Ecology, 96(7), 2015, pp. 1802–1811

Stochastic dynamics of a warmer Great Barrier Reef

Jennifer K. Cooper,[1,3] Matthew Spencer,[1,4] and John F. Bruno[2]

[1] *School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP United Kingdom*
[2] *Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599-3300 USA*

Abstract. Pressure on natural communities from human activities continues to increase. Even unique ecosystems like the Great Barrier Reef (GBR), that until recently were considered near-pristine and well-protected, are showing signs of rapid degradation. We collated recent (1996–2006) spatiotemporal relationships between benthic community composition on the GBR and environmental variables (ocean temperature and local threats resulting from human activity). We built multivariate models of the effects of these variables on short-term dynamics, and developed an analytical approach to study their long-term consequences. We used this approach to study the effects of ocean warming under different levels of local threat. Observed short-term changes in benthic community structure (e.g., declining coral cover) were associated with ocean temperature (warming) and local threats. Our model projected that, in the long term, coral cover of less than 10% was not implausible. With increasing temperature and/or local threats, corals were initially replaced by sponges, gorgonians, and other taxa, with an eventual moderately high probability of domination (>50%) by macroalgae when temperature increase was greatest (e.g., 3.5°C of warming). Our approach to modeling community dynamics, based on multivariate statistical models, enabled us to project how environmental change (and thus local and international policy decisions) will influence the future state of coral reefs. The same approach could be applied to other systems for which time series of ecological and environmental variables are available.

Key words: climate change; communities; compositional data; coral reef; dynamics; Great Barrier Reef; human impacts; local threat; long-term behavior; ocean temperature; reef state; stochastic model.

INTRODUCTION

Natural communities are under threat from human perturbation and the effects of climate change (Halpern et al. 2008, Butchart et al. 2010). Despite clear evidence of degradation in many habitat types (Duffy 2003, Worm et al. 2006), the size and direction of long-term impacts remain uncertain, because few ecological monitoring programs are older than a few decades. Coral-reef communities are one of the clearest examples of a biological system greatly altered by human activities, including overfishing, increased nutrient loading, and anthropogenic warming (Hughes et al. 2003). Globally, coral cover has declined to 10–20%, and corals have been replaced to some degree by other invertebrates such as gorgonian soft corals and sponges, by crustose coralline algae, algal microturfs, and bare carbonate substrate (collectively termed CTB; Aronson and Precht 2000), and by fleshy macroalgae (Aronson et al. 2002, Bruno and Selig 2007, Bruno et al. 2009, Schutte et al. 2010). This broad decline of coral cover has led to a general flattening or simplification of reef habitats with direct consequences for fishes and other reef inhabitants (Alvarez-Filip et al. 2009).

Ocean warming has been a primary cause of mass coral mortality and coral cover decline over the last two to three decades (Hughes et al. 2003, Hoegh-Guldberg and Bruno 2010, Selig et al. 2012). Temperatures ~1°C greater than the local seasonal maximum can disrupt the relationship between corals and their symbiotic zooxanthellae, leading to "coral bleaching" (Baker et al. 2008). In some circumstances, bleaching can cause partial or complete mortality of coral colonies. Mortality and mass bleaching have been observed across the Pacific and Indian Oceans, and the Caribbean (Glynn 1991, Baker et al. 2008, Eakin et al. 2010). Anomalously high water temperature is also associated with coral disease outbreaks (Bruno et al. 2007, Harvell et al. 2009, Rogers and Muller 2012), possibly due to an increase in susceptibility of the coral host caused by thermal stress and bleaching (Mydlarz et al. 2009).

Although the proximate causes of coral population declines (e.g., disease, bleaching, and pollution) have been identified, relatively little progress has been made in deciphering the relative importance of different drivers. Thus, our understanding of how these drivers affect entire reef communities (not just coral cover) is incomplete. Moreover, little progress has been made on using the large empirical record of reef degradation to develop analytical models of future reef composition. By

---

Manuscript received 20 January 2014; revised 4 August 2014; accepted 15 October 2014; final version received 15 November 2014. Corresponding Editor (ad hoc): R. van Woesik.

[3] Present address: ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811 Australia.

[4] Corresponding author. E-mail: m.spencer@liverpool.ac.uk

linking changes in community structure with changes in environmental conditions, we should be able to identify key environmental drivers. These data can also be used to move beyond the usual univariate studies of reef health (e.g., De'ath et al. 2012) into multivariate studies of community dynamics.

The purpose of this study was to project the composition of future coral reef benthic communities under current environmental conditions, and under environmental change scenarios. We used data from the Great Barrier Reef to build multivariate models for the effects of ocean temperature and "local threat level" (an index of local human impacts developed for the Reefs at Risk Revisited report, Burke et al. 2011) on short-term changes in reef composition. We then used these simple empirical models and a novel analytical approach to project the long-term distributions of reef composition under both current environmental conditions and increased ocean temperature, and local threat level. We also estimated the probability of undesirable reef compositions, in which coral cover is reduced to $\leq 10\%$ or when macroalgae dominates $>50\%$ of the benthos.

Methods

Data

Data from Australia's Great Barrier Reef (GBR) were obtained from quantitative reef surveys. Video transect surveys of 46 reefs (for locations, see Appendix A: Fig. A1) were performed over at least two consecutive years between 1996 and 2006 as part of the Australian Institute of Marine Science long-term monitoring program. The methods are described in Abdo et al. (2004) and summarized in Appendix A: A.1. Reef data consisted of proportional benthic cover of three biological categories: coral, macroalgae, and other (which includes CTB, sponges, gorgonians, and other invertebrates). The data we use were aggregated to reef level, and are a subset of the data in Bruno et al. (2009) and Żychaluk et al. (2012). These data formed multivariate time series of reef composition in consecutive years (62 series, median length 7 years, length range 2–11 years). We analyzed the combined data as 364 pairs of observations in consecutive years.

