

## LETTER

# Predicting coral community recovery using multi-species population dynamics models

Mohsen Kayal,<sup>1,2,3\*</sup> Hunter S. Lenihan,<sup>1</sup> Andrew J. Brooks,<sup>4</sup> Sally J. Holbrook,<sup>4,5</sup> Russell J. Schmitt<sup>4,5</sup> and Bruce E. Kendall<sup>1</sup>

### Abstract

Predicting whether, how, and to what degree communities recover from disturbance remain major challenges in ecology. To predict recovery of coral communities we applied field survey data of early recovery dynamics to a multi-species integral projection model that captured key demographic processes driving coral population trajectories, notably density-dependent larval recruitment. After testing model predictions against field observations, we updated the model to generate projections of future coral communities. Our results indicated that communities distributed across an island landscape followed different recovery trajectories but would reassemble to pre-disturbed levels of coral abundance, composition, and size, thus demonstrating persistence in the provision of reef habitat and other ecosystem services. Our study indicates that coral community dynamics are predictable when accounting for the interplay between species life-history, environmental conditions, and density-dependence. We provide a quantitative framework for evaluating the ecological processes underlying community trajectory and characteristics important to ecosystem functioning.

### Keywords

Community recovery, coral reefs, density dependence, ecosystem function, elasticity analysis, integral projection model, life-history traits, multi-species demographic model, reassembly, size structure.

Ecology Letters (2018) 21: 1790–1799

## INTRODUCTION

As the human population increases, so do the diversity and severity of disturbances to communities of organisms that shape ecosystems. Understanding what influences the recovery of communities from disturbance is therefore growing more difficult and important in terms of conservation and management (Godfray & May 2014). This is especially true for tropical coral reefs that provide a plethora of ecosystem services yet are being degraded at an increasing rate by human activities (Hughes *et al.* 2017). Coral reefs are impacted by storms, predator outbreaks, bleaching events, and other environmental perturbations that reduce live coral cover, the abundance and size of coral colonies and coral taxonomic diversity (De'ath *et al.* 2012; Riegl *et al.* 2017; Adjeroud *et al.* 2018). In turn, a decline in coral abundance, composition, and size can reduce the provision of ecosystem services, largely because mixed assemblages of corals create complex physical structures that form habitat for a diversity of organisms (Graham *et al.* 2008; Fabricius *et al.* 2014; Holbrook *et al.* 2015; Lamy *et al.* 2016; Darling *et al.* 2017), provide refuge from multiple kinds of stress (Schmitt & Holbrook 2007; Lenihan *et al.* 2008; Kayal *et al.* 2011; Bozec *et al.* 2013), as well as support fisheries that benefit millions of people (Cinner *et al.* 2012; Rogers *et al.* 2014).

An increasing number of reefs have experienced major coral loss, with an alarming portion of them shifting to a macroalgae dominated or other non-coral state (Mumby *et al.* 2007; De'ath *et al.* 2012; Anthony *et al.* 2015). Live coral cover on other reefs has recovered rapidly and repeatedly, even from catastrophic disturbance (Tomascik *et al.* 1996; Johns *et al.* 2014; Adjeroud *et al.* 2018). Recovery has been observed in cases where surviving coral colonies regrow, larval supply from remote populations facilitate recolonisation, and/or grazing fishes control macroalgal growth (Gilmour *et al.* 2013; Holbrook *et al.* 2018). However, the return of live coral cover does not necessarily imply recovery of coral taxonomic composition or size. Many recovering reefs have returned to a pre-disturbed level of live coral cover but support taxonomically and physically simplified coral communities, some with reduced species diversity and productivity (Berumen & Pratchett 2006; van Woesik *et al.* 2011; Alvarez-Filip *et al.* 2013; Rogers *et al.* 2014). To date, research designed to identify demographic mechanisms leading to coral community recovery has focused mainly on coral cover, and used a variety of field-based empirical approaches, sometime coupled with stage-structured population matrix models to examine inherently complex underlying population dynamic processes (Gilmour *et al.* 2013; Johns *et al.* 2014; Ortiz *et al.* 2014; Riegl *et al.* 2017). A greater understanding of demographic

<sup>1</sup>Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, 93106, USA

<sup>2</sup>UPVD-CNRS, Centre de Formation et de Recherche sur les Environnements Méditerranéens, UMR 5110, 52 avenue Paul Alduy, 66860 Perpignan, France

<sup>3</sup>Centre de Recherche sur les Ecosystèmes Marins (CREM), impasse du solarium, 66420 Port-Barcarès, France

<sup>4</sup>Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

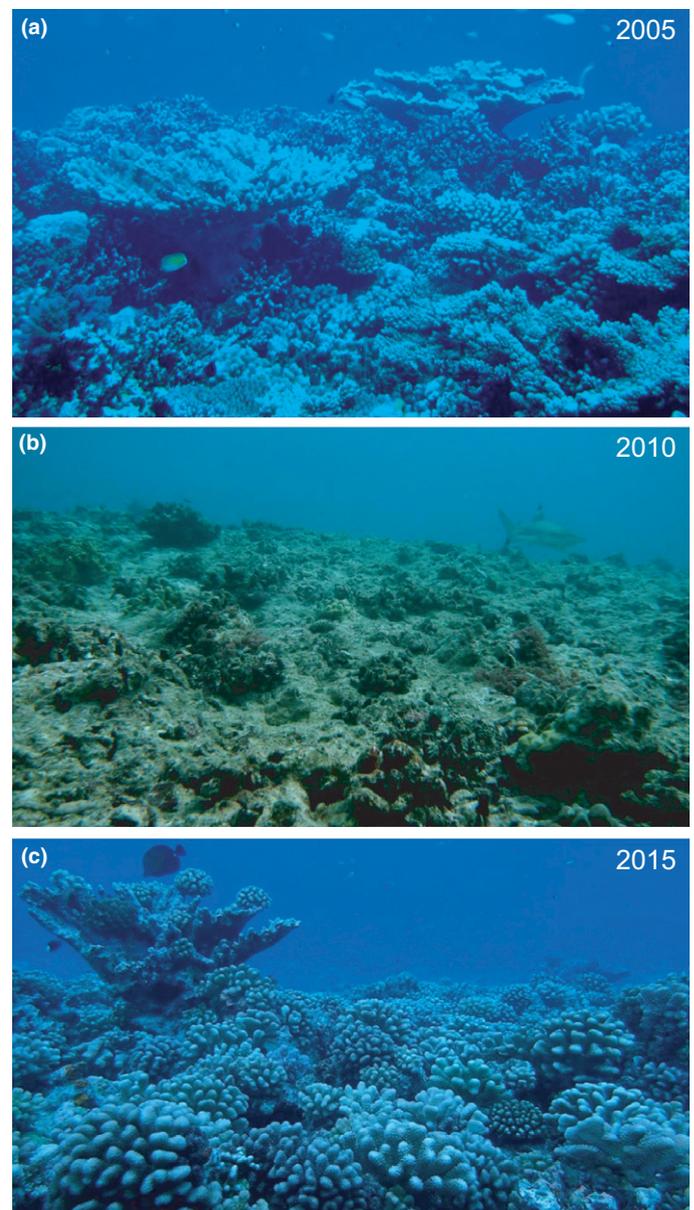
<sup>5</sup>Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA, 93106, USA

\*Correspondence: E-mail: mohsen.kayal@gmail.com

mechanisms driving the recovery of community abundance, composition, and size structure requires the application of powerful new quantitative tools, including those provided by integral projection models (Ellner *et al.* 2016).

