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Net effects of life-history traits explain persistent differences in abundance among similar species

Mike McWilliam[1] | **Maria Dornelas**[2] | **Mariana Álvarez-Noriega**[3] | **Andrew H. Baird**[4] | **Sean R. Connolly**[5] | **Joshua S. Madin**[1]

[1]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, Hawai'i, USA

[2]Centre for Biological Diversity, Scottish Oceans Institute, University of St Andrews, St Andrews, UK

[3]Centre for Geometric Biology, School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

[4]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

[5]Smithsonian Tropical Research Institute, Balboa, Panama

Correspondence
Mike McWilliam
Email: mjmcwilliam@outlook.com

Present address
Mariana Álvarez-Noriega, Australian Institute of Marine Sciences, Townsville, Queensland, Australia.

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Abstract

Life-history traits are promising tools to predict species commonness and rarity because they influence a population's fitness in a given environment. Yet, species with similar traits can have vastly different abundances, challenging the prospect of robust trait-based predictions. Using long-term demographic monitoring, we show that coral populations with similar morphological and life-history traits show persistent (decade-long) differences in abundance. Morphological groups predicted species positions along two, well known life-history axes (the fast-slow continuum and size-specific fecundity). However, integral projection models revealed that density-independent population growth (λ) was more variable within morphological groups, and was consistently higher in dominant species relative to rare species. Within-group λ differences projected large abundance differences among similar species in short timeframes, and were generated by small but compounding variation in growth, survival, and reproduction. Our study shows that easily measured morphological traits predict demographic strategies, yet small life-history differences can accumulate into large differences in λ and abundance among similar species. Quantifying the net effects of multiple traits on population dynamics is therefore essential to anticipate species commonness and rarity.

KEYWORDS
commonness, comparative demography, coral reefs, fitness, functional traits, rarity, recruitment, reproduction, trade-offs

INTRODUCTION

Ecological assemblages are typically composed of a few highly abundant species, and many rare species (May, 1975; Preston, 1948). Anticipating the identities of common versus rare species is a crucial challenge, necessary to predict species' contributions to ecosystem functions and services (Winfree et al., 2015), and the potential responses of species to environmental change (Enquist et al., 2019; Purvis et al., 2000). Species have evolved a diverse range of "functional traits," so-named because they influence individual performance, and therefore predict population turnover, standing biomass, and ultimately species roles in ecosystems (Bellwood et al., 2018; Shipley

et al., 2016; Violle et al., 2007). Since the arrival of neutral theory (Hubbell, 2001), numerous studies have identified non-neutral patterns of abundance in which species differences (traits) play a central role in community assembly (e.g., Bode et al., 2012; Dornelas et al., 2006). However, we still know surprisingly little about why certain types of species become common whereas many others remain rare, and the identities of common and rare species are often lacking when modeling species abundance distributions (Connolly et al., 2014; McGill et al., 2007).

Through a process of species sorting or filtering (akin to natural selection on ecological timescales), species with specific trait combinations are more likely to dominate in certain environments or microhabitats (Shipley et al., 2006; Southwood, 1988). Various traits have been linked with species dominance (Kunin & Gaston, 1993; Murray et al., 2002), and are often identified along environmental gradients, such as those structured by colonization versus competition (Grime, 1974; Laughlin et al., 2020). Nevertheless, the capacity of traits to produce accurate reconstructions of species abundance patterns remains limited (McGill, 2006). Associations between traits and abundances rely mostly on community-aggregated values or groups (e.g., community-weighted means), obscuring species-level variation in traits and abundance, and skipping over the population-level processes that drive commonness and rarity (Laughlin & Messier, 2015). By grouping species together, trait-based approaches ignore large differences in abundance occurring among species that share broad suites of traits. These "similar species" can differ in abundance by many orders of magnitude (e.g., Jones et al., 2002; Walker et al., 1999), revealing large variations in abundance that appear difficult to predict.

Demographic approaches can improve our understanding of trait–abundance relationships (Salguero-Gómez et al., 2018; Shipley et al., 2006). Theoretically, certain traits promote greater abundance by enhancing vital rates (survival, growth, or reproduction), and consequently the population geometric growth factor, λ, (hereafter, "population growth rate") which describes a species' average fitness in a given environment (Adler et al., 2014; Pistón et al., 2019). Numerous links between traits and vital rates have been identified: wood density affects tree growth (Wright et al., 2010), coral shapes affect colony dislodgement (Madin & Connolly, 2006), behavioral traits alter vertebrate clutch size and mortality (Jetz et al., 2008; Ozgul et al., 2010), and body size and metabolic rates are strongly linked to growth and survival across most taxa (Charnov & Ernest, 2006; Speakman, 2005). The subsequent effects of these traits on λ depend on (i) how vital rates covary along important trade-off axes to determine species life-history strategies, and (ii) how particular demographic rates influence the overall population growth rate in a given environment (Laughlin et al., 2020; Southwood, 1988). Population growth rates are therefore the driving force of the trait–abundance relationship (Shipley et al., 2016), but are rarely quantified in long-lived species because they are data-intensive, and require knowledge of how multiple vital rates interact across the life cycle (Caswell, 2000).

In this study, we monitored 11 coexisting coral populations to test the hypothesis that divergent abundances among apparently similar species can be explained by differences in fitness and population growth. We quantify the stepwise associations between morphological traits, demography, and population growth rate (λ), and test whether small but consistent differences in demographic rates can accumulate into large differences in λ and abundance within groups of similar species. Previous work has shown that groups of coral populations with similar morphological traits have similar levels of survival (Madin et al., 2014), fecundity (Álvarez-Noriega et al., 2016), growth (Dornelas et al., 2017), and partial mortality (Madin et al., 2020). However, coral populations are known to show stark differences in abundance within morphological groups (Dornelas & Connolly, 2008), and are therefore useful study groups to determine how demographically similar species can diverge in abundance, ultimately shedding light on the hidden dynamics that drive species commonness and rarity.