For each reef, we extracted data on sea surface temperature (SST) climatology (the long-term value for a 4×4 km square, as defined in Selig et al. 2010), annual mean anomalies (departure from long-term value for this 4×4 km square), and local threat level as described in Appendix A: A.1. We used one-year lags for both climatology and anomaly, and centered and scaled them to mean zero, standard deviation 1. The Reefs at Risk Revisited local threat level index (Burke et al. 2011) is a categorical variable (with four levels: 1, low; 2, medium; 3, high; and 4, very high) that summarizes information on coastal development, marine-based pollution and damage, watershed-based pollution, and overfishing, most of which was resolved to the 1-km or 3-km scale (Burke et al. 2011). It is important to note that we have little information about the effects of high and very high local threat, because we had only one reef (with five and nine pairs of observations in consecutive years) for each of these two categories. We also considered distance from the coast as another potential proxy for human activity, but this was strongly related to local threat index (Appendix A: Fig. A2), and models using distance from the coast always performed worse than corresponding models using local threat index (Appendix A: Table A1).

Short-term change in reef composition

We represent the reef compositions on a single reef in two consecutive years by the column vectors $\mathbf{y}(t)$ and $\mathbf{y}(t+1)$. Each such vector has three components $y_1(t)$, $y_2(t)$, $y_3(t)$, representing the proportions of coral, algae, and other at time t, and summing to 1. We described short-term changes in composition (from one year to the next) using perturbing vectors (Appendix A: A.2), which are themselves compositions. If there is no change in composition between two years, the corresponding perturbing vector is

$$\left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right).$$

For each element of the perturbing vector, a value greater than 1/3 indicates an increase in that component, and a value less than 1/3 indicates a decrease.

Model assumptions

We assume that the perturbing vectors on each reef are independent of those on other reefs, that future perturbing vectors are conditionally independent of past reef composition given current reef composition, that the process generating these perturbing vectors is homogeneous over time (conditional on the values of environmental variables), and that measurement error is small relative to the short-term variability in the true composition of a reef. We argued in Żychaluk et al. (2012: supporting information, section S1.2), that similar assumptions will often be approximately true, and that models based on them are useful descriptions of the regional dynamics of coral reefs.

Models for short-term change

For a single species, a linear model for changes in log abundance between successive time points is the natural starting point for an investigation of the factors affecting population dynamics, because exponential growth results in a straight-line relationship between log abundance and time. In the same way, a linear model for isometric log-ratio (ilr) transformed perturbing vectors (Appendix A: A.3) is a natural starting point, because exponential growth of all components results in a straight-line trajectory in ilr coordinates (Egozcue et al. 2003). We do not expect that all components will grow exponentially, so we include the effects of current reef composition in our model, which takes the form

$$\mathrm{ilr}\,\mathbf{p}(t) = \mathbf{c} + \mathbf{A}\mathbf{x}(t) + \boldsymbol{\beta}_1 z_1(t) + \boldsymbol{\varepsilon}(t). \tag{1}$$

Each term in Eq. 1 is a column vector with two elements. The response variable $\mathrm{ilr}\,\mathbf{p}(t)$ is the transformed short-term change in reef composition. The first term on the right of Eq. 1 ($\mathbf{c}$) is a constant for any given reef and environmental change scenario, which depends on climatology and local threat. The second term ($\mathbf{A}\mathbf{x}(t)$) is the effects of current transformed reef composition. The third term is the effect of SST anomalies. The fourth term ($\boldsymbol{\varepsilon}(t)$) describes the stochastic effects of processes such as storms, diseases, and crown of thorns starfish, for which we do not have data (and for which we assume mean vector zero and constant covariance matrix). More detail on Eq. 1 is given in Appendix A: A.4. All the parameters in Eq. 1 can be back-transformed to compositions and represented on ternary plots, in the same way as the perturbing vectors. We fitted and checked this model, tested hypotheses, and visualized parameters as described in Appendix A: A.5–A.7.

Our model is the multivariate equivalent of the widely used stochastic Gompertz model. The univariate version is a plausible description of the density-dependent dynamics in many single-species time series (e.g., Dennis et al. 2006), and the multivariate version is likewise a good way to approximate the dynamics of a multispecies community (Ives et al. 2003, Hampton et al. 2013). Independently, Gross and Edmunds (2015) arrived at a very similar model for reef dynamics.

Long-term behavior and effects of changes in sea surface temperature

Under the simplifying assumption that annual mean SST anomaly is a sequence of identically normally distributed random variables, independent of past SST anomalies and of the error term $\boldsymbol{\varepsilon}(t)$, the model in Eq. 1 may converge to a stationary distribution, which can be found analytically (Appendix A: A.8). This stationary distribution tells us about the long-term behavior of the GBR under current conditions. We then used two approaches to explore the effects of changes in the long-term mean u_2 of climatology on long-term behavior: sensitivity to infinitesimal changes and calculation of stationary distributions under a range of long-term means. We think that changing climatology rather than changing anomalies is the right way to model the effects of long-term change in SST, because the climatology parameter describes the long-term mean temperature at a site. However, we comment in the *Discussion* on the consequences of this assumption. We assumed that the variance of SST anomalies did not change, which greatly simplifies the sensitivity analysis. The evidence for changes in the temporal variability of recent and projected temperatures remains ambivalent (Huntingford et al. 2013), so it would be difficult to justify any other treatment.

It is possible to calculate the sensitivity of the stationary density at any point to changes in climatology (Appendix A: A.9). The contour of zero sensitivity is of particular interest because it separates reef compositions projected to become less likely under increased climatology (those with negative sensitivity) from reef compositions projected to become more likely under increased climatology (those with positive sensitivity). A similar approach can be used to express the long-term effects of local threat level in terms of equivalent increases in climatology (Appendix A: A.9). Although local threat effects and climatology effects do not necessarily have the same direction, the component of a local threat effect that acts in the same direction as the climatology effect tells us how much the difference between two local threat levels is worth in terms of climatology.