Coral reefs around the island of Mo'orea, French Polynesia, have been heavily disturbed several times over the past few decades (Adjeroud *et al.* 2018), including in 2006–2010 when an outbreak of predatory crown-of-thorns seastar (COTS) followed by a cyclone reduced coral cover on the fore-reefs from > 40 to < 1% (Fig. 1), greatly altering the reef ecosystem (Kayal *et al.* 2012). By 2015, coral cover on many reefs had recovered, some to greater than the pre-disturbance levels (Holbrook *et al.* 2018; Fig. S1 in Supporting Information). However, coral communities in 2015 were dominated by small pocilloporid colonies, and substantial recovery of structurally complex acroporids and massive poritids had not happened (Fig. 1c). Whether coral communities eventually recover to a pre-disturbed state, or remain in a taxonomically and physically simplified state, is difficult to predict (van Woesik *et al.* 2011; Alvarez-Filip *et al.* 2013; Osborne *et al.* 2017; Riegl *et al.* 2017). Acroporids and poritids exhibit different life history strategies than pocilloporids in French Polynesia and elsewhere (Darling *et al.* 2012; Kayal *et al.* 2015), including differences in the production of dispersive larvae that can recolonise disturbed reefs, as well as in colony survival and growth rates (Appendix S1). The recent disturbances raise particular concern about the recovery of Mo'orea's acroporids, as larvae necessary for replenishment of depopulated fore-reef populations may originate in the lagoon where prior disturbances may have reduced a historically high abundance of acroporids (Done *et al.* 1991; Berumen & Pratchett 2006; Leichter *et al.* 2013).

We used the recovery of Mo'orea's fore-reefs to test whether coral community dynamics are predictable, and to quantitatively evaluate demographic processes underlying coral recovery. To do so, we developed a quantitative framework comprised of coral demographic surveys, generalised linear mixed model (GLMM, Pinheiro *et al.* 2016) estimates of demographic functions, and a multi-taxon, open-population integral projection model (IPM, Ellner *et al.* 2016) that simulated the dynamics of coral assemblages. A key feature of our empirical model was a dynamic recruitment function that combined quantitative information from our surveys and from prior work in Mo'orea to predict larval recruitment rates as a function of the taxon, location, and abundance of coral populations (see Materials and Methods). Our model complements recent work that developed IPMs for open marine populations (Yau *et al.* 2014) and multi-species assemblages (Adler *et al.* 2010) in an effort to characterise the dynamics of communities composed of taxa with contrasting life-histories and driven by different patterns of density-dependent larval recruitment. Our model simulations predicted transient dynamics in coral abundance, composition, and size to evaluate if the reefs around Mo'orea will eventually recover to their pre-disturbed state. We developed our empirical IPM in an iterative approach in which short-term predictions of coral recovery were compared with field observations to



**Figure 1** Changes in coral communities on the fore-reef of Mo'orea, French Polynesia, associated with disturbance and recovery. The photos were taken on the north shore of the island. Data for coral cover and community composition from 2005 to 2015 are presented in Fig. S1. (a) Coral communities in 2005, prior to an *Acanthaster planci* (crown-of-thorns seastar) predator outbreak (2006–2010) and Cyclone Oli (2010), were composed mainly (73–95%) of acroporid, pocilloporid, and poritid corals. Mean proportion of the reef space covered by live coral ranged 33–46% around the island. (b) Coral communities in 2010, after disturbances reduced live coral cover around the island to 0–9%. (c) By 2015, rapid recovery of live coral cover was driven mostly by recolonisation of *Pocillopora*.

evaluate model accuracy, before a revised IPM parameterisation that corrected for major model deviances was used to produce long-term projections. Our study provides insights into the demographic processes driving the dynamics of coral taxa with contrasting life-history strategies, and predictions of community recovery and reassembly in different reef environments.

## MATERIALS AND METHODS

### Estimation of coral demographic performances

We quantified the population dynamics of the three primary habitat-forming coral genera, *Acropora*, *Pocillopora*, and *Porites*, at four fore-reef locations distributed around Mo'orea (Fig. 2; Appendix S2) by recording new recruits, estimating overall abundance, and measuring survival and changes in the size of individual colonies from 2011 to 2015 (Lenihan & Kayal 2015; Schmitt *et al.* 2017). We estimated size-specific coral survival and growth profiles for each population (Fig. 2e–l) as the average annual response observed over the two consecutive years 2011–2013. These profiles were calculated using generalised linear mixed models (GLMMs) that accounted for autocorrelation between consecutive observations (i.e. longitudinal data), and within-subject variability (random effects of the intercepts) among observations performed on different years within individually distinct plots (Pinheiro *et al.* 2016). The survival model specified that survival from time  $t$  to time  $t + 1$  is a logistic function of initial size (in  $\log_{10}(x + 1)$  scale) at time  $t$ , with a constant slope and an intercept that included random effects for years and plots. The growth model specified that final size (in  $\log_{10}(x + 1)$  scale) at time  $t + 1$  is a linear function of initial size (in  $\log_{10}(x + 1)$  scale) at time  $t$ , with a constant slope and an intercept that included random effects for years and plots. Our estimations of growth rates also accounted for occurrences of colony shrinkage (i.e. final size < initial size in consecutive surveys) as observed in populations (Fig. 2i–l). The resulting intercept and slope parameters estimated by GLMM (Table S1) were implemented in our IPM to predict size-specific coral survival and growth performances.

Variability in annual coral recruitment rates was evaluated using a semi-parametric approach that complements GLMMs with penalised splines to account for deviations from linearity in an optimised fashion given model accuracy and complexity (Ruppert *et al.* 2003). To capture the complex, multi-dimensional variability in coral recruitment as observed around Mo'orea (variability in time, space, and across genera, see Fig. 2a–d) in our IPM, we created a density-dependent recruitment function that combined an intercept parameter describing our population-specific estimates of recruitment at low coral abundance (estimated by GLMM over the first 2 years of recovery 2011–2012), with a slope parameter (Table S1) describing the density-dependent response of coral genera as estimated in a previous study (Kayal *et al.* 2015). The resulting dynamic recruitment function predicted recolonisation of the reefs by larvae from the three coral genera as a function of local population abundances. As such, our IPM encompassed the observed spatial differences in mean recruitment rates and taxonomic differences in the density dependence of recruitment (Fig. 2a–d), using a simple linearised recruitment function (see Appendix S3).

Adequacy of the GLMMs was evaluated by checking the distribution of model residuals for normality and homoscedasticity. The demographic parameters estimated by GLMM (Table S1) were implemented in our IPM to produce predictions in a deterministic approach, therefore not accounting for

uncertainty and stochasticity. All GLMMs, IPMs, and graphing were coded in R complemented by the NLME package (Pinheiro *et al.* 2016).

