UNIVERSIDADE FEDERAL DA PARAÍBA
CENTRO DE CIÊNCIAS EXATAS E DA NATUREZA
DEPARTAMENTO DE SISTEMÁTICA E ECOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
ÁREA DE CONCENTRAÇÃO ZOOLOGIA

JULIANO MORAIS

RECIFES PROFUNDOS FUNCIONAM COMO REFÚGIOS? UM TESTE COM CORAIS DO ATLÂNTICO SUL

JOÃO PESSOA - PARAÍBA
2018

JULIANO MORAIS

RECIFES PROFUNDOS FUNCIONAM COMO REFÚGIOS? UM TESTE COM CORAIS DO ATLÂNTICO SUL

Dissertação apresentada ao Programa de Pós-graduação em Ciências Biológicas, área de concentração Zoologia, da Universidade Federal da Paraíba, como parte dos requisitos para obtenção do Grau de Mestre em Ciências Biológicas (Zoologia).

Orientador: Dr. Bráulio Almeida Santos

JOÃO PESSOA - PARAÍBA
2018

Catalogação na publicação
Seção de Catalogação e Classificação

M827r Morais, Juliano.
Recifes profundos funcionam como refúgios? Um teste com corais do Atlântico Sul / Juliano Morais. - João Pessoa, 2018.
89 f. : il.

Orientação: Bráulio Almeida Santos.
Dissertação (Mestrado) - UFPB/CCEN.

1. Zoologia. 2. Corais - Costa Paraibana. 3. Ambientes recifais. I. Santos, Bráulio Almeida. II. Título.

UFPB/BC

Ata da 303ª Apresentação e Banca de Defesa de Mestrado de Juliano Morais

Ao(s) vinte e três dias do mês de fevereiro de dois mil e dezoito, às 09:00 horas, no(a) Sala 02 do DSE, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a dissertação de mestrado de **Juliano Morais**, candidato(a) ao grau de Mestre em Ciências Biológicas. A banca foi composta pelos seguintes professores/pesquisadores: **Dr. Bráulio Almeida Santos (orientador), Dr. Pablo Riul (titular) e Dra. Beatrice Padovani Ferreira (titular)**. Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra para o(a) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Juliano Morais**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"Recifes profundos funcionam como refúgio? Um teste com corais do atlântico sul".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito APROVADO. Perante a aprovação, declarou-se o(a) candidato(a) legalmente habilitado(a) a receber o grau de **Mestre** em **Ciências Biológicas**, área de concentração **Zoologia**. Nada mais havendo a tratar eu**, Dr. Bráulio Almeida Santos**, como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 23/02/2018.

Dr. Bráulio Almeida Santos (orientador)

Dr. Pablo Riul (titular)

Dra. Beatrice Padovani Ferreira (titulartitulartitular)

Ciente do Resultado:
Juliano Morais
Juliano Morais

AGRADECIMENTOS

Ao meu orientador Prof. Bráulio A. Santos, pela excelente orientação, oportunidades, ensinamentos, confiança e liberdade no desenvolvimento do trabalho. Além de um excelente orientador, foi meu grande incentivador, e um exemplo como profissional.

Aos integrantes da banca examinadora e aos suplentes, que aceitaram avaliar e contribuir com a construção deste trabalho de dissertação.

A Fundação Grupo O Boticário de Proteção à Natureza pelo financiamento do projeto, sem o qual a realização do trabalho não seria possível.

À CAPES pelo suporte financeiro, me possibilitando assim estar em tempo integral dedicado ao mestrado.

A Mar Aberto operadora de mergulho por toda a logística necessária para o trabalho de campo, sempre prestativos em proporcionar as melhores experiências no mar.

Aos mergulhadores, Ismar Dust, Michel Russi, e Orione A. Silva, pelo trabalho nos mergulhos técnicos profundos.

Ao PPGCB (Zoologia) e a todos os professores que contribuíram para minha formação.

A todos os amigos que fiz nesses dois anos, muito obrigado pela companhia e contribuições.

A minha família que, mesmo estando tão longe, esteve sempre muito presente em minhas decisões e conquistas.

A minha querida esposa Dailanne Andrade, por suportar sempre firme a esse período longo de formação, por sempre me apoiar em tudo, sendo minha maior incentivadora na busca dessa carreira.

RESUMO GERAL

A hipótese dos refúgios em recifes profundos prevê que ecossistemas recifais profundos (>30 m de profundidade) podem atuar como refúgios para a biota dos recifes rasos e recuperá-la após distúrbios humanos. Ainda que a hipótese tenha sido postulada há quase duas décadas, faltam evidências empíricas que a suportem para diversos grupos biológicos, incluindo corais. Pouco se sabe também sobre como os corais respondem a diferentes tipos de distúrbios humanos, cuja magnitude e frequência variam consideravelmente. Neste trabalho, utilizei comunidades de corais ocorrentes na costa paraibana para testar a hipótese dos refúgios em recifes profundos. Como preâmbulo, revisei a literatura (110 estudos) para identificar lacunas teóricas e geográficas sobre as respostas dos corais à acidificação do oceano, mudança climática, sobrepesca, poluição e turismo desordenado. Classifiquei os estudos de acordo com o oceano, ecorregião, tipo de perturbação, nível de organização biológica, abordagem de estudo, método de coleta de dados, profundidade em que os dados foram coletados e tipo de resposta do coral. Descobri que os estudos estão concentrados no Indo- Pacifico (36.3%) e no Caribe (31.9%) e têm utilizado abordagem observacional (59,1%) com mergulho SCUBA (37,2%) para avaliar o impacto do aquecimento do oceano (55,4%) nas comunidades de corais (58,1%), especialmente em águas rasas (até 27 m). Estes resultados revelam a escassez de informações sobre respostas de corais à poluição, turismo, sobrepesca e acidificação, particularmente em ecossistemas recifais profundos e em ecorregiões fora do Indo-Pacífico e Caribe. Para o teste da hipótese do refúgio, utilizei uma abordagem no nível de comunidade capaz de particionar a diversidade em seus componentes alfa e beta ao longo de um gradiente de 3 a 61 m. Amostrei, através de mergulho SCUBA, 7 recifes rasos (<30 m) e 12 profundos (>30 m). Contrário às expectativas, os recifes rasos apresentaram maior diversidade gama que os profundos (13 vs. 7 espécies); maior proporção de espécies especialistas em profundidade (77% vs. 57%); diversidade alfa similar porém maior diversidade beta de espécies raras, típicas e comuns; e funções exclusivas não encontradas nas áreas profundas (e.g. corais moles). Esses resultados refutam a hipótese de que os recifes profundos funcionam como refúgios para corais. Entretanto, revelam que recifes rasos e profundos são complementares, sendo fundamental conservar todo o gradiente de profundidade para proteger integralmente a diversidade regional de corais.

Palavras chaves: Mudanças climáticas; distúrbios humanos; ecossistemas de corais mesofóticos; hipótese de refúgio; número de Hill; recifes de corais.

ABSTRACT

The hypothesis of deep reef refuges predicts that deep reef ecosystems (> 30 m depth) may act as refuges for the biota of shallow reefs and recover it after human disturbances. Although the hypothesis has been postulated almost two decades, empirical evidence is lacking that support it for diverse biological groups, including corals. Little is known about how corals respond to different types of human disorders, whose magnitude and frequency vary considerably. In this work, I used coral communities on the coast of Paraíba to test the hypothesis of deep reef refuges. As a preamble, I reviewed the literature (110 studies) to identify theoretical and geographic gaps on coral responses to ocean acidification, climate change, overfishing, pollution, and disordered tourism. I ranked the studies according to the ocean, ecoregion, type of disturbance, level of biological organization, study approach, method of data collection, depth at which data were collected and type of coral response. I have found that the studies are concentrated in the Indo-Pacific (36.3%) and the Caribbean (31.9%) and have used an observational approach (59.1%) with SCUBA diving (37.2%) to assess the impact of ocean warming 55.4%) in coral communities (58.1%), especially in shallow waters (up to 27 m). These results reveal the scarcity of information on coral responses to pollution, tourism, overfishing and acidification, particularly in deep reef ecosystems and in ecoregions outside the Indo-Pacific and Caribbean. For the test of the hypothesis of the refuge, I used a community-level approach capable of partitioning the diversity in its alpha and beta components along a gradient of 3 to 61 m. Through SCUBA diving, I found 7 shallow reefs (<30 m) and 12 deep reefs (> 30 m). Contrary to expectations, shallow reefs presented greater range diversity than the deep ones (13 vs. 7 species); highest proportion of specialist species in depth (77% vs. 57%); similar alpha diversity but higher beta diversity of rare, typical and common species; and unique functions not found in deep areas (e.g., soft corals). These results refute the hypothesis that deep reefs function as refuges for corals. However, they reveal that shallow and deep reefs are complementary, being essential to conserve the entire depth gradient to fully protect regional coral diversity.

Key words: climate change; human disturbances; mesophotic coral ecosystems, refuge hypothesis, Hill number; coral reef.

SUMÁRIO

INTRODUÇÃO GERAL

Recifes de corais possuem a maior densidade de biodiversidade de todos os ecossistemas, sendo considerados os ecossistemas mais diversos dos mares e uma das estruturas mais antigas da Terra constituídas por organismos vivos (Budd and Pandolfi 2010) Os recifes de corais ocupam somente 0,2% de toda área dos oceanos (Spalding and Grenfell 1997), porém aproximadamente 25% de todas as espécies marinhas dependem deles para viver (Davidson 1998). São típicos de águas tropicais quentes e claras, locais onde durante o inverno, a temperatura do mar permanece acima dos 18°C (Wilkinson 2008). No entanto, muitas comunidades de corais são também observadas em maiores latitudes, como na Austrália (Harriott 1999), Japão (Nozawa et al. 2006) e na América do Sul (Castro and Pires 2001, Leão et al. 2016), em águas turvas, como as dos recifes da foz do Rio Amazonas (Moura et al. 2016).

O Brasil detêm a maior e mais rica área de recife em todo o Oceano Atlântico Sul, mas a diversidade de corais brasileiros é baixa em comparação com os recifes do Caribe, com poucas espécies de construção de recifes, mas um alto endemismo e muitas espécies de formas maciças (Castro and Pires 2001, Leão et al. 2016). A fauna de corais brasileiros é representada por 23 espécies de corais escleractíneos, 5 hidrocorais (Leão et al. 2016a) e pelo menos 22 espécies de octocorais (Castro et al. 2010). Os recifes brasileiros estão espalhados de 0º50 a 18º00, divididos em 4 regiões: a região norte, os recifes da costa do Nordeste, os recifes da costa leste e os ecossistemas dos recifes das ilhas oceânicas, ocorrendo por 3.000 km ao longo da costa (Leao et al. 2003, Ferreira et al. 2013).

Alguns levantamentos revelam que, em nível mundial, os recifes de corais contribuem em quase 375 bilhões em bens e serviços por meio de atividades como proteção costeira, pesca e turismo (Wilkinson 2002, 2008). Além disso, sustentam uma grande diversidade biológica e genética, exercendo função fundamental para o sucesso ecológico dos ecossistemas marinhos (Moberg and Folke 1999). Porém, eles estão sujeitos às alterações causadas pelo homem, tais como aquecimento global, acidificação, sobrepesca, poluição e turismo desordenado (Carpenter et al. 2008). Por exemplo, o dióxido de carbono atmosférico é o mais alto em no mínimo 15 milhões de anos (Lariviere et al. 2012). Esse grande acúmulo de carbono na atmosfera pode prejudicar os corais de duas maneiras: (1) através do aquecimento das águas oceânicas, que leva os corais a perder suas microalgas simbiontes e consequentemente ao branqueamento (Guest et al. 2016), e (2) através da acidificação dos oceanos, que interfere diretamente no processo de calcificação e construção dos recifes de corais (Edmunds et al. 2016).

A hipótese dos recifes profundos se baseia na premissa de que os recifes localizados em maiores profundidades (abaixo dos 30 m) são mais estáveis e menos afetados por distúrbios humanos que os recifes rasos, sendo menos vulneráveis e potencialmente mais resistentes a perturbações que resultem no branqueamento, incidência de doenças, mortalidade, infertilidade e falha no estabelecimento dos corais (Kahng et al. 2014). Segundo Glynn (1996) e Bongaerts et al. (2010), no caso de perturbação dos recifes rasos, os recifes profundos poderiam servir como refúgio para as espécies de corais e ajudá-las a repopular os recifes rasos quando as condições ambientais voltarem a ser adequadas.

Neste trabalho, meu objetivo principal foi testar a hipótese do refúgio em recifes profundos, utilizando comunidades de corais ocorrentes entre 3 e 61 m de profundidade na costa da Paraíba. Como preâmbulo, revisei a literatura para identificar lacunas teóricas e geográficas sobre as respostas dos corais à acidificação do oceano, mudança climática, sobrepesca, poluição e turismo desordenado. A revisão é apresentada no primeiro capítulo, a ser submetido para o periódico Marine Biology, e o teste da hipótese é apresentado no segundo capítulo, atualmente em revisão no periódico Ecology.

REFERÊNCIAS

Amado-Filho, G. M., R. L. Moura, A. C. Bastos, R. B. Francini-Filho, G. H. Pereira-Filho, R. G. Bahia, F. C. Moraes, and F. S. Motta. 2016. Mesophotic ecosystems of the unique South Atlantic atoll are composed by rhodolith beds and scattered consolidated reefs. Marine Biodiversity 46:933–936.