We also examined the effects of changes in climatology on the stationary distribution of reef composition using numerical methods. We calculated stationary distributions for a range of climatologies between the current regional minimum (rounded down to the nearest degree) and a value 3.5°C warmer than the current regional mean. These climatologies cover a plausible range of future ocean temperatures. Increases of 0.83° to 3.91°C in global mean surface temperature by 2100 compared to 2000 are projected under the four Representative Concentration Pathways (Meehl et al. 2012). Under a range of climate models, sites in the GBR may experience 0.76° to 1.01°C increase in maximum summer SST per °C increase in global mean temperature (Wooldridge et al. 2012). Thus, an increase of several °C in climatology seems plausible, despite the large uncertainty. We caution that examining plausible future climatology involves extrapolating beyond the range of currently observed climatology. In contrast, the sensitivity calculation outlined in the previous paragraph looks at the effects of small increases in climatology, and does not require extrapolation.

Probability of undesirable compositions

To summarize the changes in stationary distributions across a range of climatologies, we report the probabilities of low coral cover (the stationary probability that coral cover is less than or equal to 10%) and high algal cover (the stationary probability that algal cover is greater than 50%). The 10% low coral cover threshold is believed to be the minimum cover required for net reef accretion (Kennedy et al. 2013), whereas the 50% high algal cover threshold is a conventional definition of macroalgal dominance (Bruno et al. 2009). These statistics can be interpreted in two ways: as the long-run proportion of time we expect the composition of an individual reef to satisfy the specified condition; and as the proportion of randomly chosen reefs we expect to satisfy the specified condition, at a given point in time.

RESULTS

Short-term change in reef composition

The most obvious pattern in the raw data (Fig. 1A) was that most reefs had low algal cover most of the time, with occasional, but generally short-lived, excursions toward higher algal cover. There was a wide range of coral cover. Perturbing vectors, which represent short-term changes in composition (Fig. 1B), were clustered around the coral–other 0.5-isoproportion line, covering its whole length. Thus, large increases and decreases in algae occurred, but in general the ratio of coral to other changed little in the short term. Large decreases in macroalgal cover tended to be associated with unusually cold SST anomalies (Fig. 1B, blue symbols predominate in left half of plot). It was not easy to discern a difference in short-term changes between local threat categories (Fig. 1B, different symbol shapes).

Fitted model

Current composition, SST anomaly, and climatology, and local threat had significant effects on transformed perturbing vectors (Appendix A: Tables A2 and A3). If the ratio of algae to coral was high, the proportion of algae tended to decrease the following year, with little effect on the ratio of coral to other (Fig. 1C, light blue dot (2)). Conversely, if the ratio of other to the geometric mean of coral and algae was high, the proportion of other tended to decrease the following year, and the ratio of algae to coral tended to increase (Fig. 1C, dark blue dot (3)). A one-standard-deviation increase in SST anomaly tended to increase the proportion of algae, with little effect on the relative proportions of coral and other (Fig. 1C, green dot (4)). A one-standard-deviation increase in climatology had an effect in the same direction as the SST anomaly effect, but with a slightly smaller magnitude (Fig. 1C, pink dot