MATERIALS AND METHODS

Study design

We conducted demographic surveys of common and rare coral populations for 6 years (2009–2014) on an exposed reef crest on Lizard Island, Australia (14.699839° S, 145.448674° E). Eleven species of reef-building coral (Scleractinia) were selected to represent at least one locally common and one locally rare species from five morphological groups (Appendix S1: Figure S1). Species within each group differ only slightly in morphological structure (e.g., in corallite geometry, Veron, 2000), and therefore have a range of functional traits in common. Nevertheless, an exhaustive colony count across 270 10 m^2 belt transects in 2005 (Dornelas & Connolly, 2008) demonstrated that species with similar morphologies have striking differences in abundance. For example, the two tabular study species have near-identical morphologies, yet *Acropora hyacinthus* was 45 times more abundant than *A. cytherea*. In the massive group, *Goniastrea retiformis* was 22 times more abundant than *G. pectinata*. In the corymbose group, *A. nasuta* was seven times more abundant than

A. millepora. In the digitate group, *A. digitata* was five times more abundant than *A. humilis*. In the staghorn group, *A. intermedia* was two times more abundant than *A. robusta* (Appendix S1: Figure S2). The persistence of these abundance differences was confirmed using six 10 m line intercept transect (LIT) surveys in 2011 and 2014. Our study design therefore enabled the search for a demographic explanation for different abundances among species with very similar functional traits.

Demographic rates

To examine demographic differences within morphological groups, rates of coral growth, survival, and fecundity were quantified by monitoring 30 colonies of each species over 6 years, during a period with no large-scale disturbances (2009–2014, Madin et al., 2018). Growth was calculated as changes in planar area each year, using photographs of colonies with a scale bar, and processed with ImageJ software after correcting for lens distortion. Dead or missing colonies were identified and recorded to track rates of mortality. For each whole-colony mortality event, a new colony was tagged in its place to keep the yearly sample size at 30 per species. Yearly fecundity was measured by collecting fragments (one nubbin of *Goniastrea*, four branches of *Acropora*) from 30 colonies 1 week before spawning and counting eggs in six polyps per fragment using a dissecting microscope. Egg carbon content in 3–6 isolated colonies was measured directly to estimate egg biomass (Álvarez-Noriega et al., 2016). Size-specific fecundity (eggs per cm^2) was found by multiplying average eggs per polyp in each colony by the average polyp density of its species, where polyp densities were measured by counting all polyps (in three dimensions) across a 16 cm^2 planar area of replicate colonies (Álvarez-Noriega et al., 2016). Colony fecundity was calculated by multiplying size-specific fecundity by colony area.

Coral demographic rates are strongly dependent on colony size (Hughes & Connell, 1987). The demographic rates of each species were therefore modeled against $\log_{10}$-transformed colony sizes (planar area) on a m^2 scale (Appendix S1: Figure S3). Reproductive maturity (whether a colony produced eggs) was modeled against colony area using logistic regression (a generalized linear model with a binomial response variable and logit link function). Total fecundity (eggs per mature colony) was modeled against colony area using a negative binomial regression and a log link function (Appendix S1: Figure S3a,b; Álvarez-Noriega et al., 2016). Growth was measured using linear models of colony area at year t against area at year $t + 1$ (Appendix S1: Figure S3c; Dornelas et al., 2017). Survival was determined by whether a colony was found alive 1 year after measurement, and was modeled against colony area using logistic regression, which included a quadratic term to allow for greater mechanical vulnerability in large corals (Appendix S1: Figure S3d; Madin et al., 2014). Demographic modeling was restricted to colonies above 5 cm^2 because of low sample sizes in very small colonies. Growth parameter estimates for one species (*G. retiformis*) implied biologically implausible growth (allometric slope > 1, driven by anomalous small colonies shrinking over many years), and were therefore replaced with those of *G. pectinata*.

Population dynamics and fitness

To further examine signals of demographic differences within morphological groups, we used integral projection models (IPMs), which combine regression functions of colony size and vital rates (growth, survival, fecundity), and generate transition matrices used to project population dynamics (Coulson, 2012; Easterling et al., 2000; Merow et al., 2014). The strong dependency of demographic rates on colony size makes IPMs a useful tool for studying coral population dynamics, because IPMs treat colony size as a continuous variable, generating more accurate predictions of population change (Cant et al., 2021; Edmunds et al., 2014; Kayal et al., 2018). The number of individuals of size y at time $t + 1$ was modeled as a function of the number of individuals of size x at time t:

$$n(y, t+1) = \int [s(x)g(x,y) + r(x,y)]n(x,t)\mathrm{d}x$$

where $s(x)$, $g(x, y)$, and $r(x, y)$ represent annual survival, growth, and recruitment functions, respectively, and both size distributions x and y are on $\log_{10}$ scales. Survival rates at size x were based on fitted logistic regressions (Appendix S1: Figure S3d), and growth at size x based on the fitted linear regressions (Appendix S1: Figure S3c). The reproduction function was modeled as:

$$r(x,y) = p_{\mathrm{mat}}(x)\ n_{\mathrm{eggs}}(x)\ p_{\mathrm{rec}}\ p_{\mathrm{recsize}}(y)$$

where p_{mat} represents the probability of reproductive maturity at size x and n_{eggs} represents the total number of eggs produced at size x (Appendix S1: Figure S3a,b). p_{rec} can be interpreted in a closed-system context as the probability of ovule fertilization, larval survival, and immediate postsettlement survival, with the added probability in an open system that exported larvae are replaced by imported larvae. p_{recsize} represents the size at

recruitment, and strongly determines the "escape in size" phenomenon in corals, whereby colonies grow to avoid high mortality at smaller sizes. Both p_{rec} and $p_{recsize}$ were highly uncertain, and demographic models were therefore analyzed using a large range of p_{rec} and $p_{recsize}$ values (see Appendix S1: Section S1).

