

# How does a widespread reef coral maintain a population in an isolated environment?

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**ABSTRACT:** In a changing global environment, previously suboptimal habitats may become climate refuges for species. For instance, the ranges of some tropical reef corals are already expanding poleward. Understanding the demographic strategies by which isolated or marginal populations persist is therefore important, especially since such populations are often both vulnerable to local extinction and sources of evolutionary novelty. This study builds an integral projection model from individual-level demographic rates for a genetically isolated population of a reef coral, *Plesiastrea versipora*, in Sydney Harbour, Australia, in order to understand the population-level demographic characteristics allowing its persistence. We show that this population is thriving, with the potential to rapidly increase in benthic cover, due to high adult survivorship and at least sporadic high recruitment. Medium-sized colonies are the most important for long-term population viability due to their reproductive potential. Nonetheless, the population's persistence is sensitive to recruitment and growth rates, and protecting it from factors that affect these processes is likely to be crucial for its longer-term survival.

**KEY WORDS:** Population dynamics · Population persistence · Isolated population · Demographics · *Plesiastrea versipora* · Integral projection model

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## INTRODUCTION

Increasing environmental change and stochastic disturbance lend urgency to understanding the functioning of potential refuges and the bases for the persistence of isolated populations. Isolated populations towards the edge of their species ranges can be more vulnerable to extinction, because they often have smaller and more variable sizes than more central populations (Hardie & Hutchings 2010). However, they can also display greater stress adaptation and be a source of evolutionary novelty contributing to intraspecific genetic diversity (Lesica & Allendorf 1995). Consequently, they are of both theoretical and

practical interest, and may contribute to our understanding of range expansions or shifts (Hardie & Hutchings 2010).

Coral reefs are increasingly threatened by warming oceans (Hughes et al. 2003, 2017). Coral species can find refuge in habitats that shelter them in various ways, for example, by attenuating light in tropical waters (van Woesik et al. 2012) or by having such a strong environmental filter upon entry that only the hardy survive (Fine et al. 2013). Temperate areas can also offer a refuge for species whose tropical populations are declining in response to climate change (Greenstein & Pandolfi 2008), especially species which have some capacity for heterotrophy and

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whose expansion is not immediately limited by photosynthetically available radiation (Muir et al. 2015). Rising sea surface temperatures are already leading to poleward range expansions of tropical corals (Marsh 1992, Precht & Aronson 2004, Yamano et al. 2011, Baird et al. 2012). Corals able to live in apparently suboptimal environments (Kleypas et al. 1999, Perry & Larcombe 2003) could be better adapted to withstand environmental change, as they already tolerate environmental stress (Glynn 1996, Riegl 2003, Halfar et al. 2005). Understanding how coral populations persist in such areas is therefore important in assessing potential refuges and potential sources of diversity.

*Plesiastrea versipora*, one of the most widely distributed coral species, is found from French Polynesia to east Africa and the Red Sea, and from Japan to southern Australia (Veron et al., available at [www.coralsoftheworld.org/species\\_factsheets/species\\_fact\\_sheet\\_distribution/plesiastrea-versipora/](http://www.coralsoftheworld.org/species_factsheets/species_fact_sheet_distribution/plesiastrea-versipora/) [Version 0.01 beta, accessed 19 April 2018]). Its range includes the high-latitude (33° S) and highly urbanized Sydney Harbour, Australia, where it was recorded at least as early as 1887 (Australian Museum, Sydney, registration number G.7168). The Sydney Harbour population, which broadcast spawns (Madsen et al. 2014), is genetically isolated despite significant populations to the north and south (Rodriguez-Lanetty & Hoegh-Guldberg 2002, Madin et al. 2015), probably receiving no larval supply from other populations. Understanding how this species survives in Sydney Harbour despite reproductive isolation and urban environmental challenges may throw light on whether high-latitude locations could serve as possible climate change refuges for reef coral species. Quantifying the demographic rates of this species will determine which life history stages and processes are most sensitive to change and help guide the choice of appropriate conservation strategies. Finally, other species with similar demographic rates and life history traits could undergo successful range expansion in response to climate change (Keith et al. 2011, Sommer et al. 2014, Madin et al. 2016).

Growth, survival, and fecundity rates may be measured for individual colonies or units in a population. These rates can then be modeled and combined to estimate the population's asymptotic growth rate and to project its size structure into the future. Demographic processes in corals are generally more strongly linked to colony size than to age or discrete categorical stages (Hughes & Connell 1987), and corals are thus best modeled via continuous functions and integrals rather than traditional matrix projec-

tion models (Leslie 1945). Integral projection models (IPMs) offer a framework connecting individual-level demographic rates to a detailed quantification of population-level ecological performance (Easterling et al. 2000, Edmunds et al. 2014). Because the model for each demographic rate requires the estimation of only a few parameters, IPMs can make much more efficient use of data than matrix projection models, resulting in higher accuracy and/or lower data requirements. In addition, by allowing experimentation with parameters that differentially affect life stages and demographic rates, IPMs permit projection of the consequences of changing conditions on a population, and highlight management priorities.

In this study, we aimed to assess the ecological performance and viability of an isolated, high-latitude population of *P. versipora*. We built an IPM using demographic rates of colonies in Sydney Harbour, and examined the model for insights into the demographic characteristics of the population and into potential sensitivities on which conservation and management should focus.