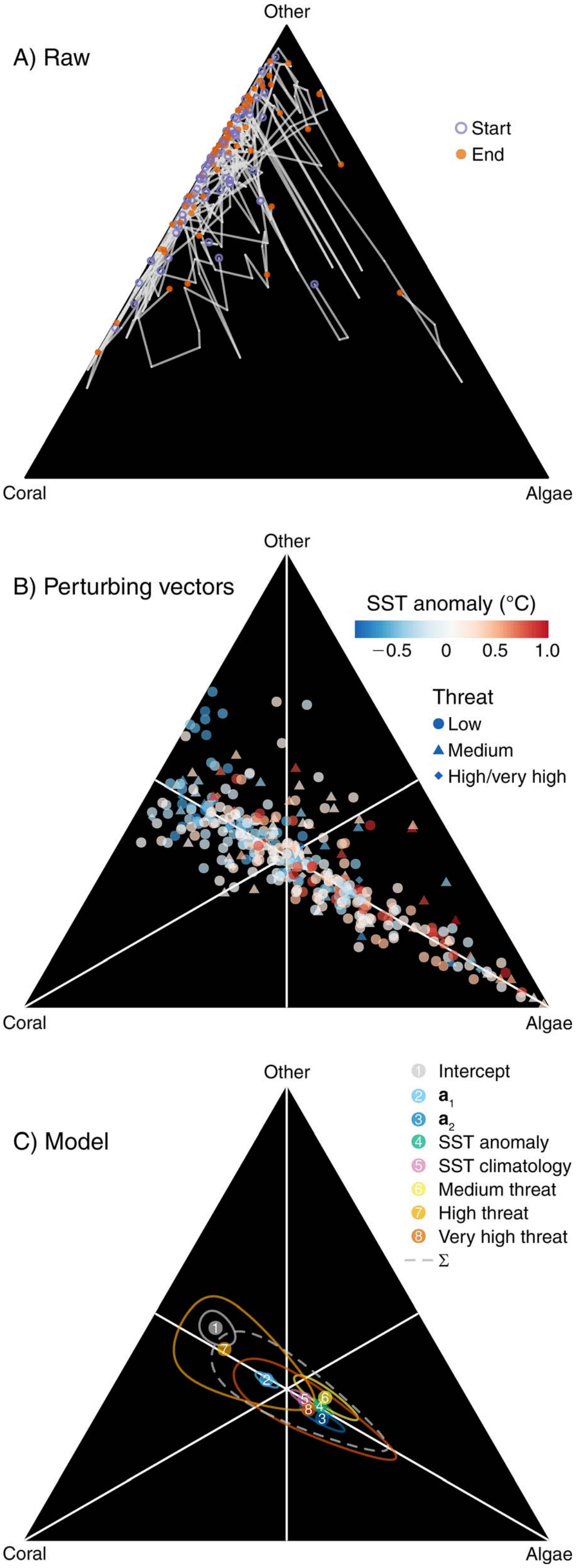

FIG. 1. (A) Time series of Great Barrier Reef (GBR) composition at 46 locations between 1996 and 2006. Each series of observations on the same reef in consecutive years is represented by a gray line, starting at an open blue circle and ending at a solid orange circle. (B) Short-term changes in reef composition for the data in (A), colored by annual mean sea surface temperature (SST) anomaly with a one-year lag. Circles indicate low local threat. Triangles indicate medium local threat. Diamonds indicate high and very high local threat. White lines are 0.5 isoproportion lines, along which two of the components of the composition have no change in relative proportions. For example, points along the line from the algae vertex to the point bisecting the coral–other edge have no change in the relative proportions of coral and other. (C) Parameters from Eq. 1 in a model for the data in (B). Each parameter is represented by its contribution to short-term change, with an approximate 95% confidence ellipse. The intersection of the white lines corresponds to no effect. Gray (1), intercept. Light blue (2) and dark blue (3), $\mathbf{a}_1$ and $\mathbf{a}_2$ columns of the matrix $\mathbf{A}$, which describes effects of reef composition. Green (4), effect of centered and scaled SST anomaly. Pink (5), effect of centered and scaled SST climatology. Yellow (6), orange (7), red (8), effects of medium, high, and very high relative to low local threat level, respectively. Gray dashed line, shape of the covariance matrix $\mathbf{\Sigma}$, represented by an ellipse at unit Mahalanobis distance around the no-effect point.

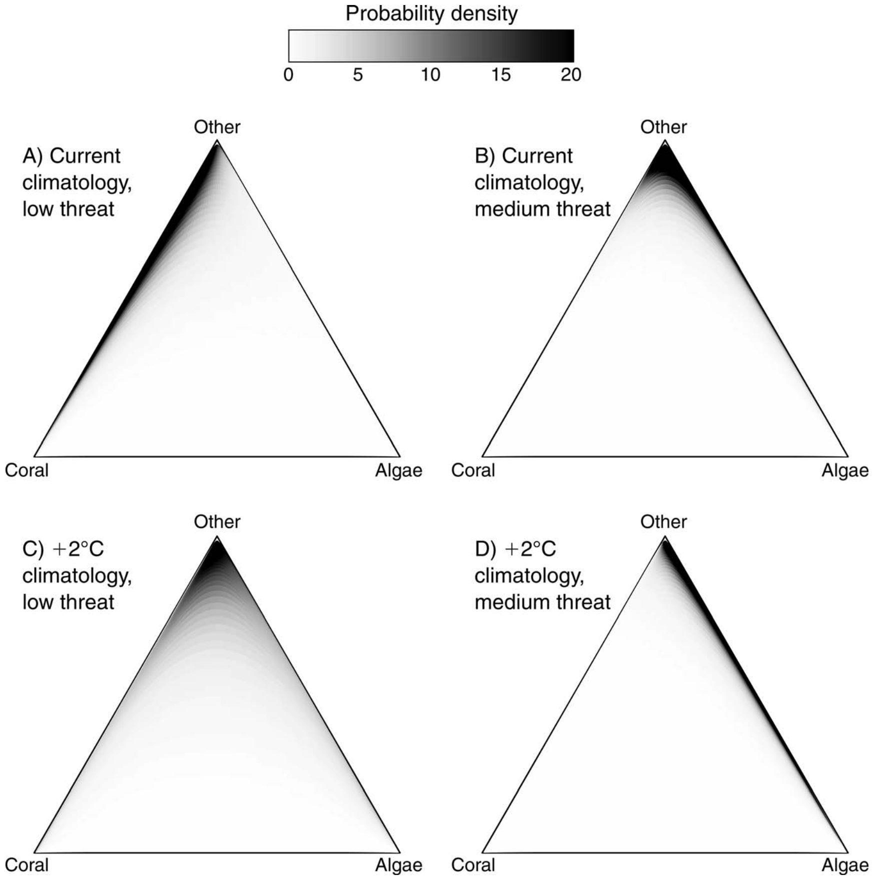

FIG. 2. Stationary distributions for the GBR at current climatology (A, low local threat; B, medium local threat), and with a 2°C increase in climatology (C, low local threat; D, medium local threat). Darker colors are more-likely compositions.

(5)). Post-hoc tests (Appendix A: Table A3) showed that only the medium local threat level was significantly different from the low local threat level. Relative to low local threat, reefs in the medium local threat category tended to have short-term changes that decreased the ratios of coral to both algae and other (Fig. 1C, yellow dot (6)). In subsequent results, we therefore looked separately at the low and medium local threat levels. The lack of evidence for effects of the high and very high local threat levels (Fig. 1C, orange (7) and red (8) dots, respectively) may be due to the small number of observations in these categories (five and nine pairs, respectively, and in each case from a single reef). Thus, although the high threat category appears to be associated with decreases rather than increases in algal cover (Fig. 1C, orange dot (7)), the confidence ellipse for this effect overlaps both the no-effect point, and the confidence ellipses for the effects of medium and very high threat.

No major departures from the model assumptions were apparent. We checked by simulation that our parameter estimates were qualitatively robust to plausible levels of observation error (Appendix A: A.6, Fig. A3). However, observation error may lead to underestimation of the effects of increased climatology (Appendix A: Fig. A4). Removing 30 out of 364 pairs of observations that were identified as outliers (Appendix A: A.7, Fig. A5) did not substantially affect parameter estimates (Appendix A: A.7, Fig. A6). It was noticeable that in observations with large increases in algae, the model under-predicted these increases (Appendix A: A.7, Fig. A7B). Although this involves relatively few observations, it may be biologically important. There were no strong patterns in residuals plotted against explanatory variables (Appendix A: Fig. A8), or time (Appendix A: Fig. A9), and residuals were not strongly spatially autocorrelated (Appendix A: Fig. A10).

Long-term behavior under current environmental conditions

There was strong evidence for the existence of a stationary distribution (Appendix A: A.10). Under current climatology, this distribution was unimodal for both low (Fig. 2A) and medium (Fig. 2B) local threat levels. The level of uncertainty in the stationary distributions was fairly high, especially for compositions with high stationary density (Appendix A: Fig. A11), but the stationary distributions of individual bootstrap replicates all had similar shapes.

In the long term, under current climatology and low local threat level, likely reef compositions had high cover of other, moderate coral cover, and low algal cover (Fig. 2A). For medium local threat level (Fig. 2B), this distribution shifted toward compositions with lower coral cover and higher other and algal cover.