Antônio-de-Souza, C., and F. D. Amaral. 2002. Variação morfométrica de alguma espécies de corais Mussidae (Cnidaria, Anthozoa) do Brasil. Tropical Oceanography, Recife 30:23–36.

Appeldoorn, R., D. Ballantine, I. Bejarano, M. Carlo, M. Nemeth, E. Otero, F. Pagan,

H. Ruiz, N. Schizas, C. Sherman, and E. Weil. 2016. Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico. Coral Reefs 35:63–75.

Barros, M. M. L. de, D. de O. Pires, and C. B. e Castro. 2003. Coral Reef Paper Sexual Reproduction of the Brazilian Reef Coral Siderastrea Stellataverrill 1868 (Anthozoa , Scleractinia). Bulletin of Marine Science 73:713–724.

Bongaerts, P., T. Ridgway, E. M. Sampayo, and O. Hoegh-Guldberg. 2010. Assessing the “deep reef refugia” hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327.

Bongaerts, P., C. Riginos, R. Brunner, N. Englebert, S. R. Smith, and O. Hoegh-guldberg. 2017. Deep reefs are not universal refuges : Reseeding potential varies among coral species. Science Advances.

Boscolo, H. K., and F. L. Silveira. 2005. Reproductive biology of Palythoa caribaeorum and Protopalythoa variabilis (Cnidaria, Anthozoa, Zoanthidea) from the southeastern coast of Brazil. Brazilian Journal of Biology 65:29–41.

Bridge, T. C. L., T. J. Done, R. J. Beaman, A. Friedman, S. B. Williams, O. Pizarro, and J. M. Webster. 2011. Topography , substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin , central Great Barrier Reef , Australia. Coral Reefs:143–153.

Bridge, T., and J. Guinotte. 2012. Mesophotic Coral Reef Ecosystems in the Great Barrier Reef World Heritage Area in the Great Barrier Reef World. Great Barrier Reef Marine Park Authority.

Budd, A. F., and J. M. Pandolfi. 2010. Evolutionary novelty is concentrated at the edge of coral species distributions. Science 328:1558–1561.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzman, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. Science 321:560–563.

Castro, C. B., M. S. Medeiros, and L. L. Loiola. 2010. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. Journal of Natural History 44:763–827.

Castro, C. B., and D. O. Pires. 2001. Brazilian coral reefs: what we already know and what is still missing. Bulletin of Marine Science 69:357–371.

Chao, A., C. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

Chao, A., K. H. Ma, and T. C. Hsieh. 2016. iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User’s Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Chao, A., and T. J. Shen. 2010. Program SPADE: species prediction and diversity estimation. Program and user’s guide. CARE, Hsin-Chu, Taiwan.

Cordeiro, R. T., B. M. Neves, J. S. Rosa-Filho, and C. D. Pérez. 2015. Mesophotic coral ecosystems occur offshore and north of the Amazon River. Bulletin of Marine Science 91:491–510.

Culter, J. K., K. B. Ritchie, S. A. Earle, D. E. Guggenheim, R. B. Halley, K. T. Ciembronowicz, A. C. Hine, B. D. Jarrett, S. D. Locker, and W. C. Jaap. 2006. Pulley reef: A deep photosynthetic coral reef on the West Florida Shelf, USA. Coral Reefs 25:228.

Davidson, O. G. 1998. The enchanted braid. Coming to the terms with nature on the Coral Reef. New York: John Wiley & Sons Inc:269.

Edmunds, P. J., S. Comeau, C. Lantz, A. Andersson, C. Briggs, A. Cohen, J.-P. Gattuso, J. M. Grady, K. Gross, M. Johnson, E. B. Muller, J. B. Ries, S. Tambutté, E. Tambutté, A. Venn, and R. C. Carpenter. 2016. Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs. BioScience 66:biw023.

Erftemeijer, P. L. A., B. Riegl, B. W. Hoeksema, and P. A. Todd. 2012. Environmental impacts of dredging and other sediment disturbances on corals : A review. Marine Pollution Bulletin 64:1737–1765.

Feitoza, B. M., R. S. Rosa, and L. A. Rocha. 2005. Ecology and zoogeography of deep-reef fishes in northeastern Brazil. Bulletin of Marine science 76:725–742.

Ferreira, B. P., M. B. S. F. Costa, M. S. Coxey, A. L. B. Gaspar, D. Veleda, and M. Araujo. 2013. The effects of sea surface temperature anomalies on oceanic coral reef systems in the southwestern tropical Atlantic. Coral Reefs:441–454.

Francini-filho, R. B., E. O. C. Coni, P. M. Meirelles, G. M. Amado-filho, F. L. Thompson, G. H. Pereira-filho, A. C. Bastos, D. P. Abrantes, P. Y. G. Sumida, N. L. Oliveira, C. M. Ferreira, F. Z. Gibran, A. Z. Gu, L. Kaufman, C. V Minte-vera, and R. L. Moura. 2013. Dynamics of Coral Reef Benthic Assemblages of the Abrolhos Bank , Eastern Brazil : Inferences on Natural and Anthropogenic Drivers. PLoS ONE 8:1–12.

Glynn, P. w. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biology 2:495–509.

Guest, J. R., J. Low, K. Tun, B. Wilson, C. Ng, D. Raingeard, K. E. Ulstrup, J. T. I. Tanzil, P. A. Todd, T. C. Toh, D. McDougald, L. M. Chou, P. D. Steinberg, A. Douglas, D. . Smith, and T. C. LaJeunesse. 2016. Coral community response to bleaching on a highly disturbed reef. Scientific Reports 6:20717.

Harriott, V. J. 1999. Coral growth in subtropical eastern Australia. Coral Reefs 18:281–291.

Hill, J., and C. Wilkinson. 2004. Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville:117.

Hinderstein, L. M., J. C. A. Marr, F. A. Martinez, M. J. Dowgiallo, K. A. Puglise, R. L. Pyle, D. G. Zawada, and R. Appeldoorn. 2010. Theme section on “Mesophotic Coral Ecosystems: Characterization, Ecology, and Management.” Coral Reefs 29:247–251.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world’s coral reefs. Marine and Freshwater Research 50:839.

Hoeksema, B. W. 2012. Extreme morphological plasticity enables a free mode of life in Favia gravida at Ascension Island (South Atlantic). Marine Biodiversity 42:289–295.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Jost, L. 2010. Independence of alpha and beta diversities. Ecology 91:1969–1974.

Kahng, S. E., Y. Benayahu, and H. R. Lasker. 2011. Sexual reproduction in octocorals.

Marine Ecology Progress Series 443:265–283.

Kahng, S. E., J. M. Copus, and D. Wagner. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Current Opinion in Environmental Sustainability 7:72–81.

Karlson, R. H. 1981. Reproductive patterns in Zoanthus spp. from Discovery Bay, Jamaica.

Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geosciences 32:1259–1269.

Kühlmann, D. H. H. 1983. Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36:183–204.

Lariviere, J. P., A. C. Ravelo, A. Crimmins, P. S. Dekens, H. L. Ford, M. Lyle, and M. W. Wara. 2012. LateMiocene decoupling of oceanicwarmth and atmospheric carbon dioxide forcing. Nature 486:97–100.

Leao, Z., U. Federal, R. Kikuchi, and U. Federal. 2003. Corals and coral reefs of Brazil.

Leão, Z. M. A. N., R. K. P. Kikuchi, B. P. Ferreira, E. G. Neves, H. H. Sovierzoski, M. D. M. Oliveira, M. Maida, M. D. Correia, and R. Jhonsson. 2016a. Brazilian coral reefs in a period of global change: A synthesis. Brazilian Journal of Oceanography 64:97–116.

Leão, Z. M. A. N., R. K. P. Kikuchi, B. P. Ferreira, E. G. Neves, H. H. Sovierzoski, M. D. M. Oliveira, M. Maida, M. D. Correia, and R. Johnsson. 2016b. Brazilian coral reefs in a period of global change: A synthesis.

Leão, Z. M. A. N., R. K. P. Kikuchi, and V. Testa. 2003. Corals and coral reefs of Brazil.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lesser, M. I. P., M. Lattery, M. I. S. Tat, M. I. O. Jimi, and R. Ates. 2010. Photoacclimatization by the coral Montastraea cavernosa in the mesophotic zone : light , food , and genetics. Ecology 91:990–1003.

Lesser, M. P., M. Slattery, and J. J. Leichter. 2009. Ecology of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 375:1–8.

Lewis, J. B. 2006. Biology and Ecology of the Hydrocoral Millepora on Coral Reefs. Advances in Marine Biology 50:1–55.

Liddell, W. D., and W. E. Avery. 2000. Temporal change in hard substrate communities 10-250 m, the Bahamas. Proceedings of the Ninth International Coral Reef Symposium. Volume 2 23–27 Octo:1053–1058.

Lins-De-Barros, M., and D. O. Pires. 2007. Comparison of the reproductive status of the scleractinian coral Siderastrea stellata throughout a gradient of 20 degrees of latitude. Brazilian Journal of Oceanography 55:67–69.

Loya, Y., G. Eyal, T. Treibitz, M. P. Lesser, and R. Appeldoorn. 2016. Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9.

Lueg, J. R., A. L. Moulding, V. N. Kosmynin, and D. S. Gilliam. 2012. Gametogenesis and Spawning of *Solenastrea bournoni* and *Stephanocoenia intersepta* in Southeast Florida, USA. Journal of Marine Biology 2012:1–13.

Luiz, O. J., J. S. Madin, D. R. Robertson, L. A. Rocha, P. Wirtz, and S. R. Floeter. 2012. Ecological traits influencing range expansion across large oceanic dispersal barriers : insights from tropical Atlantic reef fishes. Proc Roy Soc B. 279:1033–1040.

Meirelles, P. M., G. M. Amado-Filho, G. H. Pereira-Filho, H. T. Pinheiro, R. L. De Moura, J. C. Joyeux, E. F. Mazzei, A. C. Bastos, R. A. Edwards, E. Dinsdale, R. Paranhos, E. O. Santos, T. Iida, K. Gotoh, S. Nakamura, T. Sawabe, C. E. Rezende, L. M. R. Gadelha, R. B. Francini-Filho, C. Thompson, and F. L. Thompson. 2015. Baseline assessment of mesophotic reefs of the Vitória-Trindade Seamount Chain based on water quality, microbial diversity, benthic cover and fish biomass data. PLoS ONE 10:1–22.

Moberg, F. F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29:215–233.

Van Moorsel, G. 1983. Reproductive strategies in two closely related stony corals (Agaricia, Scleractinia). Marine Ecology Progress Series 13:273–283.

Morgan, K. M., C. T. Perry, S. G. Smithers, J. A. Johnson, and J. J. Daniell. 2016. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. Scientific Reports 6:29616.

Moura, R. L., G. M. Amado-Filho, F. C. Moraes, P. S. Brasileiro, P. S. Salomon, M. M. Mahiques, A. C. Bastos, M. G. Almeida, J. M. Silva, B. F. Araujo, F. P. Brito, T. P. Rangel, B. C. V. Oliveira, R. G. Bahia, R. P. Paranhos, R. J. S. Dias, E. Siegle, A. G. Figueiredo, R. C. Pereira, C. V Leal, E. Hajdu, N. E. Asp, G. B. Gregoracci, S. Neumann-Leitao, P. L. Yager, R. B. Francini-Filho, A. Froes, M. Campeao, B. S. Silva, A. P. B. Moreira, L. Oliveira, A. C. Soares, L. Araujo, N. L. Oliveira, J. B. Teixeira, R. A. B. Valle, C. C. Thompson, C. E. Rezende, and F. L. Thompson. 2016. An extensive reef system at the Amazon River mouth. Science Advances 2:e1501252–e1501252.

Moura, R. L. De, N. A. Secchin, G. M. Amado-filho, R. Bastos, M. O. Freitas, C. V. Minte-vera, J. Batista, F. L. Thompson, A. Z. Guth, R. M. Lopes, and A. C. Bastos. 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Continental Shelf Research 70:109–117.

Neves, E. G., and D. O. Pires. 2002. Sexual reproduction of Brazilian coral Mussismilia hispida (Verrill, 1902). Coral Reefs 21:161–168.

Neves, E. G., F. L. Silveira, M. Pichon, and R. Johnsson. 2010. Cnidaria, Scleractinia, Siderastreidae, Siderastrea siderea (Ellis and Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical Southwestern Atlantic. Check List 6:505–510.

Nozawa, Y., M. Tokeshi, and S. Nojima. 2006. Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. Marine Biology 149:1047–1058.

Nunes, F., R. D. NorrisS, and N. Knowlton. 2009. Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. Molecular Ecology 18:4283–4297.

de Oliveira Soares, M., M. Davis, C. C. de Paiva, and P. B. de Macêdo Carneiro. 2016. Mesophotic ecosystems: coral and fish assemblages in a tropical marginal reef (northeastern Brazil). Marine Biodiversity.

Van Oppen, M. J. H., P. Bongaerts, J. N. Underwood, L. M. Peplow, and T. F. Cooper. 2011. The role of deep reefs in shallow reef recovery : an assessment of vertical connectivity in a brooding coral from west and east Australia. Molecular Ecology 20:1647–1660.