## MATERIALS AND METHODS

### Study site and data collection

The study population of *Plesiastrea versipora* is located near Fairlight Pool, Sydney Harbour, Australia (33° 48' 3" S, 151° 16' 32" E) on a rocky shelf at 5–12 m depth. We estimated the population size structure in December 2011 by haphazardly laying two 20 × 2 m belt transects and digitally photographing 350 unconstrained colonies (i.e. not touching neighboring colonies) of *P. versipora* together with a 10 × 10 cm scale plate. Photographs were corrected for barrel distortion, and colonies were outlined and their planar areas estimated using ImageJ (Abràmoff et al. 2004). Colonies in this population grow in an encrusting form on generally flat slabs (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m594\\_p085\\_supp.pdf](http://www.int-res.com/articles/suppl/m594_p085_supp.pdf)), and their size can be captured well by planar area.

Colony growth estimates were gathered over 3 yr. In December 2011, 27 colonies of varying sizes, not in close contact with neighbors, were haphazardly selected, tagged, and photographed (Fig. S1). Fifteen of those colonies were photographed again in August 2012. Four colonies had disappeared and were treated as deaths. The fate of 8 others could not be determined, so they were removed from the data. Five additional colonies that appeared in both earlier

and later photos were measured, bringing the total to 20 growth estimates. The censuses were 266 d apart, and the ratios of later to earlier sizes were raised by the power  $365/266$  to get an annualized exponential growth rate. In December 2012, 3 permanent  $10 \times 2$  m transects were placed on the substrate in areas with relatively uncrowded colonies (growth was not constrained). Colonies were censused with  $1 \times 1$  m abutting quadrats along each side of a transect, for a total of 20 quadrats transect<sup>-1</sup>. The four  $50 \times 50$  cm quadrants within each quadrat were photographed in December 2012 and again in December 2013. Photos were corrected for barrel distortion, and colonies were outlined in ImageJ to estimate their areas. A 25 cm section of the quadrant was used for scale. We measured 45 colonies in both 2012 and 2013. Colonies that disappeared by 2013 were recorded as deaths.

Additional data on survival, reproductive status, and sex were drawn from Withers (2000, her Tables 3.4 and 3.5) and from Madsen et al. (2014) as described below.

### Modeling

An IPM can estimate the asymptotic population size structure by combining colony-level mortality, colony-level growth or shrinkage, and fecundity. Alternately, as in the present study, it can use colony-level mortality, colony-level growth or shrinkage, and the actual population size structure (as an approximation to the asymptotic size structure) to estimate fecundity. The IPM takes the form

$$N(zz, t+1) = \int [S(z, t)G(zz|z, t) + F(z, zz, t)] N(z, t) dz \quad (1)$$

where  $N(z, t)$  is the distribution of colonies of size  $z$  at time  $t$ ,  $F(z, zz, t)$  is the expected number of recruits of size  $zz$  at time  $t+1$  generated by a colony that was of size  $z$  at time  $t$ ,  $S(z, t)$  is the predicted probability of survival of a colony of size  $z$  from time  $t$  to time  $t+1$ , and  $G(zz|z, t)$  is the probability density function of expected sizes  $zz$  at time  $t+1$  given an observed size  $z$  at time  $t$ . The components of the model make use of per capita rates for colonies of size  $z$ , and thus do not rely on an estimate of abundance.

The integral in Eq. (1) was evaluated at 300 mesh points using the midpoint rule for numerical integration. The smallest and largest midpoints were set to the nominal minimum ( $0.35 \text{ cm}^2$ ) and maximum ( $1600 \text{ cm}^2$ ) colony sizes (see the Supplement for rationale for the minimum and maximum sizes modeled).

The annual growth probability density function  $G(zz|z, t)$  was a linear regression of colony sizes ( $n = 65$ ) at time  $t+1$  against sizes at time  $t$ . The residuals were examined, and normality was rejected by the Shapiro-Wilk test ( $p < 0.001$ ). The Box-Cox procedure was used to find a power transformation to increase residual homoscedasticity and normality (Rees et al. 2014), and a sixth-root transformation of size was chosen. If density-dependent effects apply, their omission might lead to overestimating the population's growth rate.

The survival function  $S(z, t)$  was the product of size-dependent and size-independent components. The size-dependent probability of survival was modeled as a logistic regression on colony size. Observations from this study ( $n = 72$ ) and Withers (2000, her Table 3.4;  $n = 384$ ) were combined, with the midpoint of each size class in Withers' table representing the sizes of Withers' data. There was no mortality among this study's 37 colonies whose earlier measurement exceeded  $20 \text{ cm}^2$  nor among 77 colonies larger than  $20 \text{ cm}^2$  which were measured twice in an earlier study near Fairlight Pool spanning 3 yr (Withers 2000). However, to avoid modeling large colonies as immortal, a size-independent survival probability was introduced. An initial size-independent mortality of several percent was considered, but yielded an extremely low probability of seeing no mortality among the 114 largest colonies. The size-independent mortality was then reduced in steps down to 1%, corresponding to a 32% probability of the observed absence of mortality. Analysis showed that the IPM was fairly insensitive to the level of size-independent mortality. The sixth root of size was taken, to increase the homoscedasticity and normality of the residuals. This was the transform suggested by the Box-Cox procedure for the growth model, and the same transform of size was both mathematically reasonable and convenient for the survival model.