Effects of changes in sea surface temperature and local threat level

The sensitivity of the stationary density to small changes in climatology provides an analytical estimate of likely effects of long-term increases in sea surface temperature. At low local threat, the zero contour representing no effect (Fig. 3A, black line) roughly divided compositions with low algal cover, which became less likely (blue), from compositions with high algal cover, which became more likely (red). The largest increases in stationary density (reddest) were for compositions with low coral and algal cover and high cover of other. For medium local threat level (Fig. 3B), the zero contour moved toward the right, so that compositions with low coral cover became more likely, and compositions with high coral cover less likely. The set of compositions with the highest increases in stationary density (reddest) was moved toward somewhat higher algal cover and lower coral cover than in the low local threat level, but the relative cover by other remained the largest component in this scenario. For both local threat levels, the uncertainty associated with sensitivity was substantial (Appendix A: Fig. A12). The long-term effect of the difference between medium and low local threat levels was equivalent to the effect of 2.8°C increase in climatology, but with high uncertainty (95% confidence interval [1.1°, 19.4°C] increase). Numerical results confirmed this pattern. With a 2°C increase in climatology, the stationary distribution under low threat level (Fig. 2C) shifted away from high coral cover, and toward high other and somewhat higher algal cover, compared with current conditions (and became more similar to the current distribution under medium local threat). At medium local threat level, a 2°C increase in climatology caused a shift away from other in the direction of higher algal cover (Fig. 2D).

Animations (available online) show more information about the relationship between the stationary distribution of reef composition and climatology. For low local threat level (Appendix A: A11), as climatology increased, coral cover declined, leading to a state with both low coral cover and low algal cover at around 1.5°C increase. At higher climatology, coral cover remained low and algal cover increased. At around 3.25°C increase, the stationary distribution was bimodal, with high density associated with low coral cover and either low algae and high other, or high algae and low other. This bimodality arises because the stationary distribution has a large enough spread that, for high climatology, the stationary mean is positioned so that large amounts of density get squashed into both the other and algae vertices. Thus, alternative stable states may be possible under some future environmental conditions. For medium local threat level (Appendix A12), coral cover was low for current climatology, and most of the probability was associated with high cover of other. The distribution moved toward increased algal cover with increases in climatology, but the stationary distribution did not appear bimodal.

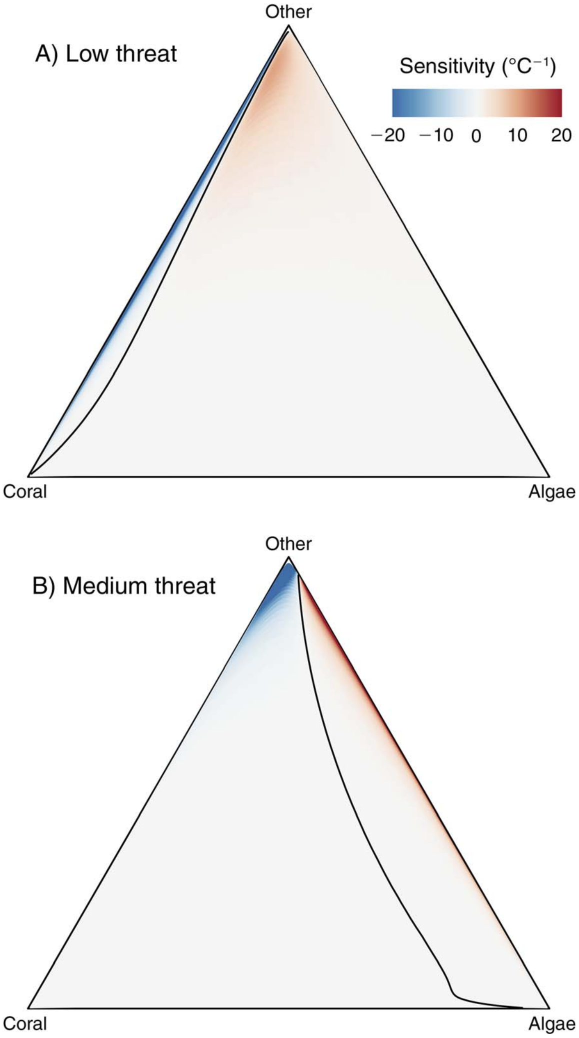

FIG. 3. Sensitivity of stationary density for the GBR to climatology, evaluated at current climatology and either (A) low or (B) medium local threat. Blue, compositions that would become less likely under small increases in climatology. Red, compositions that would become more likely under small increases in climatology. Black line, compositions that would become neither more nor less likely under small increases in climatology.

Probability of undesirable compositions

The probability of low coral cover (Fig. 4A and B) and high algal cover (Fig. 4C and D) increased with

