

Review

Responses of Cryptofaunal Species Richness and Trophic Potential to Coral Reef Habitat Degradation

Ian C. Enochs ^{1,2,*} and Derek P. Manzello ^{1,2}

¹ Cooperative Institute for Marine and Atmospheric Sciences, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149, USA; E-Mail: derek.manzello@noaa.gov

² Atlantic Oceanographic and Meteorological Laboratories (AOML), National Oceanic and Atmospheric Administration (NOAA), 4301 Rickenbacker Cswy, Miami, FL 33149, USA

* Author to whom correspondence should be addressed; E-Mail: Ian.Enochs@noaa.gov; Tel.: +1-305-361-4507; Fax: +1-305-361-4447.

Received: 17 November 2011; in revised form: 7 February 2012 / Accepted: 10 February 2012 / Published: 15 February 2012

Abstract: Coral reefs are declining worldwide as a result of many anthropogenic disturbances. This trend is alarming because coral reefs are hotspots of marine biodiversity and considered the ‘rainforests of the sea. As in the rainforest, much of the diversity on a coral reef is cryptic, remaining hidden among the cracks and crevices of structural taxa. Although the cryptofauna make up the majority of a reef’s metazoan biodiversity, we know little about their basic ecology or how these communities respond to reef degradation. Emerging research shows that the species richness of the motile cryptofauna is higher among dead (framework) vs. live coral substrates and, surprisingly, increases within successively more eroded reef framework structures, ultimately reaching a maximum in dead coral rubble. Consequently, the paradigm that abundant live coral is the apex of reef diversity needs to be clarified. This provides guarded optimism amidst alarming reports of declines in live coral cover and the impending doom of coral reefs, as motile cryptic biodiversity should persist independent of live coral cover. Granted, the maintenance of this high species richness is contingent on the presence of reef rubble, which will eventually be lost due to physical, chemical, and biological erosion if not replenished by live coral calcification and mortality. The trophic potential of a reef, as inferred from the abundance of cryptic organisms, is highest on live coral. Among dead framework substrates, however, the density of cryptofauna reaches a peak at intermediate levels of degradation. In summary, the response of the motile cryptofauna, and thus a large fraction of the reef’s biodiversity,

to reef degradation is more complex and nuanced than currently thought; such that species richness may be less sensitive than overall trophic function.

Keywords: biodiversity; reef framework structure; rainforest's of the sea; rubble

1. Introduction

Coral reefs are in a state of decline due to climate change and overpopulation [1–3]. This trend is especially disturbing as coral reefs, the “rainforests of the sea”, contain the highest concentrations of species within the marine realm and likely support the greatest number of metazoan phyla of any ecosystem on the planet [4–7]. Furthermore, the restricted ranges and high endemism of many reef species make them especially susceptible to extinction [8,9]. While there are no reef taxa known to have become globally extinct, regional coral extinctions have been documented and many fish and coral species are increasingly threatened [10–12]. Given the numbers of undescribed reef species, the probability of the disappearance of a species before it is known to science is high [13].

Carlton *et al.* [14] used species-area relationships and Reaka-Kudla's [5] estimates of total described reef species to calculate that a 5% reduction in reef habitat area would lead to the extinction of roughly 1,000–1,200 known reef species, and as many as 10,000–12,000 when one factors in potentially undescribed species. A loss of 30% of reef habitat would lead to the extinction of 6,000–8,000 described or 65,000–85,000 described and undescribed species [13]. The 1997–1998 widespread mass coral bleaching event (loss of endosymbiotic dinoflagellates due to elevated seawater temperatures [15]) was reported to have caused the “loss” or “destruction” of 16% of the world's coral reefs [16]. If we couple this estimate with the assumptions of the aforementioned calculations [14], this translates to a loss of 4,000 described coral reef species and a total loss of up to 40,000 species if one includes those both described and undescribed. Despite these alarming statistics, the “loss” of 16% of coral reefs should be more accurately labeled the decline in percent live coral cover as it is clearly stated in Wilkinson [16] that this “loss” should be viewed as temporary, with the potential for recovery. This is an important point as a decline in live coral cover does not automatically translate into the complete destruction of reef habitat or the sterilization of all ecosystem functions [17]. In reality, the dynamics of reef ecological function, biodiversity, and the physical integrity of framework structures vary across differing spatiotemporal scales, making them difficult to discern as a function of live coral. For instance, recent field experiments have shown that the presence of live coral has no effect on the abundances, biomass, or diversity of the motile cryptic fauna inhabiting the frameworks immediately below [18].