De Putron, S. J., and S. R. Smith. 2011. Planula release and reproductive seasonality of the scleractinian coral porites astreoides in bermuda, a high-latitude reef. Bulletin of Marine Science 87:75–90.

Riegl, B., and W. E. Piller. 2003. Possible refugia for reefs in times of environmental stress. International Journal of Earth Sciences 92:520–531.

Safuan, M., H. B. Wee, Y.-S. Hii, H.-C. Liew, and Z. Bachok. 2015. Optimization of Coral Video Transect Technique for Coral Reef Survey : Comparison with Intercept Transect Technique. Open Journal of Marine Science 5:379–397.

Semmler, R. F., W. C. Hoot, and M. L. Reaka. 2017. Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs ? Coral Reefs 36:433–444.

Serrano, X. M., I. B. Baums, K. O'Reilly, T. B. Smith, R. J. Jones, T. L. Shearer, F. L. D. Nunes, and A. C. Baker. 2014. Geographic differences in vertical connectivity in the Caribbean coral Montastraea cavernosa despite high levels of horizontal connectivity at shallow depths. Molecular Ecology 23:4226–4240.

Smith, T. B., J. Gyory, M. E. Brandt, W. J. Miller, J. Jossart, and R. S. Nemeth. 2016. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Global Change Biology 22:2756–2765.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. Mcmanus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. BioScience 57:573.

Spalding, M. D., and A. M. Grenfell. 1997. New estimates of global and regional coral reef areas. Coral Reefs 16:225–230.

Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–53.

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164:853–860.

Underwood., J. N., L. D. Smith., M. J. Van Oppen., and J. P. Gilmour. 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular Ecology 16:771–784.

Venn, A. A., F. K. Weber, J. E. Loram, and R. J. Jones. 2009. Deep zooxanthellate corals at the high latitude Bermuda Seamount. Coral Reefs 28:135.

Wagner, D., R. G. Waller, A. D. Montgomery, C. D. Kelley, and R. J. Toonen. 2012.

Sexual reproduction of the Hawaiian black coral Antipathes griggi (Cnidaria: Antipatharia). Coral Reefs 31:795–806.

Wilkinson, C. 2002. Status of Coral Reefs of the World. Australian Institute of Marine 2.

Wilkinson, C. 2008. Status of Coral Reefs of the World: 2008. Status of Coral Reefs of the World: 2008:5–19.

Zilberberg, C., D. P. Abrantes, J. A. Marques, L. F. Machado, and L. F. de B. Marangoni. 2016. Conhecendo os Recifes Brasileiros - Coral Vio.

Capítulo 1

Artigo a ser submetido na **MARINE BIOLOGY – Student reviews**

Research gaps of coral ecology in a changing world

Juliano Morais[1], Aline P. M. Medeiros[1], Bráulio A. Santos[2,*]

[1] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil.

[2] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil. Email: braulio@dse.ufpb.br

*Corresponding author: braulio@dse.ufpb.br, + 55 83 3216-7406

Acknowledgments

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) and Fundação de Apoio à Pesquisa do Estado da Paraíba (Fapesq-PB) for the graduate scholarships provided to JM and APMM, respectively. BAS received research grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number 310340/2016-0) and Fundação Grupo Boticário de Proteção à Natureza (grant number 1044-20152).

Abstract

Corals have long inspired marine ecologists and conservationists around the world due to their remarkable ecological and socioeconomic importance. Much knowledge on the human impacts on coral species has been accumulated, especially on coral reef ecosystems, but relevant research areas on coral ecology remain underappreciated in human-dominated seascapes. In this review we assessed 110 studies on coral responses to five major human disturbances– acidification, climate change, overfishing, pollution and non-regulated tourism –to identify geographic and theoretical gaps in applied coral ecology and help to guide further researches on the topic. We searched for papers in Web of Science published from 2000 to 2016 and classified them according to the ocean, ecoregion, disturbance type, level of biological organization, study approach, method of data collection, depth of data collected, and type of coral response. Most studies were carried out in the Indo-Pacific and Caribbean (36.3 and 31.9%, respectively) and used observational approach (59.1%) with SCUBA diving (37.2%) to assess the impact of ocean warming (55.4%) on coral communities (58.1%). Only 37 of the 232 global ecoregions were studied. All studies were restricted to shallow waters (0.5-27 m depth) and reported negative response of corals to human disturbance. Our results reinforce the notion that corals are extremely sensitive to anthropogenic changes and reveal the scarcity of information on coral responses to pollution, tourism, overfishing and acidification, particularly in mesophotic ecosystems (>30 m depth) and in ecoregions outside the Indo-Pacific and Caribbean. Experimental studies at the individual and population levels should be also encouraged.

Key words: cnidaria; human disturbance; acidification; climate change; overfishing; pollution; tourism

Introduction

Coral reefs are the most diverse marine ecosystems and one of the oldest structures on Earth constituted by living organisms (Carpenter et al. 2008; Budd and Pandolfi 2010). They provide ecosystem services like fishing, tourism, structural materials, coastal protection, medical service and biochemicals, being vital for human societies and industries (Souter and Lindén 2000). Despite this ecological and socioeconomic importance, they are subject to anthropogenic changes at varying type, intensity and frequency just like any other ecosystem around the world. Many studies have shown that global warming, ocean acidification, overfishing, pollution and non-regulated tourism are the main threats to coral reefs (McLeod et al. 2013). Combined, these human threats have significant impacts on coral abundance and distribution, affecting biodiversity from local to global scales and jeopardizing people who directly depend on coral reefs to live (Hansen et al. 2008; Bryant et al. 2011; Cinner et al. 2016).

There are innumerous studies assessing different aspects of coral physiology and ecology in face of human disturbance, including several valuable reviews (Hoegh-guldberg 2007; Baker et al. 2008a; Hoegh-Guldberg et al. 2017). In this review we spatialize the more recent information on the topic (2000-2016) to identify geographic and theoretical gaps and thus help to guide further research in applied coral ecology. We gathered information from Web of Science platform using the following keywords in the title: Coral reef* acidification, Coral reef* climate change, Coral reef* overfishing, Coral reef* pollution, Coral reef* tourism. This procedure resulted in 180 papers, but 70 were focused on taxonomic groups other than corals, such as fishes and algae. We excluded them and carefully analyzed the other 110 studies to get information on: level of biological organization, threats, ocean, location.

The review is structured in three sections. First, we briefly summarize the empirical evidence on the mechanisms underlying coral responses to the threats, including publications that came out before 2000. Second, we used the outcome of our analyses to point out the current geographical and theoretical gaps in the field. Finally, we suggest further directions for filling up the gaps and guide future applied and basic research in increasingly common human-dominated seascapes.

Threats

Ocean acidification

Large-scale human activity has caused increased CO_2 emissions, thus increasing ocean acidification levels (Feely et al. 2004). This dissolved carbon in water reduces its pH and alters its chemical components (Doney et al. 2012). About 25% of all CO_2 released into the atmosphere by anthropogenic activities annually are absorbed by the oceans (Sabine et al. 2004; Quéré et al. 2009). Basically, the increase of the CO_2 emission in the atmosphere leads to the increase of the ions of CO_2 (aqueous), HCO_3^- and hydrogen ions (H^+), and decreases CO_3^{-2} (McLeod et al. 2013). The decline in CO_3^{-2} concentration reduces the saturation state of seawater aragonite (Ωa), thus causing lower rates of calcification in reef-building corals (Tab.1); Aragonite is the mineral form of calcium carbonate ($CaCO_3$) deposited by corals (Andersson et al. 2009; Clements et al. 2017).

Acidification is considered a global impact, but nutrient and sediment loading, which occurs locally, with fertilizer-rich sewage from plantations, may influence acidification in reefs close to urban centers (Kelly et al. 2011). The increase in $C0_2$ emission from the pre-industrial period reduced calcification and coral growth by approximately 40% by inhibiting the formation of aragonite (Kleypas and Langdon

2006). During the last century, the increase in CO_2 emissions induced a reduction of the oceanic pH by ~ 0.1 units, from ~ 8.25 to ~ 8.14 (Orr et al. 2005). Estimates for the future suggest a decrease of 0.3 pH units by the end of the century (Caldeira and E.Wickett 2003). The concentration of atmospheric carbon dioxide is expected to exceed 500 parts per million by 2050, significantly exceeding the concentration of the last 420,000 years during which most of the existing marine organisms evolved (Hoegh-Guldberg et al. 2007). Thus, these changes are likely to outweigh the ability of most organisms to adapt. By the end of the century, a few tropical corals will persist, but their functions as precipitator of calcium carbonate and coastal protector will reduce (Ferrario et al. 2014; Comeau et al. 2015).

For reef-building corals, the low levels of saturation of aragonite generates a high energy cost of calcification, which ends up harming the growth and the construction of reef structure (Doney et al. 2009). Several studies show that not only coral, but all reef-building organisms suffer damage from acidification (Kroeker et al. 2010). For example, Vogel et al. (2015) showed that the studied a coral *Acropora millepora* and a algae *Halimeda opuntia*, were negatively affected by the increase in acidification and that the decrease in light availability could have an additional impact on both organisms. Using a metabolic approach, Sogin et al. (2016) show that under stressful conditions caused by acidification and rising temperatures, coral changes the pathways involved in carbohydrate metabolism, cellular structural maintenance and cell signaling. In addition, they strengthen defense mechanisms to maintain cellular activity necessary for survival at the expense of reproduction and growth. In the long run, the main consequences of ocean acidification for coral reefs are reduced survival, growth, and reproduction (Kroeker et al. 2010).

Ocean warming

The increase in the concentration of greenhouse gases is the main driver for increase the atmospheric temperature and, consequently, also end up influencing the temperature of the oceans (Tab.1), (Wilkinson 2008). The projected increase in sea surface temperature (SST) up to the middle of the century, even from an optimistic perspective regarding greenhouse gas emission reductions, can range from 0.5 to 1.5°C (Kirtman et al. 2013), and from 0.7 to 2.5°C by the end of the century (Collins et al. 2013). According to some studies, SST has increased by 0.08 every decade during 1950 until 2011 (Lough 2012), playing an important role in the distribution of reef ecosystems (Kleypas et al. 1999; Deser et al. 2010) as many organisms limit their occurrence to certain thermal conditions (Drinkwater et al. 2010).

The main consequences of ocean warming on corals are major bleaching events of mass mortality (Ainsworth et al. 2016). Most of the pigmentation within corals are composed of symbiotic interactions from zooxanthellae algae (*Symbiodinium* spp.); the term coral bleaching refers to the partial or total loss of zooxanthellae algae (Lough and Oppen 2009). Iglesias-prieto and colleagues (1992) show that endosymbionts *Symbiodinium* start to abandon the coral when exposed to 30°C temperature and leave it completely at 34-36°C. For example Hughes et al. (2017) in a recent study on Australia's large coral barrier showed a strong relationship between the temperature increase and the level of bleaching in corals. This process increases respiratory rates and susceptibility to diseases that can lead to death (Kaczmarsky 2006).

Corals live extremely close to the thermal limits because they are sensitive to temperature changes, even if they are low, 1 or 2°C elevation can result in large scale bleaching (Crabbe 2008). Because of this, most disease events are identified during or after bleaching (Cantin and Lough 2014), although they may partially or fully recover from bleaching events (Depczynski et al. 2013). Many examples of mass mortality associated with bleaching have been documented, reducing coral cover and modifying the structure and function of the entire benthic community (Thompson and Dolman 2010; Burt et al. 2011; Wild et al. 2011; Marimuthu et al. 2013; Buglass et al. 2015; Swain et al. 2016; Guest et al. 2016). Actually, the consequences of bleaching may be classified into two broad categories: immediate and longer term effects (Baker et al. 2008b). Immediate effects involve decreased tissue and skeletal growth, increased susceptibility to disease and mortality, and negative impact on coral reef organisms. Longer term effects involve reduced coral reproduction end recruitment, bioerosion, change in algal symbiont communities, and time lags in coral responses related to coral taxonomy, morphology and size (Baker et al. 2008b).

Overfishing

Overfishing is present in almost all reefs close to any human settlements (Sandin et al. 2008) and has been treated as the main driver of algae dominance in reef ecosystems (Hughes et al. 2010; Jackson et al. 2012). In healthy coral reefs, herbivory by fishes is largely responsible for controlling the accumulation of algal biomass (Rasher et al. 2012), leaving space for corals to thrive even under scenarios of fast algae growth (McClanahan et al. 2012). As the populations herbivorous fishes are reduced by overfishing (Tab.1), top-down control of algal biomass is lost and corals are gradually replaced by algae (Deron E. Burkepile and Mark E. Hay 2006; Mumby et al. 2007). According to Ceccarelli et al. (2006), the area covered by some species of algae may increase from 20 to 50% with the total exclusion of large herbivorous fishes.

In addition to the control of algae, some fishes are also responsible for the control of sponges in the reefs. In the Caribbean, in places with high overfishing, the number of sponges that were in competition with corals per space was double compared with places without overfishing (Loh et al. 2015). As a result, all species that live associated with the corals have their populations negatively affected, with cascade effects on the structure and functions of reef communities (Stella et al. 2011). In a simplistic view, we may identify four links among fishes, algae, and corals: (1) herbivorous fishes consume algae, (2) algae compete with and displace corals, (3) corals generate habitat complexity for fishes, and (4) fishes require habitat complexity for feeding, protection, nursery and reproductive sites (Mumby 2016). Therefore, any disruption in these links can collapse the reef ecosystem.

