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Cameron H. Ainsworth
University of South Florida, ainsworth@usf.edu

Peter J. Mumby
The University of Queensland

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Coral–algal phase shifts alter fish communities and reduce fisheries production

CAMERON H. AINSWORTH¹ and PETER. J. MUMBY²

¹College of Marine Science, University of South Florida, 140 7th, St. Petersburg, FL 33701, USA, ²Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St. Lucia, Qld 4072, Australia

Abstract

Anthropogenic stress has been shown to reduce coral coverage in ecosystems all over the world. A phase shift towards an algae-dominated system may accompany coral loss. In this case, the composition of the reef-associated fish assemblage will change and human communities relying on reef fisheries for income and food security may be negatively impacted. We present a case study based on the Raja Ampat Archipelago in Eastern Indonesia. Using a dynamic food web model, we simulate the loss of coral reefs with accompanied transition towards an algae-dominated state and quantify the likely change in fish populations and fisheries productivity. One set of simulations represents extreme scenarios, including 100% loss of coral. In this experiment, ecosystem changes are driven by coral loss itself and a degree of habitat dependency by reef fish is assumed. An alternative simulation is presented without assumed habitat dependency, where changes to the ecosystem are driven by historical observations of reef fish communities when coral is lost. The coral–algal phase shift results in reduced biodiversity and ecosystem maturity. Relative increases in the biomass of small-bodied fish species mean higher productivity on reefs overall, but much reduced landings of traditionally targeted species.

Keywords: acidification, bleaching, coral disease, coral reefs, Ecopath with Ecosim, ecosystem-based management, Raja Ampat, reef fish

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Introduction

Coral reefs are assailed by an array of anthropogenic stressors rapidly intensifying with the growth of human populations and the expansion of human industry. Climate change, including global warming and ocean acidification, and indirect impacts like disease and corallivore outbreaks may come to rival overexploitation and pollution as the major drivers of coral loss (Hoegh-Guldberg *et al.*, 2007; Frieler *et al.*, 2012). As we project these effects to intensify, we may expect further loss of coral structure and reduced abundance of numerous reef-associated species (Wilson *et al.*, 2006), many of which support reef fisheries (Pratchett *et al.*, 2011). Tropical reef fisheries are an indispensable source of income in many communities of the developing world and critical for food security (McManus, 1997; Bell *et al.*, 2011). In this article, we attempt to quantify in broad terms the likely impact that coral loss followed by a phase transition to an algae-dominated state may have on the reef fish assemblage and on fisheries productivity.

We select as a case study the Raja Ampat archipelago in Eastern Indonesia. Still relatively pristine, it is among

the most biodiverse regions on Earth possessing over 75% of the world's coral species and almost a thousand species of reef fish (McKenna *et al.*, 2002; Donnelly *et al.*, 2003; Halim & Mous, 2006). Although the human population is low, the coral reef ecosystem faces numerous threats including overexploitation, destructive fishing practices (blast and cyanide fishing), coral mining, crown-of-thorn (*Acanthaster planci*) outbreaks and land-based pollution (Pet-Soede & Erdmann, 1998; Kaczmarek *et al.*, 2005).

It is difficult to estimate the amount of coral loss that has occurred historically in Raja Ampat. Blast fishing is present, but estimates of the frequency vary widely (e.g. Erdmann & Pet, 2002; McKenna *et al.*, 2002; Donnelly *et al.*, 2003), while the effects on coral reefs of disease and environmental stress remain poorly studied. As few empirical data are available with which to base the rate of loss, we engage here in simulation modelling that represents a wide range of possible futures.