Concerns over the impacts of global climate change on coral reef ecosystems have focused primarily on corals and coral reef fishes. While these taxa are structurally and ecologically vital to reef ecosystems, they actually contribute relatively little towards species richness [5]. Cryptic coral reef animals, termed the cryptofauna, are similar to the rainforest insects in that they make up the majority of metazoan biodiversity, a large proportion of biomass, and are important trophic links, crucial to ecosystem function [5,19,20].

Despite the importance of coral reef cryptofauna, there has been little quantitative evidence concerning how these communities respond to coral mortality and framework degradation. The immediate collapse of all ecosystem functions is often simply assumed when there is mass coral mortality. Perhaps this is because those organisms that directly depend on live coral usually share its fate during a mortality event. For example, the abundance, species richness, and biomass of symbiotic crustaceans associated with live coral all decline after coral bleaching and mortality [21,22]. Additionally, non-obligate commensals often experience an increase in predation because they become less camouflaged against the white background of bleached coral and more conspicuous to predators [23]. However, these declines in coral-dwelling species represent only a small fraction of the total number of organisms found on reefs.

2. Evidence from Eastern Pacific Pocilloporid Reefs

Recent studies on the species richness, abundance, and biomass of naturally occurring motile cryptofauna from an eastern Pacific reef shed light on how these communities may respond to reef ecosystem degradation [24,25]. In these studies, the motile cryptofauna were sampled from live coral and four different reef framework structures (*i.e.*, dead coral) typifying progressive levels of degradation and erosion. For further information on sampling methodology, readers should refer to previous studies [24,25].

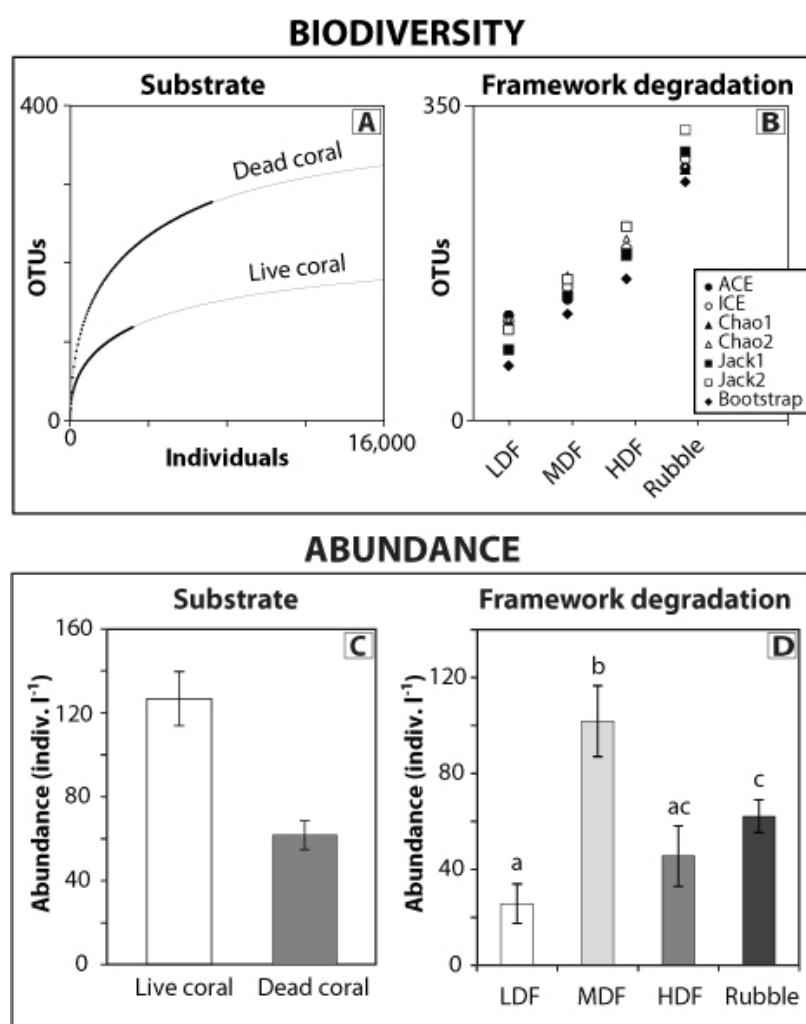
Species richness was greater among reef framework structures, or the non-living coral “rock” compared with live coral habitats (Figure 1A) [24]. One possible reason for this finding is that the entire existence of coral reefs is a result of the ability of corals to be domineering competitors, effectively excluding many other species [26]. In contrast, dead coral frameworks and rubble support a suite of sessile flora and fauna that are far less restrictive to the occupation of diverse associates. Unexpectedly, dead coral rubble was the most species rich habitat sampled and richness decreased incrementally within each successively more intact and less eroded reef framework structure (Figure 1B) [24]. Simply put, as the reef framework structure sampled became more eroded, there were successively greater numbers of species of motile cryptofauna inhabiting it.