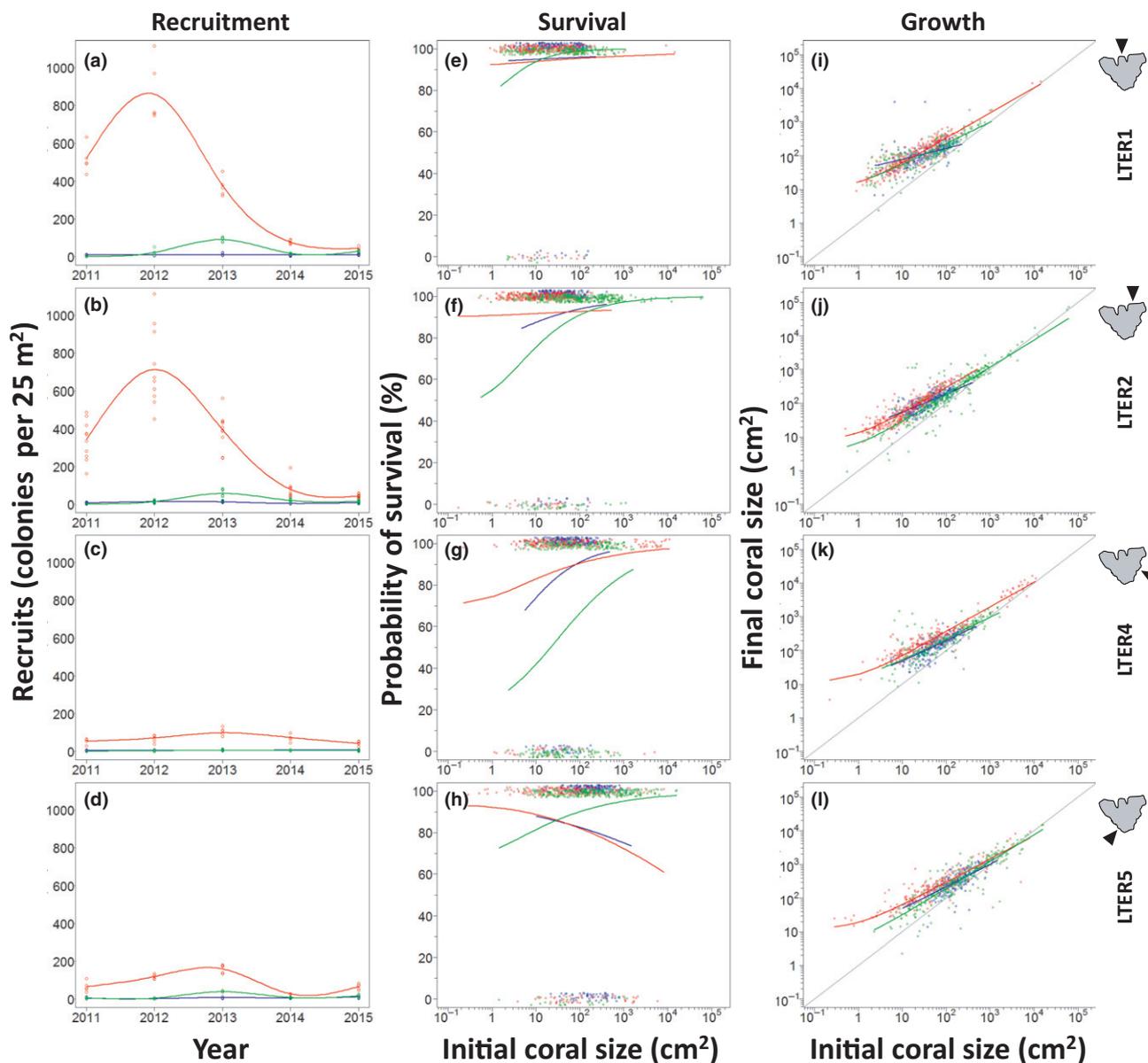
### Modeling

Integral projection models (IPMs) are constructed in a way to represent the successive stages constituting species life-cycles (Adler *et al.* 2010; Coulson 2012; Ellner *et al.* 2016). Here, we built a three-taxon, open population IPM based on a theoretical understanding of the major demographic processes driving coral community dynamics and quantitative knowledge accumulated around Mo'orea (Kayal 2017). Following early work on coral population dynamics (Hughes 1984), a large body of research confirms that coral survival and growth are strongly size dependent. Because coral abundance was exceptionally low at the onset of our study (Fig. 1b), we expected coral survival and growth to be mostly density-independent and, in the absence of major disturbance, relatively consistent across the recovery period. In contrast, as in other open marine populations, recruitment in corals is highly variable in time and space and usually hard to predict (Caley *et al.* 1996; Adjeroud *et al.* 2017). Recent studies, notably from Mo'orea, have shown that coral recruitment patterns can be related to the abundance of local populations, that is density-dependent, with responses that vary among coral genera (Hughes *et al.* 2000; Kayal *et al.* 2015; Bramanti & Edmunds 2016). A negative recruitment pattern has been observed for *Pocillopora* in relation to increasing coral assemblage surface area, regardless of taxonomic composition; a positive response is observed for *Acropora* with increasing *Acropora* abundance; and no significant density-dependent variation in recruitment has been observed for *Porites* (Kayal *et al.* 2015). Hence, our IPM combines demographic functions describing size-dependent coral survival and growth and density-dependent recruitment (Appendix S3) to predict the simultaneous dynamics of populations of the three coral taxa with the general mathematical formula

$$n(z', t + 1) = \int_L^U s(z)G(z, z')n(z, t)dz + R(\gamma, z'), \quad (1)$$

where for each population, the distribution of individuals  $n(z', t + 1)$  of final-size  $z'$  (in  $\log_{10}(x + 1)$  scale) at time  $t + 1$  is predicted as a function of the distribution of the individuals  $n(z, t)$  of all sizes  $z$  (in  $\log_{10}(x + 1)$  scale and bounded to the lower [ $L$ ] and upper [ $U$ ] limits of the size range) at time  $t$ . The functions  $s$ ,  $G$ , and  $R$  describe size ( $z$ ) dependent coral survival and growth, and density ( $\gamma$ ) dependent coral recruitment, respectively, and are detailed in Appendix S3.

Because the recent disturbances had left Mo'orea's reefs mostly denuded from live coral (Fig. 1), our initial model runs assumed empty reef space and simulated recovery of unoccupied substrata through larval recruitment only (Fig. 3, Fig. S4). After comparing model predictions against field observations, we integrated the presence of remnant corals that had survived the disturbances by reinitializing simulations with the structure of coral assemblages observed in

