Demographic insights for coral restoration

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Abstract

Coral reef decline has prompted a global surge in reef restoration initiatives. The success of initiatives that aim to sustain coral populations or assemblages will depend on demographic principles. Restoration strategies generally follow two demographic pathways: additive approaches, which increase population numbers by introducing recruits, fragments, or adults without altering vital rates; and multiplicative approaches, which enhance vital rates–growth, survival, or reproduction–either extrinsically (e.g., herbivory, habitat protection) or intrinsically (e.g., assisted evolution). We synthesized 34 coral matrix population models spanning morphologically diverse coral species from the Caribbean, Hawaii and the Great Barrier Reef, to quantify additive and multiplicative changes needed to increase population growth. Results highlight two consistent demographic leverage points for which population growth was most sensitive:(1) survival of reproductive adults and (2) successful recruitment. Achieving a 5% increase in population growth rate through additive means required ~100 recruit outplants or 5–10 adult outplants per 1,000 individuals in a population annually. For large populations typical of restoration targets (10^5–10^7 individuals), this translates to 10^3–10^4 outplants per year—efforts rarely logistically or economically feasible. By contrast, improving adult survival or recruitment rates by 20% (1.2 fold) produced equivalent population growth increases, depending on the fraction of the population affected. These findings yield two key implications. First, additive interventions are inefficient for large populations and demand sustained, large-scale effort. Second, strategies enhancing vital rates across broad population segments represent the most effective means of boosting coral abundance, including habitat protection, the alleviation of environmental stressors, and interventions which promote long-term survival and recruitment. Our demographic framework underscores that if the restoration goal is to enhance coral cover on a sustained basis, success depends less on adding individuals and more on interventions that will lead to long-term increases in vital rates.

Introduction

Coral reef conservation is transitioning from a focus on species and habitat protection to active restoration (Rinkevich 2019). Many scientists are skeptical that coral restoration can change the course of the coral reef crisis (Hughes et al. 2023), in part because of the vast geographical areas of reefs, numerous coral species, diverse life history strategies, and large coral population sizes (McWilliam et al. 2018, Deitzel et al. 2023). However, modeling efforts suggest that some local-scale actions combined with large-scale action on climate change could result in significantly different reef outcomes (Bay et al. 2017, Committee on Interventions to Increase the Resilience of Coral Reefs 2019, McManus et al. 2021). Indeed, the numbers and scales of coral reef restoration initiatives are growing rapidly (e.g., SECORE, Coral Nurture Program, RRAP, MARS, reviewed by Boström-Einarsson et al. 2020; McLeod at al. 2022; Edwards et al. 2024). Governments and nonprofits are spending millions of dollars on research and logistics supporting restoration (Bayraktarov et al. 2019, Tortolero-Langarica et al. 2020, Knapp et al. 2022, Sam et al. 2021, Dela Cruz & Harrison 2020; reviewed by Watt-Pringle et al. 2024; Segaran et al. 2024; Schmidt-Roach et al. 2025). Assessments of restoration practices are generating mixed reviews among ecologists (Boström-Einarsson et al. 2020, McLeod et al. 2022; Madin et al. 2023, Hughes et al. 2023, Streit et al. 2024; Suggett et al. 2024; Watt-Pringle et al. 2024). Meanwhile, corals continue to fare poorly (Hoegh-Guldberg et al. 2023).

Coral population growth or decline can be projected quantitatively as a matrix of transitions among various life history stages (Hughes 1984), or with higher resolution as an Integral Projection Model (e.g., McWilliam et al. 2023). Similar to most plants and animals, colonial reef building corals can be classified simply into three life history stages (Caswell 1989). The first is the recruitment stage, which represents new individuals entering the population by sexual or asexual reproduction (Hughes and Jackson 1981). Recruits tend to have low growth rates (absolute change in colony area) and exceptionally low survival rates (Carlot et al. 2021). Second is the juvenile stage, which is generally considered the point prior to reproductive maturity at which a colony is large enough to reduce post-settlement mortality and growth becomes steady and predictable (Stearns 1989, Doropoulos et al. 2016). Third is the adult stage where growth slows and colonies become reproductively mature. Reproductive output scales with the number of polyps which, in turn, scales with colony size (Hall and Hughes 1996; Padilla-Gamiño & Gates 2012; Álvarez-Noriega et al 2016; Johnston et al. 2020). A complete population matrix describes transitions between each of these stages (including recruitment, growth, shrinkage, and survival, Fig. 1A), and the dominant eigenvalue of the matrix (known as lambda, λ) reflects the intrinsic growth rate of the population, which can be used as a common currency for comparing population dynamics (Edmunds et al. 2014; Cant et al. 2021). Values above one ($\lambda > 1$) translate to population growth, and those below one ($\lambda < 1$) indicate population decline. Lambda is also a metric of population resilience following disturbances, as it reflects the capacity for a population to grow back to pre-disturbance levels (Madin et al. 2012; McWilliam et al. 2023), and is, therefore, a useful tool for guiding conservation decisions (Crowder et al. 1982; Doak et al. 2021; Edmunds et al. 2014; Edmunds & Riegl 2020).

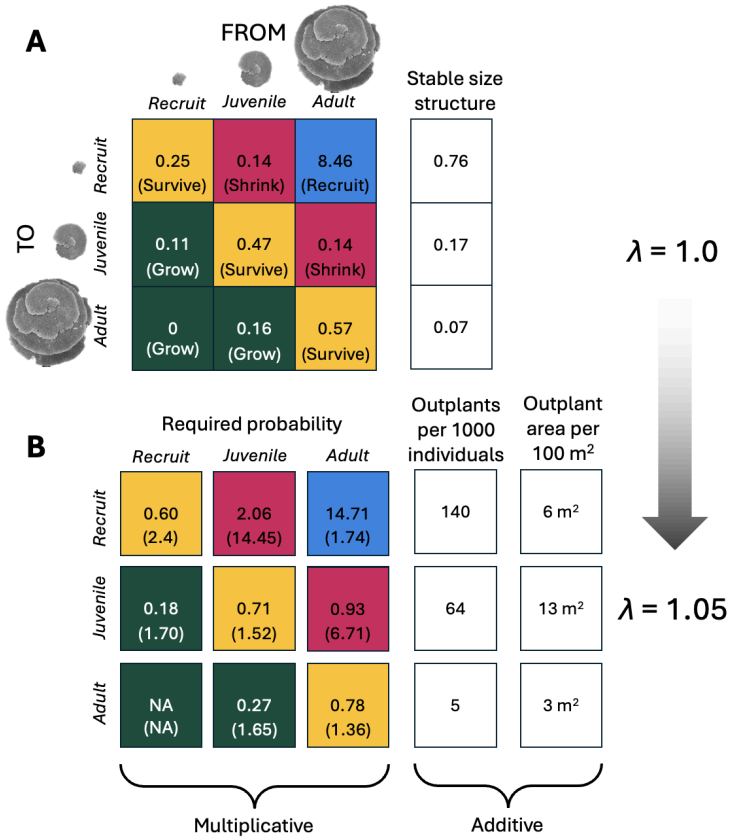

Figure 1. The yearly stage transitions for a population of *Acropora cytherea* sensu Veron 2000 at Lizard Island on the Great Barrier Reef. (**A**) Most cells show probabilities of moving between stages in one year. The blue cell represents the number of recruits that return to the population per year from a single adult for the population growth to be at stasis (λ=1.0). The stable size structure is the expected proportions of each stage when the population has stabilized. (**B**) The transition cell value required to increase the intrinsic population growth rate to λ=1.05, a 5% increase. Each cell was calculated independently, while the others remained constant. (Proportional changes are given in parentheses.) Note that cell values greater than 1 imply the addition of individuals. On the right are the number of individuals and outplant cover required for each stage to increase λ=1.05 without changing transition probabilities.

From a demographic perspective, there are two general approaches for increasing a population's intrinsic growth rate: (1) the "multiplicative approach," which manipulates matrix transition probabilities and (2) the "additive approach," which artificially increases population numbers. Table 1 summarizes some common restoration activities and the demographic approach used. For example, increasing individual growth, survival, reproductive and recruitment rates are all multiplicative levers for changing long-term population growth rate, if those increases are sustained through time. Under traditional coral reef management, such changes have been conducted by improving the environment (e.g., reducing pollution [Vega Thurber et al. 2013; Lapointe et al. 2019; Gove et al. 2023], and removing competitors [Ceccarelli et al. 2018] and predators [Pratchett et al. 2017, Raker et al. 2023]). Nevertheless, as a response to the increasingly negative effects of climate change, the focus has shifted to more active interventions such as moving corals or gametes between environments (assisted migration [Vitt et al. 2009; Hagedorn et al. 2021; Barreto et al. 2023]) and selective breeding

(assisted evolution [van Oppen et al. 2015; Humanes et al. 2021; Drury et al. 2022; Bay et al. 2023]), or by increasing population numbers via outplanting of coral larvae, fragments, or whole colonies (reviewed by Boström-Einarsson et al. 2020; Edwards et al. 2024). Theoretically, adding new individuals to the population each year can have the same demographic outcome as altering survival probabilities, because new individuals contribute to successful growth and reproduction. However, this can be a very costly strategy (Bayraktarov et al. 2019; Hughes et al. 2023), as those numbers must come from outside the population (e.g., a nursery or corals of opportunity or previously harvested fragments), and be actively deployed every year. A review of coral restoration in Indonesia found that 84% of projects reported an additive approach (i.e., some form of coral transplantation) and 16% relied on natural larval recruitment upon artificial reefs (Watt-Pringle et al. 2024). The two demographic approaches are not mutually exclusive; for example, genetically different or selectively bred corals can be added to potentially increase survival and reproduction (Drury et al. 2022, Bay et al. 2017). Ultimately, demographic approaches are needed to assess the relative utility of additive versus multiplicative modifications to population and their effectiveness for reef conservation.