The higher community richness associated with degraded, dead coral substrates is consistent with the predictions of the intermediate disturbance hypothesis [4]. In low disturbance environments, contiguous stands of high coral cover restrict the recruitment of cryptofauna to the cracks and crevices in the frameworks below. However, in more degraded areas, such as rubble zones, cryptofaunal diversity is elevated because there are fewer barriers to recruitment. Furthermore, the structure of intact frameworks is less conducive to the occupation of cryptofauna. Physical and biologically-mediated erosion creates shelters and cavities within which these diverse communities may live [27]. Finally, the high substrate mobility of rubble zones effectively limits the proliferation of space domineering competitors and therefore supports high diversity [28]. At the highest levels of reef framework degradation, characterized by fine sediment and silt, diversity is much lower than what occurs in more structurally complex and shelter-rich habitats [29]. It is noted that the intermediate disturbance hypothesis does not fully explain the observed trends because richness peaks in zones exhibiting higher than intermediate disturbance.

Patterns in abundance, and by extension trophic potential, are markedly different than those of species richness. The abundance of cryptic organisms does indeed decline with coral mortality, as

cryptofaunal abundances and biomass were highest on live coral (per volume substrates) (Figure 1C) [25]. Various metabolic by-products and food sources are concentrated on the highly productive live coral colonies (tissues, mucus, fat bodies, captured plankton and particulate organic matter). However, these sources of nutriment are exploited by a less diverse, albeit more abundant suite of specialized organisms (e.g., *Trapezia* spp., *Alpheus lottini* [30–32]).

Figure 1. Individual-based rarefaction of motile cryptofauna associated with live and dead coral substrates (A) and nonparametric richness estimators of cryptofaunal communities associated with dead frameworks in four zones of increasing degradation (B) [24]. In B, symbols correspond to the particular estimator employed. Abundances of individuals associated with live and dead coral substrates, per volume substrate (C) and with differing framework materials (D), Low Degradation Framework (LDF), roughly 80% or greater coral cover, intact three-dimensional frameworks with greatest vertical relief; Medium Degradation Framework (MDF), 20–80% coral cover, semi-eroded large framework pieces; High Degradation Framework (HDF), <20% coral cover, highly eroded and loose framework with little three-dimensional relief) [25]. In D, bars that share a common letter are not significantly different.



The greatest numbers of cryptofauna of all the dead coral materials, per liter substrate, were found on substrates of intermediate degradation (Figure 1D) [25]. In these areas, structural relief provides habitat and shelter from predators, as well as more habitat space than the intact frameworks [27]. Undisturbed high-relief framework structures (LDF) directly below contiguous stands of high coral cover contained surprisingly low densities of cryptofauna, being no different than the more degraded and eroded low-relief framework structures. Densities of cryptofauna within the rubble zone were no different than the highly degraded frameworks, but were still higher than the intact, high-relief framework structures. The recent decline in topographic complexity of Caribbean reefs [33] is thus of particular concern, as it may indicate an impairment of the trophic functioning of these reefs due to declines in the abundance and biomass of the motile cryptofauna [25].

3. Predicting Ecosystem Responses to Climate Change

We propose the following conceptual model to illustrate how the motile cryptofauna respond to coral mortality and reef structural degradation (Figure 2). Coral mortality shifts the balance between calcium carbonate production and its breakdown such that in extreme cases of mass mortality, a coral reef becomes a net-erosional system [34]. Poor recovery of live coral will subsequently lead to decreases in framework complexity and ultimately result in a habitat of little or no relief. Declines in coral cover coincide with an increase in motile cryptofaunal species richness by freeing space occupied by live coral, thereby allowing the recruitment and proliferation of a more diverse suite of biota. Greater numbers of eurytopic taxa inhabit rubble zones, rather than the limited subset of coral-specialist species found among live corals.