The fecundity function  $F(z, zz, t)$  was the product of the probability that a colony was reproductive, the probability that it was female, and the number of recruits for a reproductive female colony of size  $z$  (i.e. fecundity was assumed to be oocyte-limited. If it is limited by sperm supply instead [Yund 2000, Ritson-Williams et al. 2009], the fecundity function could be incorrect):

$$F(z, zz, t) = \text{Pr}(\text{size-}z \text{ colony is reproductive}) \times \text{Pr}(\text{size-}z \text{ colony is female}) \times R(z, zz, t) \quad (2)$$

*P. versipora* occasionally reproduces asexually, e.g. by fission, but this is uncommon (Withers 2000) and was not included in the model. In addition, while par-

tial colony mortality can reduce the reproductive area of a colony, such effects were not measured directly in this study. Instead, partial mortality was captured by the growth function, where net growth is the sum of biological growth and partial mortality, and consequently reflected in the colony size  $z$ .

The probability of a colony being reproductive was estimated as a logistic regression against colony size by combining observations from Withers (2000, her Table 3.5;  $n = 114$ ) and Madsen et al. (2014;  $n = 140$ ). Withers (2000) reported no reproductive colonies (0/57) smaller than 5 cm<sup>2</sup>, 18% (5/28) between 5 and 10 cm<sup>2</sup>, and 38% (11/29) between 10 and 100 cm<sup>2</sup>; sizes for these data were approximated with the midpoint of each size class. Madsen et al. (2014) found that 106 of 140 (76%) colonies studied were reproductive and ranged in size from 21.6 cm<sup>2</sup> to 1278 cm<sup>2</sup>. The sizes of 80 reproductive colonies measured by Madsen et al. (2014) were available to us, and the remainder of Madsen's data was simulated by randomly drawing 60 colony sizes from the set of 80 known reproductive sizes. Of the 60 randomly drawn sizes, 26 were randomly assigned to be reproductive, matching the total of 106 reproducing colonies, and 34 were assigned to be non-reproductive. Again, a sixth-root transformation of size was used to increase the homoscedasticity and normality of the residuals.

The probability of a colony being female was modeled as a logistic regression on untransformed size, using the 80 colonies of known size from Madsen et al. (2014).

Recruits were modeled as having an initial size of 0.35 cm<sup>2</sup> (i.e. approximately 0.67 cm in diameter), and the population was modeled as closed to outside recruitment (Edmunds et al. 2014). Per-polyp fecundity is not strongly related to the size of reproducing colonies (Madsen et al. 2014), and therefore the recruitment rate was modeled as a multiplier of colony area (and hence number of polyps):

$$R(z, zz, t) = \begin{cases} Qz & \text{for } zz = 0.35 \text{ cm}^2 \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

The number of recruits per reproductive female colony area,  $Q$ , was estimated by maximizing the likelihood of the empirical size structure of the 209 colonies larger than 20 cm<sup>2</sup> given the IPM's stable size distribution. Thus, the empirical size structure was treated as the best available estimate of the population's actual long-term size structure. The minimum size threshold of 20 cm<sup>2</sup> was used because of the difficulty of detecting smaller colonies in the transect photographs. During the process of likelihood maximization,  $Q$  was varied from 0.01 to 0.07 in steps of

0.0001. A likelihood-based 95% confidence interval for  $Q$  was also calculated (Meeker & Escobar 1995).

The estimated population asymptotic growth rate  $\lambda$  and stable size distribution were obtained from the dominant eigenvalue and corresponding right eigenvector, respectively, of the discretized integral projection model (Easterling et al. 2000). The sensitivities of the population growth rate and the stable size distribution to the vital rates were examined by increasing and decreasing each estimated vital rate parameter individually by 1%. This showed which parameters had the greatest impact on the model and hence were most important to estimate accurately. Sensitivity and elasticity matrices for the model projection surface indicated the size transitions most sensitive to change (de Kroon et al. 2000, Merow et al. 2014).

All data and code are available at [dx.doi.org/10.6084/m9.figshare.5410810](https://dx.doi.org/10.6084/m9.figshare.5410810).

## RESULTS

The growth rate of colonies decreased with increasing colony size, tending to yield net growth at smaller sizes and net shrinkage at larger sizes. On average, colonies of *Plesiastrea versipora* smaller than about 250 cm<sup>2</sup> increased in size (Fig. 1a). However, the slope of the relationship between colony sizes in consecutive years was  $<1$  ( $\sim 0.91$ , Table S1 in the Supplement), reflecting slowing growth at larger sizes. At sizes larger than about 250 cm<sup>2</sup> (i.e. where the regression line of the growth model crosses the 45° angle line in Fig. 1a), colony growth tended to be outweighed by partial mortality (shrinkage). An alternate measure of growth is the change in arithmetic mean radius, which averaged 3.6 mm yr<sup>-1</sup>.

Colony size was strongly linked to survivorship and reproductive potential. Yearly probability of survival increased with size, from about 85% for 0.35 cm<sup>2</sup> recruits to over 98% for colonies larger than 50 cm<sup>2</sup> (Fig. 1b). Larger colonies were also more likely to be reproductive (Fig. 1c), with 50% of 45 cm<sup>2</sup> colonies being reproductive and 90% of 290 cm<sup>2</sup> colonies being reproductive. Colonies larger than about 160 cm<sup>2</sup> were more likely to be male (Madsen et al. 2014; Fig. 1d). The probability of being female was highest at small sizes, dropping to 50% at approximately 150 cm<sup>2</sup> and 10% at about 400 cm<sup>2</sup>. Because the probability of a colony being female decreases with size while the probability of being reproductive increases, the maximum probability of a colony being a reproductive female was reached at an intermediate size ( $\sim 100$  cm<sup>2</sup>; Fig. 2a).