Population growth rate (λ) was determined by the dominant eigenvalue of the IPM kernels. This density-independent measure of population growth is likely to be a key parameter for understanding long-term abundance averages in this system because the location is affected by regular small-scale disturbances (Madin et al., 2018), and adults of each species had negligible competitive limits to growth during the study period (Álvarez-Noriega et al., 2018). Rates of recovery from low density are therefore likely to strongly influence long-term patterns of abundance. Estimates of λ were bootstrapped by resampling colonies with replacement 1000 times while keeping sample sizes the same, then re-fitting demographic models and calculating λ. Differences in abundance were projected through time by multiplying an initial population of 100 corals in the smallest size classes by the IPM matrices, and then repeating for 100 generations (years) to identify the time needed to generate observed differences in abundance within each group. The sensitivity of this process to variations in initial colony size and population size was also tested.

Demographic variation

Numerous life-history traits were calculated from demographic models (Appendix S1: Table S1) to explore demographic variation within and between morphological groups. These life-history traits included partitioned maximum growth and partial mortality rates following Madin et al. (2020), size-specific fecundity measured as the intercept of a constant-slope size-fecundity model, the minimum size at reproductive maturity, and average rates of survival and total fecundity across all sizes (Appendix S1: Table S1). Generation times were estimated from the demographic models following Ellner et al. (2016) as $\log(R_0)/\log(\lambda)$ where R_0 is the per-generation rate of increase. Variation in demographic parameters was analyzed within and between morphological groups using both principal components analysis (PCA) and within-group sum of squares calculation. Furthermore, we identified the source of differences in λ among similar species by re-fitting demographic models (Appendix S1: Figure S3) by each morphological group rather than each species, and subsequently calculating λ differences when only one demographic rate (growth, survival, or reproduction) was allowed to vary between species within morphological groups. By keeping all but one demographic rate constant within morphological groups, we identified the effect of a particular demographic rate on shifts in population dynamics among similar species.

RESULTS

Life history and abundance

A synthesis of independent vital rates over 6 years (2009–2014) revealed two key dimensions of demographic variation across the study species, summarizing important life-history trade-offs (Figure 1; Appendix S1: Figure S4). Accounting for the size-dependency of demographic rates across four orders of magnitude (5 cm^2 to 1 m^2, Figure 1a), we find that species were strongly separated along a trade-off axis from fast growth and low survival to slow growth and high survival (Figure 1b), reflecting the widely observed "fast-slow" continuum of life histories. Total colony fecundity aligned with the "fast" end of this primary axis, as faster-growing colonies tended to have larger areas, and thus exponentially more egg-producing polyps (Figure 1b; Appendix S1: Figure S3), although they required larger colony sizes to reach reproductive maturity (Figure 1b; Appendix S1: Figure S3). An alternate measure of fecundity describing reproductive investment (eggs per cm^2 of colony planar area) was aligned with a secondary PCA axis, and was highest in species with moderate levels of growth and survival (Figure 1b; Appendix S1: Figure S3).

Species with similar morphologies were highly clustered in demographic parameter space, indicating similar demographic rates. Yet, large differences in abundance within morphological groups were persistent over nearly a decade (2005–2014; Figure 1b,c). Arborescent and tabular species pairs had rapid growth, high partial mortality, and were 10 times larger than the smallest species on average, thus producing the largest number of eggs per individual. Midsize corymbose species had moderate growth and survival, while investing in the largest number of eggs per unit area. The smallest species pairs were digitate and massive ("boulder-like"), which had slow growth, high survival rates, and reached reproductive maturity at small sizes (Figure 1b). Morphology was therefore strongly linked with species positions along two demographic trade-off axes. Nevertheless, at least one species within each morphological group was persistently common and another persistently rare, whereas only one corymbose species (*A. nasuta*) became relatively less common in its group over time (Figure 1c; Appendix S1: Figure S2). These results indicate that species with similar