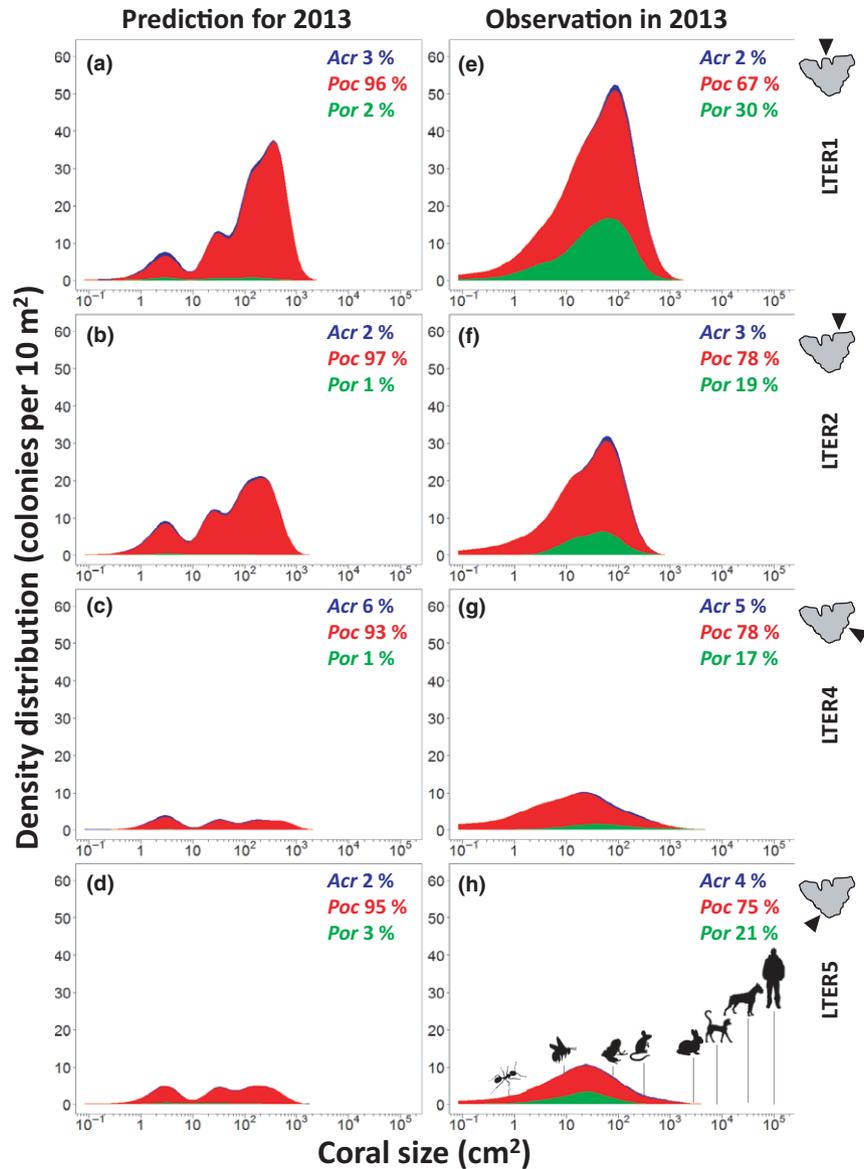


**Figure 2** Annual coral recruitment, survival, and growth rates measured on the four reefs (Long Term Ecological Research fore-reef sites, LTER 1, 2, 4 and 5). Colour codes distinguish different coral genera, *Acropora* (blue), *Pocillopora* (red), and *Porites* (green). Points represent field observations and lines are generalised linear mixed model (GLMM) estimates which, for the recruitment curves (a–d), are complemented by penalised splines to account for nonlinear variation. Note that these curves represent patterns estimated over observed data, and do not represent what was implemented into integral projection models (IPMs, see below). (a–d) Coral recruitment rates observed from 2011 to 2015. (e–l) Size-dependent survival and growth rates estimated over the first 2 years of recovery, in 2011–2013. The survival and growth curves deviate from the conventional logistic and linear shapes, respectively, because the axes represent  $\log_{10}(x)$  while a  $\log_{10}(x + 1)$  transformation was applied to coral size (Appendix S2). The diagonal grey line in (i–l) represents the null-growth threshold (final size = initial size), values below this line indicate colony shrinkage. In IPMs, survival and growth functions were implemented with parameters estimated by the GLMMs (e–h and i–l, respectively) whereas a different approach was used to capture the nonlinear recolonisation of reefs observed in a–d. Indeed, the recruitment functions in IPMs combined an intercept parameter representing the post-disturbance larval recolonisation rates (mean values measured in populations in 2011–2012), with a slope parameter representing the density-dependent response of each genus to local crowding (see Appendix S3). Table S1 provides a list of all the parameters used to represent recruitment, survival, and growth in the IPMs. Diagrams on the right indicate the positions of each of the reefs around Mo’orea.

2013 (Fig. 4). Similarly, while a common recruit size was assumed for the three coral taxa in our initial model runs, recruit size was increased for *Acropora* in subsequent simulations to match observed size distributions (Appendix S3). Each model iteration simulated coral assemblage dynamics in 10 m<sup>2</sup> of reef space over a 1-year period.

**Model performance and diagnosis of recovery dynamics**

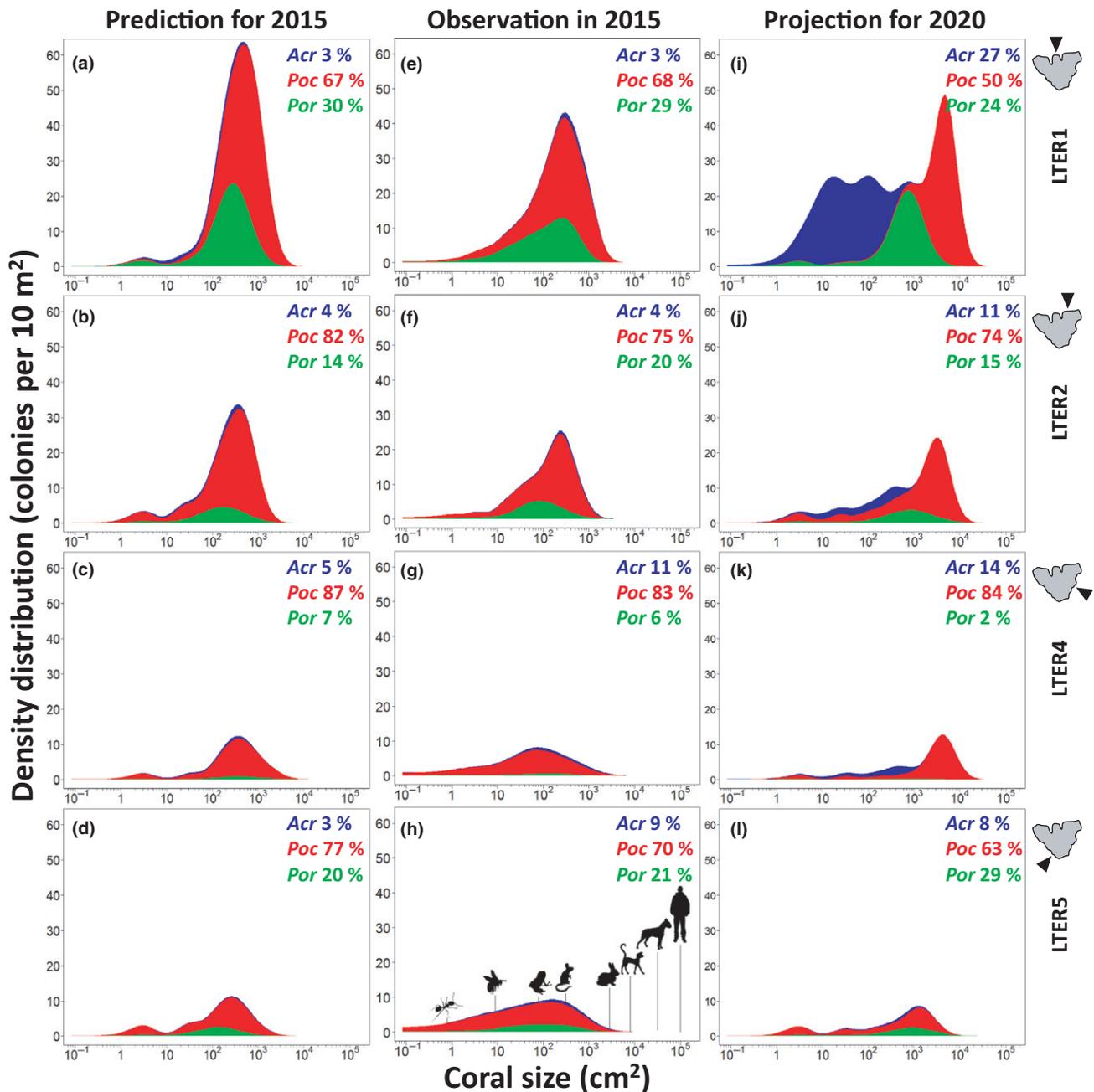
We evaluated model performance by comparing our predictions of the structure of coral assemblages after 3 and 5 years of reef recovery, with that of the actual assemblages observed in 2013 and 2015. Model simulations were considered