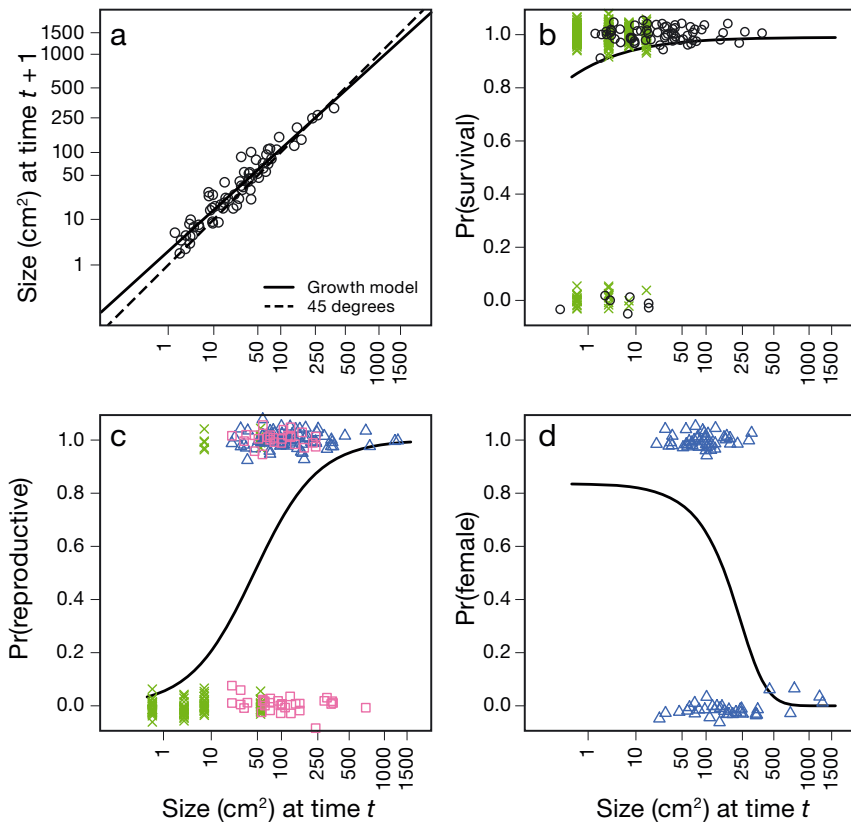


Fig. 1. Data points and fitted functions for *Plesiastrea versipora* (a) growth, (b) probability of survival, (c) probability of being reproductive, and (d) probability of being female, plotted against size. Points in plots (b,c,d) are vertically dithered to enhance visualization. Black circles indicate data collected in this study; green Xs show data from Withers (2000); blue triangles, data from Madsen et al. (2014); and pink squares are resampled data simulating missing sizes from Madsen et al. (2014)

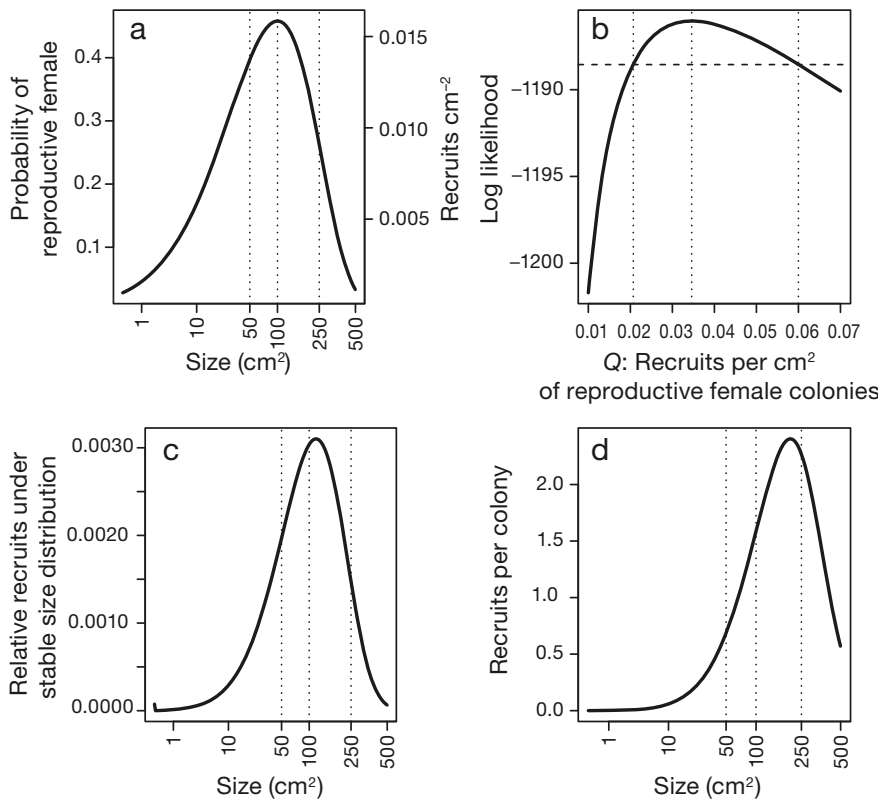


Fig. 2. (a) Probability of a *Plesiastrea versipora* colony being a reproductive female (left axis) and number of recruits  $\text{cm}^{-2}$  (right axis), against size. The number of recruits  $\text{cm}^{-2}$  is  $\text{Pr}(\text{colony is a reproductive female}) \times Q$  (where  $Q$  is defined below panel b). (b) Log likelihood of the observed size distribution under the predicted stable size distribution, which varies as a function of  $Q$ . Vertical dotted lines indicate, from left to right, the lower 95% confidence limit, maximum likelihood estimate, and upper 95% confidence limit. (c) Number of recruits predicted from colonies of a given size, multiplied by the predicted stable size distribution. For example, under the stable size distribution, about twice as many recruits would be produced by colonies of  $100 \text{ cm}^2$  as by colonies of  $40 \text{ cm}^2$ . (d) Recruits per colony as a function of colony size  $z$ , i.e.  $Q \times z \times \text{Pr}(\text{colony of size } z \text{ is female})$ . Vertical dotted lines in (a,c,d) are to aid comparison