We present simulations for a range of coral loss, up to 100%, from the Raja Ampat ecosystem. We refer to these as 'conjectural' simulations because the effect of coral loss lies outside of the observed historical range for any such large area (Raja Ampat model encompasses 45 000 km²; Ainsworth *et al.*, 2008b). However, similar losses of coral have been observed at the scale of individual reefs after coral bleaching events

Correspondence: Cameron Ainsworth, tel. 727-553-3373, fax 727-553-1189, e-mail: ainsworth@usf.edu

(Edwards *et al.*, 2001; Mumby *et al.*, 2001) and corresponding fish population impacts have been studied (Sano, 2004; Pratchett *et al.*, 2008). We assume some degree of habitat dependency for reef fish species and drive ecosystem changes by removing coral from the model. We also assume space-limited growth by macroalgae.

A second set of simulations, more firmly grounded in empirical data, drives changes in the ecosystem not by coral loss directly, but by changes in the fish assemblage that result from coral loss (as documented by Wilson *et al.*, 2006). In this case, model predictions are made concerning the wider fish community and we present overall ecosystem impacts as the combination of data from Wilson's observations and predictions made by the model. For comparison, it is worth noting that the assemblage changes presented by Wilson are driven, on average, by a 33.4% loss of coral relative to the initial (2012) coral biomass value (i.e. from 100% down to 66.6%). Thus, the Wilson simulation corresponds to a moderate change in coral reef status relative to the conjectural simulations.

Materials and methods

EwE models

Working with nongovernmental and academic partners, Ainsworth *et al.* (2008a,b) constructed a suite of ecosystem models using Ecopath with Ecosim (EwE: Christensen & Pauly, 1992; Walters *et al.*, 1997) and Ecospace (Walters *et al.*, 1998) representing various regions in Raja Ampat. Development of the models utilized field information from dive transects, fish stomach sampling, community interviews and coastal surveys. The models were tuned to historical catch and biomass data (1990–2006; including illegal removals, Varkey *et al.*, 2010 and anecdotal biomass information Ainsworth *et al.*, 2008c) and used to reconstruct the history of exploitation in the region and to answer practical management and conservation questions posed by the Indonesian Ministry of Marine Affairs and Fisheries (Departemen Kelautan dan Perikanan, DKP). A thorough technical description of the model, including all input data, assumptions, fits to observational data and diagnostic testing is available in Ainsworth *et al.*, 2008b located at <http://www.fisheries.ubc.ca/node/3755>. Applications of the model include Varkey *et al.*, 2012; Pitcher & Ainsworth, 2010 and Ainsworth *et al.*, 2008a.

We employ the present-day Raja Ampat model (assumed representative of 2012), representing the entire archipelago bounded at the north-west coordinate 129°12' E, 0°12' N and the south-east coordinate 130°30' E, 2°42' S. This model is described in Ainsworth *et al.* (2008b), so we will present only the information most relevant to this study. The most important parameter is the degree of species' dependency on coral reefs, which we represent by use of EwE's mediation functions (Christensen *et al.*, 2005). These can be used to represent

changes in the vulnerability of prey to predator by some third mediating species group (e.g. Cox *et al.*, 2002) or affect the productivity of a group according to the biomass of a mediating group (e.g. Okey *et al.*, 2004). Ainsworth *et al.* (2008a,b) developed four mediation functions for the Raja Ampat models that affect prey vulnerability according to the biomass of a mediating group. These describe tuna facilitating small pelagic predation by birds, coral protection of fish and invertebrates, cleaner wrasse symbiosis with large reef fish and sea grass/mangrove protection of juvenile reef fish (Fig. 1). The protection effect from coral is particularly relevant to this study as it establishes the response of reef-associated fish to coral loss (an assumption relaxed under the Wilson simulation). The function is modelled so that the vulnerability of the prey species changes in inverse linear proportion to coral biomass. All predators are affected equally (effectively we assume a similar mode of attack). The vulnerabilities are free to increase to a maximum of 2× the baseline value during periods of low coral biomass and can decrease to near 1 during periods of high coral biomass. Note that in high complexity reefs, certain size classes of prey may be disproportionately affected by coral loss (Rogers *et al.*, 2014).