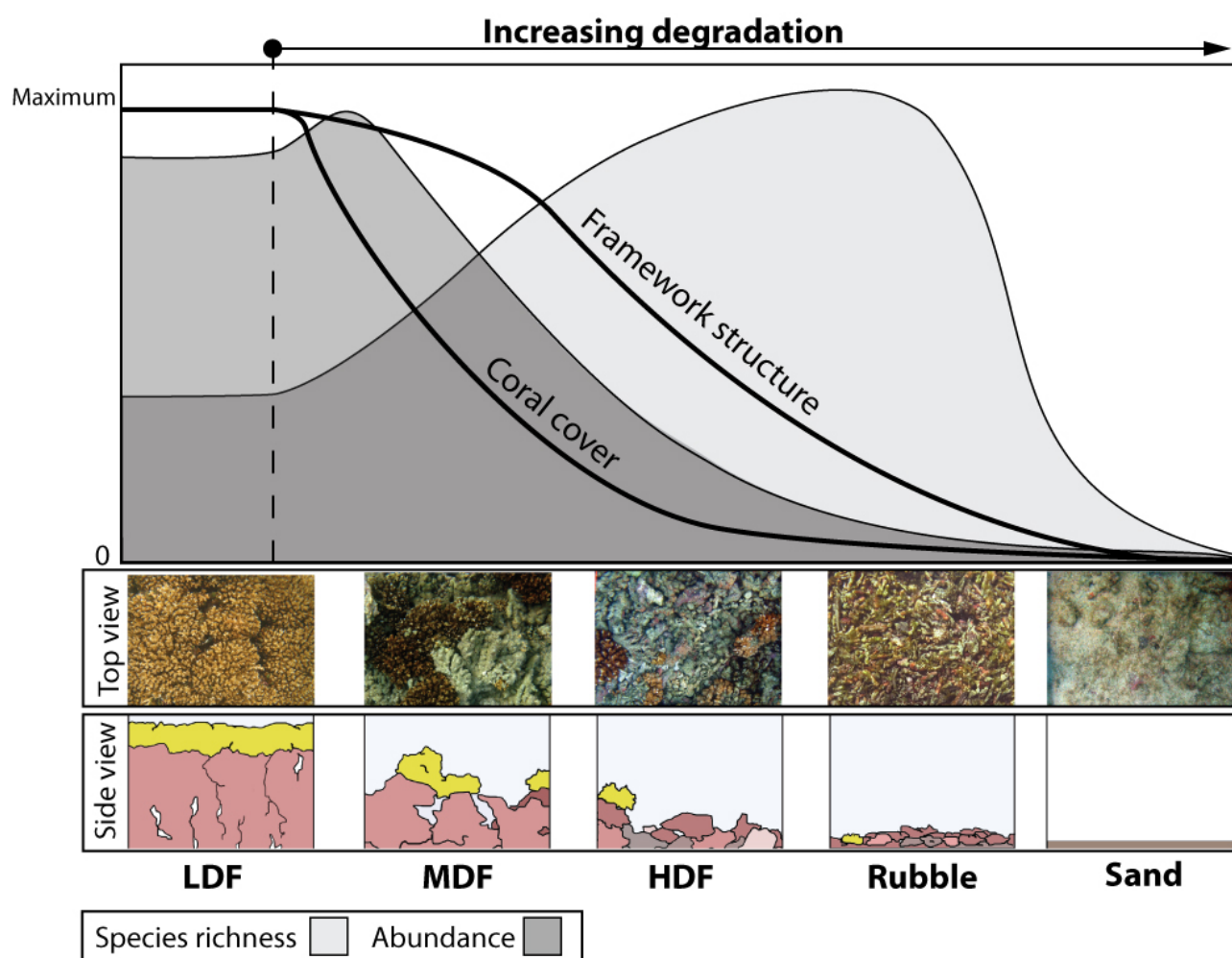
We hypothesize that the diversity of the cryptofauna will decline precipitously only after reef framework structures and rubble are broken down to sand and silt [26]. Of course, live coral cover is important for reef biodiversity in that calcification must equal or exceed erosion in order to maintain reef frameworks and thus supply the requisite structure that fosters the high diversity. The prolonged absence of live coral cover coupled with high bioerosion rates will result in the elimination of important reef habitats after decades. In certain cases, where rates of bioerosion are exceedingly high, such as the Galápagos Islands, framework structures can be lost in as little as a decade [34,35].