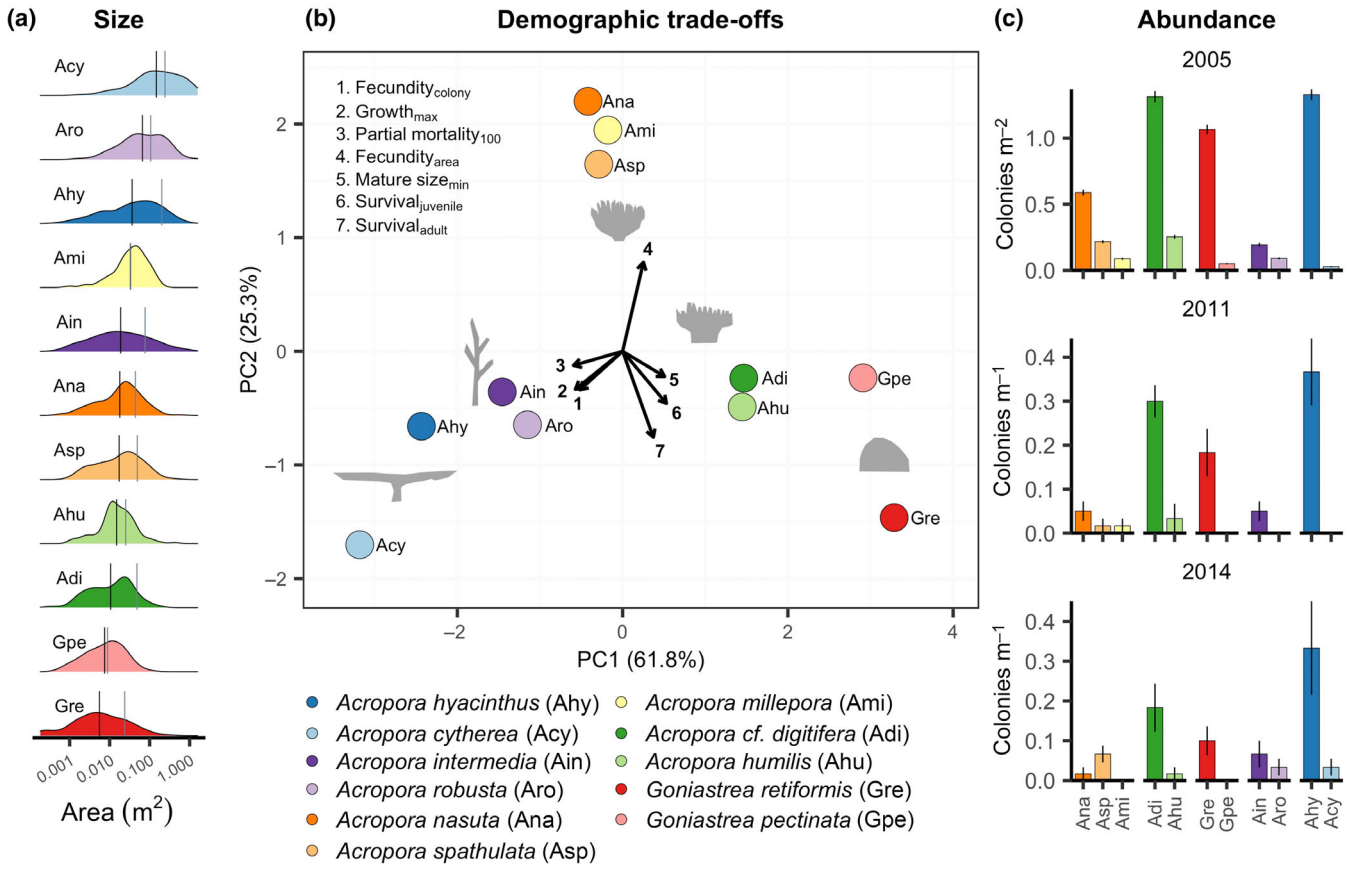

FIGURE 1 Commonness and rarity are poorly explained by morphological and life-history traits. Color pairings indicate species with similar morphologies. Dark colors within each pair reflect higher abundance. (a) Planar area distributions of all colonies in the study area. Separate distributions are shown for each study species, ranked top–bottom by mean size (black lines). Mean size of colonies for which demographic information was obtained was typically higher (gray lines). (b) Principal components analysis of 11 species by demographic parameters obtained from size-structured models (Appendix S1: Table S1). (c) Decadal abundances of study species measured using 270 10 m^2 belt transects (2005) and six 10 m line intercept transects (2011–2014). Separate horizontal panels are shown for each morphological group.

morphologies and similar rates of growth, survival, and reproduction can maintain large differences in abundance for at least 9 years (Figure 1b,c).

Population growth differences

Comparisons of IPMs within morphological groups indicate that common species tended to have higher population growth rates (population "fitness" or λ) than rare or declining species (Figure 2). IPMs summarizing size-dependent growth, survival, and reproduction (Figure 2a; Appendix S1: Figure S5) were combined with estimates of recruitment probabilities to quantify λ in each study species. Holding recruitment parameters constant (genus-level averages of fitted p_{rec} values; Figure 2b), we find that λs were consistently higher in common species than rare species, and were robust to bootstrapping (distributions of λs, Figure 2c). Additions to λ in common relative to rare species varied from 0.04 (in the massive group) to 0.49 (in the tabular group), and were generally larger in taxa with shorter (<15 year) generation times such as tabular, staghorn, and corymbose *Acropora* (Figure 2c,d). Notably, the corymbose group with large differences in λ exhibited shifting patterns of dominance and rarity during the study, with the declining species showing extremely low values (Figure 2c; Appendix S1: Figure S2).

Higher population growth rates in common species were consistent across a wide range of recruitment probabilities (Figure 2b; Appendix S1: Figure S6). The boundaries of possible recruitment probabilities (p_{rec}) ranged between ~1/100 and 1/10,000 (Figure 2b; Appendix S1: Section S1), reflecting the high variability in fertilization, settlement, and juvenile survival that can occur from year to year. Within the bounds of these estimates, population trajectories of each species varied from declining ($\lambda < 1$) to growing ($\lambda > 1$). Nevertheless, common species had higher λ than rare species across a wide