These four functions are applied to appropriate species in the model (Table 1). In this study, we have added a fifth affecting benthic algal productivity (Fig. 2). As coral biomass declines, productivity of benthic algae increases. Adding this mediation effect is necessary to capture space-limited growth in algae as moderated by competitive exclusion by coral. Without the mediation effect, algal growth in EwE is moderated only by herbivory. Note that increased productivity is realistic with coral decline if fleshy macroalgae are replaced by fast-turnover benthic turfs (Hatcher, 1988) – our benthic algae group implicitly includes both. Although the potential for algal phase shifts are well documented (Done, 1992; Norström *et al.*, 2009) and an important assumption in our modelling methodology, Carassou *et al.*, 2013 note that macroalgae density is related to coral coverage only in degraded reef systems. However, due to the large spatial domain of the model (45 000 km²; Ainsworth *et al.*, 2008b), we represent here the net effect in a mosaic of degraded and healthy reefs.

Conjectural simulations

We force the biomass of coral to decline from 0% to –100% in eleven 20-year simulations (2012–2032). Results are presented at the end state of the simulations (in 2032). For each of the simulations, we estimated fisheries productivity in kg C km⁻² yr⁻¹ based on an annual catch rate and assuming a 1 : 20 dry to wet weight conversion ratio (Cushing *et al.*, 1958) and Redfield element proportions C : N : P = 106 : 16 : 1 (Redfield, 1934). To calculate the productivity and biomass of the ecosystem under the most extreme coral decline scenario (–100%), we generated a new Ecopath model based on the end state of the simulation utilizing the .eii file input/output procedure available in EwE (Christensen *et al.*, 2005). Ecosystem productivity is determined as the sumproduct of biomasses and production-per-unit-biomass (P/B) across species groups. A weighted average of biomass/production (B/P)

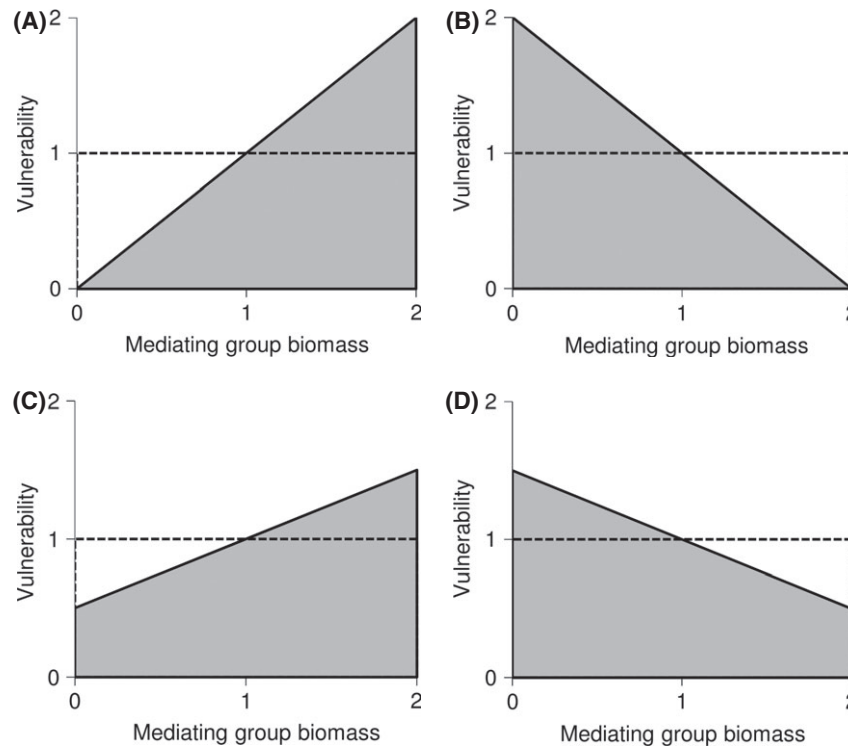


Fig. 1 Ecosim mediation functions. Vulnerability of prey vs. mediating group biomass: (A) tuna facilitating small pelagic predation by birds; (B) reef-building coral protection of reef fish and invertebrates; (C) cleaner wrasse symbiosis with large reef-associated fish; (D) sea grass and mangrove protection of juvenile reef fish. x - and y -axes are relative to model baseline values. Reproduced from Ainsworth *et al.*, 2008b.