The trophic potential of cryptofaunal populations will ultimately decline with coral mortality and extreme levels of framework erosion. When we consider cryptofauna community abundance as a function of the individuals associated with both live coral and the underlying dead framework, we hypothesize that abundances peak at very low levels of disturbance between LDF and MDF (Figure 2). The reasons for this peak are twofold. First, obligate live coral symbionts increase in abundance as contiguous stands of live coral are fragmented into isolated hemispherical colonies [21,25]. Secondly, among communities associated with dead coral, abundances increase per liter substrate in MDF (Figure 1D), likely a result of erosion leading to greater habitat complexity and shelter availability [25,27]. While these patterns suggest a slight increase in trophic potential at low levels of degradation, abundances ultimately decline with the loss of live coral food sources and decreases in reef framework structural complexity.

The conceptual model proposed herein has implications for the entire coral reef ecosystem. Reductions in coral cover have been shown to have limited effects on the diversity of coral reef

fishes [36]. The abundances of facultative reef fishes often lag behind coral mortality by 3–4 years, paralleling the loss of framework structures [37,38]. Cryptofaunal populations are known to be an important food source for reef fishes [39], thus the decrease in their abundances during the breakdown of reef framework structures [25] may explain the concomitant declines in reef fishes several years after coral mortality events.

Figure 2. Response of coral reef cryptofaunal richness and community abundance to declines in coral cover and framework degradation. Communities modeled in this figure represent total numbers and species of cryptofauna, including those associated with both live and dead coral substrates. Solid lines represent changes in the habitat of cryptofauna following the progression of reef framework degradation. Coral cover refers to percent live coral cover, whereas framework structure refers to habitable framework depth and porosity [25]. Colored trajectories plot the species richness (light gray) and abundances (dark gray) of cryptofaunal communities. Different reef framework types defined in caption to Figure 1.



These data predict maximum species richness and abundances at separate points along a continuum of disturbance. Therefore, managers targeting both ecosystem function and species diversity need to preserve degraded rubble environments in addition to pristine stands of live coral, as these different habitats provide unique and valuable ecosystem services. The high diversity of communities associated

with rubble coupled with the elevated abundances of individuals associated with frameworks of intermediate degradation support the concept that artificial reef structures may be powerful tools for remediation of reef habitat loss, provided that they are of sufficient structural complexity [18].

Coral reef frameworks in the Indo-West Pacific and Caribbean are constructed by a more diverse suite of scleractinian corals compared to the low diversity eastern Pacific [40] and these reefs likely contain more diverse communities of obligate symbionts. However, in these regions, as in the eastern Pacific, the relative number of obligate coral associates is low compared with the more ubiquitous taxa that inhabit dead coral substrates [41]. Furthermore, on reefs where massive coral morphologies are more prevalent, epilithic coral associates are likely depressed due to insufficient shelters [27]. In these ecosystems, possibly more so than the eastern Pacific, dead coral substrates likely host proportionally more species as the erosion/degradation of geometrically simple massive colonies would be needed to create shelters and habitat for cryptic organisms [42–44].

4. Parallels with Forest Ecosystems

The concept that disturbance is important for the maintenance of biodiversity has a long history for tropical rainforests [4,45] and for reef corals [4,46]. In these communities, disturbance of homogeneous climax communities (trees and corals) facilitates the colonization of less competitive species. It is therefore not surprising that on reefs, the diversity of motile cryptic species which occupy these disturbed structural taxa increases along with the heterogeneity of the sessile substrate.

Additional parallels with terrestrial forests are numerous. In temperate woodlands, a large proportion of species (roughly 20–25%) are saproxylic, relying on dead wood for food or shelter [47]. Such organisms are similar to the cryptic reef taxa, which shelter on, within, and/or beneath dead coral. Within natural forests, smaller size classes of dead wood are occupied by more diverse communities per unit volume [48,49], mirroring the higher cryptofauna richness observed in highly eroded reef substrates. Maintenance of these dead wood materials is crucial to the preservation of forest ecosystem biodiversity [47,50]. Our data show that continuous stands of living coral with few dead coral habitats would limit cryptofauna diversity and we therefore suggest that dead coral is equally or even more important in reef ecosystems than dead wood in forests.