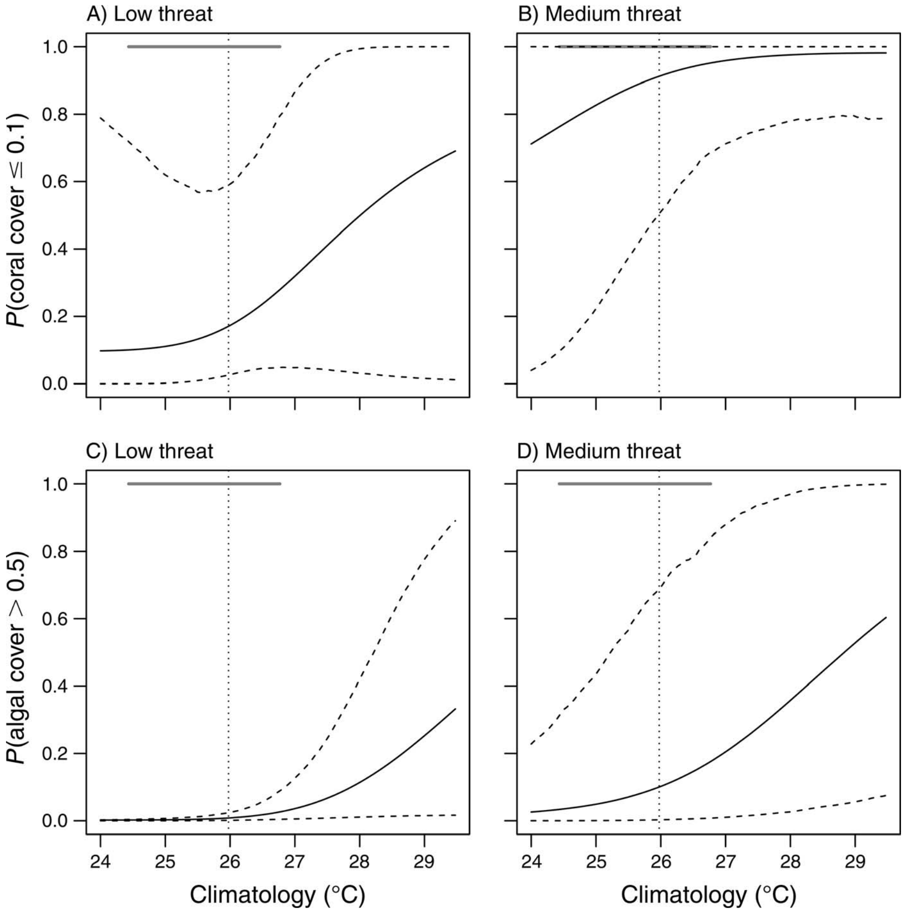

FIG. 4. Probability of low coral cover (A and B, less than or equal to 10%) and high algal cover (C and D, more than 50%) in the GBR over a range of climatology from the current minimum (rounded down to the nearest degree) to 3.5°C warmer than the current mean. Solid black lines, bootstrap mean probability. Dashed lines, 95% bootstrap confidence interval. Vertical dotted line, current mean climatology. Horizontal gray bar, observed range of climatology.

climatology. However, the probability of low coral cover was greater than the probability of high algal cover at any given climatology (this must be partly because the current stationary distribution has most of its mass much further from the 50% algal threshold than from the 10% coral threshold). Compared with the low local threat level, the probability of low coral cover was greatly increased at medium local threat level (Fig. 4A vs. 4B), but there was less change in the probability of high algal cover (Fig. 4C vs. 4D). All these probabilities had high uncertainty for most climatologies.

DISCUSSION

Observed and projected effects of ocean warming

Our results highlighted differences between observed short-term and projected long-term responses of reef composition to ocean warming. Over the period (1996–2006) covered by our data, the observed short-term effect of increased ocean temperatures on reef composition was to increase macroalgal cover, with proportional decreases in coral and other. However, moderate future warming (~2°C) in our long-term projections led to dominance by other (a category including organisms such as sponges, gorgonians, and CTB), with algal dominance only projected under extreme warming (>2°C). Empirical evidence for phase shifts from coral to other states (Aronson et al. 2002, Norström et al. 2009), and for the relative rarity of macroalgal dominance at the global scale (Bruno et al. 2009), is consistent with our analysis. Thus, it may be more appropriate to think of macroalgae as fast-colonizing ephemeral taxa rather than as competitive dominants under current conditions on the GBR (Connell 1987). However, the potential for dynamics within the dominant other category (Aronson et al. 2002) makes resolving this category more finely a priority. The differences between the observed short-term response to warming and our projected long-term dynamics occurred because short-term increases in algae are modified in the long-term by reef composition in all successive years (Fig. 5, Appendix A: A.9). The result that short- and long-term effects of environmental change are in different directions is a general one, and is likely to apply to almost all ecosystems (Appendix A: A.9).

Although moderate warming moves the stationary mean toward dominance by other rather than by macroalgae, such warming also increases the proportions of reefs projected to have high algal (>50%) and low coral (≤10%) cover (Fig. 4). This is because the whole of the stationary distribution is shifted clockwise, around the edge of the simplex, moving its tails away from the coral vertex and toward the algal vertex (see animations in Appendices B and C). These proportions can be thought of in two ways. For a single reef, they are the proportions of time a single reef spends at low coral, or high algal cover. For a population of reefs with the same environmental conditions, they are the proportions of reefs with low coral and/or high algal cover at a given time. The 10% threshold for coral cover is somewhat arbitrary, but is generally believed to be the approximate minimum value required for net-reef accretion (Kennedy et al. 2013). Current coral cover on the GBR is only ~14%, down from 28% in the mid-1980s, and even more so from a probable historical baseline of >50% (Hughes et al. 2011, Bruno 2013). Our results suggest that warming of an additional 1–2°C may lead to further coral loss.

When studying the effects of increased temperature, we used the climatology parameter rather than the anomaly parameter to model the effects of long-term warming. The estimated effect of climatology on year-to-year changes includes the effects of spatial differences in species composition and local adaptation, which may explain why the estimated climatology effect is weaker than the estimated anomaly effect. We implicitly assume that changes in species composition and opportunities for local adaptation can occur temporally, as well as spatially. If this is not the case, then we will have underestimated the effects of long-term warming. Nevertheless, because the directions of the climatology and anomaly parameters are very similar, the model's direction for the long-term effect of warming is likely approximately correct.

Local threats

Being in the medium local threat category (compared with the low local threat category) had an effect on short-term changes in composition roughly equivalent to 2.8°C of warming. Consequently, medium threat reefs are expected to have high levels of other even under current conditions, and low levels of coral and high levels of macroalgae are more likely than on low threat reefs. The local threat metric encapsulates impacts from coastal development, marine-based pollution and damage, watershed-based pollution, and overfishing (Burke et al. 2011). For example, terrestrial run-off of sediment, nutrients, pesticides, etc. have a variety of negative effects on corals, and can benefit sponges and seaweeds, effectively shifting community composition away from corals, and toward other and/or algae, as our model projected (Fabricius 2005). Most of the study reefs were in the low local threat category, so there may be little scope for further reduction in local threat. Furthermore, because ocean temperature increases of 1–2°C are likely (IPCC 2007), maintaining reefs in the low local threat category will not alone be sufficient to secure the future of the GBR. Reducing both human perturbations and the effects of climate change is necessary (Hoegh-Guldberg et al. 2007, Mumby and Steneck 2008, Sale 2008). Because Reefs at Risk Revisited is a static classification, we can say nothing about how these threat categories might vary over time. Also, because the classification integrates a wide variety of local threats, it would not be easy to design a management policy based specifically around these threat categories.