Table 1 Assignment of mediation functions (Med.) in Raja Ampat EwE model. A, B, C and D are defined as in Fig. 1. Reproduced from Ainsworth *et al.*, 2008b

Prey group	Med.	Prey group	Med.	Prey group	Med.	Prey group	Med.
Ad groupers	B, C	Ad coral trout	B, C	Juv small reef assoc.	B, D	Ad eroding grazers	B, C
Sub groupers	B	Juv coral trout	B, D	Ad large planktivore	B, C	Juv eroding grazers	B, D
Juv groupers	B, D	Ad small pelagic	A	Juv large planktivore	B, D	Ad scraping grazers	B, C
Ad snappers	B, C	Juv small pelagic	A	Ad small planktivore	B	Juv scraping grazers	B, D
Sub snappers	B	Ad large reef assoc.	B, C	Juv small planktivore	B, D	Penaeid shrimps	D
Juv snappers	B, D	Juv large reef assoc.	B, D	Ad anchovy	A	Shrimps and prawns	D
Ad Napoleon wrasse	B, C	Ad medium reef assoc.	B, C	Juv anchovy	A	Octopus	B
Sub Napoleon wrasse	B	Juv medium reef assoc.	B, D	Ad macroalgal browsing	B, C	Small crabs	B
Juv Napoleon wrasse	B, D	Ad small reef assoc.	B	Juv macroalgal browsing	B, D		

(units: yr) is used as an indicator of ecosystem maturity after Odum (1969).

Wilson simulation

For the Wilson simulation, we force biomass of seven fish groups. Biomass change is based on Fig. 2 in Wilson *et al.* (2006), which provides biomass change at the species level relative to the change in coral cover. Wilson's species are aggregated (averaged) to the level of EwE functional groups and the absolute change in biomass is determined relative to the

coral decline projected by the model. The coral decline amounts to an 8.3% loss over the 20 year simulation. This rate represents the effects of coral mining, blast fishing, cyanide fishing and corallivory by bioeroding fish and crown-of-thorns starfish and was set by Ainsworth *et al.*, 2008a to reflect trends in Raja Ampat (McKenna *et al.*, 2002). It is similar to the 7.4% decline observed in the Indo-Pacific over the same period by Bruno & Selig (2007). The programmed loss of coral in the model ensures that trophodynamic effects impacting species whose biomass is not forced are realistically portrayed. Based on this technique, the following biomass changes from Wilson

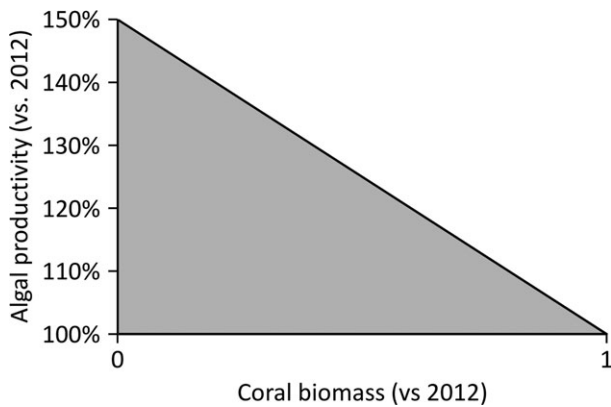


Fig. 2 Mediation function boosts algal productivity when coral biomass is low.

are inferred: butterflyfish -7.6% , cleaner wrasse -4.8% , large reef-associated fish $+1.0\%$, medium reef-associated fish -1.5% , small reef-associated fish -5.0% , scraping grazers $+1.8\%$ and small planktivores -2.5% . We assume a linear increase or decrease in species group biomass leading to these values in the final year of a 20-year simulation (relative to initialization biomass). Biodiversity is assessed using two methods, the Shannon index (Shannon & Weaver, 1949), which measures evenness, and the Q90 index (Ainsworth & Pitcher, 2006), which measures evenness and richness. All simulations run from 2012 to 2032 and we assume that current (2012) fishing mortalities are maintained into the future.