**Figure 3** Abundance, composition, and size distribution of coral assemblages in 2013 on the four reefs (Long Term Ecological Research fore-reef sites, LTER 1, 2, 4 and 5) as predicted by our initial integral projection model (IPM) simulations and as observed. The graphs characterise the coral assemblages as the distribution of coral colony density ( $y$ -axis) across the size range of colonies ( $x$ -axis, log-scale). The size range represents the estimated surface area of living tissue of three-dimensional corals. Examples of animals with equivalent dimensions are depicted in panel (h) for reference (from the size of an ant = 0.5 cm, to that of a human = 180 cm). Colour codes distinguish the proportions of the different genera, *Acropora* (blue), *Pocillopora* (red), and *Porites* (green), whose population density curves are stacked to illustrate the total coral assemblage abundances. The relative proportion of the coral assemblage surface area represented by each taxon is indicated as text on the plots. (a–d) Model predictions of the coral assemblages in 2013, after 3 years of reef recovery. These predictions result from model simulations of coral recovery in unoccupied reef space, and thus do not take into account the presence of remnant corals that had survived the disturbances (see Materials and Methods). (e–h) Actual coral assemblages as observed in 2013. Diagrams on the right indicate the positions of each of the reefs around Mo’orea.

statistically accurate if the predicted population densities and surface areas (i.e. sum of the individual colony sizes) fell within the limits of the confidence intervals of observations made on the actual populations (Figs S2 and S5). We also compared the predicted and observed size distribution of coral assemblages to identify portions of the coral size range where colony abundances were over- or under-represented regardless of differences in abundance (Figs S3 and S6), and used Kolmogorov–Smirnov tests to quantify the distance between the

size distribution functions. We did not expect an exact overlap in the structure of predicted and observed populations, given that our model constituted a relatively simple virtual representation of complex coral dynamics (Hughes & Jackson 1985; Kayal *et al.* 2015) designed to capture the major demographic processes driving coral community recovery and its variability in time, space, and across genera. Instead, we evaluated how closely the observed population dynamics were captured by model predictions (Figs S7–S8), and used differences to



**Figure 4** Abundance, composition and size distribution of coral assemblages in 2015 and 2020 on the four reefs (Long Term Ecological Research fore-reef sites, LTER 1, 2, 4 and 5) as predicted by our updated integral projection model (IPM) simulations and as observed. The graphs characterise the coral assemblages as the distribution of coral colony density (y-axis) across the size range of colonies (x-axis, log-scale). The size range represents the estimated surface area of living tissue of three-dimensional corals. Examples of animals with equivalent dimensions are depicted in panel (h) for reference (from the size of an ant = 0.5 cm, to that of a human = 180 cm). Colour codes distinguish the proportions of the different genera, *Acropora* (blue), *Pocillopora* (red), and *Porites* (green), whose population density curves are stacked to illustrate the total coral assemblage abundances. The relative proportion of the coral assemblage surface area represented by each taxon is indicated as text on the plots. Fig. 1c provides a photograph of the coral assemblage characterised in plot (e). (a–d) Model prediction of the coral assemblages in 2015, after 5 years of reef recovery. These predictions were generated by applying the demographic functions describing coral performance on the different reefs (Appendix S3, Table S1) to the 2013 assemblages (Fig. 3e–h), which included the presence of remnant corals that had survived the disturbances (see Materials and Methods). (e–h) Actual coral assemblages as observed in 2015. (i–l) Model projections of coral assemblages in 2020. Diagrams on the right indicate the positions of each of the reefs around Mo’orea.

improve our understanding and projections of coral recovery in an iterative approach. We used elasticity analyses (Ellner *et al.* 2016; Figs S9–S10, Tables S2–S3) to evaluate to what extent the predicted surface area of the simulated populations for

2013 and 2015 responded to variations in each of the parameters describing recruitment, survival, and growth in our IPM (Table S1). This evaluation provided a diagnosis designed to help identify which demographic processes were most

influential in the recovery of coral populations at the different stages of reef recovery. Elasticity analyses were coded in R complemented by the numDeriv package (Gilbert & Varadhan 2016).

### Model projections and prognosis of community recovery

We used the GLMM estimates of coral demographic performance during early reef recovery in 2011–2013 (Fig. 2, Table S1) and data of the abundance and size distribution surveyed in 2015 (Fig. 4e–h) to predict the structure of coral assemblages in 2020 (barring further major disturbance). For these simulations, we also performed elasticity analyses (Fig. S11, Table S4). We were unable to directly compare coral abundance and size distribution between 2005 and 2020 because communities were characterised using two-dimensional, live coral cover data in 2005 (Edmunds 2015), and our 2020 simulations generated three-dimensional, total living coral surface area. Instead, we compared the relative proportions of *Acropora*, *Pocillopora*, and *Porites* as predicted by our model for 2020 (Fig. 4i–l) with those observed within communities in 2005 (Fig. S1e–h). The capacity of the ecosystem for recovery was evaluated by the ability of reefs to reassemble coral assemblages similar in composition to that observed prior the disturbances, and dominated by large colonies that can fulfil their ecological function of providing structural habitat and refuges for diverse communities (Nash *et al.* 2014; Rogers *et al.* 2014).

## RESULTS AND DISCUSSION

### Predicting coral community recovery

The simulation models correctly predicted that coral assemblages would contain predominantly small (~ 5 cm diameter) *Pocillopora* (Fig. 3), as expected given their capacity to saturate open reef space through high larval settlement (Penin *et al.* 2010). Model simulations were relatively accurate in predicting *Pocillopora* and *Acropora* abundance across the four reefs in 2013, but largely underestimated *Porites* populations (Fig. 3, Fig. S2). While we did not expect a deterministic model to exactly match the dynamics of populations subject to environmental and demographic stochasticity, the consistent and large bias in *Porites* abundance suggested that the model was incomplete. Indeed, the simulations underestimated *Porites* abundance because our initial models predicted recovery of coral-denuded substrata through larval recruitment only, whereas the actual reefs contained small patches of *Porites* colonies that survived the disturbances (Kayal *et al.* 2012) and grew to occupy substantial space (Fig. 3e–h). *Porites* exhibits a high tolerance to disturbance and stress compared with other coral taxa, and a massive growth form that favours coral persistence through shrinkage and fission rather than full colony mortality (Darling *et al.* 2012; Kayal *et al.* 2015). Deviance from model predictions therefore revealed that remnant corals that survive disturbance can produce large populations, even for taxa with low recruitment rates like *Porites* (Fig. 2a–d). Model simulations were generally accurate in predicting coral size distribution on the different reefs (Fig. S3).