Table 1. Common approaches for coral restoration and conservation and their demographic approach.

Activity	**Demographic Approach**	**Description**	**Examples**
Allee Effect Mitigation	Multiplicative	Increasing density beyond the minimum required for successful fertilization.	Ricardo et al. 2025
Artificial habitat	Multiplicative	Deployment of artificial structures for attracting coral and other biodiversity with a focus on the recruitment stage.	Knoester et al. 2023; Reichert et al. 2024; Tanaya et al. 2025
Assisted evolution	Multiplicative	A range of interventions that speed up the natural process of coral adaptation that might improve growth and survival.	Van Oppen et al. 2015; Caruso et al. 2021; Drury et al. 2022
Assisted migration	Multiplicative	The delivery of corals with environmental tolerances to another based on anticipated environmental changes.	Van Oppen et al. 2014; Caruso et al. 2021
BioRock Electric Reef	Additive / Multiplicative	Similar to substrate stabilisation, but with the addition of low voltage electricity applied to metal mesh to promote calcification	Goreau & Prong 2017; Goreau 2022
Coral gardening	Additive	The asexual propagation of corals onto a reef typically following a nursery phase.	Page et al. 2018; Tortolero-Langracia et al. 2020; Knapp et al. 2022
Coral repositioning	Additive	Securing dislodged corals back onto the reef. In some cases corals will be fragmented before being repositioned. Similar to coral gardening and transplantation, but without a nursery phase.	Garrison & Ward 2008; Nava & Figueroa-Camacho 2017; Sam et al. 2021
Coral seeding	Additive	The settlement of coral larvae or attachment of small fragments onto structures for reef deployment.	Forsman et al. 2015; Lindal 2003; Suzuki et al. 2011

Coral superfoods / probiotics	Additive Multiplicative (if sustained)	Administering nutrients or supplementing coral microbiomes to boost survival and growth. Note that this intervention must be sustained to be multiplicative.	Doering et al. 2021; Peixoto et al. 2017
Coral Transplantation	Additive / Subtractive	Similar to assisted migration or coral seeding, corals are moved from one place to another, but environmental tolerances are not considered and adult colonies are generally used. Supplementing existing populations with individuals destined for mortality due to development, without a nursery phase. An umbrella term that can also include coral gardening and repositioning.	Lindal 2003; Kilbane et al. 2008; Rogers et al. 2017; Forrester et al. 2019; Kikuzawa et al. 2021
Early maturity	Multiplicative	Selecting for maturity at smaller sizes.	Randall et al. 2020
Herbivore fishing restrictions	Multiplicative	Decreasing competition for space on the reef and improving recruitment, growth and survival of coral. However, recruitment can be hindered by herbivores in the absence of habitat complexity.	Penin et al. 2011; Bonaldo et al. 2017 Morais & Bellwood 2018; Strain et al. 2018
Larval-based restoration	Additive	Supplying large numbers of coral larvae to damaged reef areas.	Harrison et al. 2021
Macroalgae removal	Multiplicative / Additive	Suppress macroalgae proliferation to facilitate coral recovery. In some cases paired with urchin releases.	Neilson et al. 2018; Smith et al. 2021
Pollution & sedimentation mitigation	Multiplicative	Generally improving the environment improves all demographic rates.	Donovan et al. 2021; Donovan et al. 2020; Gove et al. 2023
Spawn capture and rearing	Additive	Collecting reproductive gametes during spawning events for culturing.	Dela Cruz & Harrison 2020
Substrate stabilisation	Multiplicative	Laying an artificial substrate (e.g., mesh) over areas of unconsolidated reef rubble.	Fox et al. 2019; Chesney & Richards 2022; Ceccarelli et al. 2020
Urchin releases	Multiplicative	Similar to herbivore fishing restrictions, but potentially more disruptive to coral recruitment.	Neilson et al. 2018; Barrows et al. 2023

Optimal restoration approaches will likely differ among geographic locations and coral taxa with different sensitivities to demographic change across their life cycle. Coral species exhibit an array of life history strategies because of energetic trade-offs among growth, survival and reproductive rates (Edmunds et al. 2014, McWilliam et al. 2023; Stearns 1989). Indeed, this array of strategies supports coexistence among species (Chesson 2000) and is essential for reef ecosystem function (Bellwood et al. 2004). For corals, major morphological groups (or growth forms) tend to reflect life history strategies (Jackson 1982; McWilliam et al. 2023; Dornelas et al. 2017). For instance branching and tabular coral growth forms are specialised to compete for reef space via early and rapid growth (Baird & Hughes 2000), but typically have lower survival rates across life stages (Madin et al. 2016). Reproductive output varies

dramatically among coral taxa, yet tends to be similar within growth forms, and highest in taxa which reach large colony sizes (Hall and Hughes 1996; Álvarez-Noriega 2016). Identifying life stages in which lambda is sensitive to change in specific vital rates is therefore necessary to design suitable conservation and restoration plans, acknowledging that these may vary across species.

In this study, we use demographic modeling to explore how changes to population structures can shift a population from decline to recovery for the purposes of coral conservation. We collated existing coral matrix population models capturing a range of geographic locations and coral morphologies (Table 2) to address a basic question that all reef resource managers and restoration practitioners should ask: what changes in transition probabilities or outplant numbers are needed to increase a population's yearly growth by a given amount? We explicitly compare two approaches to reef conservation, the additive approach in which colonies are outplanted, and the multiplicative approach in which vital rates are modified, quantifying the relative effort needed for each to affect population growth rates. We also examine the different life stages of coral in which changes in vital rates or abundances have the largest effects on population growth across different taxa. Our study highlights that demographic approaches are needed to inform decisions regarding the allocation of effort when attempting to preserve and restore coral populations.

Methods

We collated 34 projection transition matrices, representing recruit, juvenile, and adult life history stages, spanning 22 species from six growth forms of reef-building corals (Table 2). Of these matrices, 17 were already three-by-three stage matrices representing recruits, juveniles and adults from the Comadre database (Salguero-Gómez et al. 2016). Only complete matrices that captured unmanipulated population growth were included from Comadre. Another 11 species matrices were generated from the Trimodal dataset (Lizard Island, Great Barrier Reef; Madin et al. 2023) by transposing yearly colony growth and survival data into three-by-three matrices using the stage size classifications in Table 2 (see Supporting Methods, Fig. S1 and Fig. S2). Six more species matrices were generated from NOAA's Coral Reef Conservation Program-funded Vital Rate Project across the Hawaiian Archipelago (Rodriguez et al 2022). For those matrices that began as larger than three-by-three, we selected transition sizes from recruit to juvenile according to the observed decline in mortality rates (Fig. S1), and from juvenile to adult according to estimated size of first reproduction (Fig. S2).

Table 2. A summary of the 34 matrices by species. Each life history stage shows the range of planar areas for each stage. In parentheses are the areas used to estimate population areas, which are roughly the midpoints of stages. [a]Mercado-Molina et al. (2015); [b]Madin et al. 2023; [c]Hughes & Tanner 2000; [d]Rodriguez et al 2022; [e]Hernández-Pacheco et al. 2011. Growth form was collected from the Coral Trait Database (Madin et al. 2016).