Results

Detailed model results for conjectural and Wilson simulations are provided in the supplement. Tables S1 through S6 provide biomass, catch and catch value results; Tables S7 and S8 show changes in ecosystem trophic level; Table S9 shows mixed trophic impacts from Ecopath indicating net trophic effects for impacted-impacting group combinations (see Ulanowicz & Puccia, 1990 and Christensen *et al.*, 2005). Table S10 shows changes in production rates for the conjectural simulation. Figures S1 through S6 show Shannon and Q90 biodiversity trajectories. Figure S7 shows average ecosystem biomass/production.

Conjectural simulations

Biomass trajectories for the conjectural simulations are presented in Fig. 3A. When coral is eliminated, the ecosystem shifts towards algal dominance. Herbivorous fish increase 14% and urchins increase 117% under the extreme coral loss scenario (relative to the 0% loss scenario). However, the reef fish groups' biomasses decrease on average by 46% , with some reef-dependent groups showing severe depletions

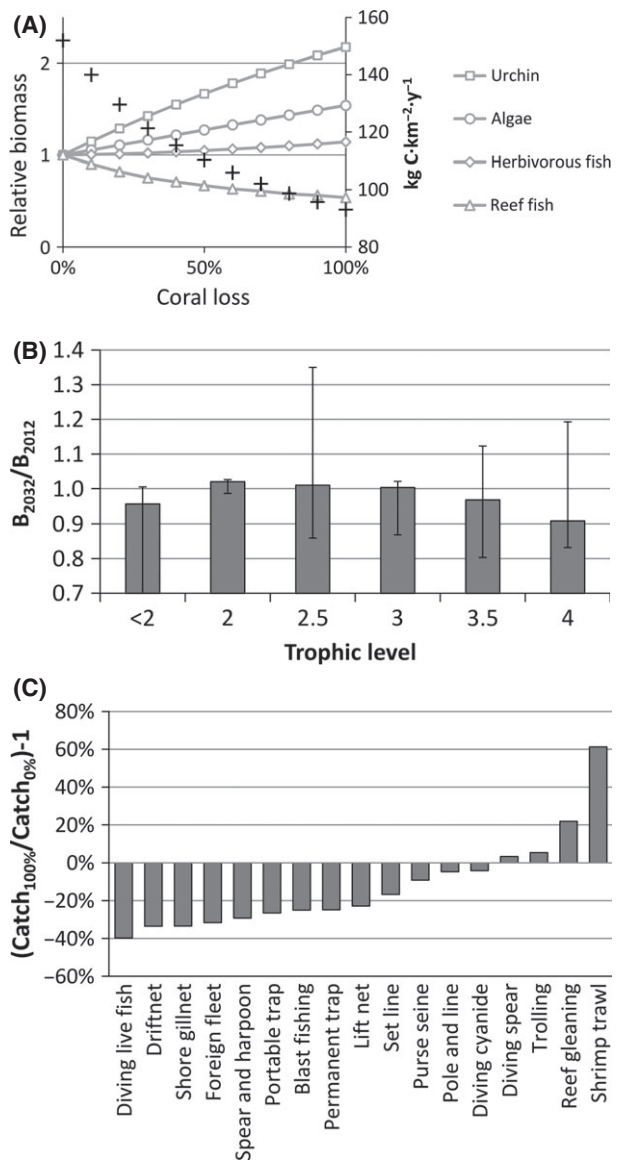


Fig. 3 Simulation results. (A) Transition from coral-dominated ecosystem (left) to algae-dominated ecosystem (right). Data represent end-points of 20-year simulations. Results are from the conjectural simulations (0% , 10% ... 100% coral loss scenarios). Grey lines: biomass changes relative to initialization (2012) biomass; black hatches: reef fisheries productivity in kg C km⁻² yr⁻¹. (B) Biomass changes per trophic level under the 100% coral loss scenario (all species groups). Error bars show the range for species groups within these trophic levels. (C) Fisheries catch by fleet under the 100% coral loss scenario relative to 0% loss scenario. Catch for the year 2032 is compared.