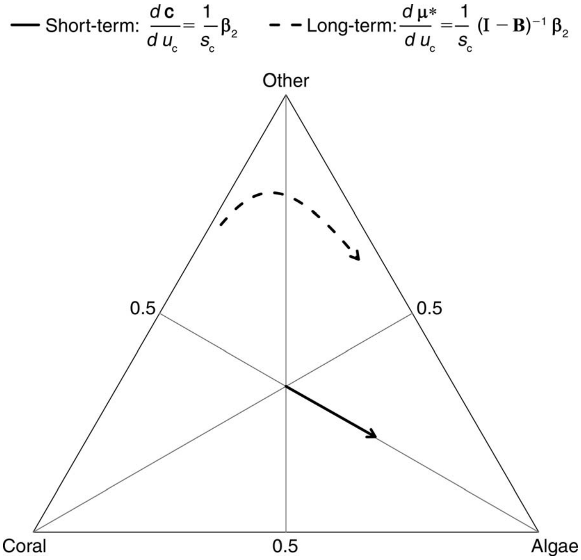

FIG. 5. Differences between short- and long-term effects of climatology on reef composition. Solid arrow, direction of short-term effect of increased climatology on isometric log-ratio (ilr)-transformed perturbing vector (tail of vector at the point representing a zero effect). Dashed arrow, direction of long-term effect of increased climatology on stationary mean reef composition (tail of arrow at current stationary mean, low local threat). The dashed arrow is a straight line in ilr coordinates. Both arrows are scaled by an amount corresponding to a 3.5°C increase in climatology. Variables in equations are **c**, intercept vector in Eq. 1; u_c, mean climatology (°C); s_c, sample standard deviation of climatology (°C); $\boldsymbol{\beta}_2$, coefficient vector for centered and scaled climatology; $\boldsymbol{\mu}^*$, mean vector for stationary distribution of reef composition; **I**, 2 × 2 identity matrix; and **B**, 2 × 2 coefficient matrix of effects of current transformed reef composition on next year's transformed reef composition.

Complementary modelling approaches

We have greatly expanded the scope of our previous work on statistical models of reef dynamics (Żychaluk et al. 2012), and addressed the concern that these models ignored among-reef heterogeneity in environmental conditions (Mumby et al. 2013). Conceptually, our approach (a multivariate statistical model for reef dynamics) is closely related to statistical summaries of empirical data on changes in coral cover (e.g., De'ath et al. 2012). However, using a multivariate model reveals a difference in the direction of environmental change effects between the short and long term, that would be undetectable using univariate analyses. Recently, simple analytical models (e.g., Fung et al. 2011, Baskett et al. 2014) have advanced our understanding of how the range of possible reef dynamics depends on biological features such as macroalgal growth rates and coral life history characteristics. Our model is much less sophisticated as a description of reef dynamics, although it can be viewed as a linear approximation of a more complicated nonlinear dynamical system (Ives et al. 2003), and can answer some of the same questions about dynamics. For example, Gross and Edmunds (2015), using a method very similar to ours, showed that coral reefs from different habitats in the U.S. Virgin Islands varied in their stability properties in ways consistent with known features of coral life histories. Our model knows much less biology than ambitious and sophisticated models of reef dynamics (e.g., Melbourne-Thomas et al. 2011, Kennedy et al. 2013, Sebastian and McClanahan 2013). Unlike these models, we cannot even attempt to predict what might happen to an individual reef. However, we can make projections about the statistical properties of ensembles of reefs (analogous to "climate" rather than to "weather"). We see these diverse modeling approaches as complementary. Given their differences in assumptions, it may even be productive to use multimodel ensembles (Gardmark et al. 2013) to look for robust projections about coral reef futures.

In summary, our models allowed us to explore regional community dynamics of the GBR. The short- and long-term responses of the system to environmental change were quite different, because of population-dynamic effects. This is likely to be true in many other systems. Statistical models of community dynamics have the potential to bridge the gap between analytical theory and field data, and have been found useful in systems including freshwater plankton (Ives et al. 2003, Hampton et al. 2013) and marine fisheries (Lindegren et al. 2009), as well as coral reefs (Gross and Edmunds 2015).

Acknowledgments

This work developed out of an undergraduate project by J. Cooper, supported by the School of Environmental Sciences, University of Liverpool. Further work was done under a short-term visit grant (supporting J. Cooper and J. Bruno) and a sabbatical fellowship awarded to M. Spencer by the National Institute for Mathematical and Biological Synthesis, an Institute sponsored by the National Science Foundation, the U.S. Department of Homeland Security, and the U.S. Department of Agriculture through NSF Award #EF-0832858, with additional support from the University of Tennessee, Knoxville. Further funding was provided by the Natural Environment Research Council grant NE/K00297X/1 to M. Spencer. We are grateful to Kevin Gross and Peter Edmunds for generously sharing their unpublished manuscript on a similar analysis, and to Rob Marrs and Jon Green for comments on the manuscript. The manuscript was greatly improved by constructive criticism from three anonymous reviewers and Robert van Woesik. This work would not have been possible without data supplied by the Australian Institute of Marine Science.

Literature Cited

Abdo, D., S. Burgess, G. Coleman, and K. Osborne. 2004. Surveys of benthic reef communities using underwater video. Long-term monitoring of the Great Barrier Reef Standard Operational Procedure Number 2. Australian Institute of Marine Science, Townsville, Australia.

Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Cote, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society B 276:3019–3025.

Aronson, R. B., and W. F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnology and Oceanography 45:251–255.

Aronson, R. B., W. F. Precht, M. A. Toscano, and K. H. Koltes. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. Marine Biology 141:435–447.