Pollution

Contamination of coastal waters with residential and industrial sewage has been a major concern in developing tropical countries (Byamukama et al. 2005). Some studies addressing the impacts of pollution on coral reefs indicate that the elevated content of inorganic nutrients could lead to increased algae growth and coral diseases (Fabricius et al. 2005). Others suggest that areas with high levels of pollution are characterized by low local coral diversity, low coral recruitment, high mortality rates, low skeletal density, reduced depth distribution, high bioerosion rates, and for shifting community dominance from hard corals to organisms that are not capable of building reefs (West and Woesik 2001). A study conducted in French Polynesia showed widespread contamination at all sampling sites and in all species studied with herbicide derivatives and insecticides (Roche et al. 2011), indicating the potential for large-scale shifts in coral populations.

Like overfishing, pollution favors algal dominance in reef ecosystems by weakening the bottom-up regulation of algae populations, as the input of nutrients is translated into increased algal biomass (Zaneveld et al. 2016). A work on the Red Sea showed that a 50% increase in nutrients from floating fish farms, causing benthic algal blooms, 50% of coral mortality and reducing calcification by 3-4 times (Loya et al. 2004). The models estimating pollution in coral reefs around the world show that 22% of all coral reefs are classified as highly threatened and 12% as average (Bryant et al. 2011). Pollution is also associated with deforestation and countries with high deforestation levels (Tab.1), such as Taiwan and Vietnam, have a higher percentage of reefs at risk, around 50% (Bourke et al. 2002). In general, pollution is as important for reef conservation as bleaching and acidification, but efforts to understand this impact have been less.(Fabricius 2005).

Non-regulated tourism

In many tropical countries, coral reef-based tourism is growing at a faster rate than any other tourism segment (Tab.1), as well as being a key component of the global tourism industry (Milazzo et al. 2002). For example, Cesar et al. (2003) estimated that reefs generate $29.8 billion in global net benefits per year, while Richmond (1993) in the Great Barrier Reef estimated that tourism generates $1.5 billion per year for Queensland, Australia. Tourism activities directly affect the corals through physical contact with diver fins, anchors, and collision of boat bottom with the corals (Dearden et al. 2007). They also affect the corals indirectly by the addition of pollutants and other toxic substances from tourists and vessels, and by increasing water turbidity (Dearden et al. 2007; Reopanichkul et al. 2009).

Evidence shows that non-regulated tourism degrades the reef and reduces its value as tourist spot, attracting fewer tourists due to loss of quality in visiting experience (Hasler and Ott 2008). A study showed that about 90% of divers assumed that they had physical contacts with the corals during diving, where the biggest causes of damage were the fins (45.5%), followed by hands (19.5%) and equipment (15.9%) (Barker and Roberts 2004; Ku and Chen 2013; Roche et al. 2016). In Akumal, Mexico, there is a clear link between snorkel-based tourism and the decline in coral cover over time and space (Gil et al. 2015). Because the loss of coral cover is often paralleled by fish impoverishment, tourists prefer to visit more conserved coral reefs. In this sense, adjusting the quantity of visitants to the biotic features of the reef is mandatory to conciliate sustainable exploration and conservation (Uyarra et al. 2009).

Knowledge gaps

Geographic gaps

As expected, most studies were performed in regions where coral diversity is greatest: the Indo-Pacific, with 36.3% of all studies, and the Caribbean with 31.9% (Fig. 1). The other works were distributed across the Southwestern Atlantic (3.6%), Pacific Islands (8.1%), Asia (5.4%), some seas of Africa (5.4%), and in the central part of the Indian (2.7%), plus some studies that did not mention the location (6.6%). Besides concentrating the global richness of coral species, the Indo-Pacific and the Caribbean are close to countries that historically funding research in coral ecology (Fig 1). For example, in Australia we find many studies because it is a country with great investment in the science and conservation of coral reefs. The United States of America also supports coral research historically. However, there are other countries that have not presented many studies but are also of great importance for the world's coral reefs. An example of this are the corals of the Southwestern Atlantic, largely hosted by Brazilian reefs.

Brazilian coral species richness is low compared with that of Caribbean reefs (Leão et al. 2016). It has fewer reef-building species, but higher levels of endemism and are predominantly composed of massive forms (Castro and Pires 2001). Environmental conditions, such as strong solar radiation, low light levels and high sediment influx, eventually establish the tolerance levels of most Brazilian coral species (Leão et al. 2003; Sassi et al. 2015). Only the most adapted species tolerate the stressful conditions of the Southwestern Atlantic waters (Leão et al. 2016), and as such, it is possibly that they are less sensitive to human disturbances than Caribbean and Indo-Pacific species.

Another example is the Red Sea, which has a great wealth of coral fauna, and also has many endemic species. For example, about 14% of its reef fishes are endemics, including 7 unique species of butterfly fishes (Randall 1998). The Persian Gulf is another example, with a low diversity but with species well adapted to the harsh conditions. Such species are able to withstand the cold temperatures of the winter and summer temperatures much warmer than in any other reef around of the world (Coles and Riegl 2013). This fact creates an important point of study to understand the adaptations and the effects of temperature in coral species (Bryant et al. 2011; Coles and Riegl 2013).

Our results indicated only 37 of the 232 ecoregions have been studied. It is evident that corals are not present in all of them due to extreme conditions in greater latitudes or other natural constraints (e.g. lack of suitable substrate), but it is also clear that corals are not restricted to the 37 revealed by our analyses. We found only three ecoregions with more than five studies, two in the Caribbean and one in the great barrier reef of Australia, indicating that our current knowledge on coral response to human disturbances is quite biased geographically. We will be unable to guide successful environmental-friendly management actions in coral reefs unless this geographic gap is rapidly filled up.

Theoretical gaps

More than half of the studies focused on ocean warming (55.4%), which could be directly linked with global warming and its influence with SST increasing. In second place appears acidification (13.6%), followed by tourism (10.9%), overfishing (10%), and pollution (9.2%) (Fig. 2). This demonstrates that we are still unable to draw conclusions on how coral species couple with most anthropogenic alterations in human-dominated seascapes. Consequently, we are not totally prepared to support decision-makers and protected coral diversity from human threats, even in the most studied sites.

In terms of biological organization, most studies focused on the community level (58.1%) taking into consideration all groups of coral species (e.g. soft, hard), 24.5% were conducted at the ecosystem level and a few addressed issues at the individual (8.2%) or population levels (9.2%) (Fig. 2). It is well known that populations and individuals may respond differently to changes in the environment (Edmunds et al. 2016) and therefore the scarcity of studies avoids us to properly estimate the level of species plasticity under contrasting disturbance scenarios. In addition, once different species may have different functions in the community, this knowledge gap results in uncertainty about how coral communities and the whole ecosystem respond to human disturbances (Clements 2000).

In almost 60% of the studies the approach used was the observational. Only 22% of the studies had an experimental approach, and 18% gathered data from the literature. The experimental approach is valuable because the environment and the conditions for obtaining results capable of forecasting the future of corals can be manipulated. Observational studies are critical as well, but experiments may be established in situ to reduce costs, isolate variables and complement the correlative evidence derived from observational approaches. Such manipulation is more indicated for individual- or population-level studies (Bongaerts et al. 2017), but communities may be also artificially structured and designed to answer specific questions (Edmunds et al. 2016).

Despite the ocean, ecoregion, depth, level of biological organization, and methods used, all studies reported negative response of corals to all human disturbances considered. Such sensitivity is not novel, but observing 100% of negative responses was quite surprising. The negative responses was noticed by whitening (27.2%), mortality (13.6%), reduced calcification (10.9%), among others such as disease, intoxication, physical damage, reduced coverage, immune response and metabolic loss. This alarming finding reinforces the notion that corals are extremely vulnerable to anthropogenic changes(Freeman et al. 2013; Edmunds et al. 2014; Hoegh-Guldberg et al. 2017).

Another very important gap was the absence of studies below the 30 m depth, revealing that there is no work examining how mesophotic coral species respond to human disturbances. Since the deep reef refugia hypothesis was postulated about two decades ago (Glynn 1996), many studies have been developed but often describing some aspect of coral biology along the gradient of depth (Bongaerts et al. 2010; Loya et al. 2016; Shlesinger et al. 2017). Studies comparing mesophotic reefs with contrasting levels of human disturbance or monitoring the same mesophotic reef following different anthropogenic impacts are lacking yet. Without this information, it is hard to estimate the potential of deep corals to replenish not only human-disturbed shallow reefs, as the hypothesis predicts, but also other deep reefs impacted by humans.

One of the explanations for the lack of studies in the mesophotic reefs are the logistic and methodological requirements involved in data collection (Kahng et al. 2010; Hinderstein et al. 2010). In recent years, technology has helped a lot in expanding our knowledge on the abundance and distribution of deep coral species (Kahng et al. 2014), as going below the 40 m requires at least tech divers. Remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) may replace divers and are very promising, but their elevated cost usually makes the research unfeasible (Menza et al. 2007; Wynn et al. 2014). This might explain why we found no work using such vehicles in data collection. In fact, most studies collected their data with SCUBA diving (37.2%) at shallow depths smaller than 27 m; all other studies adopted a myriad of methodological procedures, from snorkel, interviews and controlled environment to satellite images, fossil records, and secondary data.

Future directions

We suggest five directions for future research on coral ecology in human-dominated seascapes. First, giving more attention to regions outside the Indo-Pacific and the Caribbean. Many places with relevant importance for global coral diversity are sub-sampled. For example, the corals of the Southwestern Atlantic with its high level of endemism (Leão et al. 2016), and the corals of the Persian Gulf with their capacity of supporting remarkable amplitude of variation in temperature (Coles and Riegl 2013). Even within the most studied regions, sampling ecoregions other than Greater Antilles, Western Caribbean, and Central and Southern Great Barrier Reef, which concentrate the current information. Second, assessing the effects acidification, pollution, non-regulated tourism and overfishing on coral growth, mortality, reproduction, dispersal, abundance and distribution. That does not mean that the consequences of ocean warming are completely understood. There is much to be documented on the outcome of SST on corals (Hughes et al. 2017), but the other threats are becoming increasingly common and deserve the same attention.

Third, concentrating efforts on corals occupying the mesophotic zones (Esser et al. 2010), identifying depth-specialists and depth-generalists species. The depth-generalists, i.e. those species occurring in shallow and deep waters, are particularly important for the recovery of shallow reefs and should be identified (Bongaerts et al. 2010). However, they will be not helpful if they are sensitive to one or more threats analyzed here, thus their vulnerability to human disturbance should be also estimated. Four and linked to that is the developing of more cost-effective technology for assessing deep waters, such as cheaper ROVs, AUVs, and rebreathers. These technologies should be available for researchers in both developing and developed countries.

Our last suggestion is to produce more experimental studies to uncover between-individual and between-population differences along gradients of human disturbance, and if possible, quantify the relative contribution of genetic and phenotypic drivers. We should also identify the winner species that will benefit from each of the human threats, jointly or separately. By identifying these species, we may forecast the taxonomic and functional composition of the future coral community, and shed light into the functioning of the future coral reefs. Given the biogeographic history of the oceans

(Spalding et al. 2007), this procedure should be performed for the biogeographic units independently.

Finally, we should be fast and skillful enough to translate the scientific knowledge into conservation actions soon. We have functionally lost at least 25% of the world's coral reefs, and a third of all coral species are threatened with extinction (Carpenter et al. 2008). Since 1970 the coral cover in the Caribbean has been lost from approximately 80% (Gardner et al. 2003), and total coral cover in the Indo-Pacific has been reduced by 1 to 2% annually (Scopelitis et al. 2009). These alarming numbers can be explained by the major threats considered here, plus low legal protection of coral reefs, urbanization, development of ports among others that also jeopardize marine biodiversity (Sarkar and Ghosh 2013). We expect that the research gaps we have pointed out help to protect corals around the world as well.

References

Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, Eakin CM, Leggat W (2016) Climate change disables coral bleaching protection on the Great Barrier Reef. Science (80-) 352:338–342. doi: 10.1017/CBO9781107415324.004

Andersson AJ, Kuffner IB, Mackenzie FT, Jokiel PL, Rodgers KS, Tan A (2009) Net Loss of CaCO 3 from a subtropical calcifying community due to seawater acidification : mesocosm-scale experimental evidence. Biogeosciences 1811–1823.

Baker AC, Glynn PW, Riegl B (2008a) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471. doi: 10.1016/j.ecss.2008.09.003

Baker AC, Glynn PW, Riegl B (2008b) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471. doi: 10.1016/j.ecss.2008.09.003

Barker NHL, Roberts CM (2004) Scuba diver behaviour and the management of diving impacts on coral reefs. Biol Conserv 120:481–489. doi: 10.1016/j.biocon.2004.03.021

Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the "deep reef refugia" hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327. doi: 10.1007/s00338-009-0581-x

Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-guldberg O (2017) Deep reefs are not universal refuges : Reseeding potential varies among coral species.

Bourke L, Selig E, Spalding M (2002) Reefs at Risk in Southeast Asia. World Resour Institute, Cambridge 72.

Bryant D, Burke L, McManus J, Spalding M (2011) Reefs at risk.