Species	Region	Matrices	Recruit (cm^2)	Juvenile (cm^2)	Adult (cm^2)	Growth form
Acropora cervicornis [a]	Carribean	2	0-100 (50)	100-1000 (550)	>1000 (1500)	Arborescent
Acropora cf. digitifera [b]	GBR	1	0-150 (75)	150-300 (225)	>300 (375)	Digitate
Acropora cytherea [b]	GBR	1	0-500 (250)	500-2000 (1250)	>2000 (3000)	Tabular
Acropora humilis [b]	GBR	1	0-200 (100)	200-300 (250)	>300 (350)	Digitate
Acropora hyacinthus [b]	GBR	1	0-200 (100)	200-1000 (600)	>1000 (1400)	Tabular
Acropora intermedia [b]	GBR	1	0-150 (75)	150-500 (325)	>500 (675)	Arborescent
Acropora millepora [b]	GBR	1	0-150 (75)	150-300 (225)	>300 (375)	Corymbose
Acropora nasuta [b]	GBR	1	0-150 (75)	150-300 (225)	>300 (375)	Corymbose
Acropora robusta [b]	GBR	1	0-200 (100)	200-500 (350)	>500 (650)	Arborescent
Acropora spathulata [b]	GBR	1	0-150 (75)	150-700 (425)	>700 (1050)	Corymbose
Agaricia agaricites [c]	Carribean	2	0-20 (10)	20-100 (60)	>100 (150)	Laminar
Goniastrea pectinata [b]	GBR	1	0-20 (10)	20-200 (110)	>200 (300)	Massive
Goniastrea retiformis [b]	GBR	1	0-20 (10)	20-200 (110)	>200 (300)	Massive
Helioseris cucullata [c]	Carribean	3	0-20 (10)	20-100 (60)	>100 (150)	Laminar
Montipora capitata [d]	*Hawaii*	1	0-20 (10)	20-100 (60)	>100 (150)	Laminar
Montipora patula [d]	*Hawaii*	1	0-20 (10)	20-100 (60)	>100 (150)	Laminar
Orbicella annularis [b,e]	Carribean	8	0-50 (25)	50-150 (100)	>150 (225)	Massive
Pocillopora meandrina [d]	*Hawaii*	1	0-150 (75)	150-700 (425)	>700 (1050)	Corymbose
Porites astreoides [a]	Carribean	2	0-50 (25)	50-150 (100)	>150 (225)	Massive

Species	Region	Matrices	Recruit (cm^2)	Juvenile (cm^2)	Adult (cm^2)	Growth form
Porites lichen [d]	*Hawaii*	1	0-50 (25)	50-150 (100)	>150 (225)	Massive
Porites lobata [d]	*Hawaii*	1	0-50 (25)	50-150 (100)	>150 (225)	Massive
Porites lutea [d]	*Hawaii*	1	0-50 (25)	50-150 (100)	>150 (225)	Massive

To compare the demographic effects of restoration across coral taxa, we assumed that all populations were at stasis when matrix data were collected—neither growing nor declining. To do this, we modified the recruitment rates of taxa (which were not recorded in field studies) and used a least squares function and the *optimize* function in R to estimate the amount of recruitment generated by adults that would result in a population with λ=1 (R Core Team 2025; Fig. S3A). Estimated levels of recruitment per adult colony required to make λ=1 were consistent with other levels reported in the literature (Madin et al. 2012; McWilliam et al. 2023).

We used a least squares function to estimate transition cell changes (multiplicative) and outplant numbers (additive) required to achieve population growth increases of 1, 2, 5 and 10%. For the multiplicative approach, we increased a given transition cell value, while holding all other cells constant, until attaining levels of λ=1.01, 1.02, 1.05 or 1.1 (e.g., Fig. S3A). Cell values were allowed to increase above 1, which is theoretically the maximum transition probability for all cells that do not reproduce. However, we only report changes for the species for which cell values reflecting transition probabilities were one or less. We did not include the calculated changes for “shrinkage” cells, as the perturbation resulted in impossibly large values. That is, increasing population growth rate by elevating transitions from a large stage to a smaller stage can only occur when total survival probability in the resulting stage is above one, which can only be accomplished by adding individuals to the population, such as by reproduction.

For the additive approach, we increased each stable size structure (SS) value, while holding all others constant, until the summed matrix multiplication of the baseline transition matrix and the SS reached 1.01, 1.02, 1.05 or 1.1 (e.g., Fig. S3B). The amount of SS increase for a stage was multiplied by 1000 to express the number of outplants required per 1,000 individuals in the population. We also present these numbers in terms of the outplanted coral area per year (i.e., the planar area of coral required from an outside source), which was done by multiplying the number of individuals in each stage by the midpoint stage sizes in Table 2. We multiplied these values by 10,000 to express as outplant area per hectare (10,000 m^2) of population cover. Note that additive metrics only reflect the levels required in the first year; that is, proportionally more additions are required as the population size increases.

We estimated typical coral population sizes and population domain areas (i.e., the total area of living coral in a population) using NOAA’s National Coral Reef Monitoring Program (NCRMP) data on coral colony density across the US-affiliated central Pacific. The NCRMP effort includes

a stratified random survey of reef sites across 37 islands which enumerates coral colonies, returning colony-level taxonomic identification, colony density, and survey sector reef area (Towle et al. 2022). From this data set, we highlight 80 taxa that represent the most-robust species-level identifications present in the dataset, and then relied on the survey design estimates of sector-level colony number; that is, the estimated census population size at the sector scale (Smith et al 2011; Winston et al 2019). The NCRMP survey design assesses adult colony density in three depth-dependent strata per sector (0-6 m, 6-18 m, 18-30 m), so sector-level abundance (population size) for each representative species was calculated as the product of strata-level mean colony density and stratum area, summed across the three strata in each sector (Smith et al 2011; Winston et al 2019). Here, the sector represents roughly 10s of km of coastline; i.e., island scale for small islands (e.g., Jarvis, Pagan) or side-of-island scale for larger islands (e.g., O‘ahu, Guam). Previous work on the modeled distribution of juvenile colony density, show an apparent stock-recruitment at sector scale, which suggests this scale is a reasonable proxy for a demographically coupled population (Couch et al 2023). While we are presenting projection matrices from three regions (Caribbean, Australia, Central US-Pacific), we only present the estimates of population sizes from the US Pacific.

Results

Across the 34 population matrices, yearly survival probabilities tended to increase as colonies got larger (Fig. 2). Growth probabilities declined slightly with increasing size, and growth from recruit to adult (skipping the juvenile phase) had the lowest probability, and it was only observed in some massive and laminar species populations. Shrinkage (partial mortality or fission) to smaller stages tended to occur more for the adult stage. By way of example, Fig. 1A shows the matrix for *Acropora cytherea* and the blue transition cell represents the estimated number of successful recruits generated by an average adult colony per year; in this case, for the population to remain in stasis, only 8-9 of the hundreds of thousands of larvae generated by an adult colony must recruit back into the population. The green cells show probabilities of surviving and growing to larger stages; yellow cells show probabilities of surviving and remaining at the same stage; and red cells show surviving and shrinking via partial mortality or fission to smaller stages. The vector to the right of the transition matrix in Fig. 1A is the population’s stable size structure (i.e., the transition matrix’s eigenvector): the proportion of colonies at each stage once the population has stabilized (i.e., 76% of the colonies would be recruits, 17% juveniles and 7% adults; Caswell 1981).

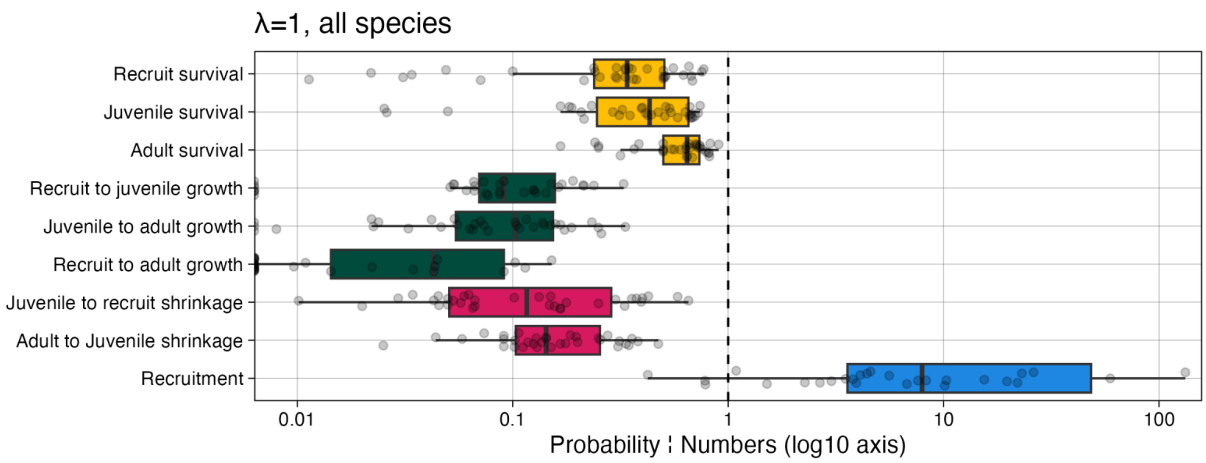

Figure 2. Boxplots for transition cells values for the 34 species matrices. The color scheme reflects that of Fig. 1 with survival probabilities in yellow, growth and survival probabilities in green, shrinkage in red, and contribution of adults to recruitment in blue.

Demographic models captured the changes in colony numbers and transition values needed to shift populations from stasis to growth. Using *Acropora cytherea* as an example, we find that increasing population size by 5% (equivalent to increasing λ to 1.05) would require outplanting of either 140 recruits, 64 juvenile or 5 adult colonies per 1000 colonies in a population per year (Fig. 1B). Similarly, for a summed planar area of 100 m^2, we find that 3% of this area (3 m^2) would need to be outplanted as new adult corals each year to increase population growth rate by 5%. Taking a multiplicative approach, a 5% increase in λ can be achieved by increasing recruit survivorship from 0.25 to 0.6 (assuming all other transition probabilities remain the same; Fig. 1B), equivalent to a 2.4-fold increase in recruit survival rates (parentheses, Figure 1B). On the other end of the life-stage spectrum, increasing survival of adult colonies from 57% to 78% achieves a 5% increase in population growth, equivalent to a 1.36-fold increase in adult survival. Finally, 5% increases in population growth of *A. cytherea* can be achieved by increasing the survival of juvenile colonies that grow into adults and the probability of recruitment; each of these requiring an approximately 1.7-fold change.