However, the absence of remnant *Porites* in simulations allowed for higher initial recruitment by *Pocillopora*, which translated into higher proportions of large (> 10 cm diameter) colonies than were observed in 2013. This difference in *Pocillopora* dynamics (Fig. 3, Fig. S4) suggested the models responded realistically to changes in coral abundance as predicted by density-dependent regulation.

We updated our model simulations to account for the presence of remnant *Porites*. Data on coral size distribution was not available prior to 2013 due to differences in survey methodology (see Appendix S2), a feature that prevented us from initiating our simulations with the structures of the actual remnant assemblages in 2011. Therefore, we initiated simulations with the structure of assemblages observed in 2013 (Fig. 3e–h), and used the same demographic functions describing coral performance on the four reefs (Table S1) to produce predictions for coral assemblages in 2015. Although our initial model runs diverged substantially from field observations in 2013 and 2015 by underestimating *Porites* populations (see Fig. 3 and Fig. S4, respectively), accounting for remnant corals by using the 2013 distributions predicted the actual dynamics in abundance, composition, and size distribution of the coral assemblages in 2013–2015 relatively accurately (Fig. 4a–h, Figs. S5–S8). Remaining divergences between model predictions and field observations included an underestimated growth potential of *Acropora* to large (> 10 cm diameter) colony sizes (Fig. S6e–h), particularly on the north shore where the resulting deviance in model predictions was compensated by an overestimation of recolonisation rates (Fig. S7a), resulting in small differences in population surface (Fig. S7d). The model also tended to underestimate variance in the growth of large corals for all species (Fig. S6). Such differences were reasonable as demographic performances cannot be assumed to remain constant as the system moves away from the initial conditions during which coral performances were quantified. *Acropora* colonies were small recruits when we quantified coral performance in 2011–2013 (Fig. 2i–l), and differences in coral growth variances may result from regulatory mechanisms not represented in our relatively simple model, such as the effect of competition on species growth rates (e.g. Adler *et al.* 2010). Nevertheless, confronting model predictions with independent field data (the updated model did not use post-2013 demographic data) revealed no consistent biases, thus indicating that our updated models successfully captured the major regulatory mechanisms driving the first 5 years of reef recovery around Mo'orea.

### From recovery dynamics to community reassembly

We evaluated reef reassembly by comparing coral assemblages after 5 years of recovery (2015) with those observed prior to disturbance (2005), and used model elasticities to identify preponderant demographic processes acting at different stages of recovery. By 2015, the two reefs on the north shore had recovered in coral cover but the composition of the assemblages was different than in 2005 (Fig. S1). Elasticity analyses indicated that recovery of these reefs was initially driven by the high *Pocillopora* recruitment observed shortly after the disturbances in 2010–2013 (Fig. 2a,b), whereas colony growth appeared

most influential on the trajectory of these populations in 2013–2015 (Figs S9–S10). On the east and west coasts where recruitment was low (Fig. 2c,d), coral composition had returned to pre-disturbed states by 2015, whereas coral cover had not (Fig. S1). Unlike the other reefs, the east coast was not physically damaged by the cyclone, only overrun by COTS, thereby leaving many dead coral skeletons that have since decayed and broken apart (Adam *et al.* 2014). This process produced poor substrate quality that reduced the survival of coral recruits (Fig. 2g). Colony growth had a strong influence on recovery trajectories on this reef (Figs S9–S10), probably because the survival of small corals increased rapidly with colony size as the effect of substrate instability on mortality diminished (Lenihan *et al.* 2011). The west coast reef experiences throughout the year big waves that can break and dislodge large corals (Leichter *et al.* 2013), especially branching and tabular genera like *Pocillopora* and *Acropora* (Madin *et al.* 2014). Therefore, hydrodynamic disturbance may explain why these taxa suffered higher mortality with increasing colony size on the west coast (Fig. 2h), and why the influence of survival on the recovery trajectories increased through time (Figs S9–S10). In general, full recovery of habitat-forming corals around Mo'orea appears dependent upon further recolonisation by *Acropora* on the north shore, and the survival and continued growth of already established but small (~ 10 cm diameter) colonies of the three coral genera on all reefs (Fig. 4e–h).

#### Projections of future coral assemblages

IPM projections of coral assemblages for 2020 were generated by applying the demographic functions describing coral performance on the four reefs (Table S1) to the structure of assemblages observed in 2015 (Fig. 4e–h). Projections indicated that by 2020, barring major disturbance, reefs on the east and west shores will develop large (20–30 cm diameter) corals and assemblages that are relatively similar in composition to those observed in 2005 (Fig. 4k–l, Fig. S1). On the north shore, projections indicated that coral composition will not fully reassemble by 2020, and instead continue to support higher proportions of *Pocillopora* than in 2005 (Fig. 4i,j). Simulations predicted substantial recovery of *Acropora* on these reefs, driven mainly by positive density-dependent recruitment (Fig. S11a,b). However, our simulations tended to underestimate *Acropora* growth potential to large (> 10 cm diameter) sizes (Fig. 4i–l, Fig. S6e–h). If large *Acropora* colonies continue to redevelop on the north-shore, reefs should reassemble to their pre-disturbed states thereby also demonstrating resilience to the recent disturbances.

#### Demographic drivers of coral community dynamics

Our results reveal that the relative importance of recruitment, survival, and growth in coral trajectory varies substantially as a function of species life-history, local reef environment and stages of recovery, thus helping to resolve the ongoing debate about what ecological processes control the dynamics of open populations (Caley *et al.* 1996; Osenberg *et al.* 2002; Adjerdoud *et al.* 2017). In Mo'orea's recovering reef system, recruitment played a key role in early recolonisation by *Pocillopora* and

drove the return of *Acropora* at later stages of recovery, but had little influence on the trajectories of *Porites* populations. When recruitment was limited, coral growth was most influential on the recovery trajectories except where survival was particularly low (Fig. 2, Fig. S9–S10). In the present era of coral decline (Hughes *et al.* 2017), such fine-scale quantitative diagnosis of species demography is crucial for identifying suitable management actions that can influence the trajectory of coral communities. For example, when efforts should be dedicated to species reintroductions to compensate for a limiting recruitment, or to stress mitigation to improve post-recruitment growth or survival (Precht 2006; Anthony *et al.* 2015).

Coral communities in Mo'orea have not been affected by major disturbances since 2010, despite the occurrence of a global coral bleaching event in 2015–2017 (Hughes *et al.* 2017). Our results indicate that the reefs around the island follow different recovery trajectories yet can reassemble within 10 years to their pre-disturbed states in coral abundance, composition, and size, thus providing a unique example of outstanding island-scale ecosystem resilience. This finding is encouraging in the present context of global coral reef decline, and contrasts with the numerous instances of delayed coral community recovery and lack of reassembly (van Woesik *et al.* 2011; De'ath *et al.* 2012; Johns *et al.* 2014; Osborne *et al.* 2017; Riegl *et al.* 2017). We encourage the use of quantitative approaches, like the one we developed for Mo'orea, to help forecast coral community dynamics and identify demographic processes that limit population trajectories. This could particularly benefit management for resilience of species that are vulnerable to environmental change, such as structurally complex acroporids which are fundamental to reef ecosystem function but whose populations are declining in many regions (Berumen & Pratchett 2006; Alvarez-Filip *et al.* 2013; Osborne *et al.* 2017; Riegl *et al.* 2018).