Baker, A. C., P. W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine Coastal and Shelf Science 80:435–471.

Baskett, M. L., N. S. Fabina, and K. Gross. 2014. Response diversity can increase ecological resilience to disturbance in coral reefs. American Naturalist 184:E16–E31.

Bruno, J. F. 2013. Coral reef baselines survey: what do we think is natural? figshare. http://dx.doi.org/10.6084/m9.figshare.774627

Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS ONE:e711.

Bruno, J. F., E. R. Selig, K. S. Casey, C. A. Page, B. L. Willis, C. D. Harvell, H. Sweatman, and A. M. Melendy. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. PLoS Biology 5:e124.

Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484.

Burke, L., K. Revtar, M. Spalding, and A. Perry. 2011. Reefs at risk revisited. World Resources Institute, Washington, D.C., USA.

Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. Science 328:1164–1168.

Connell, J. H. 1987. Change and persistence in some marine communities. Pages 339–352 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific Publications, Oxford, UK.

De'ath, G., K. E. Fabricius, H. Sweatman, and M. Puotinen. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences USA 109:17995–17999.

Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density dependence, process noise, and observation error. Ecological Monographs 76:323–341.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Eakin, C. M., et al. 2010. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. PLoS ONE 5:e13969.

Egozcue, J. J., V. Pawlowsky-Glahn, G. Mateu-Figueras, and C. Barcelo-Vidal. 2003. Isometric logratio transformations for compositional data analysis. Mathematical Geology 35: 279–300.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50:125–146.

Fung, T., R. M. Seymour, and C. R. Johnson. 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92:967–982.

Gardmark, A., et al. 2013. Biological ensemble modeling to evaluate potential futures of living marine resources. Ecological Applications 23:742–754.

Glynn, P. W. 1991. Coral reef bleaching in the 1980s and possible connections with global warming. Trends in Ecology and Evolution 6(6):175–179.

Gross, K., and P. J. Edmunds. 2015. Stability of Caribbean coral communities quantified by long-term monitoring and autoregression models. Ecology 96:1812–1822.

Halpern, B. S., et al. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Hampton, S. E., E. E. Holmes, L. P. Scheef, M. D. Scheuerell, S. L. Katz, D. E. Pendleton, and E. J. Ward. 2013. Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. Ecology 94:2663–2669.

Harvell, C. D., S. Altizer, I. M. Cattadori, L. Harrington, and E. Weil. 2009. Climate change and wildlife diseases: when does the host matter the most? Ecology 90:912–920.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. Science 328:1523–1528.

Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742.

Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Hughes, T. P., D. R. Bellwood, A. H. Baird, J. Brodie, J. F. Bruno, and J. M. Pandolfi. 2011. Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). Coral Reefs 30:653–660.

Huntingford, C., P. D. Jones, V. N. Livina, T. M. Lenton, and P. M. Cox. 2013. No increase in global temperature variability despite changing regional patterns. Nature 500: 327–330.

IPCC. 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. Estimating community stability and ecological interactions from time-series data. Ecological Monographs 73: 301–330.

Kennedy, E. V., et al. 2013. Avoiding coral reef functional collapse requires local and global action. Current Biology 23: 912–918.

Lindegren, M., C. Moellmann, A. Nielsen, and N. C. Stenseth. 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proceedings of the National Academy of Sciences USA 106:14722–14727.

Meehl, G. A., A. Hu, C. Tebaldi, J. M. Arblaster, W. M. Washington, H. Teng, B. M. Sanderson, T. Ault, W. G. Strand, and J. B. White III. 2012. Relative outcomes of climate change mitigation related to global temperature versus sea-level rise. Nature Climate Change 2:576–580.

Melbourne-Thomas, J., C. R. Johnson, T. Fung, R. M. Seymour, L. M. Cherubin, J. E. Arias-Gonzalez, and E. A. Fulton. 2011. Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system. Ecological Applications 21:1380–1398.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in Ecology & Evolution 23:555–563.

Mumby, P. J., R. S. Steneck, and A. Hastings. 2013. Evidence for and against the existence of alternate attractors on coral reefs. Oikos 122:481–491.

Mydlarz, L. D., C. S. Couch, E. Weil, G. Smith, and C. D. Harvell. 2009. Immune defenses of healthy, bleached and diseased *Montastraea faveolata* during a natural bleaching event. Diseases of Aquatic Organisms 87:67–78.

Norström, A. V., M. Nyström, J. Lokrantz, and C. Folke. 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Marine Ecology Progress Series 376:295–306.

Rogers, C. S., and E. M. Muller. 2012. Bleaching, disease and recovery in the threatened scleractinian coral *Acropora palmata* in St. John, US Virgin Islands: 2003–2010. Coral Reefs 31:807–819.

Sale, P. F. 2008. Management of coral reefs: where we have gone wrong and what we can do about it. Marine Pollution Bulletin 56:805–809.

Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Marine Ecology Progress Series 402:115–122.

Sebastian, C. R., and T. R. McClanahan. 2013. Description and validation of production processes in the coral reef ecosystem model CAFFEE (coral-algae-fish-fisheries ecosystem energetics) with a fisheries closure and climatic disturbance. Ecological Modelling 263:326–348.

Selig, E. R., K. S. Casey, and J. F. Bruno. 2010. New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. Global Ecology and Biogeography 19:397–411.

Selig, E. R., K. S. Casey, and J. F. Bruno. 2012. Temperature-driven coral decline: the role of marine protected areas. Global Change Biology 18:1561–1570.

Wooldridge, S. A., T. J. Done, C. R. Thomas, I. I. Gordon, P. A. Marshall, and R. N. Jones. 2012. Safeguarding coastal coral communities on the central Great Barrier Reef (Australia) against climate change: realizable local and global actions. Climatic Change 112:945–961.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Żychaluk, K., J. F. Bruno, D. Clancy, T. R. McClanahan, and M. Spencer. 2012. Data-driven models for regional coral-reef dynamics. Ecology Letters 15:151–158.

Supplemental Material

Ecological Archives

Appendices A–C and the Supplement are available online: http://dx.doi.org/10.1890/14-0112.1.sm