Changes in transition values needed to achieve 5% increase in population growth varied across the 34 matrices in the analysis, though some consistencies emerged across different life histories and biogeographic regions (Fig. 3). Species for which required transition values became greater than one (Fig. 3A, red points) indicated that the multiplicative approach was not a variable option. For instance, improving adult survivorship in order to increase population growth rate by 5% was only viable for 79% of our populations. Considering only the population for which a strategy is possible, two transition cells—adult survival and recruitment—required the least change in value to achieve a 5% increase in population growth (Fig. 3B), which were also reflected in matrix elasticities for adult survival and recruitment that quantify the relative sensitivity of population growth to the various transitions (Fig. S4; Caswell 1989). Increases in successful recruitment or adult survival present the most consistent, demographically efficient means to increase population growth, with the caveat that the adult survival approach is only viable for 27 of the 34 populations. The small changes in recruitment and adult survival needed

to boost population growth were largely consistent across coral growth forms (Fig. 3C). Changes required for other transition cells were higher and more variable, reflecting the sensitivity of growth forms to different changes in demographic rates. For example, the low growth in massive taxa and the low juvenile survival in laminar taxa required higher necessary changes in transition probability to boost population growth (Fig 3c; Fig S5). Meanwhile, higher recruit survival in massive taxa meant that smaller shifts in recruit survival were needed relative to other growth forms (Fig 3; Fig S5). The small changes in recruitment and adult survival needed to boost population growth were also consistent across biogeographic regions (Figure 3D). With the exception that the Caribbean showed greater efficacy (lower transition multiplier) of elevated recruitment survival for some species, but not all as reflected by high levels of variation.

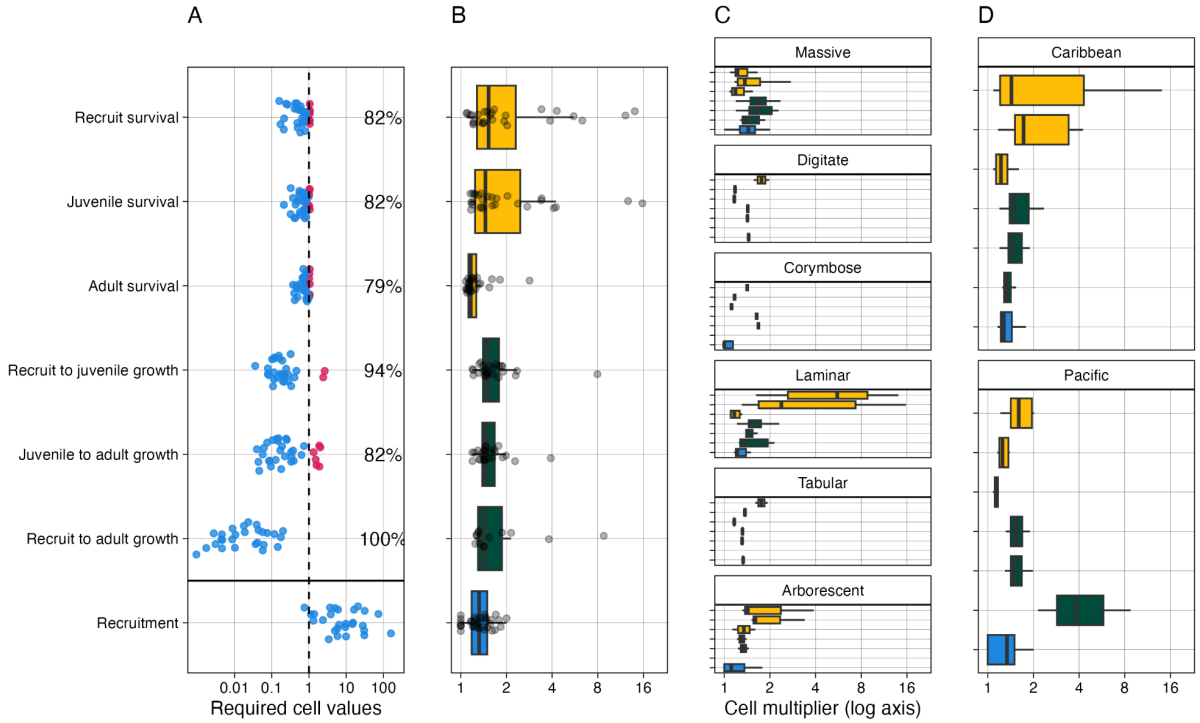

Figure 3. The multiplicative approach. (**A**) The cell values required to increase population growth rate by 5% (λ=1.05) summarised for all species. Transition values cannot exceed one for cells that do not generate individuals (red points) unless individuals are artificially added. The percent of species for which changing cell values is possible are given. (**B**) The proportional change in cell values required to increase population growth rate by 5%, only for species for which the approach is possible. Proportional change is also shown for (**C**) species growth form and (**D**) biogeographic region. The color scheme reflects that of Fig. 1 with survival probabilities in yellow, growth and survival probabilities in green, and contribution of adults to recruitment in blue.

Increasing population growth by adding numbers required approximately 100 recruits or juveniles per 1000 colonies in the population in the first year (Fig. 4A, left), or 5–10 adults; and this number would increase proportionally as the population size increased. These numerical additions translate into similar amounts of live coral area for recruits and adults of approximately 2–5 m^2 yearly for every 100 m^2 of adult coral area in a population (Fig. 4A, right). In contrast,

juveniles require approximately an order of magnitude more coral material since they require large numbers of corals (comparable with recruits) but with substantially increased areas of 20–500 cm^2 (Table 2). These results were consistent among growth forms, with notable deviations for massive and laminar growth forms. For example, significantly more recruits or juveniles would be required relative to adults for the laminar populations due to low early survival rates, suggesting that a strategic focus on adults may more efficiently elevate population growth. Conversely, fewer recruits would be required to elevate population growth for massive species relative to other growth forms, likely because of higher rates of recruit survival (Fig. 2). Desired levels of population growth rate scale approximately linearly with the amount of coral material added to the population each year (Fig. 4B). For instance, for a population size of 1000 individuals, adding one adult per year is estimated to increase population growth by 1% and adding 10 adults would increase it by 10%.