Budd AF, Pandolfi JM (2010) Evolutionary Novelty Is Concentrated at the Edge of Coral Species Distributions. Science (80-) 328:1558–1561. doi: 10.1126/science.1188947

Buglass S, Donner SD, Alemu I JB (2015) A study on the recovery of Tobago's coral reefs following the 2010 mass bleaching event. Mar Pollut Bull 104:198–206. doi: 10.1016/j.marpolbul.2016.01.038

Burt J, Al-Harthi S, Al-Cibahy A (2011) Long-term impacts of coral bleaching events on the world's warmest reefs. Mar Environ Res 72:225–229. doi:

10.1016/j.marenvres.2011.08.005

Byamukama D, Mach RL, Kansiime F, Manafi M, Farnleitner AH (2005) Discrimination Efficacy of Fecal Pollution Detection in Different Aquatic Habitats of a High-Altitude Tropical Country , Using Presumptive Coliforms , Escherichia coli , and Clostridium perfringens Spores. Appl Environ Microbiol 71:65–71. doi: 10.1128/AEM.71.1.65

Caldeira K, E.Wickett M (2003) Anthropogenic carbon and ocean pH. Nature 425:2003.

Cantin NE, Lough JM (2014) Surviving coral bleaching events: Porites growth anomalies on the great barrier reef. PLoS One. doi: 10.1371/journal.pone.0088720

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. Science (80-) 321:560–563. doi: 10.1126/science.1159196

Castro CB, Pires DO (2001) Brazilian coral reefs: what we already know and what is still missing. Bull Mar Sci 69:357–371.

Ceccarelli DM, Hughes TP, Mccook LJ (2006) Impacts of simulated overfishing on the territoriality of coral reef damselfish. Mar Ecol Prog Ser 309:255–262.

Cesar H, Burke L, Pet-Soede L (2003) The Economics of Worldwide Coral Reef

Degradation.

Cinner JE, Pratchett MS, Graham NAJ, Messmer V, Fuentes MMPB, Ainsworth T, Ban N, Bay LK, Blythe J, Dissard D, Dunn S, Evans L, Fabinyi M, Fidelman P, Figueiredo J, Frisch AJ, Fulton CJ, Hicks CC, Lukoschek V, Mallela J, Moya A, Penin L, Rummer JL, Walker S, Williamson DH (2016) A framework for understanding climate change impacts on coral reef social-ecological systems. Reg Environ Chang 16:1133–1146. doi: 10.1007/s10113-015-0832-z

Clements JC, Bourque D, Mclaughlin J, Stephenson M, Comeau LA (2017) Extreme ocean acidification reduces the susceptibility of eastern oyster shells to a polydorid parasite. J Fish Dis 40:1573–1585. doi: 10.1111/jfd.12626

Clements WH (2000) Integrating effects of contaminants across levels of biological organization: An overview. J Aquat Ecosyst Stress Recover 7:113–116. doi: 10.1023/A:1009927612391

Coles SL, Riegl BM (2013) Thermal tolerances of reef corals in the Gulf: A review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. Mar Pollut Bull 72:323–332. doi: 10.1016/j.marpolbul.2012.09.006

Collins M, Arblaster J, Dufresne J-L, Fichefet T, Pierre Friedlingstein, Gao X, Jr WJG, Johns T, Gerhard Krinner, Shongwe M, Tebaldi C, Weaver AJ, Wehner M (2013) Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cam- bridge.

Comeau S, Carpenter RC, Lantz CA, Edmunds PJ (2015) Ocean acidification accelerates dissolution of experimental coral reef communities. Biogeosciences 12:365–372. doi: 10.5194/bg-12-365-2015

Crabbe MJC (2008) Climate change, global warming and coral reefs: Modelling the effects of temperature. Comput Biol Chem 32:311–314. doi: 10.1016/j.compbiolchem.2008.04.001

Davis J, Grady APO, Dale A, Arthington AH, Gell PA, Driver PD, Bond N, Casanova M, Finlayson M, Watts RJ, Capon SJ, Nagelkerken I, Tingley R, Fry B, Page TJ, Specht A (2015) Science of the Total Environment When trends intersect : The challenge of protecting freshwater ecosystems under multiple land use and hydrological intensification scenarios. Sci Total Environ 534:65–78. doi: 10.1016/j.scitotenv.2015.03.127

Dearden P, Bennett M, Rollins R (2007) Perceptions of Diving Impacts and Implications for Reef Conservation Perceptions of Diving Impacts and Implications. Coast Manag 37–41. doi: 10.1080/08920750601169584

Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, Holmes TH, Moore JAY, Radford BT, Thomson DP, Tinkler P, Wilson SK (2013) Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. Coral Reefs 32:233–238. doi: 10.1007/s00338-012-0974-0

Deron E. Burkepile and Mark E. Hay (2006) Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. Ecology 87:3128–3139. doi: 10.1890/0012-9658(2006)87[3128:HVNCOM]2.0.CO;2

Deser C, Alexander MA, Xie S, Phillips AS (2010) Sea Surface Temperature

Variability : Patterns and Mechanisms. Ann Rev Mar Sci. doi: 10.1146/annurev-marine-120408-151453

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean Acidification : The Other CO 2 Problem. Ann Rev Mar Sci 169–194. doi: 10.1146/annurev.marine.010908.163834

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012) Climate Change Impacts on Marine Ecosystems. Annu Rev Ecol Evol Syst. doi: 10.1146/annurev-marine-041911-111611

Drinkwater KF, Beaugrand G, Kaeriyama M, Kim S, Ottersen G, Perry RI, Pörtner H, Polovina JJ, Takasuka A (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388. doi: 10.1016/j.jmarsys.2008.12.014

Edmunds PJ, Adjeroud M, Baskett ML, Baums IB, Budd AF, Carpenter RC, Fabina NS, Fan TY, Franklin EC, Gross K, Han X, Jacobson L, Klaus JS, McClanahan TR, O'Leary JK, Van Oppen MJH, Pochon X, Putnam HM, Smith TB, Stat M, Sweatman H, Van Woesik R, Gates RD (2014) Persistence and change in community composition of reef corals through present, past, and future climates. PLoS One. doi: 10.1371/journal.pone.0107525

Edmunds PJ, Comeau S, Lantz C, Andersson A, Briggs C, Cohen A, Gattuso J-P, Grady JM, Gross K, Johnson M, Muller EB, Ries JB, Tambutté S, Tambutté E, Venn A, Carpenter RC (2016) Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs. Bioscience 66:biw023. doi: 10.1093/biosci/biw023

Esser MIPL, Lattery MARCS, Tat MIS, Jimi MIO, Ates RUTHDG (2010) Photoacclimatization by the coral Montastraea cavernosa in the mesophotic zone : light , food , and genetics. Ecology 91:990–1003.

Fabricius K, Ath G De, Mccook L, Turak E, Mcb D (2005) Changes in algal , coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar Pollut Bull 51:384–398. doi: 10.1016/j.marpolbul.2004.10.041

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Mar Pollut Bull 50:125–146. doi: 10.1016/j.marpolbul.2004.11.028

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of Anthropogenic CO 2 on the CaCO 3 System in the Oceans. Science (80-) 305:362–366.

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoldi L (2014) The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat Commun 5:1–9. doi: 10.1038/ncomms4794

Freeman LA, Kleypas JA, Miller AJ (2013) Coral reef habitat response to climate change scenarios. PLoS One 8:1–14. doi: 10.1371/journal.pone.0082404

Gardner TA, Côté IM, Gill JA, Grant A, Andrew R (2003) Long-Term Region-Wide Declines in Caribbean Corals. Science (80-) 301:958–960.

Gil MA, Renfro B, Figueroa-Zavala B, Peni?? I, Dunton KH (2015) Rapid tourism growth and declining coral reefs in Akumal, Mexico. Mar Biol 162:2225–2233. doi: 10.1007/s00227-015-2748-z

Glynn P w. (1996) Coral reef bleaching: facts, hypotheses and implications. Glob

Chang Biol 2:495–509. doi: 10.1111/j.1365-2486.1996.tb00063.x

Guest JR, Low J, Tun K, Wilson B, Ng C, Raingeard D, Ulstrup KE, Tanzil JTI, Todd PA, Toh TC, McDougald D, Chou LM, Steinberg PD (2016) Coral community response to bleaching on a highly disturbed reef. Sci Rep 6:20717. doi: 10.1038/srep20717

Hansen J, Sato M, Kharecha P, Beerling D, Masson-delmotte V, Pagani M, Raymo M, Royer DL, Zachos JC (2008) Target Atmospheric CO 2 : Where Should Humanity Aim ? Open Atmos Sci 2:217–231.

Hasler H, Ott JA (2008) Diving down the reefs ? Intensive diving tourism threatens the reefs of the northern Red Sea. Mar Pollut Bull 56:1788–1794. doi: 10.1016/j.marpolbul.2008.06.002

Hilborn R, Stokes K (2011) Defining Overfished Stocks: Have We Lost the Plot? Fisheries 35:113–120. doi: 10.1577/1548-8446-35.3.113

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, Appeldoorn R (2010) Theme section on “Mesophotic Coral Ecosystems: Characterization, Ecology, and Management.” Coral Reefs 29:247–251. doi: 10.1007/s00338-010-0614-5

Hoegh-guldberg O (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science (80-). doi: 10.1126/science.1152509

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science (80-) 318:1737–

1742. doi: 10.1126/science.1152509

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral Reef Ecosystems under Climate Change and Ocean Acidification. Front Mar Sci. doi: 10.3389/fmars.2017.00158

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642. doi: 10.1016/j.tree.2010.07.011

Hughes TP, Kerry JT, Simpson T (2017) Large-scale bleaching of corals on the Great Barrier Reef. Ecology 2–3. doi: 10.1111/ijlh.12426

Iglesias-prieto R, Matta JL, Robins WA, Trench RK (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate Symbiodinium microadriaticum in culture. Ecology 89:10302–10305.

IPCC (2007) Climate Change 2007: Impacts, Adaptation and Vulnerability.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH (2012) Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science (80-). doi: 10.1126/science.1059199

Kaczmarsky L (2006) Coral disease dynamics in the central Philippines. Dis Aquat Organ 69:9–21. doi: 10.3354/dao069009

Kahng S, Copus J, Wagner D (2014) Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Curr Opin Environ Sustain 7:72–81. doi:

10.1016/j.cosust.2013.11.019

Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. Coral Reefs 1–21. doi: 10.1007/s00338-010-0593-6

Kelly RP, Foley MM, Fisher WS, Feely RA, Halpern BS, Waldbusser GG (2011) Mitigating Local Causes of Ocean Acidification with Existing Laws. Science (80-) 332:1036–1037.

Kirtman B, Akintayo John Adedoyin GJB, Bojariu R, Camilloni I, Doblas-Reyes F, Fiore AM, Kimoto M, Meehl G, Prather M, Sarr A, Schär C, Sutton R, Geert Jan van Oldenborgh GV, Wang H-J (2013) Near-term Climate Change: Projections and Predictability. In: In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung AJ, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate Change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on.

Kleypas JA, Langdon C (2006) Coral reefs and changing seawater chemistry. Coast Estuar Stud 110:61–73.

Kleypas JA, McMaus JW, Menez LAB (1999) Environmental Limits to Coral Reef Development: Where Do We Draw the Line? Am Zool 39:146–159. doi: 10.1093/icb/39.1.146

Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol Lett 1419–1434. doi: 10.1111/j.1461-0248.2010.01518.x

Ku K, Chen T (2013) A conceptual process-based reference model for collaboratively managing recreational scuba diving in Kenting National Park. Mar Policy 39:1–10. doi: 10.1016/j.marpol.2012.09.008

Leão ZMAN, Kikuchi RKP, Testa V (2003) Corals and coral reefs of Brazil.

Leão ZMAN, Kikuchi RKP, Ferreira BP, Neves EG, Sovierzoski HH, Oliveira MDM, M. Maida, Correia MD, Jhonsson R (2016) Brazilian coral reefs in a period of global change: A synthesis. Brazilian J Oceanogr 64:97–116. doi: 10.1590/S1679-875920160916064sp2

Loh T, Mcmurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs : sponges overgrow reef-building corals. PeerJ 13. doi: 10.7717/peerj.901

Lough JM (2012) Small change , big difference : Sea surface temperature distributions for tropical coral reef ecosystems , 1950 – 2011. J Geophys Res Ocean. doi: 10.1029/2012JC008199

Lough JM, Oppen MJH Van (2009) Introduction : Coral Bleaching - Patterns , Processes , Causes and Consequences. In: Springer, p. 1-4 2009. (ed) Coral Bleaching - Patterns, Processes, Causes and Consequences. pp 1–6

Loya Y, Lubinevsky H, Rosenfeld M, Kramarsky-Winter E (2004) Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. Mar Pollut Bull 49:344–353. doi: 10.1016/j.marpolbul.2004.06.011

Loya Y, Eyal G, Treibitz T, Lesser MP, Appeldoorn R (2016) Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9. doi: 10.1007/s00338-016-1410-7

Marimuthu N, Jerald Wilson J, Vinithkumar N V., Kirubagaran R (2013) Coral reef recovery status in south Andaman Islands after the bleaching event 2010. J Ocean Univ China 12:91–96. doi: 10.1007/s11802-013-2014-2

McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Alemu I. JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby PJ, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing Key Resilience Indicators to Support Coral Reef Management in a Changing Climate. PLoS One. doi: 10.1371/journal.pone.0042884

McLeod E, Anthony KRN, Andersson A, Beeden R, Golbuu Y, Kleypas J, Kroeker K, Manzello D, Salm R V., Schuttenberg H, Smith JE (2013) Preparing to manage coral reefs for ocean acidification: Lessons from coral bleaching. Front Ecol Environ 11:20–27. doi: 10.1890/110240

Menza C, Kendall M, Rogers C, Miller J (2007) A deep reef in deep trouble. Cont Shelf Res 27:2224–2230. doi: 10.1016/j.csr.2007.05.017

Milazzo M, Chemello R, Badalamenti F, Camarda R, Riggio S (2002) The Impact of Human Recreational Activities in Marine Protected Areas : What Lessons Should Be Learnt in the Mediterranean Sea ? Mar Ecol 1:280–290.