5. Conclusions

The existence of coral reefs as ‘rainforests of the sea’ is dependent on the natural breakdown of framework structures. Therefore, decreases in live coral cover, often cited as harbingers of reef degradation [16,51], may not directly correlate with an immediate, catastrophic decline in the biodiversity of all reef communities. Similarly, those organisms that actively degrade reef frameworks, termed bioeroders, are more diverse among dead rather than live coral [52]. It is cautioned that this model reflects only one component, albeit a large fraction, of a coral reef’s total metazoan biodiversity and that other communities (e.g., epibenthic, nektonic, planktonic) may respond differently.

This model suggests that management strategies which simply aim to increase or conserve live coral cover may be unknowingly ignoring cryptofauna biodiversity. Our data show that the conservation of reef rubble substrates is therefore of paramount importance to preserving this large fraction of coral reef biodiversity.

Conversely, rubble environments provide poor trophic resources for the myriad of taxa which rely on cryptofauna as a food source. Instead, trophic potential is dependent, in large part, on structurally complex reef habitats and the metabolic products of live coral substrates. Management strategies which aim to simply increase the number of organisms, irrespective of biodiversity, should strive to maximize coral cover and reef framework complexity. This may be accomplished in some instances with artificial reef structures provided that they possess a high degree of complexity and numerous, diverse shelters.

A comprehensive management strategy would seek to simultaneously maximize all ecosystem services, including biodiversity and trophic potential. For this reason, managers should attempt to preserve the full spectrum of reef habitats, ranging from stands of live coral to superficially barren rubble patches. Coral reef habitats with intermediate levels of coral cover and high structural complexity may be the healthiest and most productive reef environments, despite having a lower aesthetic value than coral thickets.

Acknowledgments

Financial support was provided by the Lerner-Gray Fund, the American Museum of Natural History, and National Science Foundation grant to Peter W. Glynn, #OCE-0526361. We are grateful for the field assistance of V. Brandtneris and L. Toth. P.W. Glynn built the foundation of knowledge on which this work stands and provided humble mentoring at all stages of this project.

References

1. Jackson, J.B.C.; Kirby, M.X.; Berger, W.H.; Bjorndal, K.A.; Botsford, L.W.; Bourque, B.J.; Bradbury, R.H.; Cooke, R.; Erlandson, J.; Estes, J.A.; *et al.* Historical overfishing and the recent collapse of coastal ecosystems. *Science* **2001**, *293*, 629–638.
2. Pandolfi, J.M.; Bradbury, R.H.; Sala, E.; Hughes, T.P.; Bjorndal, K.A.; Cooke, R.G.; McArdle, D.; McClenachan, L.; Newman, M.J.H.; Paredes, G.; *et al.* Global trajectories of the long-term decline of coral reef ecosystems. *Science* **2003**, *301*, 955–958.
3. Hughes, T.P.; Baird, A.H.; Bellwood, D.R.; Card, M.; Connolly, S.R.; Folke, C.; Grosberg, R.; Hoegh-Guldberg, O.; Jackson, J.B.C.; Kleypas, J.A.; *et al.* Climate change, human impacts, and the resilience of coral reefs. *Science* **2003**, *301*, 929–933.
4. Connell, J.H. Diversity in tropical rain forests and coral reefs. *Science* **1978**, *199*, 1302–1310.
5. Reaka-Kudla, M.L. The global biodiversity of coral reefs. In *Biodiversity II: Understanding and Protecting Our Biological Resources*; Reaka-Kudla, M.L., Wilson, D.E., Wilson, E.O., Eds.; Joseph Henry Press: Washington, DC, USA, 1997; pp. 83–108.
6. Adrianov, A.V. Current problems in marine biodiversity studies. *Russ. J. Mar. Biol.* **2004**, *30*, S1–S16.
7. Small, A.; Adey, W.; Spoon, D. Are current estimates of coral reef biodiversity too low? The view through the window of a microcosm. *Atoll Res. Bull.* **1998**, *458*, 1–20.
8. Reaka, M.L.; Rodgers, P.J.; Kudla, A.U. Patterns of biodiversity and endemism on Indo-West Pacific coral reefs. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 11474–11581.