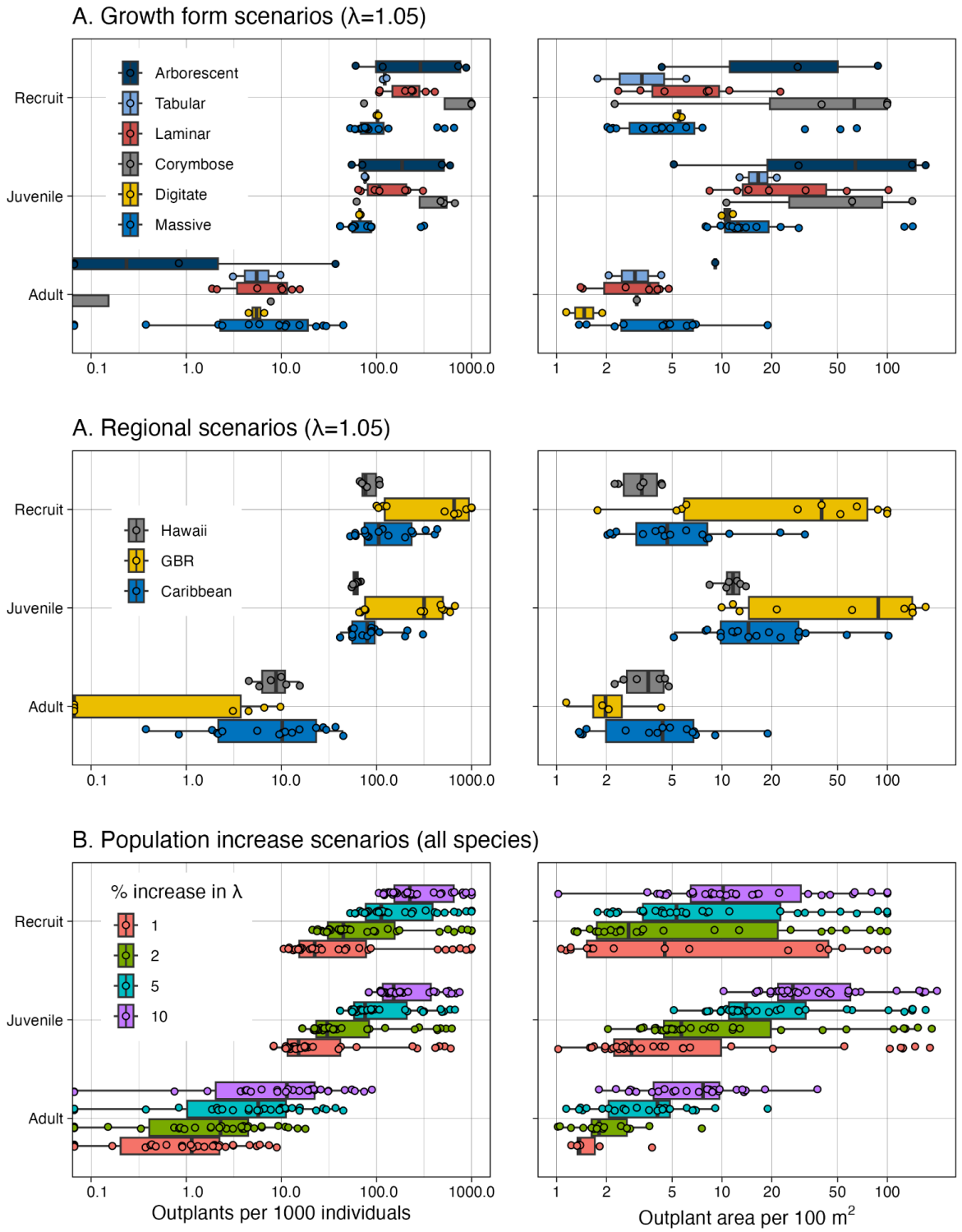

Figure 4. The numbers approach. (**A**) Boxplots of the number of outplants (left) and outplant area (right) for each life history stage required to increase yearly population growth rate by 5% (λ=1.05), summarised by growth form. (**B**) Boxplots of the number of outplants per 1000 individuals (left) and outplant area per 100 m^2 of population area (right) for each life history stage required to increase yearly population growth rate by 1, 2, 5, and 10% for all species.

Both additive and multiplicative restoration approaches depend on the scale of implementation (Fig. 5). The number of yearly adults that need to be outplanted to achieve a 5% increase in population growth differs by two orders of magnitude across species (Fig. 5B). Assuming that sector-scale population sizes seen across the US-affiliated Pacific are reasonable estimates for other populations, and based on mean estimates of census population size (~625,000 individuals, Fig. 5A), a minimum of 26 (*Acroopora millepora*) and a maximum of 28,000 (*Montastrea annularis*) adult colony outplants per year are necessary to alter the dynamics of a population. Orders of magnitude greater numbers of additional recruits are necessary to alter population growth by 5%, with a minimum of 33,000 and a maximum of 630,000 recruits added to the natural rates every year, based on the average population size in the dataset (Fig. 5C). Such numbers highlight the difficulty of altering population growth at large (regional) scales using the additive approach.

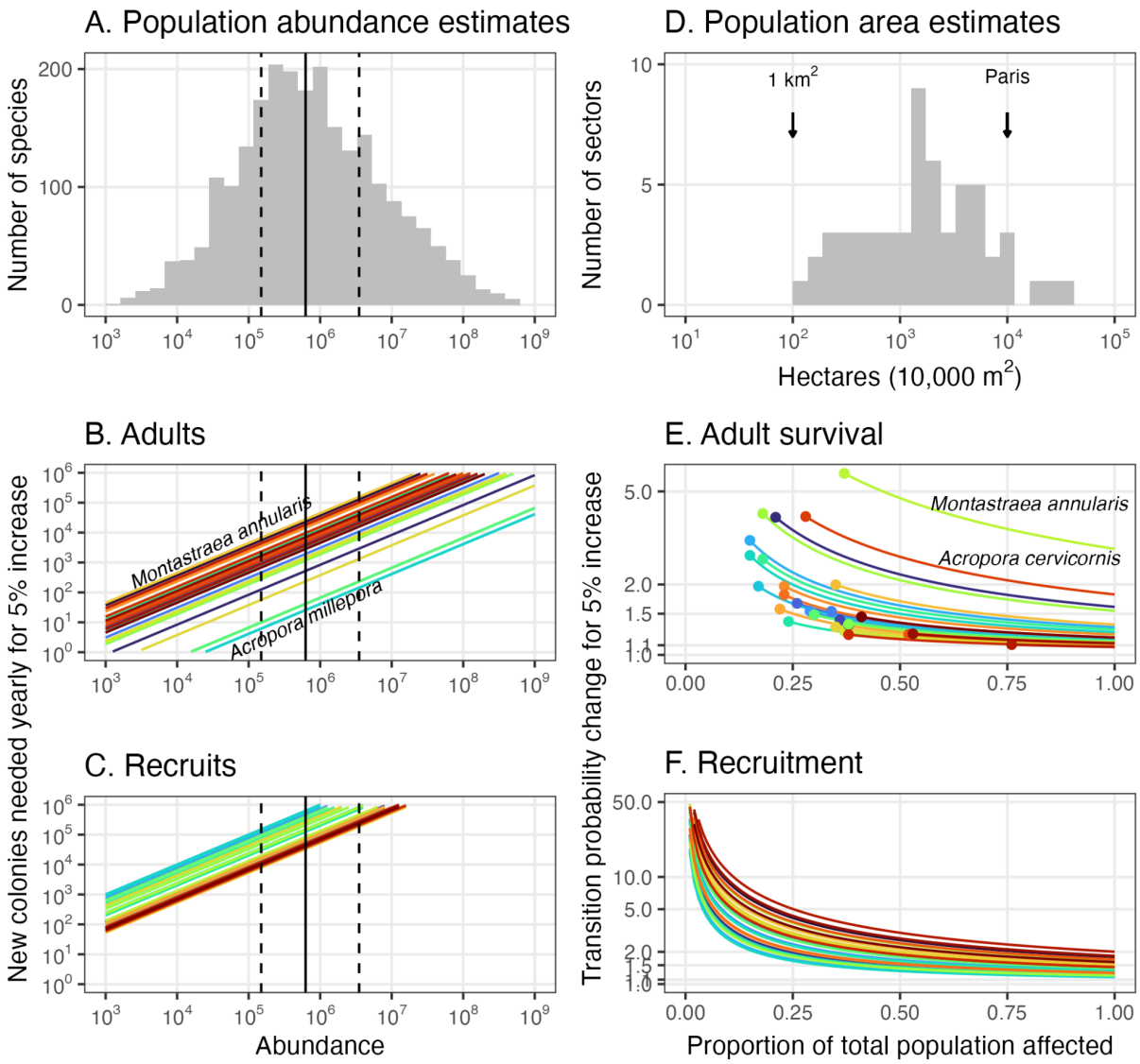

Figure 5. (**A**) Population abundance for 80 species estimated from NOAA NCRMP Pacific benthic survey data. Comparison of approaches relative to species population sizes. (**B**) The number of yearly adult outplants required to increase population growth rate by 5%, with each colored line representing one of the 34 examined transition matrices. The species at either end of the range are labeled. (**C**) The number of yearly recruit-sized outplants needed to increase population growth by 5% for each of the 34 matrices. (**D**) Population-scale reef area estimates from NOAA Pacific benthic survey data. (**E**) The change in adult survival probability needed to increase population growth rate by 5% when considering the proportion of the population affected by a conservation measure for each of the 34 matrices. Points indicate the theoretical limit; that is, where adult survival probability is 100%. (**F**) The change in recruitment probability needed to increase population growth rate by 5% for each of the 34 matrices.

Elevating adult survival probability is also likely to be most effective if the benefit can be implemented across the entire population (Fig. 5D). However, when we model a realistic intervention that does not benefit the entire coral population, we can show that elevated vital rates required to meet a 5% shift in population growth rate (lambda) are relatively stable when only subsets of the population are affected (Fig. 5D-E). Indeed, for many taxa the necessary improvement to survival remains stable (< 1.5-fold increase) as long as > 50% of the population is affected (Fig. 5E). Similarly, a five-fold increase in recruitment was sufficient to shift lambda to 1.05 for all taxa as long as > 25% of the population was affected by the changes (Fig. 5F). Nevertheless, the number of additional recruits required becomes exceedingly high if small portions of the population are impacted (Fig 5F). Moreover, we identify a critical threshold in survival beyond which a 5% change in lambda is theoretically impossible because survival has already reached 100% (points in Fig. 5E). For many taxa, this threshold occurs between 25-50% of the population affected, demonstrating the importance of capturing large proportions of the population to achieve meaningful shifts in lambda, a feat that requires conservation action to be implemented across large areas (Fig 5D).

Discussion

Our analysis suggests that modifying vital rates at critical stages of the life cycle is the most effective way to grow coral populations. This “multiplicative” approach focuses on modifying factors that influence survival, growth and recruitment, and shows considerable promise if it can be applied over large portions of the effective population (Fig. 5D-F). A wide range of conservation measures can be employed to modify vital rates (Table 1), yet demographic models suggest that those which affect adult survival and recruitment rates are likely to be the most successful because they require the least change. If applied to the whole population, a 1.2-fold increase in survival (20% increase) or a 1.5-fold increase in recruitment (50%, on average) was sufficient to boost population growth by 5%. In contrast, relying solely on outplanting additional colonies to modify coral population growth rate—the additive approach—is likely to be inefficient for most species, particularly those with high abundances (Fig. 5A-C). While it was possible to boost population growth by adding colonies, we find that yearly additions of 5-10% of the existing population size in recruit form, or 0.5-1% of the existing population size in adult form, were necessary to alter population trends (Fig. 4). Genetic models suggest that a similar level of adult transplantation (2-5% of the population per year) could prevent extinction, but not population decline, under moderate emissions scenarios (formerly

RCP6.0) only if transplanted corals were pre-adapted to warming conditions (Bay et al. 2017). Depending on the population size, the number of new colonies needed can be exceedingly large (Fig. 5A-C).