Recruitment was estimated by adjusting  $Q$  to find the stable size distribution most similar to the empirical size structure. The model stable size distribution best fit the population's empirical size structure when  $Q$  was 0.0347 (recruits  $\text{yr}^{-1} \text{cm}^{-2}$  of reproductive female coral cover), or 347 recruits  $\text{yr}^{-1} \text{m}^{-2}$  of reproductive female colony (Fig. 2b). The average number of recruits  $\text{yr}^{-1} \text{cm}^{-2}$  of reproductive females over all sizes from 0.35 to 1600  $\text{cm}^2$  (i.e. integrating Fig. 2a) was 62. If the population matches the stable size distribution (i.e. integrating Fig. 2c), 48 recruits  $\text{yr}^{-1}$

$\text{cm}^{-2}$  of coral are predicted (95% confidence interval: 29–85). Reproductive output decreases slowly as colonies exceed intermediate size, with larger size partially balancing the lower probability of being female (Fig. 2d).

Fig. 3a compares the population's empirical size structure to the best-fit stable size distribution generated by the model. The IPM's intrinsic population growth rate  $\lambda$  was 1.164, or approximately 16% annual growth in population planar area, corresponding to population size doubling every 4.6 yr given

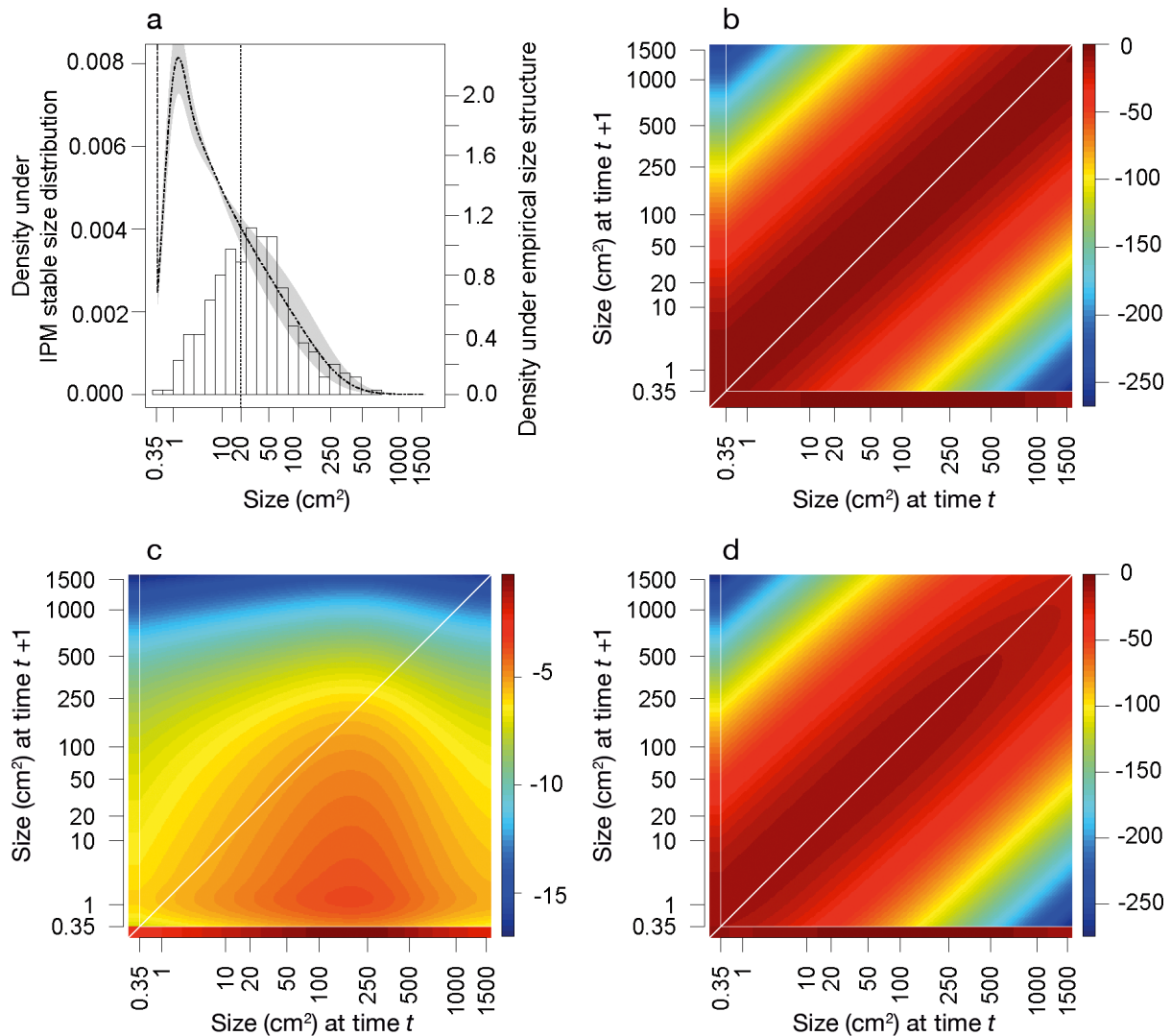


Fig. 3. (a) Histogram of empirical size structure of *Plesiastraea versipora* (right axis), with the dotted-dashed line showing integral projection model (IPM) stable size distribution (left axis). The IPM stable size distribution was fitted to the empirical size structure only for sizes greater than 20  $\text{cm}^2$ , indicated by a dotted vertical line. The grey shaded region around the stable size distribution curve corresponds to the 95% confidence interval for  $Q$  (as defined in 'Materials and methods; Modeling'). (b) Kernel, on kernel log scale. The highest- (lowest-) probability size transitions are dark red (blue). (c) Sensitivity and (d) elasticity of the kernel matrix, both plotted as natural logs to reduce the visual difference between the recruits and all other sizes. Larger (smaller) log probability values are dark red (blue). To increase the visibility of the row and column corresponding to 0.35  $\text{cm}^2$  recruits, these are shown as wider bands at the left and bottom of the plots, separated by thin white lines. The matrix diagonals are shown with a white line

unconstrained colony growth. This should be regarded as a candidate upper bound on population growth, as colony growth can be constrained by competition or other factors, though many colonies are uncrowded (J. S. Madin pers. obs., R. M. Woods pers. obs.). The shapes of the empirical size structure and the model stable size distribution were very different for smaller colonies. The model predicts many more juveniles and recruits, and fewer colonies of 25–65 cm<sup>2</sup>, than were counted in the field.

The effects of changes in each demographic parameter on the growth rate of the population and on the stable size distribution are shown in Fig. S2 in the Supplement. The growth function relating a colony's size at time  $t$  to its size at time  $t+1$ , in particular the slope of this function, has by far the greatest impact on the population's growth rate and size distribution.

Combining growth, survival and recruitment functions with colony size gives the probability of a colony of any size  $z$  at time  $t$  transitioning to any size  $zz$  at time  $t+1$ , that is, the IPM kernel in Eq. (1). Key features of this kernel (Fig. 3b) are (1) the nearly diagonal high probability (i.e. dark red) ridge, which shifts from positive growth for smaller colonies to negative growth for larger ones, and (2) the red horizontal band along the bottom that represents a colony's contribution to recruitment and that indicates that the greatest recruitment (darkest red) comes from colonies of intermediate sizes.