(small reef fish -97% , medium reef fish -61% , large planktivores -78%) (see Table S1). The total production rate of reef-associated groups increases by about 40% as high-turnover smaller species replace slow-growing larger species (Table S10). This finding is corroborated as mean ecosystem trophic level also

drops from 1.62 to 1.56 between 2012 and 2032 (Table S8), reflecting a major structural change. Larger species tend to be higher trophic level, and we see a skewing of the trophic pyramid towards smaller-bodied consumers (Fig. 3B). In the 100% coral loss scenario, Shannon biodiversity decreases and then recovers incompletely (Figure S1), Q90 biodiversity decreases steadily (Figure S2).

When corals are removed, total ecosystem biomass increases 18.5% (Table S1). With trophic chains shortened, fewer trophic steps result in less energy lost through thermodynamic inefficiencies. However, the increased biomass does not occur in groups targeted by fisheries. Annual reef fish landings decline by 39%, from 152 to 93 kg C km⁻² yr⁻¹ [contrast this against Rogers *et al.* (2014) who estimated a 55% decline in predator productivity under similar conditions in the Caribbean]. Reef fish biomass has been halved from 373 to 202 kg C km⁻² (Table S1). Midtrophic level species, which previously acted as a conduit for vertical energy flow, are reduced in biomass (small pelagic fish -45%, small reef fish -97%, anchovy -43%) (Table S1). This is from a combination of top-down and bottom-up effects (Table S9). Macroalgal grazers increase in biomass because of the abundance of algae in coral loss scenarios, yet they do not eat algae exclusively. A small fraction of their diet includes forage species (e.g. about 19% of predation mortality on small pelagic fish is due to this group) so there is increased predation from macroalgal grazers. There is also a decrease in availability of small herbivorous zooplankton, an important prey item for forage fish. This is due to a trophic cascade connecting herbivorous zooplankton to carnivorous zooplankton to reef-associated fish (Table S9).

Structural changes are further evidenced by a decrease in ecosystem maturity (Figure S7), with the greatest reduction in B/P occurring in the 100% coral

loss scenario. The only fisheries that clearly benefit from the loss of coral structure are those targeting shrimp and other benthic invertebrates (Fig. 3C). Biomass increases in both the penaeid shrimp (+64%) and nonfished shrimp groups (+42%) (Table S1). The mixed trophic impacts routine (Ulanowicz & Puccia, 1990) suggests that this is due to a decrease in predation mortality by carnivorous macrobenthos, which is a result of coral loss (Table S9). A small increase in the availability of detritus may also contribute.

Wilson simulation

Forcing EwE with Wilson *et al.* biomass changes in reef fish leads to a 10–30% decline in biomass over 20 years in fished groups like large pelagic fish, groupers and snappers (Table S4). There is a steady decrease in ecosystem biodiversity from 2012 to 2032 according to the Shannon index, but the Q90 index decreases and then recovers (Figures S3 and S4). This disagreement between the metrics implies that evenness has been impacted, but ecosystem biomass eventually recovers (although not necessarily in the same groups as those that declined). Considering biodiversity within the reef fish assemblage, both biodiversity metrics indicate steady decline (Figures S5 and S6). As in the conjectural simulations, there is an increase in shrimp biomass (Fig. 4). Penaeid shrimp and nonfished shrimp increase 7% and 6% respectively (Table S4), while the shrimp trawl fleet benefits from a 9% increase in the annual catch rate (Table S6).