The population size affected by a conservation initiative strongly influences both the multiplicative and additive approaches, which ultimately depend on the spatial scale of conservation. At the likely scale of demographically connected populations (i.e. stock-recruitment scale) we estimate the census population sizes of most coral species to be in the range of 10^5 to 10^7 individuals (Fig. 5A). These island-scale values are lower than many Pacific coral population estimates, as estimates that span full species ranges suggest that roughly two-thirds of species have population sizes exceeding 100 million colonies and one-fifth exceeding a billion colonies (Dietzel et al. 2021). Quantifying population growth at this more local scale is challenging, and more precise estimates would require information on dispersal dynamics and spatial differences in vital rates (Hunter & Caswell et al. 2005). Nevertheless, our simplified extrapolation of population growth suggests that outplanting as few as 500 adult colonies per year for rare species, or as many as 50,000 for common species, was necessary for a 5% increase in population growth at the scale of the NCRMP sectors (Fig. 5B-C). This result demonstrates the challenges of this strategy for typical coral population sizes unless a substantial amount of coral material is available, or the population is small or limited to an area with high levels of self-recruitment, like an embayment. In contrast, multiplicative reef conservation measures, which focus on enhancing vital rates, can often effectively capture large components of a coral population. For example, networks of Marine Protected Areas can cover a large geographic space (> 1000 hectares; Selig & Bruno 2010; Smith et al. 2025) and thus boost coral vital rates (e.g., improved herbivory and coral recruitment) across a large portion of a coral population. Similarly, reducing greenhouse gas emissions is likely to benefit most, if not all, of a coral population by reducing mortality from climate stressors, such as recurrent bleaching (Hughes et al. 2023; Jury et al. 2024).

For local interventions, multiplicative approaches also offer the greatest chance of boosting coral population growth at the site or reef scale, especially if they limit the need for costly yearly intervention. For example, artificial structures can boost local recruitment by providing substrate, modifying water flow, and enhancing settlement probabilities (Nguyen et al. 2022; Higgins et al. 2022; Fig. 6). Our calculations suggest that if a small fraction of the incoming recruits experience a 10-fold or more increase in settlement success (as has been shown possible, Fig. 6), this is more than sufficient to boost local population growth by 5%. Coral populations on reefs can still be vast (e.g., a 1 hectare reef with one coral per m^2 has a population of 10,000), thus requiring hundreds of new recruits and multiple adult colonies to be outplanted every year to modify population growth, even at a small scale. Boosting local population growth is fundamentally dependent on recruitment, which is highly variable over time and space owing to the open nature of coral populations. Understanding this variability and source-sink metapopulation dynamics will ultimately be crucial for a demographically-informed approach to coral conservation (Crowder et al. 2000; Hansen 2011).

We find two critical demographic transitions whereby small changes had strong effects on population growth. First, adult survival universally required the least change in probability to increase population growth. This result was expected, given that corals produce many offspring that mostly perish (Type III survivorship; Crowder et al. 1982; Tsounis & Edmunds 2016). For example, a 20% increase in average adult survival can enhance population growth by 5% (Fig. 2B), which is remarkably consistent across growth forms (Fig. 2C). Past studies suggest that focusing on adult survivorship provides the most efficient use of resources, delivering significant population benefits for smaller interventions. For instance, protecting mature female turtles from trawling led to population increases in the endangered loggerhead turtle (Crouse et al. 1987). However, our analysis suggests that this approach is not viable for all species populations, with 21% of the populations requiring increases in survival surpassing 100% (Fig. 3A; Supplementary Table 1). Furthermore, increasing adult survivorship across large areas for sessile corals is complex, and would typically involve addressing environmental stressors like thermal anomalies or mitigating local stressors (Ateweberhan et al. 2013; Good & Bahr 2021; Donovan et al. 2021; Gove et al. 2023). Increasing adult survivorship is also an important focus of many restoration strategies (Table 2), including substrate stabilization (Fox et al. 2019; Chesney & Richards 2022; Ceccarelli et al. 2020), macroalgal removal (Neilson et al. 2018; Smith et al. 2021), artificial evolution (Van Oppen et al. 2015; Caruso et al. 2021; Drury et al. 2022), and artificial migration (Van Oppen et al. 2014; Caruso et al. 2021).

Increasing recruitment success was the second leverage point for enhancing population growth(Fig. 3B). Despite the impressive fecundity of corals, recruitment and post-recruitment processes represent possibly the largest bottleneck for coral population growth (Arnold et al. 2010; Ritson-Williams et al. 2009; Tsounis & Edmunds 2016; Doropoulos et al. 2021).We find that population growth can be consistently increased by 5% with a less-than 2-fold improvement in recruitment. Recruitment operates differently to other life stage transitions, because it is a multiplier of population numbers, rather than a probability of transition for a single individual, and so multiplicative changes are not bounded by one and are potentially easier to manipulate via management actions (Randall et al. 2020, Harrison et al. 2021). Given the large potential for larvae supply, capturing just a small fraction of wasted larvae has extraordinary potential for scalable restoration. Spawn capture and nursery-rearing of recruits is promising (Dela Cruz & Harrison 2020), but still faces the same limitations as coral gardening, relying on consistent outplanting to maintain its efficacy (Table 1). However, improving the passive capture of even a small fraction of wasted larvae has extraordinary potential for restoration. For instance, by conservatively improving settlement by just 2-fold, population growth could be increased by 10%. Reef managers could achieve such improvements by enhancing environmental conditions, such as reducing sedimentation or contaminants (Nalley et al. 2021), promoting herbivorous fishes and urchins, restoring suitable habitats, stabilizing unconsolidated hard substrate, or deploying settlement substrates for coral larvae (Table 1). For instance, data from settlement structures with cryptic recesses routinely demonstrate improvements of 50-200-fold over natural reefs (Doropoulos et al 2016, Reichert et al.2025; Fig. 6). While density dependent processes (i.e., crowding and competition) act to thin these early life gains, the chances that

increased numbers of juveniles make it through the early life bottleneck increases, sometimes dramatically (e.g., 20-50-fold after one year; Reichert et al 2025).

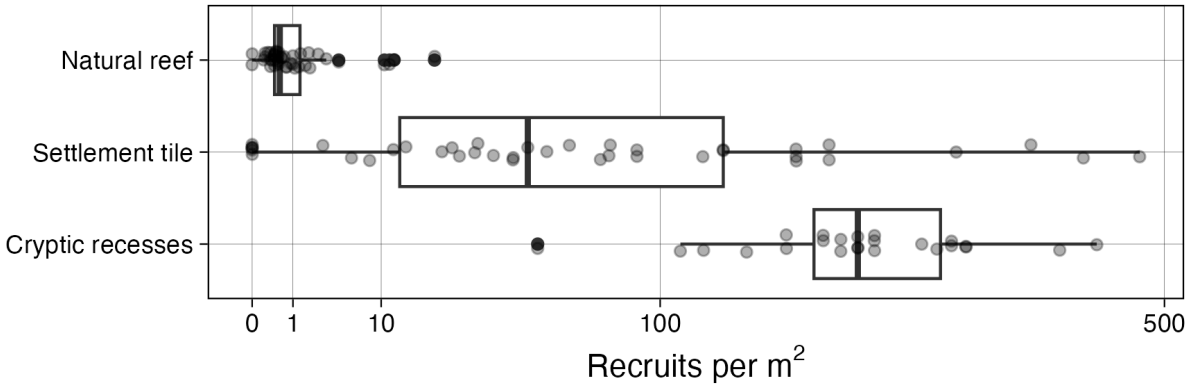

Figure 6. The density of coral recruits on natural reefs (Reichert et al. 2025), traditional settlement tiles (Bramanti and Edmunds 2016; Edmunds 2022; Brown 2004; Friedlander and Brown 2006), and structures designed with cryptic recesses (Doropoulos et al 2016; Reichert et al. 2025). See supplemental methods for details.

This paper considered various approaches to coral restoration from demographic first principles. The collation of simple population matrix models, and a straightforward analysis looking at the influence of multiplicative and additive changes for coral populations, demonstrates the salient features of current restoration approaches and their likely success. There are contexts in which "additive" restoration at achievable scales can improve population outcomes, especially in small, restricted populations or those experiencing Allee effects. However, in many coral populations, raising population growth rates above replacement by simply outplanting more colonies into declining populations will require efforts at scales unlikely to be cost-effective. On the other hand, our demographic analysis suggests that "multiplicative" efforts to the rates of survivorship and/or recruitment through combinations of traditional management and process-focused active interventions are likely the more effective strategy for responding to declining coral populations.Every coral conservation effort is unique and context-dependent, but we hope our demographic framework will provide resource managers and restoration practitioners a framework to understand and predict how restoration efforts will translate into meaningful outcomes.