#### Implications for community ecology and management

Our results imply that community dynamics can be predicted from population models that capture key regulatory mechanisms pertaining to demography in multi-species environments. In our study system, coral community recovery, in terms of abundance, composition, and size of the three major habitat-forming taxa, was captured in different reef environments by a relatively simple model that accounted for size-dependent variability in coral survival and growth rates, as well as a density-dependent regulation of larval recruitment. Modeling coral community dynamics not only enabled us to predict whether the recovering reefs are on paths to reassemble to their pre-disturbed states, but also to quantitatively evaluate how different demographic processes influenced the population trajectories in time and space. Furthermore, developing our model in an iterative manner, where predictions were confronted with empirical data to identify shortcomings, helped identify key processes that were initially overlooked, such as the capacity of massive corals to regenerate large populations from small patches of remnant colonies.

Our study expands seminal quantitative approaches to community dynamics in coral reefs (Tanner *et al.* 2009; Ortiz *et al.* 2014; Riegl *et al.* 2017) and other ecosystems (Pacala

*et al.* 1996; Purves *et al.* 2008; Adler *et al.* 2010) by developing an IPM framework that facilitates realistic representation of the demography of assemblages of species with contrasting life-histories and regulated by density-dependent recruitment. By yielding a method to advance quantitative understanding, prediction, and diagnosis of community dynamics, our empirical-modeling approach may assist managing for resilience of diverse communities, particularly for habitat-forming species whose spatial distributions and physical structures are crucial for the health and functions of ecosystems (Pacala *et al.* 1996; Hastings *et al.* 2007; Nash *et al.* 2014; Taubert *et al.* 2015).

## ACKNOWLEDGEMENTS

We thank B. Billups, H. Ake, E. Winslow, C. Applewhite, D. Cook and K. Seydel for help in the field and with data entry, and T. You Sing, J. You Sing and other University of California Berkeley's Gump Research Station staff for logistical assistance. We also thank G. Gastil-Buhl for data management as well as P. Edmunds and anonymous reviewers for improvements on the manuscript. The study was supported by NSF through the Mo'orea Coral Reef LTER (four awards including OCE1637396), University of California Santa Barbara's Sustainable Aquaculture Research Center, and the Gordon and Betty Moore Foundation. MK benefited from a grant from the Walter-Zellidja Foundation.

## AUTHORSHIP

MK and HSL designed the project. MK, HSL, AJB, SJH and RJS collected the data. MK performed the data analysis and developed the model with inputs from BEK. MK, HSL and BEK wrote the manuscript with contributions from all authors.

## DATA ACCESSIBILITY STATEMENT

Datasets supporting the results of this study are available from the MCR LTER website: multi-species coral population dynamics data (Lenihan & Kayal 2015, available at: <https://doi.org/10.6073/pasta/98855475790bfb012066f9dc802ecc31>), coral recruit density data (Schmitt *et al.* 2017, available at: <https://doi.org/10.6073/pasta/18178cf49b8e939b39e9ae5901b2b249>), live coral cover data (Edmunds 2015, available at: <https://doi.org/10.6073/pasta/1f05f1f52a2759dc096da9c24e88b1e8>). Computer code developed for this study is available from the GitHub repository: R code for constructing a multi-species, open-population integral projection model of coral assemblage dynamics (Kayal 2017, available at: <https://doi.org/10.5281/zenodo.573772>).

## REFERENCES

Adam, T.C., Brooks, A.J., Holbrook, S.J., Schmitt, R.J., Washburn, L. & Bernardi, G. (2014). How will coral reef fish communities respond to climate-driven disturbances? Insight from landscape-scale perturbations. *Oecologia*, 176, 285–296.

Adjeroud, M., Kayal, M. & Penin, L. (2017). Importance of recruitment processes in the dynamics and resilience of coral reef assemblages. In: *Marine Animal Forests* (eds Rossi, S., Bramanti, L., Gori, A. & Saco del Valle, C.O.). Springer, Switzerland, pp. 549–569.

Adjeroud, M., Kayal, M., Iborra-Cantonnet, C., Vercelloni, J., Bosserelle, P., Liao, V. *et al.* (2018). Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Sci. Rep.*, 8, 9680.

Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecol. Lett.*, 13, 1019–1029.

Alvarez-Filip, L., Carricart-Ganivet, J.P., Horta-Puga, G. & Iglesias-Prieto, R. (2013). Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Sci. Rep.*, 3, 3486.

Anthony, K., Marshall, P.A., Abdulla, A., Beeden, R., Bergh, C., Black, R. *et al.* (2015). Operationalizing resilience for adaptive coral reef management under global environmental change. *Global Change Biol.*, 21, 48–61.

Berumen, M.L. & Pratchett, M.S. (2006). Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs*, 25, 647–653.

Bozec, Y.M., Yakob, L., Bejarano, S. & Mumby, P.J. (2013). Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. *Oikos*, 122, 428–440.

Bramanti, L. & Edmunds, P.J. (2016). Density-associated recruitment mediates coral population dynamics on a coral reef. *Coral Reefs*, 35, 543–553.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. & Menge, B.A. (1996). Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Evol. Syst.*, 1, 477–500.

Cinner, J.E., McClanahan, T.R., Graham, N.A.J., Daw, T.M., Maina, J., Stead, S.M. *et al.* (2012). Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Glob. Environ. Change*, 22, 12–20.

Coulson, T. (2012). Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos*, 121, 1337–1350.

Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., Côté, I.M. & Bellwood, D. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.*, 15, 1378–1386.

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S. & Wilson, S.K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, 36, 561–575.

De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl Acad. Sci.*, 109, 17995–17999.

Done, T.J., Dayton, P.K., Dayton, A.E. & Steger, R. (1991). Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. *Coral Reefs*, 9, 183–192.

Edmunds, P. (2015). MCR LTER: coral reef: long-term population and community dynamics: corals, ongoing since 2005. Environmental Data Initiative. Available at: <https://doi.org/10.6073/pasta/1f05f1f52a2759dc096da9c24e88b1e8>.

Ellner, S.P., Childs, D.Z. & Rees, M. (2016). *Data-Driven Modeling of Structured Populations: A Practical Guide to the Integral Projection Model*. Springer, Switzerland.

Fabricius, K.E., De'ath, G., Noonan, S. & Uthicke, S. (2014). Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proc. R. Soc. B*, 281, 20132479.

Gilbert, P. & Varadhan, R. (2016). Accurate numerical derivatives. CRAN. Available at: <https://optimizer.r-forge.r-project.org>.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science*, 340, 69–71.

Godfray, H.C.J. & May, R.M. (2014). Open questions: are the dynamics of ecological communities predictable? *BMC Biol.*, 12, 22.

Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S. *et al.* (2008). Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS ONE*, 3, e3039.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G. *et al.* (2007). Ecosystem engineering in space and time. *Ecol. Lett.*, 10, 153–164.