Mumby PJ (2016) Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. Fish Fish 17:266–278. doi: 10.1111/faf.12078

Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101. doi: 10.1038/nature06252

O’Gorman KD (2009) Philosophical Issues in Tourism (Aspects of Tourism). Tour. Manag. 31:293–294.

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Slater RD, Totterdell IJ, Weirig M, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686. doi: 10.1038/nature04095

Pauly D (1988) Some Definitions of Overfishing Relevant to Coastal Zone Management in Southeast Asia. Trop Coast Area Manag 3:14–15.

Quéré C Le, Raupach MR, Canadell JG, Marland G (2009) Trends in the sources and sinks of carbon dioxide. Nat Geosci 1–6. doi: 10.1038/ngeo689

Randall JE (1998) Zoogeography of shore fishes of the Indo-Pacific region. Zool Stud 37:227–268.

Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME (2012) Effects of herbivory , nutrients , and reef protection on algal proliferation and coral growth on a tropical reef. Oceanography 187–198. doi: 10.1007/s00442-011-2174-y

Reopanichkul P, Schlacher TA, Carter RW, Worachananant S (2009) Sewage impacts coral reefs at multiple levels of ecological organization. Mar Pollut Bull 58:1356–1362. doi: 10.1016/j.marpolbul.2009.04.024

Richmond RH (1993) Coral Reefs: Present Problems and Future Concerns Resulting from Anthropogenic Disturbance. Am Zool 33:524–536.

Roche HR, Salvat BS, Ramade FR (2011) Assessment of the pesticide pollution of coral reef communities from French Polynesia. Rev d'Ecologie 66:3–10.

Roche RC, Harvey C V, Harvey JJ, Kavanagh AP, Mcdonald M, John VRS (2016) Recreational Diving Impacts on Coral Reefs and the Adoption of Environmentally

Responsible Practices within the SCUBA Diving Industry. Environ Manage 58:107–116. doi: 10.1007/s00267-016-0696-0

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng T, Kozyr A (2004) The Oceanic Sink for Anthropogenic CO 2. Science (80-) 305:367–372.

Sandin SA, Smith JE, Demartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS One. doi: 10.1371/journal.pone.0001548

Sarkar S, Ghosh AK (2013) Coral bleaching a nemesis for the Andaman reefs: Building an improved conservation paradigm. Ocean Coast Manag 71:153–162. doi: 10.1016/j.ocecoaman.2012.09.010

Sassi R, Francisca C, Sassi C, Gorlach-lira K, Fitt WK (2015) Pigmentation changes in Siderastrea spp . during bleaching events in the costal reefs of northeastern Brazil. Lat Am J Aquat Res 43:176–185. doi: 10.3856/vol43-issue1-fulltext-15

Scopelitis J, Andrefouet S, Phinn S, Chabanet P, Naimc O, Tourrand C, Done T (2009) Changes of coral communities over 35 years : Integrating in situ and remote-sensing data on Saint-Leu Reef. Estuar Coast Shelf Sci 84:342–352. doi: 10.1016/j.ecss.2009.04.030

Shlesinger T, Grinblat M, Rapuano H, Amit T, Loya Y (2017) Can mesophotic reefs replenish shallow reefs? Reduced coral reproductive performance casts a doubt. Ecology 12:3218–3221. doi: 10.1002/ecy.2098

Sogin EM, Putnam HM, Anderson PE, Gates RD (2016) Metabolomic signatures of increases in temperature and ocean acidification from the reef-building coral, Pocillopora damicornis. Metabolomics 12:1–12. doi: 10.1007/s11306-016-0987-8

Souter DW, Lindén O (2000) The health and future of coral reef systems. Ocean Coast Manag 43:657–688. doi: 10.1016/S0964-5691(00)00053-3

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson J (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57:573–583. doi: 10.1641/B570707

Stella JS, Munday PL, Jones GP (2011) Effects of coral bleaching on the obligate coral-dwelling crab Trapezia cymodoce. Coral Reefs 30:719–727. doi: 10.1007/s00338-011-0748-0

Swain TD, DuBois E, Gomes A, Stoyneva VP, Radosevich AJ, Henss J, Wagner ME, Derbas J, Grooms HW, Velazquez EM, Traub J, Kennedy BJ, Grigorescu AA, Westneat MW, Sanborn K, Levine S, Schick M, Parsons G, Biggs BC, Rogers JD, Backman V, Marcelino LA (2016) Skeletal light-scattering accelerates bleaching response in reef-building corals. BMC Ecol 16:10. doi: 10.1186/s12898-016-0061-4

Thompson AA, Dolman AM (2010) Coral bleaching: One disturbance too many for near-shore reefs of the Great Barrier Reef. Coral Reefs 29:637–648. doi: 10.1007/s00338-009-0562-0

Uyarra MC, Watkinson AR, Côté IM (2009) Managing dive tourism for the sustainable use of coral reefs: Validating diver perceptions of attractive site features. Environ

Manage 43:1–16. doi: 10.1007/s00267-008-9198-z

Vogel N, Meyer FW, Wild C, Uthicke S (2015) Decreased light availability can amplify negative impacts of ocean acidification on calcifying coral reef organisms. Mar Ecol Prog Ser 521:49–61. doi: 10.3354/meps11088

West K, Woesik RV an (2001) Spatial and Temporal Variance of River Discharge on Okinawa (Japan): Inferring the Temporal Impact on Adjacent Coral Reefs.

Wild C, Hoegh-guldberg O, Naumann MS, Colombo-pallotta MF, Ateweberhan M, Fitt WK, Iglesias-prieto R, Palmer C, Bythell JC, Ortiz J, Loya Y, Woesik R Van (2011) Climate change impedes scleractinian corals as primary reef ecosystem engineers. Mar Freshw Res 62:205–215.

Wilkinson C (2008) Status of Coral Reefs of the World: 2008. Status Coral Reefs World 2008 5–19.

Williams C (1997) Combatting marine pollution from land-based activities: Australian initiatives. Ocean Coast Manag 33:87–112.

Wynn RB, Huvenne VAI, Le Bas TP, Murton BJ, Connelly DP, Bett BJ, Ruhl HA, Morris KJ, Peakall J, Parsons DR, Sumner EJ, Darby SE, Dorrell RM, Hunt JE (2014) Autonomous Underwater Vehicles (AUVs): Their past, present and future contributions to the advancement of marine geoscience. Mar Geol 352:451–468. doi: 10.1016/j.margeo.2014.03.012

Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, Mcminds R, Welsh R, Correa AMS, Lemoine NP, Rosales S, Fuchs C, Maynard JA, Thurber RV (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nat Commun 1–12. doi: 10.1038/ncomms11833

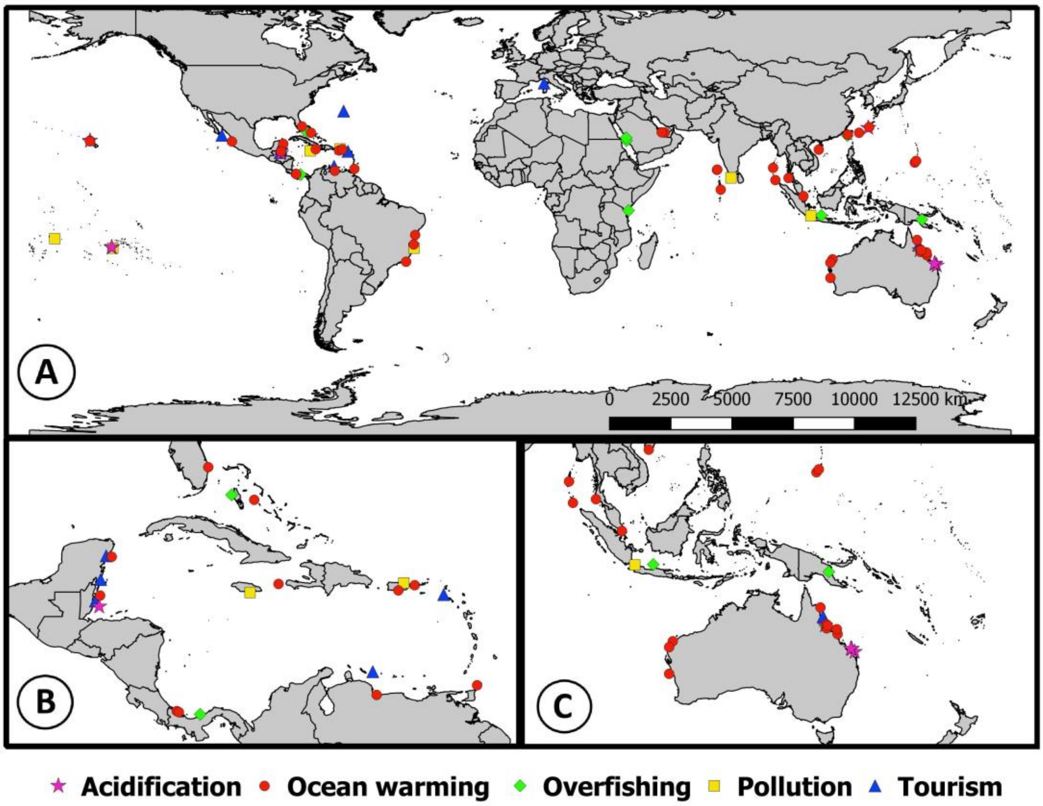


Figure 1: Location where each study was carried out and the type of threat. (A) Caribbean region. (B) Indo-pacific region.

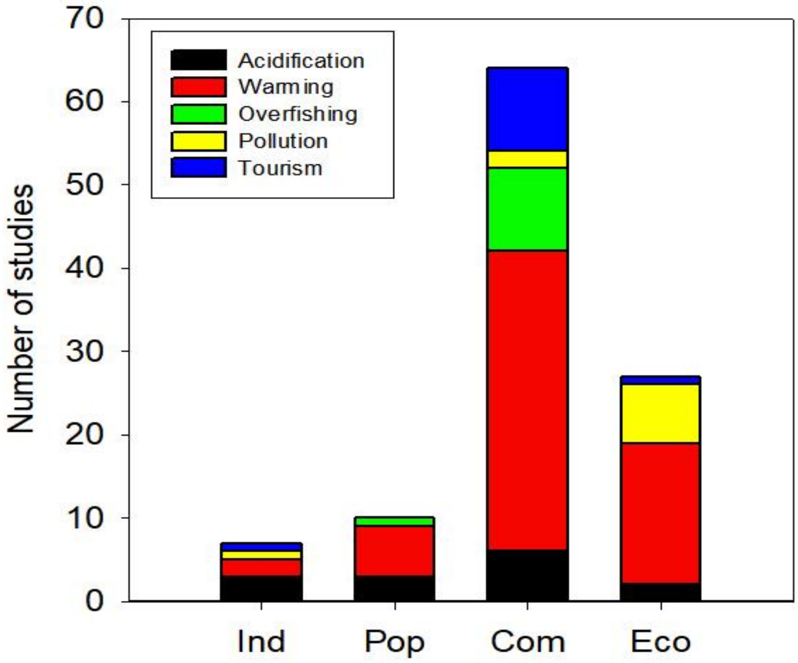


Figure 2: Number of studies per type of threat and level of level of biological organization.

Table 1: Definition of the five major threats affecting coral species.