Discussion

The Raja Ampat ecosystem is exceptionally biodiverse and may serve as a sensitive test site for coral loss studies. In other ways, the ecosystem is typical of coral reef

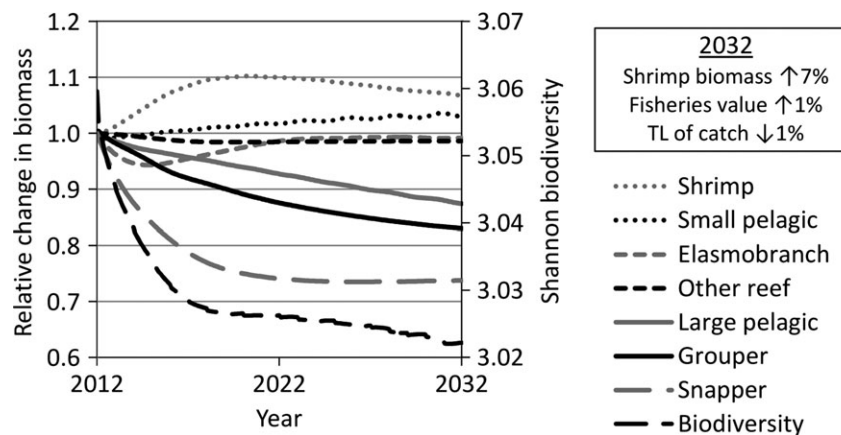


Fig. 4 Ecosystem biomass changes in Raja Ampat from 2012 to 2032 using Wilson *et al.*, 2006 biomass forcing.

areas: it endures a multitude of threats with environmental and human-related stressors on the rise. We have simulated in this article both a typical pattern of coral loss, similar to the recent world case studies summarized by Wilson *et al.* (2006), and more dramatic losses as may become common in years to come.

The conjectural simulations, in which up to 100% of coral biomass was removed, result in fundamental shifts in ecosystem structure and function. The ecosystem transitions from a coral-dominated state to an algal-dominated state, although these algae are primarily envisaged to be short turfs rather than fleshy macroalgae, and do not necessarily pose a threat to ecosystem recovery (*sensu* Arnold *et al.*, 2010). This is consistent with evidence from the Indo-Pacific (Mumby *et al.*, 2013).

The model predicts that transition towards algal dominance results in increases in herbivorous species and decreases in reef-associated fauna and high trophic level piscivorous species, the main targets of fisheries (Sano, 2004; Pratchett *et al.*, 2008). Evidence for a herbivore numerical response may be ambiguous in the Indo-Pacific (Wismer *et al.*, 2009; Carassou *et al.*, 2013; Heenan & Williams, 2013) although some studies found indications of such (Cheal *et al.*, 2008; Gilmore *et al.*, 2013). Moreover, these relationships are common in the Caribbean (Williams *et al.*, 2001; Mumby *et al.*, 2005, 2006, Newman *et al.*, 2006; Carpenter, 1990) and this lends credence to the model's behaviour. Food limitation in herbivorous fish contributes to the numerical response (Ainsworth *et al.*, 2008b). A nonlinear effect may occur at low population sizes where herbivore fish response is decoupled from algal density (Hernández-Landa *et al.*, 2014), but this is unlikely to affect our results as herbivore fish biomass remains relatively high in Raja Ampat (Ainsworth *et al.*, 2008b). Differentiation within the herbivore guild is missed by our model due to species aggregation, so it is difficult to infer which functional roles (see Heenan & Williams, 2013) remain present after the phase shift and therefore implications for reef resiliency (Cheal *et al.*, 2008).

The shift in biomass towards lower trophic level species indicates that trophic chains are shortened overall and the food web is simplified. The model predicts that less energy passes to the upper food web and through fewer conduits. This is indicated by a decrease in the average trophic level, reduced biomass in forage species (caused by simultaneous top-down and bottom-up effects), and reduced ecosystem biodiversity – a finding supported by observation (Jones *et al.*, 2004; but see Cheal *et al.*, 2008). Finally, ecosystem maturity decreases as long-lived species are replaced with high-turnover species.