9. Roberts, C.M.; McClean, C.J.; Veron, J.E.N.; Hawkins, J.P.; Allen, G.R.; McAllister, D.E.; Mittermeier, C.G.; Schueler, F.W.; Spalding, M.; Wells, F.; *et al.* Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **2002**, *295*, 1280–1284.
10. Munday, P.L. Habitat loss, resource specialization, and extinction on coral reefs. *Glob. Change Biol.* **2004**, *10*, 1642–1647.
11. Carpenter, K.E.; Abrar, M.; Aeby, G.; Aronson, R.B.; Banks, S.; Bruckner, A.; Chiriboga, A.; Cortés, J.; Delbeek, J.C.; DeVantier, L.; *et al.* One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **2008**, *321*, 560–563.
12. Glynn, P.W. In tandem reef coral and cryptic metazoan declines and extinctions. *Bull. Mar. Sci.* **2011**, *87*, 1–28.
13. Wilson, E.O. *The Diversity of Life*; W. W. Norton and Company: New York, NY, USA, 1992.
14. Carlton, J.T.; Geller, J.B.; Reaka-Kudla, M.L.; Norse, E.A. Historical extinctions in the sea. *Ann. Rev. Ecol. Syst.* **1999**, *30*, 515–538.
15. Baker, A.C.; Glynn, P.W.; Riegl, B. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast Shelf Sci.* **2008**, *80*, 435–471.
16. Wilkinson, C. *Status of Coral Reefs of the World: 2000*; Australian Institute of Marine Science: Townsville, Australia, 2000.
17. Maynard, J.A.; Baird, A.H.; Pratchett, M.S. Revisiting the Cassandra syndrome; the changing climate of coral reef research. *Coral Reefs* **2008**, *27*, 745–749.
18. Enochs, I.C.; Toth, L.T.; Brandtneris, V.W.; Afflerbach, J.C.; Manzello, D.P. Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. *Mar. Ecol. Prog. Ser.* **2011**, *438*, 105–118.
19. Ginsburg R.N. Geological and biological roles of cavities in coral reefs. In *Perspectives on Coral Reefs*; Barnes, D.J., Ed.; Australian Institute of Marine Science; Townsville, Australia, 1983; pp. 148–153.
20. Richter, C.; Wunsch, M.; Rasheed, M.; Kötter, I.; Badran, M.I. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature* **2001**, *413*, 726–730.
21. Caley, M.J.; Buckley, K.A.; Jones, G.P. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* **2001**, *82*, 3435–3448.
22. Enochs, I.C.; Hockensmith, G. Effects of coral mortality on the community composition of cryptic metazoans associated with *Pocillopora damicornis*. In *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, FL, USA, 7–11 July 2008; pp. 1368–1372.
23. Coker, D.J.; Pratchett, M.S.; Munday, P.L. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behav. Ecol.* **2009**, *20*, 1204–1210.
24. Enochs, I.C.; Manzello, D.P. Species richness of motile coral reef cryptofauna across a gradient of framework erosion in Pacific Panamá. *Coral Reefs* **2012**, in press.
25. Enochs, I.C. Motile cryptofauna associated with live and dead coral substrates: Implications for coral mortality and framework erosion. *Mar. Biol.* **2012**, in press.
26. Lang, J.C.; Chornesky, E.A. Competition between scleractinian reef corals: A review of mechanisms and effects. In *Ecosystems of the World: Coral Reefs*; Dubinsky, Z., Ed.; Elsevier Press: Amsterdam, The Netherlands, 1990; pp. 209–252.