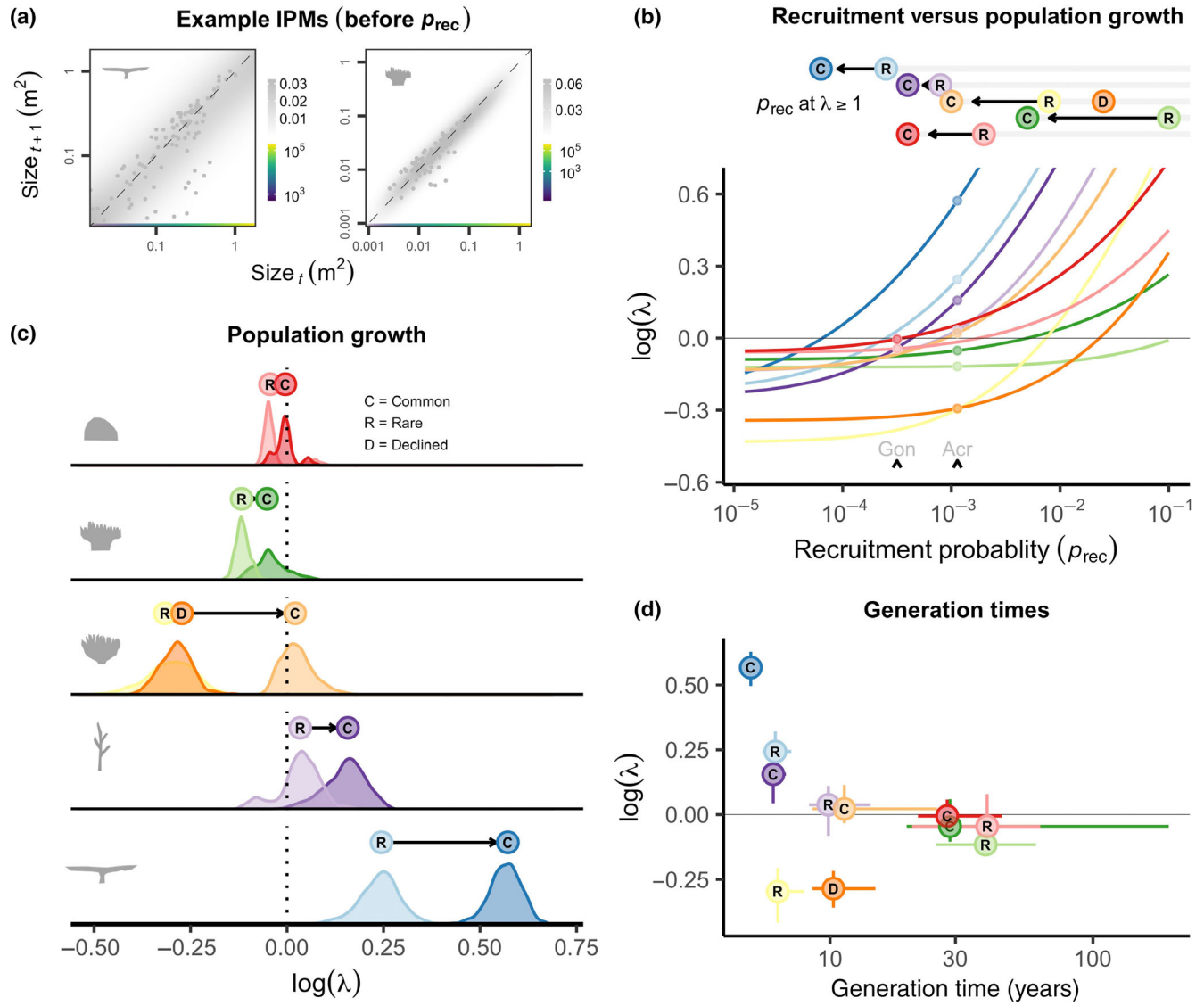

FIGURE 2 Demographic models of population growth in common and rare species. (a) Examples of annual transition matrices used for integral projection models in two species (Ahy, Adi). Grayscale indicates transition probabilities from one year to the next. The dashed line shows the 1:1 slope (stasis in colony size). Reproductive transitions (coloured scale bars) are shown prior to applying a recruitment filter, p_{rec}. (b) Probability of recruitment (p_{rec}) versus intrinsic population growth (log λ) in 11 species (colors as in Figure 1). Upper gray bars indicate the p_{rec} needed for population growth (lines, log λ > 0) or stability (points, log λ = 0) in common (C), rare (R), and declining (D) species. Mean p_{rec} values for *Acropora* (Acr) and *Goniastrea* (Gon) are derived from transects (Appendix S1: Figure S4). (c) Bootstrapped estimates of population growth rates at constant (mean) recruitment. (d) The generation times of coral populations and their relationship with population growth rates.

range of p_{rec} values (curved lines, Figure 2b). We estimate that for rare species populations to grow faster than common species, their recruitment probabilities must be between 2 and 20 times larger, depending on the morphological group (upper gray bars, Figure 2b). Consequently, assuming that recruitment probabilities (in addition to recruit sizes, $p_{recsize}$) are similar within morphological groups, we can project consistently higher population growth in common species (Figure 2d; Appendix S1: Figure S6).

Demographic decoupling

Differences in population growth rates within morphological and life-history groups allowed large differences in abundance to be projected in short (ecological) timeframes (Figure 3). Although growth, survival, and fecundity varied little within morphological groups (3%–8%, including no variation in IPM recruitment parameters), λ was more variable among morphologically similar species (23%). By projecting populations through time