Fig. 3c shows the sensitivity of the IPM, i.e. the absolute change in population growth rate  $\lambda$  that is caused by a small absolute change in the probability of a transition between any 2 sizes. The dark red band at the bottom indicates that  $\lambda$  is most sensitive to changes in recruitment, particularly from intermediate-sized colonies (approximately 100–250 cm<sup>2</sup>), suggesting a strong role for reproduction in maintaining positive population growth. The relatively high (orange) values below the diagonal in this figure also show that for intermediate-sized colonies, shrinkage affects population growth much more than increasing size does. Population elasticity is a sensitivity measure that takes into account the probabilities of size transitions (e.g. while the population is sensitive to medium-sized colonies shrinking to very small ones, the kernel shows that the probability of this happening is not high; Fig. 3b). The population elasticity surface indicates that population growth depends primarily on successful recruitment, and secondarily on growth to sizes up to about 250 cm<sup>2</sup> (Fig. 3d). Loss of recruits or small to medium-sized colonies will have the greatest negative effect on population viability.

Parameter estimates for the component models are given in Table S1, together with the equation for the IPM including all parameter estimates.

## DISCUSSION

Our results indicate that high survivorship and at least sporadic high recruitment are important for the viability of the isolated, high-latitude population of *Plesiastrea versipora* in Sydney Harbour. Indeed, this population has the potential to increase rapidly, doubling in area every 4.6 yr if growth of individuals remains unconstrained by neighboring colonies. This is perhaps surprising given possible exposure to chemical contaminants, sewage, and storm water run-off from the urban Sydney Harbour catchment (Mayer-Pinto et al. 2015, Woods et al. 2016). The population's high survivorship of individuals, especially large ones, allows it to remain viable despite its apparent isolation and what could be irregular intervals between substantial recruitment events. Large colonies occupy a disproportionate part of the population's total area and tend to be male (Fig. 1d; Madsen et al. 2014). If sexual reproduction is oocyte-limited and would remain so even without the large male colonies, these large colonies make important genetic but not numerical contributions of new individuals via sexual reproduction. Rather, medium-sized colonies of roughly 70–185 cm<sup>2</sup> are crucial to long-term population viability, because they are both reproductive and female. These colonies generate about half of the eggs in the population. This unusual reproductive pattern, in which mid-sized rather than the largest colonies are the most numerically productive, suggests that suitable habitat could eventually fill with large colonies with high survivorship (Fig. 1b), thereby leading to a decline in population-level reproductive output.

The lower number of smaller colonies in the empirical size structure compared to the model stable size structure could indicate a lack of any significant recruitment for a few years or a period of high mortality for smaller colonies. In this case, the mode in the empirical size structure would represent a cohort from the last large, surviving recruitment pulse (possibly a 'mast year,' Hughes & Tanner 2000) and the current rapid population growth would be temporary. The empirical size structure is the result of all past conditions, while the model stable size structure is derived using observations of recent, short-term individual colony growth and mortality. Thus, the disparity may suggest that the population is currently

experiencing higher growth than its past average, and that the growth reflected in the model will decline unless there is a new recruitment pulse. The 16% growth rate estimated here is higher than the 6–15% annual increase in benthic cover by *P. versipora* observed at Fairlight in 1996–1998 by Withers (2000), providing some support for this hypothesis. An alternative explanation for the difference in small-colony numbers between the empirical size structure and the model stable size structure is that smaller colonies are difficult to see in the photographs due to uneven surfaces and other benthic organisms. A third explanation for the disparity could be that fusion of neighboring colonies provides smaller colonies a route to accelerated growth and potentially reduced mortality (Forsman et al. 2015), resulting in ‘missing’ sizes in the population. The most likely scenario involves all 3 explanations. Another possibility is that the growth or survival functions are not good fits for the smallest colonies.