Threat	Definition	References
Acidification	The predictable outcome of increased atmospheric CO_2 resulting from anthropogenic activity. As the amount of CO_2 absorbed by the oceans increases, the concentration of hydrogen ions increases, thus decreasing seawater pH.	Clements et al. (2017)
Ocean warming	A global phenomenon that often expresses itself in local and regional vulnerable systems and communities by modifying temperature and rainfall regime, affecting profoundly aquatic habitats and ecological functions and processes.	Davis et al. (2015) IPCC (2007)
Overfishing	Term usually used to refer to high exploitation rates, defined as a fishery at a level of effort higher than that which maximizes the economic rent, the differences between gross returns and fishing costs and declining catches.	Pauly (1988) Hilborn and Stokes (2011)
Pollution	The introduction by man, directly or indirectly, of substances or energy into the marine environment, which results or is likely to result in such deleterious effects as harm to living resources and marine life, hazards to human health, hindrance to marine activities, including fishing and other legitimate uses of the sea, impairment of quality for use of the sea water and reduction of amenities	United Nations Convention on the Law of the Sea (1982), in Williams (1997)
Tourism	Comprises the activities of people traveling to and staying in places outside their usual environment for not more than one consecutive year for leisure, business and other purposes not related to the exercise of an activity remunerated from within the place visited.	Uyarra et al. (2009) O’Gorman (2009)

Capítulo 2

Artigo sob revisão na **Ecology - Report**

Running head: Testing the deep reef refugia hypothesis

Testing the deep reef refugia hypothesis with tropical Southwestern Atlantic corals

JULIANO MORAIS,[1] BRÁULIO A. SANTOS,[2]*

[1]Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, CEP: 58051-900 - João Pessoa, PB, Brazil. E-mail: juliano-bio@live.com
[2]Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Cidade Universitária, CEP: 58051-900 - João Pessoa, PB, Brazil. Email: braulio@dse.ufpb.br
*Corresponding author

Abstract (200 words)

The deep reef refugia hypothesis predicts that deep coral reefs may act as refuges against major disturbances affecting shallow reefs, but to date a few studies have explicitly examined it. We test it using a community-level approach able to partition the coral diversity into independent alpha and beta components along a 3-61 m depth gradient in Northeast Brazil. If the hypothesis holds, shallow reefs (<30m) should host less species than deep reefs (>30m); depth-specialist species should be rarer in shallow than deep reefs; alpha diversity should be greater in deep reefs to allow immigration into shallow areas; beta diversity should be smaller among shallow reefs due homogenization driven by successive disturbances, and the functional composition of shallow reefs should be a subset from that of deep reefs. Contrary to expectations, coral communities in shallow reefs hosted twice more species, presented greater proportion of depth-specialists (77% vs. 57%), similar alpha but greater beta diversities of either rare, typical and dominant species, and exclusive functional attributes. Our findings provide little support for the deep reef refugia hypothesis, highlight the complementary nature of shallow and deep areas for regional coral diversity, and suggest small vertical connectivity and limited reseeding potential of deep reefs.

Key words: anthropogenic disturbance; biodiversity; cross-shelf; Hill numbers; mesophotic coral ecosystems; ocean; true diversity.

INTRODUCTION

The deep reef refugia hypothesis, formerly postulated by Glynn (1996), predicts that deep coral reefs may act as refugia against major disturbances affecting shallow reefs. It stipulates that deep reefs (>30 m depth) are protected or dampened from disturbances that affect shallow reefs (<30 m), such as pollution, unregulated tourism and overfishing. The hypothesis was firstly related to global warming and its massive, but non-uniform effects on coral bleaching and mortality (Hoegh-Guldberg 1999); some benign habitats such as deep, sunlit reef substrates, oceanic shoals and relatively high latitude locations, might escape from increased sea surface temperature or solar radiation and offer refuge for coral populations (Glynn 1996). As the hypothesis gained attention, evidence from mesophotic coral ecosystems indicated that the deep reefs could also act as a viable reproductive source for shallow reef areas following disturbance, expanding the notion of thermal refuge to source of propagules as well (Lesser et al. 2009, Bongaerts et al. 2010).

Much empirical evidence has been generated since the hypothesis was proposed two decades ago (Loya et al. 2016), but considering its global relevance for marine ecology and management, the number of studies explicitly designed to validate its assumptions or test its predictions is minuscule (e.g. Smith et al. 2016, Semmler et al. 2017, Bongaerts et al. 2017). For instance, the assumption that cooler environments protect corals from bleaching has been recently challenged, as Caribbean mesophotic corals (30-75 m depth) have lower bleaching threshold temperatures than shallow corals (Smith et al. 2016). The prediction of high vertical connectivity between deep and shallow reefs has been genetically supported for the broadcasting species *Stephanocoenia intersepta*, but not for the brooding species *Agaricia fragilis* (Bongaerts et al. 2017). Mixing results have been also reported at the community level (e.g. Riegl and Piller 2003, Semmler et al. 2017), revealing the need for more explicit evaluations of this important hypothesis.

The reseeding potential of deep areas into shallow ones assumes that the shallow-deep continuum encompasses a metacommunity, i.e. a set of local communities (coral reefs) that are linked by dispersal of multiple interacting species (Leibold et al. 2004). Regardless the type of connectivity among reefs (if physical or functional) and if the coral metacommunity constitutes a patch-dynamic, species-sorting, mass-effect, or even a neutral model (Leibold et al. 2004), a substantial portion of the coral diversity will be observed among, rather than within, local communities (Jost 2007). This beta component of coral diversity is expected to be lower in more disturbed reefs due to cumulative species loss, but as the alpha component, it is strongly dependent on species relative frequency. A given species can be extremely dominant below the 30 m, but if it is a depth-specialist due to physiological, ecological or life-history constraints, it will be not able to colonize a disturbed shallow reef. Other species may tolerate varied environmental conditions (depth-generalist), but being rare at any depth and thus contributing little to shallow reef recovery. Under real conditions, these dominant depth-specialists and rare depth-generalists should co-occur with numerous rare depth-specialists and a few dominant depth-generalists, generating patterns of beta diversity along the depth gradient poorly understood until now.

The concern with species frequency is well-known in the growing literature assessing the role of deep reefs as refugia at community level. Most studies have gone beyond species richness and used abundance-based metrics such as Shannon-Wiener and Gini-Simpson indices (e.g. Riegl and Piller 2003, Semmler et al. 2017). Nonetheless, these traditional metrics actually measure entropy rather than diversity, do not obey the replication principle and do not allow to partition the regional diversity into independent alpha and beta components (Jost 2007). This last point is particularly relevant to quantify the magnitude of the differences in diversity between shallow and deep reefs. Furthermore, to be a refugium, a deep reef should encapsulate the functions observed in the shallow reefs (e.g. reproduction mode, growth habit), otherwise the functional recovery will be not achieved in disturbed shallow reefs.

The reefs of the tropical Southwestern Atlantic province, along with those of the North Brazil shelf, comprise the largest and richest reef formation of the South Atlantic ocean (Spalding et al. 2007, Leão et al. 2016b). The Brazilian coral fauna is low compared to the Caribbean reefs, being currently represented by 23 scleractinian species, 5 hydrocorals, and 22 species of octocorals (Castro et al. 2010, Leão et al. 2016b). In contrast to the shallow reefs, the mesophotic coral ecosystems of the Southern Atlantic are still poorly studied (Oliveira et al. 2016). Even with the recent advances in the deep reefs of oceanic islands (Amado-Filho et al. 2016), submarine mountains (Meirelles et al. 2015), and the mouth of the Amazon river (Cordeiro et al. 2015), the potential role of deep reefs to serve as refugia for coral species has been not yet assessed.

In this study we test the deep reef refugia hypothesis using a community-level approach able to partition the coral diversity into independent alpha and beta components. We sample coral communities in 19 reefs of the Northeastern Brazil ecoregion (Spalding et al. 2007), varying from 3 to 61 m depth. Following the predictions of Glynn's hypothesis, we expected that (1) the deep reefs would host more species (gamma diversity) than shallow ones; (2) depth-specialist species should be rarer in shallow (<30 m) than deep reefs (>30 m); (3) alpha diversity should be greater in deep reefs to allow immigration into shallow areas; (4) beta diversity should be smaller among shallow reefs due homogenization driven by successive disturbances; and (5) the functional composition of shallow reefs should be a subset from that of deep reefs. As a preambule, we describe the substrate cover and taxonomic composition along the depth gradient and report new records for the region.

METHODS

Study area

We conducted the study in the eastern coast of Northeast Brazil near the metropolitan region of João Pessoa, state of Paraíba (Appendix S1). The continental shelf in this area is relatively short (35-km wide), most of it lies at depths smaller than 40 m and the break occurs at 75 m (O. A. Silva et al., unpublished data). Water temperature is relatively constant around 28-29°C up to the 50 m; after this depth a sharp thermocline of unknown seasonality reduces the temperature to about 23-24°C (Feitoza et al. 2005). The shallow reefs of this and other tracts of the Northeastern Brazil ecoregion are relatively well studied; some reefs are attached to the coast and others are several kilometers offshore, generally lying parallel to the coast at depths of approximately 5 m to 10 m (Leão et al. 2016b). The deep reefs of the region, on the other hand, are virtually unknown. The only study developed so far (Feitoza et al. 2005) describes the fish communities of 14 reefs between 35 m and 70 m depth and concludes that the deep reefs may function as a faunal corridor between southeastern Brazil and the Caribbean.

Data survey

To identify the reefs to be surveyed within the limits of our study area, we first consulted fishermen and local dive operators on possible reef locations. Subsequently, we confirmed the locations through exploratory SCUBA dives and bathymetric data from a portable hydrographic echo sounder system (SonarMite), which located potential submerged pinnacles and shelf valleys with potential to house corals. This procedure resulted in 19 reefs to be sampled: seven shallow reefs distant 15.5 km (1.5-25.8 km) (min-max) to each other and 12 deep reefs, 26.7 km (0.34-52.2 km) apart from each other. At each reef, we performed SCUBA dives using compressed air, Nitrox, or Trimix depending on the depth, and adapted the coral video transect method to sample the communities (Safuan et al. 2015). We used GoPro Hero 4 to record the digital videos along 20-m transects 1 m above the seafloor (modified from Morgan et al. 2016). We usually filmed four transects per reef with a minimum distance of 20 m between transects. Four reefs had five or six transects, but because transects were pooled together by reef in the analyses and sample coverage was close to 100% (see Appendix S2), this difference had no influence on the estimation of alpha and beta diversities.

We identified all colonies of scleractinian corals, hydrocorals, and octocorals recorded in the video transects and classified them according to four categorical functional traits: type of skeleton (reef-building, hard, or soft), reproductive mode (brooding or broadcast), symbiosis with zooxanthella (zooxanthellate or not), and sexual pattern (hermaphrodite and/or gonochoric) (Bongaerts et al. 2010 and references therein). To describe the substrate cover we took one frame every 10 seconds from each video transect (Hill and Wilkinson 2004, Morgan et al. 2016). We analyzed the frames through the point counting method with the program CPCe® (Coral Point Count with Excel Extensions; Kohler and Gill 2006), using a set of 20 random points per frame. We classified the points as sand, rock, sponge, algae, or coral, and reported their relative cover in percentage.

Sample coverage and diversity metrics

To compare the coral diversity across the depth gradient we first assessed the inventory completeness of each reef using the coverage estimator recommended by Chao and Jost (2012) (Appendix S2). To partition the diversity into independent alpha and beta components, we used multiplicative diversity decompositions of effective numbers of species (so-called Hill numbers, ${}^{q}D$) in its unweighted form (Jost 2007). We considered diversity of rare (${}^{0}D$), typical (${}^{1}D$) and dominant (${}^{2}D$) species (Appendix S3).

RESULTS

Overall, coral cover was relatively small, only 3.4%, varying from 0.3% to 20.2%. The reef cover was largely dominated by rock with 38.9%, followed by macroalgae (31.4%), sand (15.2%) and sponges (1.0%), and still 10.1% undistinguishable cover. We recorded 861 coral colonies belonging to17 species and 14 families: 11 scleractinea species, 1 octocoral, 1 black coral, 1 hydrocoral, and 3 zoanthids (Appendix S4). The scleractinea coral *Agaricia fragilis* and the black coral *Cirripathes* sp. represented new records for state of Paraiba, Brazil. The most abundant species were the reef-building, depth generalist *Siderastrea stellata* (74.7% of the colonies) and *Montastrea cavernosa* (18.5%). Only three species occurred along the entire depth gradient: *S. stellata*, *M. cavernosa* and *Mussismilia hispida*. Ten species were observed only in the shallow reefs (>58% of the regional richness), while four occurred exclusively in the deep reefs (Appendix S5).

The three metrics of alpha diversity (${}^{0}D$, ${}^{1}D$, ${}^{2}D$) varied from 1 to 5 species per reef but did not respond to depth (Fig. 1). Compared with deep reefs, shallow reefs showed 50% more beta diversity of rare species (${}^{0}D$; 4.5 vs. 3.0 communities) and 30%

more beta diversity of dominant species (^2D; 1.6 vs. 1.2 communities) (Fig. 2). This greater beta diversity also resulted in greater gamma diversity in shallow reefs, which almost doubled the gamma diversity recorded in the deep areas (13 vs. 7 species).

Because *S. stellata* and *M. cavernosa* dominated the depth gradient, coral communities were dominated by reef-building, zooxanthellated, gonochoric corals with brooding or broadcast reproductive mode. However, soft corals were observed only in shallow reefs and non-zooxanthellated corals were recorded only in deep reefs.

DISCUSSION

Our community-level approach using Southwestern Atlantic corals do not support the deep reef refugia hypothesis. Compared with deep reefs, coral communities in shallow areas (1) hosted almost twice more species (gamma diversity), (2) presented proportionally more depth-specialists, (3) exhibited similar alpha but greater beta diversities of either rare, typical and dominant species, and (4) showed exclusive functional groups not found below the 30 m. If any, the refugia may be inverted in our study region, with more diverse, heterogeneous shallow reefs rescuing less diverse, homogeneous deeper areas, but that is not case either. The elevated proportion of depth-specialist species in both shallow and deep reefs and the exclusivity in some functions (i.e. soft corals in shallow areas and non-zooxanthellated in deep areas) reveal the complementary nature of the reefs along the depth gradient. It is worthy to mention that our deep reefs were in the upper limit of the mesophotic zone (up to 61 m), where the differences between shallow and deep areas should be minimum and the hypothesis strongly supported (Loya et al. 2016).