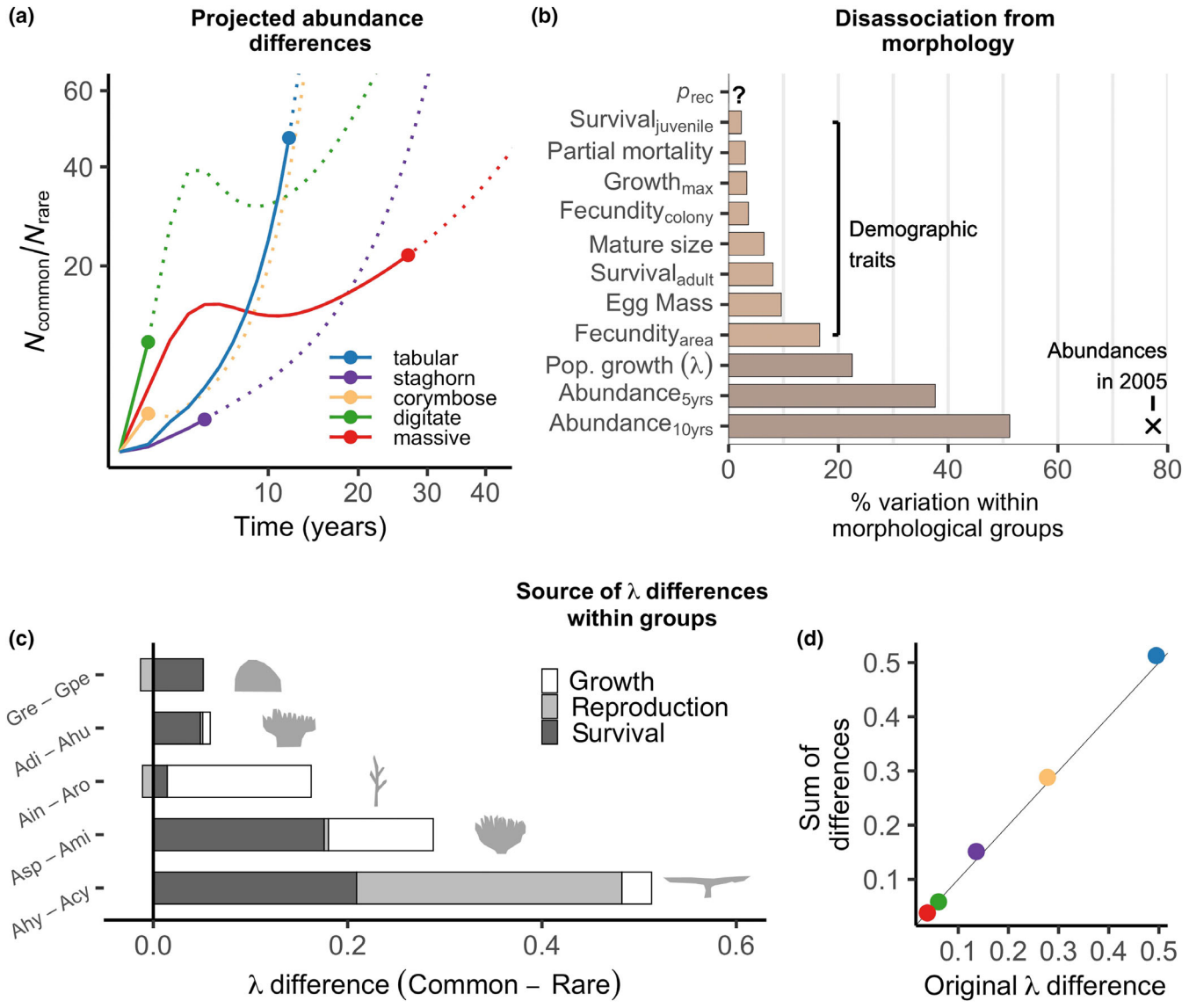

FIGURE 3 Dissociations of population dynamics from morphological and life-history groups. (a) Projected change in the abundance of common species relative to rare species through time for each morphological group, based on λs at fixed recruitment probabilities (Figure 2c). Solid lines show the number of years needed to project observed differences in abundance from 2005. Each axis is on a square-root scale. (b) Demographic variation within morphological groups. Values are the sums of squares of residuals derived from a one-way ANOVA of individual demographic traits and population-level metrics (λ and projections of abundance). The cross shows the original 79% variation in abundances within morphological groups in 2005. (c) The contribution of growth, survival, and reproduction to differences in λ within morphological groups. The analysis is based on fitting demographic models to morphological groups and allowing only one demographic rate to vary within groups. (d) The 1:1 relationship (black line) between the sum of λ differences when one demographic rate varies and the total λ differences for each morphological group (coloured dots).

(Figure 3a), 23% variation in λ within morphological groups generated 38% within-group variation in abundance in 5 years, and 51% in 10 years (Figure 3b). Under these projections, abundance differences observed on transects in 2005 (between 2- and 45-fold) were projected in less than 12 years in the fast-growing groups (tabular, staghorn, digitate and corymbose *Acropora*), and in 27 years in the slower-growing massive group (Figure 3a). These patterns reveal a stepwise "decoupling" of population dynamics from morphology, driven first by heightened variability in λ among morphologically similar species compared with individual demographic rates, and second by differences in population growth accumulating through time to generate large gaps in abundance.

Differences in population growth rates within morphological groups were produced by additive variability in growth, survival, and reproduction (Figure 3c). By calculating λ when only one demographic rate (growth,

survival, or reproduction) was allowed to vary within morphological groups, we identified the source of λ differences among similar species. Differences in survival increased the fitness of dominant species in every morphological group (positive bars, Figure 3c), manifesting primarily during early life stages (Appendix S1: Figure S3d), and were almost the exclusive source of variation in massive and digitate species (although differences in growth were unquantified in the massive group). Growth differences increased the λ of dominant species in tabular, corymbose, and especially staghorn species. Differences in reproduction drove large λ differences in the tabular group, but favored the rare species in the staghorn and massive groups (negative bars, Figure 3c). The sum of the partitioned λ differences closely matched the total λ differences when all demographic rates were allowed to vary (Figure 3d), indicating that shifts in population growth rates among similar species represented the summed effects of multiple demographic rates.