Nonlinear or threshold effects may actually worsen this problem at low coral densities (Pratchett *et al.*, 2014). We conclude that human communities relying on this depauperate ecosystem would likely be required to abandon traditional target species in favour of less valuable but more abundant species. As the EwE model we have employed does not consider opportunistic fishing behaviour or market effects, it is difficult to estimate the change in fisheries profitability. Despite great abundance, these high-turnover species of fish and invertebrates are likely to fluctuate with environmental variability more than the longer lived species that are the traditional mainstay of fisheries. This could carry implications for the consistency of fisheries benefits and food security.

The conjectural simulations and the Wilson simulation agree that loss of coral results in large decreases in reef-associated fauna, and that smaller reef-associated fish species are particularly impacted. This shift in size structure has been noticed empirically (Graham *et al.*, 2007; Ledlie *et al.*, 2007). Also, the conjectural simulations and the Wilson simulation agree that an increase in shrimp biomass and shrimp landings is likely when coral is depleted. This effect can be traced to reduced predation on shrimp by carnivorous macrobenthos, which are dependent on reefs, and a greater availability of detritus.

Qualitative agreement between the Wilson and conjectural simulations within the range of historically observed coral declines in this region lends credibility to the more extreme coral loss scenarios ventured by the conjectural simulations. However, one conspicuous disagreement is that the conjectural simulations predict a decrease in small midtrophic level fish with implications for vertical flow of energy to the upper food web. This behaviour is not present in the Wilson simulation. The (inputted) fish abundance data drawn from Wilson *et al.* (2006) does in fact include a 5% decrease in small reef-associated fish (one of the largest changes observed by those authors), but our simulation does not predict a similar decrease in small pelagic fish. Rather, it predicts a small increase in those groups leaving the pelagic forage assemblage intact. One possible explanation is that greater losses of coral are required to elicit this effect (more akin to the extreme scenarios tested in the conjectural simulations). An alternative explanation is that the conjectural simulations, which assumed a uniform effect of coral loss on different size categories of reef-associated fish, lost nuanced differences that were more properly represented by the Wilson simulation.

This study uses a combination of modelling the potential effects of major coral loss (conjectural simulations) with more empirically grounded simulations of the consequences of a modest decline in coral cover

(the Wilson *et al.* simulations). In both cases, the productivity of reef fisheries declines severely. This is a concern for food security given the high dependence on fish protein that often exists in tropical coastal areas (Burke *et al.*, 2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

- Table S1.** Conjectural simulation results (biomass by species group, all simulations).
- Table S2.** Conjectural simulation results (catch and value rates by species group, selected simulations).
- Table S3.** Conjectural simulation results (catch and value rates by fishery, selected simulations).
- Table S4.** Wilson simulation results (biomass by functional group).
- Table S5.** Wilson simulation results (catch and value rates by functional group).
- Table S6.** Wilson simulation results (catch and value by fishery).
- Table S7.** Trophic level at initialization (2012) and end state (2032) for Wilson simulation.
- Table S8.** Trophic level at initialization (2012) and end state (2032) for conjectural simulations.
- Table S9.** Mixed trophic impacts.
- Table S10.** Production rate in 2032 under 100% coral loss scenario.
- Figure S1.** Shannon biodiversity for conjectural simulations (0%, 50% and 100% coral loss scenarios).
- Figure S2.** Q90 biodiversity for conjectural simulations (0%, 50% and 100% coral loss scenarios).
- Figure S3.** Shannon biodiversity for Wilson simulation (all groups).
- Figure S4.** Q90 biodiversity for Wilson simulation (all groups).
- Figure S5.** Shannon biodiversity for Wilson simulation (reef fish groups).
- Figure S6.** Q90 biodiversity for Wilson simulations (reef fish groups).
- Figure S7.** Average group biomass/production ratios in the ecosystem.