (e.g. Bruno et al. 2011; Madin et al. 2012; Zychaluk et al.

303   2012; Elahi et al. 2016; Kayal et al. 2018; Precoda et al. 2018; Scavo Lord et al. 2020; Cant et

304   al. 2021; Carlot et al. 2021). Finally, studying the dynamics, particularly the transient

305   characteristics, of coral populations is made increasingly accessible by the development of

306   demographic analysis packages such as *popdemo* (Stott et al. 2012).

307   It is not our intention to dismiss previous efforts to evaluate the dynamics of coral

308   populations using asymptotic characteristics. Changes in individual vital rates can of course

309   have critical repercussions on the dynamics of populations (e.g. Bellier et al. 2018), and

310   asymptotic characteristics provide valuable insights for the management of threatened

311   populations (e.g. Johnson et al. 2010). However, as we have illustrated here, the asymptotic

312   characteristics of populations do not represent indicators of population resilience. Here, we

313   advocate for a greater commitment towards investigating the transient dynamics of coral

314   populations that more accurately reflect their dynamics within natural environments (Ezard et

315   al. 2010; Stott et al. 2011; Capdevila et al. 2020). With changing climatic regimes and increased

316   anthropogenic interference exposing global reef ecosystems to increasingly frequent

317   disturbances (Hoegh-Guldberg et al. 2017), evaluating the transient dynamics of coral

318   populations, and their mechanistic drivers, will provide a new effective lens on coral reef

319   resilience.

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