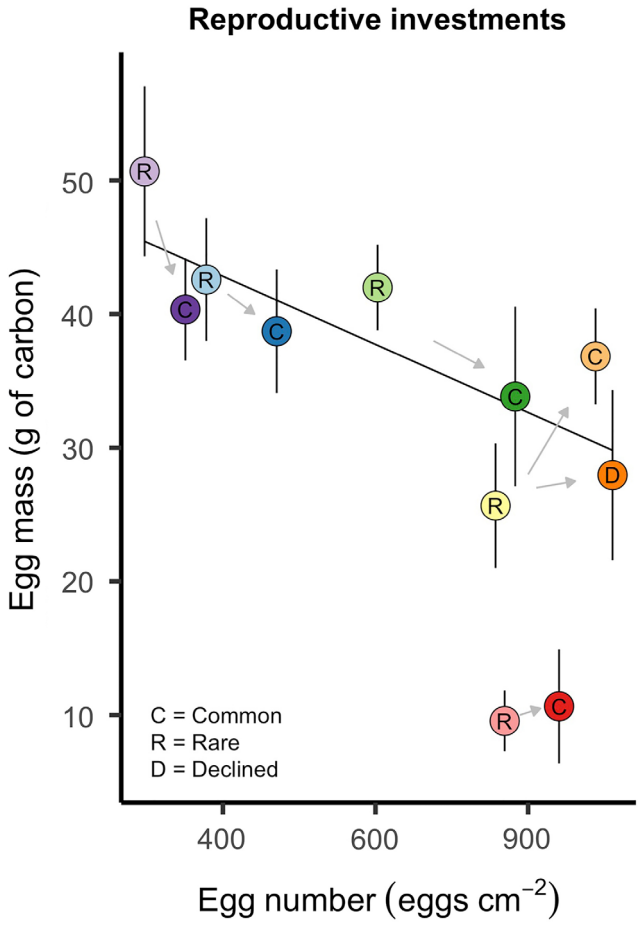

FIGURE 4 A trade-off in size-specific fecundity (eggs cm^{-2}) and egg biomass (carbon content as a proxy for energy content) across 11 species (colors as in Figure 1). The relationship indicates alternate patterns of reproductive investment, and possible sources of variation in recruitment parameters, p_{rec} and $p_{recsize}$, that were not included in IPM-derived measurements of population growth. Differences within morphological groups are indicated by arrows.

Two critical life-history traits that did not directly influence our IPM projections are size-specific fecundity and egg energy content, which together demonstrate a trade-off between offspring size and number. Common species consistently produced more eggs per unit area than rare species, often at the cost of high-biomass eggs (Figure 4), particularly in the *Acropora*. Furthermore, size-specific fecundity and egg energy content were the most variable individual demographic traits within morphological groups (16.6% and 9.6%, respectively; Figure 3b), revealing dissociations of reproductive traits from morphology relative to other demographic rates. Although these parameters did not affect the modeled life-history differences directly (Figure 3c), they reveal consistent differences in reproductive investment among morphologically similar species that may generate variations in p_{rec} or $p_{recsize}$ that are unaccounted for here. Consequently, differences in population dynamics summarizing 6 years of growth, survival, and reproduction, but without recruitment differences, may be enhanced by directional shifts in reproductive investment among similar species.

DISCUSSION

Life-history strategies and their associated traits can determine a species' fitness in a given environment (Shipley et al., 2016; Violle et al., 2007), yet our capacity to reconstruct species abundance patterns using traits remains elusive. In this study, colony growth form was a powerful predictor of growth, survival, and reproduction, reinforcing evidence that morphology is closely linked to many aspects of coral life-history (Darling et al., 2012; Hughes & Jackson, 1985). Morphologically similar species occupied similar positions along two life-history axes, describing (i) the fast-slow continuum from fast growth to high survival (Dornelas et al., 2017; Madin et al., 2014; Salguero-Gómez et al., 2016), which aligned with total fecundity driven by colony size (Álvarez-Noriega et al., 2016), and (ii) size-specific fecundity, describing the relative allocation of resources to reproduction (Figure 1b, Rüger et al., 2018). Nevertheless, species with similar morphological traits showed opposing patterns of commonness and rarity over a decade, challenging the notion that abundances can be anticipated with easily measured attributes of organisms. Instead, we show that moderate differences in population growth rates within morphological groups were enough to generate alternate, long-term population trajectories within realistic timeframes, and create persistent (decade-long)

differences in abundance among similar species. These results indicate that commonness and rarity are driven by interspecific demographic differences, but that the net influence of multiple traits must be quantified to predict the identities of the "dominant few" species.

A wide variety of traits have been linked to species abundance (Cornwell & Ackerly, 2010; Stanley Harpole & Tilman, 2005), generating the assumption that easily measured traits reflect adaptations (increased fitness) in particular environments. However, the assumption that traits drive abundance depends on at least three relationships (Southwood, 1988). First, energetic or biophysical trade-offs revealed by traits must scale up to demographic trade-offs, and therefore describe different levels of investment into growth, survival, or reproduction. Second, life-history strategies must be optimized to face the challenges of certain environments, meaning particular combinations of demographic rates (at the individual level) must maximize births minus deaths (at the population level) in specific habitats. A classic example is the different investments into roots, stems, leaves, or seeds among terrestrial plants, which reveal trade-offs between fast growth and long lifespan (Adler et al., 2014), and thereby dictate fitness along gradients of resource availability, disturbance, or adversity (Grime, 1974; Tilman, 1990; Westoby, 1998). The third relationship is between population growth and abundance, which is not necessarily positive (e.g., McGill, 2012), and is likely to depend on the way λ is calculated (e.g., density-dependent versus independent λ). We analyzed each of these stepwise relationships (traits–demography–fitness–abundance), and found that morphological traits were strongly aligned with life-history strategies, yet long-term fitness and abundance were poorly affiliated with any trait or demographic rate measured individually (Figure 4a,b). Easily measured and demographically critical traits (e.g., morphology) can therefore show limited associations with abundance.