27. Moran, D.P.; Reaka, M.L. Bioerosion and availability of shelter for benthic reef organisms. *Mar. Ecol. Prog. Ser.* **1988**, *44*, 249–263.
28. Jackson, J.B.C. Distribution and ecology of clonal and aclonal benthic invertebrates. In *Population Biology and Evolution of Clonal Organisms*; Jackson, J.B.C., Buss, L.W., Cook, R.E., Eds.; Yale University Press: New Haven, CT, USA, 1985; pp. 297–355.
29. Bailey-Brock, J.; Brock, R.; Kam, A.; Fukunaga, A.; Akiyama, H. Anthropogenic disturbances on shallow cryptofaunal communities in a marine life conservation district on Oahu, Hawai'i. *Int. Rev. Hydrobiol.* **2007**, *92*, 291–300.
30. Patton, W.K. Community structure among the animals inhabiting the coral *Pocillopora damicornis* at Heron Island, Australia. In *Symbiosis in the Sea*; Vernberg, W., Ed.; University of South Carolina Press: Columbia, SC, USA, 1974; pp. 219–243.
31. Stimson, J. Stimulation of fat-body production in the polyps of the coral *Pocillopora damicornis* by the presence of mutualistic crabs of the genus *Trapezia*. *Mar. Biol.* **1990**, *106*, 211–218.
32. Rotjan, R.D.; Lewis, S.M. Impact of coral predators on tropical reefs. *Mar. Ecol. Prog. Ser.* **2008**, *367*, 73–91.
33. Alvarez-Filip, L.; Dulvy, N.K.; Gill, J.A.; Côté, I.M.; Watkinson, A.R. Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proc. Roy. Soc. Lond. B* **2009**, *276*, 3019–3025.
34. Manzello, D.P. Reef development and resilience to acute (El Niño Warming) and chronic (high-CO₂) disturbances in the eastern tropical Pacific: A real-world climate change model. In *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, FL, USA, 7–11 July 2008; pp. 1299–1304.
35. Reaka-Kudla, M.L.; Feingold, J.S.; Glynn, P.W. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. *Coral Reefs* **1996**, *15*, 101–107.
36. Wilson, S.K.; Dolman, A.M.; Cheal, A.J.; Emslie, M.J.; Pratchett, M.S.; Sweatman, H.P.A. Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* **2009**, *28*, 3–14.
37. Graham, N.A.J.; Wilson, S.K.; Jennings, S.; Polunin, N.V.C.; Robinson, J.; Bijoux, J.P.; Daw, T.M. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* **2007**, *21*, 1291–1300.
38. Graham, N.A.J.; Wilson, S.K.; Pratchett, M.S.; Polunin, N.V.C.; Spalding, M.D. Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodiver. Conserv.* **2009**, *18*, 3325–3336.
39. Peyrot-Clausade, M. Motile cryptofauna of Tuléar reef flats. *Mar. Biol.* **1980**, *59*, 43–47.
40. Veron, J.E.N. *Corals of the World*; Australian Institute of Marine Science: Townsville, Australia, 2000.
41. Coles, S.L. Species diversity of decapods associated with living and dead reef coral *Pocillopora meandrina*. *Mar. Ecol. Prog. Ser.* **1980**, *2*, 281–291.
42. Shirayama, Y.; Horikoshi, M. A new method of classifying the growth form of corals and its application to a field survey of coral-associated animals in Kabira Cove, Ishigaki Island. *J. Oceanogr. Soc. Jpn.* **1982**, *28*, 193–207.

43. Kirsteuer, E. Quantitative and qualitative aspects of the Nemertean Fauna in tropical coral reefs. In *Proceedings of the 1st International Symposium Coral Reefs*, Mandapam Camp, India, 12–16 January 1969; pp. 363–371.
44. Preston, N.P.; Doherty, P.J. Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. I. Agile shrimps. *Mar. Ecol. Prog. Ser.* **1990**, *66*, 47–61.
45. Grime, J.P. Competitive exclusion in herbaceous vegetation. *Nature* **1973**, *242*, 344–347.
46. Grigg, R.W.; Maragos, J.E. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* **1974**, *55*, 387–395.
47. Siitonen, J. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* **2001**, *49*, 11–41.
48. Schiegg, K. Saproxylic insect diversity of beech: Limbs are richer than trunks. *For. Ecol. Manag.* **2001**, *149*, 295–304.
49. Nordén, B.; Ryberg, M.; Götberg, F.; Olausson, B. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biol. Cons.* **2004**, *117*, 1–10.
50. Nilsson, S.G.; Hedin, J.; Niklasson, M. Biodiversity and its assessment in boreal and nemoral forests. *Scand. J. For. Res. Suppl.* **2001**, *3*, 10–26.
51. Gardner, T.A.; Côté, I.M.; Gill, J.A.; Grant, A.; Watkinson, A.R. Long-term region-wide declines in Caribbean corals. *Science* **2003**, *301*, 958–960.
52. Peyrot-Clausade, M.; Hutchings, P.; Richard, G. Temporal variations of macroborers in massive *Porites lobata* on Moorea, French Polynesia. *Coral Reefs* **1992**, *11*, 161–166.