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Data and Code

Data and code are available at https://github.com/jmadinlab/restoration-focus

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Supporting Materials

Supporting Methods–A key uncertainty with the matrices used in this study were the transition boundaries between recruits, juveniles and adults. Boundaries for the Comadre matrices were set during the design of the original studies and these cannot be changed. Survival rates in the recruit stage were consistently lower than the juvenile stage (Fig. 2), and the boundary between juvenile and adult was in the vicinity of reported mature colony sizes in the literature (Table 1). For the Trimodal species we are able to fine-tune the boundaries based on fecundity and survival data. For instance, we defined the recruit-juvenile boundary as the colony size where survival rate stabilized (Fig. S1) and the juvenile-adult boundary as the colony size where approximately 75% of colonies were reproductive (Fig. S3).

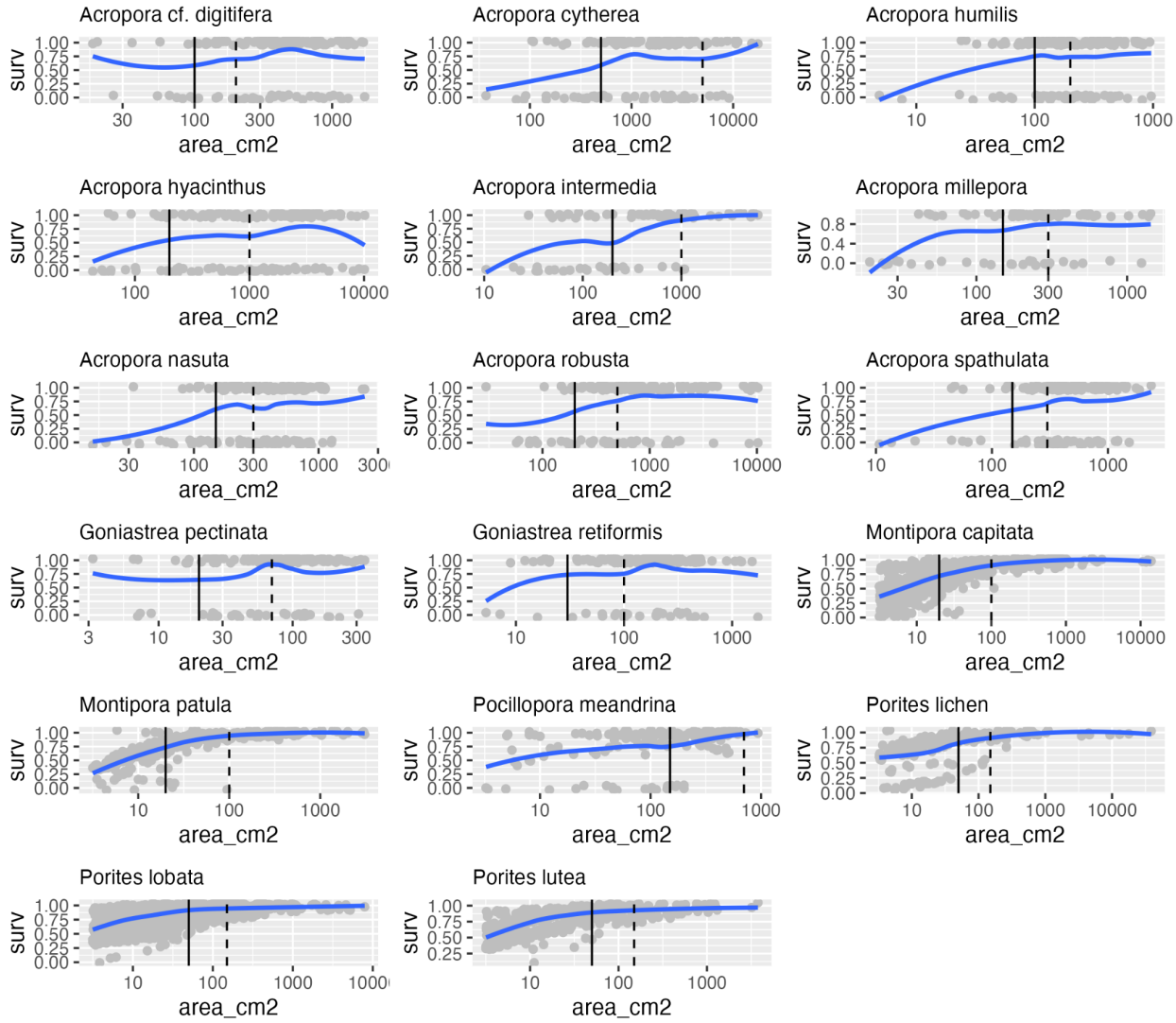

Figure S1. Yearly survival probability for Trimodal (Madin et al. 2023) and NOAA (Rodriguez et al 2021) species as a function of colony size showing transition boundaries used for recruit-juvenile (solid vertical lines) and juvenile adult (dashed lines corresponding with Fig. S2). Blue lines are loess smoothers to illustrate underlying size-survival patterns.

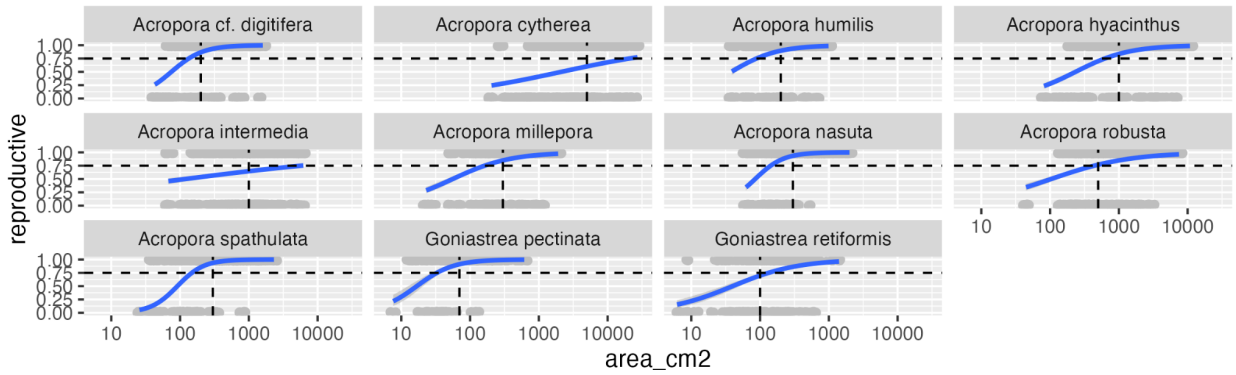

Figure S2. Size at reproduction for the 11 trimodal species (Madin et al. 2023) with logistic model fits (blue lines). We used the approximate size at which 75% of colonies are reproductive as the juvenile-adult boundary for transition matrices.

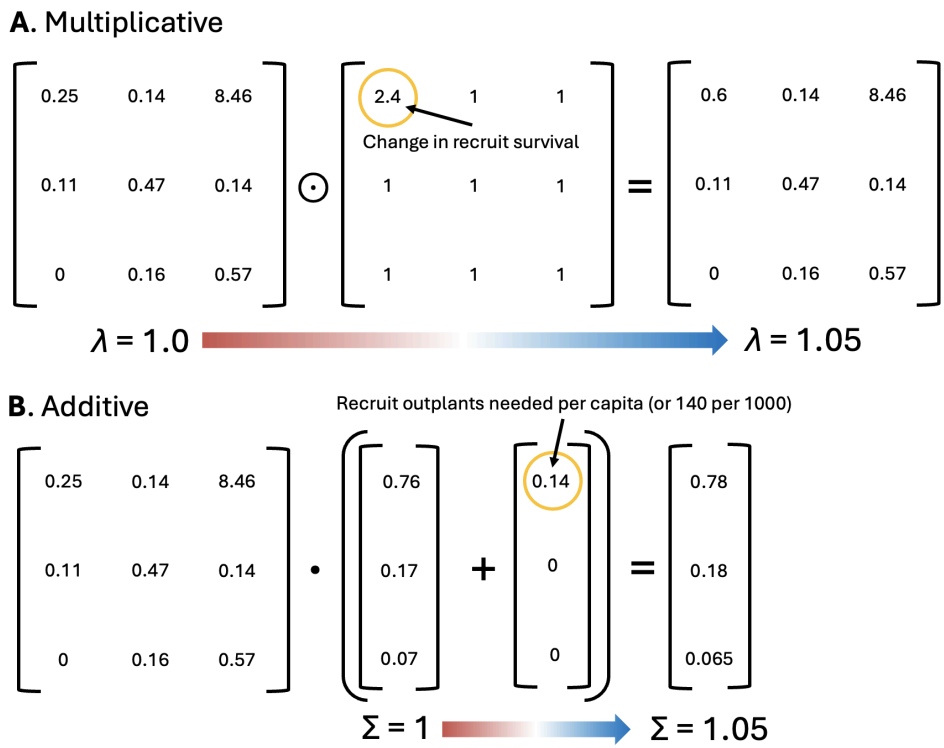

Figure S3. A demonstration of the matrix operations for (**A**) multiplicative and (**B**) additive approaches to increasing year on year population growth by 5% for *Acropora cytherea*. ⊙ represents the Hadamard product and • represent the matrix product. Σ represents the sum. This example represents best estimates of recruit survival change in A and yearly recruit outplanting in B. The values circled in yellow were found using least square optimization in R.