Species with similar traits and different dynamics are widely observed in nature (Shlesinger & van Woesik, 2021; Sugihara et al., 2003), and are an integral part of coexistence theory ("limiting similarity," MacArthur & Levins, 1967) and evolutionary theory (Scheffer & van Nes, 2006). Moreover, similar species with different dynamics can provide insurance against species losses, and are therefore an essential component of ecosystem resilience ("response diversity," McWilliam et al., 2020; Walker et al., 1999). These alternate dynamics among similar species have previously been explained by single traits that vary slightly, but have disproportionate effects on fitness. For example, the first reported trait difference between common and rare species with similar traits (in the same functional group) was made by Rabinowitz (1978), who found that rare prairie grasses have smaller seeds and higher dispersal abilities than common species, and suggested that they persist as "ephemeral colonists" (see also, Rabinowitz & Rapp, 1981). Compared with rare species in the same functional group, common woodland shrubs produce more seeds (Murray & Westoby, 2000), dominant cacti have higher fecundity (Esparza-Olguín et al., 2005), and abundant thistles have lower seed mortality (Munzbergova, 2005). These analyses suggest that a single reproductive trait can drive apart abundances among similar species (Kunin & Gaston, 1993). Our study offers an alternate explanation for differences in abundance among similar species based on compounding variation in numerous demographic rates and the multidimensionality of fitness (Laughlin & Messier, 2015; Pistón et al., 2019). Rather than a single trait, higher fitness in dominant species was generated by the combined effects of small differences in growth, survival, and reproduction (Figure 4c,d), occurring primarily during early (juvenile) life-history stages (Appendix S1: Figure S2d). The net sum of multiple life-history traits should therefore be quantified to anticipate divergences in population dynamics and abundance among similar species.

Beyond modeled life-history differences (Figure 3c), the disproportionate effects of critical reproductive traits are likely to enlarge gaps in fitness among similar species in our study. Size-specific fecundity can be highly variable among similar coral species (Babcock, 1991), and is weakly associated with the fast-slow continuum of life histories (Figure 1b; Rüger et al., 2018). Like some plants (Murray & Westoby, 2000; Rabinowitz, 1978), we find that size-specific fecundity is consistently higher in common species than rare species (at the cost of egg size, Figure 4). Because fecundity rates are often consistent across large scales (Hughes et al., 2000; Tan et al., 2016), variation in size-specific fecundity may drive large differences in regional larval abundances, adding to differences in population growth by favoring greater immigration and recruitment (p_{rec}) in dominant species. Recruitment differences are therefore a crucial missing link in our analysis, and may explain why λ differences projected only a portion of the observed variation in abundance within morphological groups (Figure 3b). Strong demographic effects of a single reproductive trait are therefore open to speculation because of the "blind spot" of recruitment dynamics in broadcast spawning species, and the heightened sensitivity of coral populations to recruitment processes (Doropoulos et al., 2015). Nevertheless, relationships between particular reproductive traits and abundance are often system or taxon dependent (Bevill & Louda, 1999; Murray et al., 2002), and quantifying population growth rates is likely to have more consistent predictive effects.

Long-term estimates of population growth were able to reconstruct persistent differences in abundance that were observed on coral surveys (Figure 3a,b). At our study sites, fast-growing and mechanically vulnerable species (e.g., *Acropora*) had the highest and lowest population growth estimates (Figure 2d), possibly reflecting their "boom and bust" population dynamics, and their adaptation and dominance under periodic disturbances (Pratchett et al., 2020). These density-independent population growth rates were consistently higher in locally dominant species, and large abundance differences in disturbance-susceptible taxa (e.g., fine-branching *Acropora*) were generated in 1–2 decades (Figure 4a), consistent with previous windows of recovery between large-scale disturbances (Madin et al., 2018; McWilliam et al., 2020). Abundance differences in massive species required longer timeframes (Figure 4a), yet this slow divergence is facilitated by the greater capacity of these taxa to survive disturbances. Density-independent drivers of abundance found here contrast those from tropical forests, where density-dependent processes such as conspecific competition have been argued to be the main drivers of abundance (Comita et al., 2010). Although we cannot discount the possibility that differential sensitivity to density-dependent processes contributes to abundance differences (especially at the settlement stage: Doropoulos et al., 2017; Sims et al., 2021), our study shows that calculating the density-independent population growth factor using established projection modeling approaches (Caswell, 2000; Easterling et al., 2000; Merow et al., 2014) can help to anticipate species abundances in this system.

CONCLUSION

The predictive value of species traits is still debated, particularly with respect to the universal law that assemblages are composed of many rare and a few highly abundant species. Group-based trait metrics are highly useful when predictions rely on aggregated species information, such as when measuring community trait dynamics (Cornwell & Ackerly, 2010; Rüger et al., 2020) or ecosystem functions (Garnier et al., 2004). Yet, species-level variations in dynamics and abundance are rarely predicted using traits (with most exceptions coming from low-diversity systems, e.g., Shipley et al., 2006). Our study helps to resolve this limitation by identifying a demographic basis for persistent abundance differences among species with very similar traits. We find that numerous, small demographic differences accumulate into large differences in population growth rates among similar species, indicating that alternate patterns of dominance and rarity are inherently predictable, and driven by consistent, nonneutral demographic forces (Bode et al., 2012; McGill et al., 2005). Nevertheless, the traits driving species abundances may neither be the most measurable, nor the most variable. Neither survival, growth, nor size-specific fecundity were independently responsible for dominance in this assemblage (Figure 1). Rather, abundance patterns were the product of the net effects of multiple lifetime demographic rates (Laughlin et al., 2020), and poorly understood trait differences at the earliest, smallest, and most sensitive life stages (Figure 4). Trait-based predictions of population dynamics and abundance must therefore account for the multidimensional nature of fitness and compounding effects of subtle variations in life-history traits.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (McWilliam & Madin, 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.6908911.

ORCID

Mike McWilliam https://orcid.org/0000-0001-5748-0859
Maria Dornelas https://orcid.org/0000-0003-2077-7055
Mariana Álvarez-Noriega https://orcid.org/0000-0003-1295-6897
Sean R. Connolly https://orcid.org/0000-0003-1537-0859
Joshua S. Madin https://orcid.org/0000-0002-5005-6227

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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