- Holbrook, S.J., Schmitt, R.J., Messmer, V., Brooks, A.J., Srinivasan, M., Munday, P.L. *et al.* (2015). Reef fishes in biodiversity hotspots are at greatest risk from loss of coral species. *PLoS ONE*, 10, e0124054.
- Holbrook, S.J., Adam, T.C., Edmunds, P.J., Schmitt, R.J., Carpenter, R.C., Brooks, A.J. *et al.* (2018). Recruitment drives spatial variation in recovery rates of resilient coral reefs. *Sci. Rep.*, 8, 7338.
- Hughes, T.P. (1984). Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.*, 123, 778–795.
- Hughes, T.P. & Jackson, J.B.C. (1985). Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.*, 55, 141–166.
- Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschanivskyj, N.A., Pratchett, M.S., Tanner, J.E. *et al.* (2000). Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology*, 81, 2241–2249.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B. *et al.* (2017). Coral reefs in the Anthropocene. *Nature*, 546, 82–90.
- Johns, K.A., Osborne, K.O. & Logan, M. (2014). Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. *Coral Reefs*, 33, 553–563.
- Kayal, M. (2017). R code for constructing a multi-species, open-population integral projection model of coral assemblage dynamics. GitHub repository. Available at: <https://doi.org/10.5281/zenodo.573772>.
- Kayal, M., Lenihan, H.S., Pau, C., Penin, L. & Adjeroud, M. (2011). Associational refuges among corals mediate impacts of a crown-of-thorns starfish *Acanthaster planci* outbreak. *Coral Reefs*, 30, 827–837.
- Kayal, M., Vercelloni, J., Lison de Loma, T., Bosserelle, P., Chancerelle, Y., Geoffroy, S. *et al.* (2012). Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS ONE*, 7, e47363.
- Kayal, M., Vercelloni, J., Wand, M.P. & Adjeroud, M. (2015). Searching for the best bet in life-strategy: a quantitative approach to individual performance and population dynamics in reef-building corals. *Ecol. Complex.*, 23, 73–84.
- Lamy, T., Galzin, R., Kulbicki, M., Lison de Loma, T. & Claudet, J. (2016). Three decades of recurrent declines and recoveries in corals belie ongoing change in fish assemblages. *Coral Reefs*, 35, 293–302.
- Leichter, J.J., Alldredge, A.L., Bernardi, G., Brooks, A.J., Carlson, C.A., Carpenter, R.C. *et al.* (2013). Biological and physical interactions on a tropical island coral reef: transport and retention processes on Moorea, French Polynesia. *Oceanography*, 26, 52–63.
- Lenihan, H.S. & Kayal, M. (2015). MCR LTER: Coral Reefs: long-term coral population and community dynamics: annual island wide coral demography survey 2011 to present. Environmental Data Initiative. Available at: <https://doi.org/10.6073/pasta/98855475790bfb012066f9dc802ecc31>.
- Lenihan, H.S., Adjeroud, M., Kotchen, M.J., Hensch, J.L. & Nakamura, T. (2008). Reef structure regulates small-scale spatial variation in coral bleaching. *Mar. Ecol. Prog. Ser.*, 370, 127–141.
- Lenihan, H.S., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. (2011). Influence of corallivory, competition, and habitat structure on coral community shifts. *Ecology*, 92, 1959–1971.
- Madin, J.S., Baird, A.H., Dornelas, M. & Connolly, S.R. (2014). Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecol. Lett.*, 17, 1008–1015.
- Mumby, P.J., Hastings, A. & Edwards, H.J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450, 98–101.
- Nash, K.L., Allen, C.R., Angeler, D.G., Barichievy, C., Eason, T., Garmestani, A.S. *et al.* (2014). Discontinuities, cross-scale patterns, and the organization of ecosystems. *Ecology*, 95, 654–667.
- Ortiz, J.C., Bozec, Y.M., Wolff, N.H., Doropoulos, C. & Mumby, P.J. (2014). Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. *Nat. Clim. Change*, 4, 1090–1094.
- Osborne, K., Thompson, A.A., Cheal, A.J., Emslie, M.J., Johns, K.A., Jonker, M.J. *et al.* (2017). Delayed coral recovery in a warming ocean. *Global Change Biol.*, 23, 3869–3881.
- Osenberg, C.W., St Mary, C.M., Schmitt, R.J., Holbrook, S.J., Chesson, P. & Byrne, B. (2002). Rethinking ecological inference: density dependence in reef fishes. *Ecol. Lett.*, 5, 715–721.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996). Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.*, 66, 1–43.
- Penin, L., Michonneau, F., Baird, A.H., Connolly, S.R., Pratchett, M.S., Kayal, M. *et al.* (2010). Early post-settlement mortality and the structure of coral assemblages. *Mar. Ecol. Prog. Ser.*, 408, 55–64.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2016). Linear and nonlinear mixed effects models. CRAN. Available at: <https://cran.r-project.org>.
- Precht, W.F. (2006). *Coral Reef Restoration Handbook*. CRC Press, Boca Raton, FL.
- Purves, D.W., Lichstein, J.W., Strigul, N. & Pacala, S.W. (2008). Predicting and understanding forest dynamics using a simple tractable model. *Proc. Natl Acad. Sci.*, 105, 17018–17022.
- Riegl, B., Cavalcante, G., Bauman, A., Feary, D.A., Steiner, S. & Purkis, S. (2017). Demographic mechanisms of reef coral species winnowing from communities under increased environmental stress. *Front. Mar. Sci.*, 4, 344.
- Riegl, B., Johnston, M., Purkis, S., Howells, E., Burt, J., Steiner, S.C.C. *et al.* (2018). Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Global Change Biol.*, 24, 2447–2462.
- Rogers, A., Blanchard, J.L. & Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr. Biol.*, 24, 1000–1005.
- Ruppert, D., Wand, M.P. & Carroll, R.J. (2003). *Semiparametric Regression*. Cambridge University Press, Cambridge, UK.
- Schmitt, R.J. & Holbrook, S.J. (2007). The scale and cause of spatial heterogeneity in strength of temporal density dependence. *Ecology*, 88, 1241–1249.
- Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Adam, T. & Lenihan, H.S. (2017). MCR LTER: Coral Reefs: coral recruitment to 25 m<sup>2</sup> plots on the forereef surrounding Moorea, French Polynesia, 2011–2015. Environmental Data Initiative. Available at: <https://doi.org/10.6073/pasta/18178cf49b8e939b39e9ae5901b2b249>.
- Tanner, J.E., Hughes, T.P. & Connell, J.H. (2009). Community-level density dependence: an example from a shallow coral assemblage. *Ecology*, 90, 506–516.
- Taubert, F., Jahn, M.W., Dobner, H.J., Wiegand, T. & Huth, A. (2015). The structure of tropical forests and sphere packings. *Proc. Natl Acad. Sci.*, 112, 15125–15129.
- Tomascik, T., van Woesik, R. & Mah, A.J. (1996). Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. *Coral Reefs*, 15, 169–175.
- van Woesik, R., Sakai, K., Ganase, A. & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.*, 434, 67–76.
- Yau, A.J., Lenihan, H.S. & Kendall, B.E. (2014). Fishery management priorities vary with self-recruitment in sedentary marine populations. *Ecol. Appl.*, 24, 1490–1504.

## SUPPORTING INFORMATION

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

Editor, Tim Coulson

Manuscript received 10 April 2018

First decision made 15 May 2018

Manuscript accepted 29 June 2018