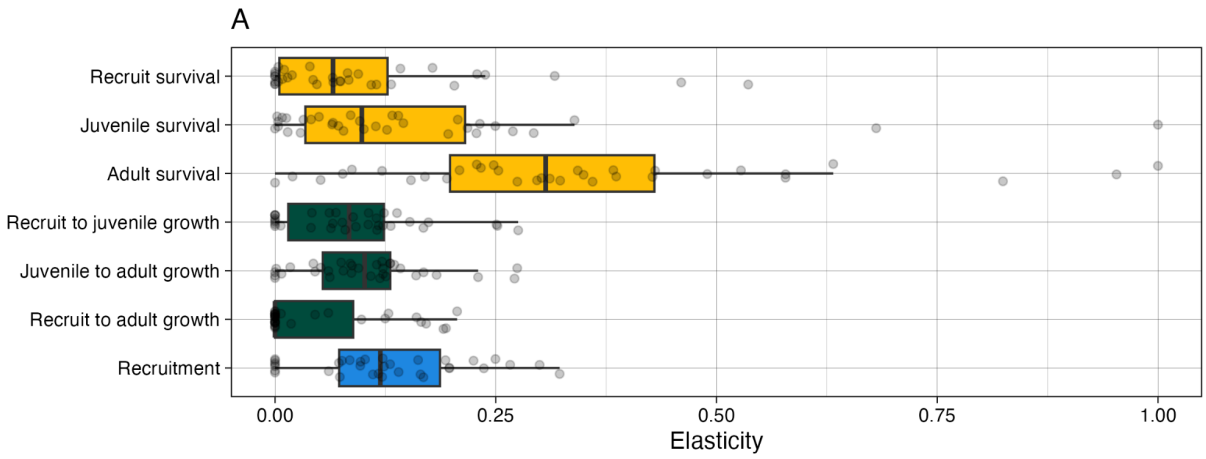

Figure S4. Elasticities.

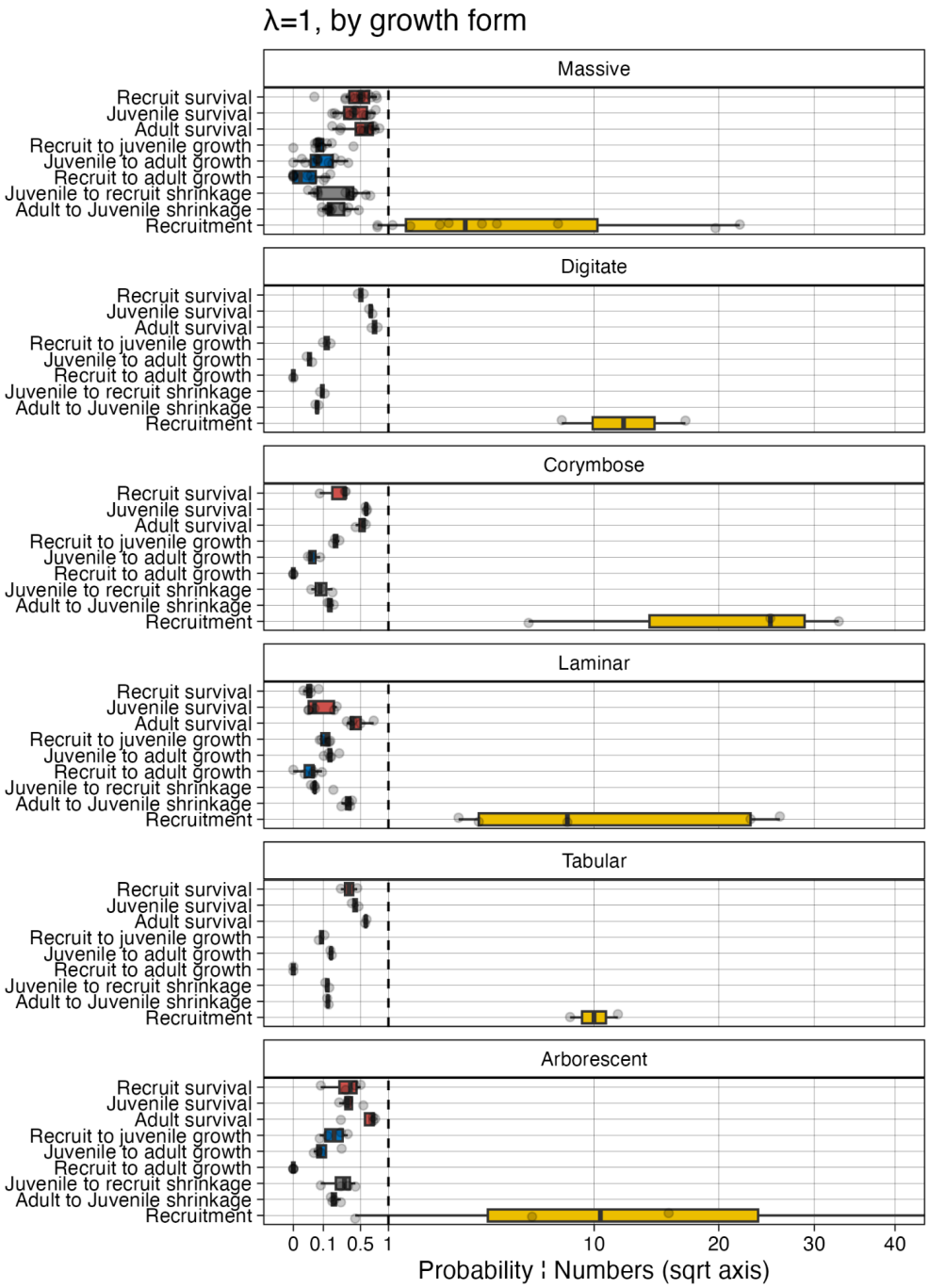

Figure S5. Boxplots for transition cells for the 34 species matrices summarised by growth form. Color coding matches Fig. 1.

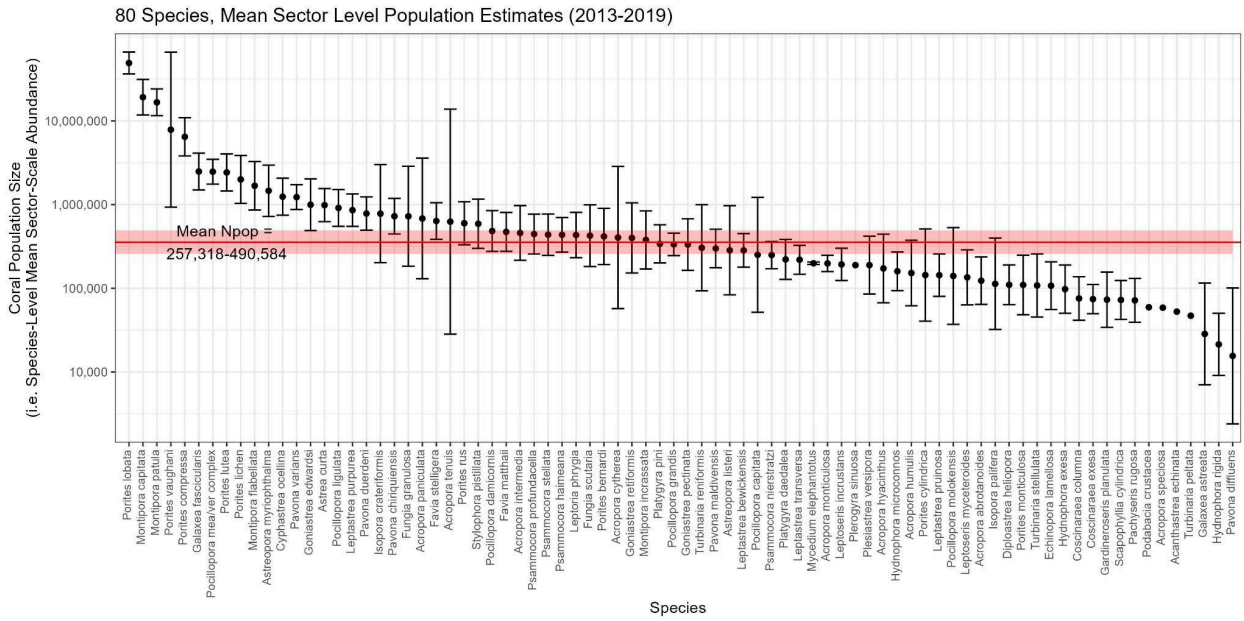

Figure S6. Population estimates for 80 species from NOAA sectors; see main text Methods for details.