If recruitment success is highly variable, another way to handle it would be to introduce annual variability in recruitment into the model, rather than deriving an average recruitment from the integrated performance reflected in the empirical size distribution. Similar treatment might be suitable for survivorship in this population as well. The model treats mortality as a function of size alone, occurring at a constant rate over time and affecting each colony independently. However, total colony mortality was not observed for any colony larger than 17 cm<sup>2</sup>, and mortality might be caused by something that affects many colonies simultaneously and that occurs too infrequently to be captured by a model with annual time steps. For example, bleaching was observed in this population in April 2016 (J. S. Madin pers. obs.). Such an event is likely to induce mortality as well as having sub-lethal effects on growth and reproduction.

The model assumes the population is closed, with no outside larval supply, based on its genetic homogeneity and significant genetic differences from other populations on the east coast of Australia (Rodriguez-Lanetty & Hoegh-Guldberg 2002). Under that assumption, the estimated rate of recruitment was 48 recruits yr<sup>-1</sup> m<sup>-2</sup> of coral. At the same location, Withers (2000) observed 93 recruits over 1996–1998 within a 3.9 m<sup>2</sup> area with about 18% coral cover, or roughly 44 recruits yr<sup>-1</sup> m<sup>-2</sup> of coral, within our estimate’s confidence bounds. This similarity in recruitment rates suggests that, while there may not have been significant recruitment recently, large recruitment pulses may be common. There is also precedent for high

recruitment followed by rapid population growth of *P. versipora*. For example, in Western Australia, colonies per site quadrupled over about 7 yr, possibly due to competitive release (Tuckett et al. 2017).

The model thus implies that *P. versipora* uses 2 strategies to persist as an isolated population in a potentially stressful, high-latitude environment: sporadic high-recruitment pulses and mortality rates low enough to bridge low recruitment periods. The mortality rate is lower than or comparable to rates reported or modeled for other scleractinian coral species (e.g. Table S2 in the Supplement), and the colony growth rate as change in arithmetic mean radius, 3.6 mm yr<sup>-1</sup>, is relatively high compared to other encrusting corals (Table S3 in the Supplement). Intermediate-size colonies are the most important for ongoing population viability. The largest colonies, which tend to be male, might not contribute numerically to recruitment, but could help maintain genetic diversity and thus support the population’s resilience to environmental variation. The population’s growth is most sensitive to recruitment, as with corals in harsh, episodically disturbed environments (Riegl & Purkis 2009, Riegl et al. 2009). Although the current population trajectory is for growth, clearly a long-term lack of recruitment would eventually lead to population decline. However, corals at an isolated reef system in Western Australia suffered over 70% mortality and a more than 16-fold reduction in recruitment lasting 6 yr after a bleaching event, yet rebounded within 12 yr (Gilmour et al. 2013). Thus, the low mortality of colonies in the Sydney Harbour population may provide insurance against extended recruitment failure and allow the population to persist.

This population of *P. versipora* is thriving. Nonetheless, its persistence is sensitive to recruitment and growth, and conservation efforts should aim to control factors that affect adult survivorship and sporadic high recruitment. In Sydney Harbour, a major threat given these demographic traits is terrestrial runoff, which can carry excess nutrients and pollutants that affect colony survival, fertilization success, and larval survival (Fabricius 2005, Woods et al. 2016).

As coral populations at species range edges are an important source of evolutionary novelty (Budd & Pandolfi 2010), protecting such populations is likely to be crucial to species survivorship in the longer term. The demographic characteristics of these populations can play a role in how they can be effectively protected. For example, while the distributions of marine species which have a highly mobile larval stage are strongly influenced by currents in addition



to habitat suitability (Dunstan & Bax 2007), modeling results indicate that populations with low adult mortality rates, such as the study population of *P. versipora*, or shorter larval durations may be less constrained by current-induced boundaries (Gaylord & Gaines 2000). We speculate that other reef coral species with demographic characteristics similar to those found here may also be able to persist as isolated populations.

## LITERATURE CITED

- Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. *Biophoton Int* 11:36–42
- ✦ Baird AH, Sommer B, Madin JS (2012) Pole-ward range expansion of *Acropora* spp. along the east coast of Australia. *Coral Reefs* 31:1063, doi:10.1007/s00338-012-0928-6
- ✦ Budd AF, Pandolfi JM (2010) Evolutionary novelty is concentrated at the edge of coral species distributions. *Science* 328:1558–1561
- ✦ de Kroon H, van Groenendael J, Ehrlén J (2000) Elasticities: a review of methods and model limitations. *Ecology* 81:607–618
- ✦ Dunstan PK, Bax NJ (2007) How far can marine species go? Influence of population biology and larval movement on future range limits. *Mar Ecol Prog Ser* 344:15–28
- ✦ Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708
- ✦ Edmunds PJ, Burgess SC, Putnam HM, Baskett ML and others (2014) Evaluating the causal basis of ecological success within the Scleractinia: an integral projection model approach. *Mar Biol* 161:2719–2734
- ✦ Ellner SP, Rees M (2006) Integral projection models for species with complex demography. *Am Nat* 167:410–428
- ✦ Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Pollut Bull* 50:125–146
- ✦ Fine M, Gildor H, Genin A (2013) A coral reef refuge in the Red Sea. *Glob Change Biol* 19:3640–3647
- ✦ Forsman ZH, Page CA, Toonen RJ, Vaughan D (2015) Growing coral larger and faster: micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ* 3:e1313
- ✦ Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am Nat* 155:769–789
- ✦ Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69–71
- ✦ Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. *Glob Change Biol* 2:495–509
- ✦ Greenstein BJ, Pandolfi JM (2008) Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. *Glob Change Biol* 14:513–528
- ✦ Halfar J, Godínez-Orta L, Riegl B, Valdez-Holguin JE, Borges JM (2005) Living on the edge: high-latitude *Porites* carbonate production under temperate eutrophic conditions. *Coral Reefs* 24:582–592
- ✦ Hardie DC, Hutchings JA (2010) Evolutionary ecology at the extremes of species' ranges. *Environ Rev* 18:1–20
- ✦ Hughes TP, Connell JH (1987) Population dynamics based on size or age? A reef-coral analysis. *Am Nat* 129:818–829
- ✦ Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263
- ✦ Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- ✦ Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG and others (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373–377
- ✦ Keith SA, Herbert RJ, Norton PA, Hawkins SJ, Newton AC (2011) Individualistic species limitations of climate-induced range expansions generated by meso-scale dispersal barriers. *Divers Distrib* 17:275–286
- ✦ Kleypas JA, McManus JW, Meñez LA (1999) Environmental limits to coral reef development: Where do we draw the line? *Am Zool* 39:146–159
- ✦ Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? *Conserv Biol* 9:753–760
- ✦ Leslie PH (1945) On the use of matrices in certain population mathematics. *Biometrika* 33:183–212
- ✦ Madin JS, Kuo CY, Martinelli JC, Mizerek T, Baird AH (2015) Very high coral cover at 36°S on the east coast of Australia. *Coral Reefs* 34:327
- Madin JS, Allen AP, Baird AH, Pandolfi JM, Sommer B (2016) Scope for latitudinal extension of reef corals is species specific. *Front Biogeogr* 8:e29328
- ✦ Madsen A, Madin JS, Tan CH, Baird AH (2014) The reproductive biology of the scleractinian coral *Plesiastrea versipora* in Sydney Harbour, Australia. *Sex Early Dev Aquat Org* 1:25–33
- Marsh LM (1992) The occurrence and growth of *Acropora* in extra-tropical waters off Perth, Western Australia. *Proc 7th Int Coral Reef Symp* 2:1233–1238
- ✦ Mayer-Pinto M, Johnston EL, Hutchings PA, Marzinelli EM and others (2015) Sydney Harbour: a review of anthropogenic impacts on the biodiversity and ecosystem function of one of the world's largest natural harbours. *Mar Freshw Res* 66:1088–1105
- Meeker WQ, Escobar LA (1995) Teaching about approximate confidence regions based on maximum likelihood estimation. *Am Stat* 49:48–53
- ✦ Merow C, Dahlgren JP, Metcalf CJE, Childs DZ and others (2014) Advancing population ecology with integral projection models: a practical guide. *Methods Ecol Evol* 5:99–110
- ✦ Muir PR, Wallace CC, Done T, Aguirre JD (2015) Limited scope for latitudinal extension of reef corals. *Science* 348:1135–1138
- ✦ Perry CT, Lecombe P (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22:427–432
- ✦ Precht WF, Aronson RB (2004) Climate flickers and range shifts of reef corals. *Front Ecol Environ* 2:307–314
- ✦ Rees M, Childs DZ, Ellner SP (2014) Building integral projection models: a user's guide. *J Anim Ecol* 83:528–545
- ✦ Riegl B (2003) Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs* 22:433–446
- ✦ Riegl BM, Purkis SJ (2009) Model of coral population response to accelerated bleaching and mass mortality in a changing climate. *Ecol Model* 220:192–208
- ✦ Riegl B, Purkis SJ, Keck J, Rowlands GP (2009) Monitored and modeled coral population dynamics and the refuge concept. *Mar Pollut Bull* 58:24–38
- ✦ Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJ, Paul VJ (2009) New perspectives on ecological

mechanisms affecting coral recruitment on reefs. *Smithson Contrib Mar Sci* 38:437–457

- ✦ Rodriguez-Lanetty M, Hoegh-Guldberg O (2002) The phylogeography and connectivity of the latitudinally widespread scleractinian coral *Plesiastrea versipora* in the Western Pacific. *Mol Ecol* 11:1177–1189
- ✦ Sommer B, Harrison PL, Beger M, Pandolfi JM (2014) Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* 95:1000–1009
- ✦ Tuckett CA, de Bettignies T, Fromont J, Wernberg T (2017) Expansion of corals on temperate reefs: direct and indirect effects of marine heatwaves. *Coral Reefs* 36:947–956
- ✦ van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol Evol* 2: 2474–2484
- ✦ Withers KJ (2000) Empire building colonials: the implications of size in the hard coral *Plesiastrea versipora*. PhD dissertation, University of Sydney
- ✦ Woods RM, Baird AH, Mizerek TL, Madin JS (2016) Environmental factors limiting fertilisation and larval success in corals. *Coral Reefs* 35:1433–1440
- ✦ Yamano H, Sugihara K, Nomura K (2011) Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophys Res Lett* 38:L04601
- ✦ Yund PO (2000) How severe is sperm limitation in natural populations of marine free-spawners? *Trends Ecol Evol* 15:10–13

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