The coral metacommunity comprised by the 17 species distributed along the depth gradient follows a species-sorting model, in which two species dominate local communities anywhere in the region (*Siderastrea stellata* and *Montastrea cavernosa*) and the others are separated into spatial (depth) niches and limited in terms of dispersion (Leibold et al. 2004). Sedimentation and turbidity, common in shallow and deep reefs of our region, are known to negatively affect corals and select a few species more adapted to the stressful conditions (Erftemeijer et al. 2012). *M. cavernosa* is recognized as a species with high sediment removal capacity and one of the most important reef-building corals of the South Atlantic and the Caribbean (Francini-filho et al. 2013, Leão et al. 2016b). Its physiological and morphological adaptations to tolerate greater depths has been documented as well (Lesser et al. 2010). *S. stellate*, by far the most abundant coral species in our region, seems to be even more tolerant to depth, sedimentation and turbidity than *M. cavernosa* (Antônio-de-Souza and Amaral 2002, Leão et al. 2003). These characteristics certainly explain its ecological success throughout the coast of Paraíba and other Brazilian reefs, such as the Vitória-Trindade seamount chain (Meirelles et al. 2015), Abrolhos bank (Moura et al. 2013), Rocas Atoll (Amado-Filho et al. 2016) and mesophotic reefs of the Ceará coast in Northeast Brazil (Oliveira et al. 2016).

Several factors, besides depth, might be involved in coral distribution pattern and explain the deviation from the hypothesis predictions. One possibility is that competition for consolidate substrate (Liddell and Avery 2000, Wilkinson 2008) and/or level of human disturbance (Appeldoorn et al. 2016) are greater in deep than shallow reefs. However, most reef surface of shallow and deep reefs was uncovered and classified as rock (see smaller rock cover in Bridge et al. 2011, Bridge and Guinotte 2012, Meirelles et al. 2015, Cordeiro et al. 2015), indicating that there would be enough space to expand coral cover by 10 times at any depth. In addition, there is no evidence supporting increased pressures of fishing, pollution, and tourism in the deep reefs (Leão et al. 2003). In fact, these threats are more common in shallow areas due to the proximity from the coast. Thus, the depth – and its intrinsic covariates (i.e. light, pressure, temperature) – is more likely to be the main driver of community organization at our study region.

The deviation from the hypothesis might be also explained by the geographic (horizontal) distance between the shallow and deep reefs, which exacerbates the taxonomic differentiation between coral communities. While shallow reefs were attached to the coast or a kilometer offshore lying at depths of up to 10 m, the deep reefs were often more than 20 km offshore (see Appendix S1). This horizontal gap is very likely to favor the depth specialism in the region, limit the vertical connectivity between shallow and deep areas, and reduce the role of deep reefs as a source of larvae from shallow reefs (Hinderstein et al. 2010). In addition, some studies have shown that larval dispersion may be as low as 100 m (Underwood. et al. 2007), challenging the idea that deep reefs could be helpful in recovering the shallow reefs of the Paraíba coast.

One possibility for measuring the capacity of mesophotic coral populations to replenish shallow reefs after disturbance is to measure the extent and direction of gene flow between these habitats (Van Oppen et al. 2011). To this end, the characteristics of each species will ultimately determine the dispersal potential. For example, the large eggs of *M. cavernosa* can increase the survival time of the larvae, the dispersion capacity, and the survival of the post-release (Nunes et al. 2009). But studies that tested this ability demonstrated that vertical connectivity can vary greatly between species within the same reef (Bongaerts et al. 2017) and within the same species but on different reefs (Serrano et al. 2014). We encourage further studies to investigate gene flow of *M. cavernosa* and *S. stellata* among reefs at the same and different depths in our study region to disentangle the drivers of vertical and horizontal connectivity among reefs.

The greater beta diversity in the shallow areas was quite surprising, given that the human pressures close to the coast should have homogenized the coral communities (Leão et al. 2003). The smaller average pairwise distance of shallow reefs (15.5 km) compared with that of deep reefs (26.7 km) would also support lower beta diversity in the shallow areas, but the analyses revealed the opposite. This suggests high dispersal limitation of most species at smaller spatial scales, especially rare and typical ones, or strong differences in resource quality for corals from one reef to another, affecting local demography of species and the outcomes of local species' interactions (Leibold et al. 2004). At the metacommunity level, the increased depth – an unsuitable natural condition for shallow-specialist corals – seems to be more dramatic for corals than fishing, pollution, and tourism together. This does not mean that human activities do not affect these sessile invertebrates, but rather that we could have found more distinct coral communities in the absence of human use.

The low number of species we recorded (17 species) is naturally expected for this region. According to Leão et al. (2016), we found 83% of the species expected for scleractinea and 50% for Hydrozoa, besides 20% of the species expected for octocorals (Castro et al. 2010). The Brazilian reefs have three main characteristics: the low biodiversity compared to North Atlantic reefs, the main reef builders are endemics (e.g. *S. stellata*), and species of massive form are dominant. One of the factors that may explain the low coral diversity in the South Atlantic is the geographical barrier formed by the plume of the Amazon River, which prevents the migration of most species from the Caribbean (Luiz et al. 2012) and allows a few species that tolerate great depths and high levels of sedimentation to cross (Leão et al. 2003, Neves et al. 2010).

In summary, the deep reefs are unlikely to serve as refugia for Southwestern Atlantic corals that occupy the shallow areas. If any, they have potential to replenish shallow reefs with only two depth-generalist species, *S. stellata* and *M. cavernosa*, but this possibility remains to be properly assessed by genetic analyses. Because beta diversity is very high, especially in shallow reefs, and many species are specialized on particular depths, conservation actions in the region should integrate the protection of shallow and deep reefs to conserve the regional coral diversity.

ACKNOWLEDGEMENTS

We thank the Fundação Grupo O Boticário de Proteção à Natureza (grant number 1044-20152) for funding this study and the Mar Aberto Dive Center for logistical support. The Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided research grant to BAS (310340/2016-0) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a graduate scholarship to JM. Technical divers O. A. Silva, M. Russi, and I. Just supported the fieldwork. We also thank two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

LITERATURE CITED

Amado-Filho, G. M., R. L. Moura, A. C. Bastos, R. B. Francini-Filho, G. H. Pereira-Filho, R. G. Bahia, F. C. Moraes, and F. S. Motta. 2016. Mesophotic ecosystems of the unique South Atlantic atoll are composed by rhodolith beds and scattered consolidated reefs. Marine Biodiversity 46:933–936.

Antônio-de-Souza, C., and F. D. Amaral. 2002. Variação morfométrica de alguma espécies de corais Mussidae (Cnidaria, Anthozoa) do Brasil. Tropical Oceanography, Recife 30:23–36.

Appeldoorn, R., D. Ballantine, I. Bejarano, M. Carlo, M. Nemeth, E. Otero, F. Pagan, H. Ruiz, N. Schizas, C. Sherman, and E. Weil. 2016. Mesophotic coral ecosystems under anthropogenic stress: a case study at Ponce, Puerto Rico. Coral Reefs 35:63–75.

Barros, M. M. L. de, D. de O. Pires, and C. B. e Castro. 2003. Coral Reef Paper Sexual Reproduction of the Brazilian Reef Coral Siderastrea Stellataverrill 1868 (Anthozoa , Scleractinia). Bulletin of Marine Science 73:713–724.

Bongaerts, P., T. Ridgway, E. M. Sampayo, and O. Hoegh-Guldberg. 2010. Assessing the "deep reef refugia" hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327.

Bongaerts, P., C. Riginos, R. Brunner, N. Englebert, S. R. Smith, and O. Hoegh-guldberg. 2017. Deep reefs are not universal refuges : Reseeding potential varies among coral species. Science Advances.

Boscolo, H. K., and F. L. Silveira. 2005. Reproductive biology of Palythoa caribaeorum and Protopalythoa variabilis (Cnidaria, Anthozoa, Zoanthidea) from the southeastern coast of Brazil. Brazilian Journal of Biology 65:29–41.

Bridge, T. C. L., T. J. Done, R. J. Beaman, A. Friedman, S. B. Williams, O. Pizarro, and J. M. Webster. 2011. Topography , substratum and benthic macrofaunal relationships on a tropical mesophotic shelf margin , central Great Barrier Reef , Australia. Coral Reefs:143–153.

Bridge, T., and J. Guinotte. 2012. Mesophotic Coral Reef Ecosystems in the Great Barrier Reef World Heritage Area in the Great Barrier Reef World. Great Barrier Reef Marine Park Authority.

Budd, A. F., and J. M. Pandolfi. 2010. Evolutionary novelty is concentrated at the edge of coral species distributions. Science 328:1558–1561.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzman, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts. Science 321:560–563.

Castro, C. B., M. S. Medeiros, and L. L. Loiola. 2010. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. Journal of Natural History 44:763–827.

Castro, C. B., and D. O. Pires. 2001. Brazilian coral reefs: what we already know and what is still missing. Bulletin of Marine Science 69:357–371.

Chao, A., C. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

Chao, A., K. H. Ma, and T. C. Hsieh. 2016. iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User’s Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Chao, A., and T. J. Shen. 2010. Program SPADE: species prediction and diversity estimation. Program and user’s guide. CARE, Hsin-Chu, Taiwan.

Cordeiro, R. T., B. M. Neves, J. S. Rosa-Filho, and C. D. Pérez. 2015. Mesophotic coral ecosystems occur offshore and north of the Amazon River. Bulletin of Marine

Science 91:491–510.

Culter, J. K., K. B. Ritchie, S. A. Earle, D. E. Guggenheim, R. B. Halley, K. T. Ciembronowicz, A. C. Hine, B. D. Jarrett, S. D. Locker, and W. C. Jaap. 2006. Pulley reef: A deep photosynthetic coral reef on the West Florida Shelf, USA. Coral Reefs 25:228.

Davidson, O. G. 1998. The enchanted braid. Coming to the terms with nature on the Coral Reef. New York: John Wiley & Sons Inc:269.

Edmunds, P. J., S. Comeau, C. Lantz, A. Andersson, C. Briggs, A. Cohen, J.-P. Gattuso, J. M. Grady, K. Gross, M. Johnson, E. B. Muller, J. B. Ries, S. Tambutté, E. Tambutté, A. Venn, and R. C. Carpenter. 2016. Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs. BioScience 66:biw023.

Erftemeijer, P. L. A., B. Riegl, B. W. Hoeksema, and P. A. Todd. 2012. Environmental impacts of dredging and other sediment disturbances on corals : A review. Marine Pollution Bulletin 64:1737–1765.

Feitoza, B. M., R. S. Rosa, and L. A. Rocha. 2005. Ecology and zoogeography of deep-reef fishes in northeastern Brazil. Bulletin of Marine science 76:725–742.

Ferreira, B. P., M. B. S. F. Costa, M. S. Coxey, A. L. B. Gaspar, D. Veleda, and M. Araujo. 2013. The effects of sea surface temperature anomalies on oceanic coral reef systems in the southwestern tropical Atlantic. Coral Reefs:441–454.

Francini-filho, R. B., E. O. C. Coni, P. M. Meirelles, G. M. Amado-filho, F. L. Thompson, G. H. Pereira-filho, A. C. Bastos, D. P. Abrantes, P. Y. G. Sumida, N. L. Oliveira, C. M. Ferreira, F. Z. Gibran, A. Z. Gu, L. Kaufman, C. V Minte-vera, and R. L. Moura. 2013. Dynamics of Coral Reef Benthic Assemblages of the Abrolhos Bank , Eastern Brazil : Inferences on Natural and Anthropogenic Drivers.

PLoS ONE 8:1–12.

Glynn, P. w. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biology 2:495–509.

Guest, J. R., J. Low, K. Tun, B. Wilson, C. Ng, D. Raingeard, K. E. Ulstrup, J. T. I. Tanzil, P. A. Todd, T. C. Toh, D. McDougald, L. M. Chou, P. D. Steinberg, A. Douglas, D. . Smith, and T. C. LaJeunesse. 2016. Coral community response to bleaching on a highly disturbed reef. Scientific Reports 6:20717.

Harriott, V. J. 1999. Coral growth in subtropical eastern Australia. Coral Reefs 18:281–291.

Hill, J., and C. Wilkinson. 2004. Methods for ecological monitoring of coral reefs. Australian Institute of Marine Science, Townsville:117.

Hinderstein, L. M., J. C. A. Marr, F. A. Martinez, M. J. Dowgiallo, K. A. Puglise, R. L. Pyle, D. G. Zawada, and R. Appeldoorn. 2010. Theme section on “Mesophotic Coral Ecosystems: Characterization, Ecology, and Management.” Coral Reefs 29:247–251.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world’s coral reefs. Marine and Freshwater Research 50:839.

Hoeksema, B. W. 2012. Extreme morphological plasticity enables a free mode of life in Favia gravida at Ascension Island (South Atlantic). Marine Biodiversity 42:289–295.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Jost, L. 2010. Independence of alpha and beta diversities. Ecology 91:1969–1974.

Kahng, S. E., Y. Benayahu, and H. R. Lasker. 2011. Sexual reproduction in octocorals.

Marine Ecology Progress Series 443:265–283.

Kahng, S. E., J. M. Copus, and D. Wagner. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). Current Opinion in Environmental Sustainability 7:72–81.

Karlson, R. H. 1981. Reproductive patterns in Zoanthus spp. from Discovery Bay, Jamaica.

Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers and Geosciences 32:1259–1269.

Kühlmann, D. H. H. 1983. Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36:183–204.

Lariviere, J. P., A. C. Ravelo, A. Crimmins, P. S. Dekens, H. L. Ford, M. Lyle, and M. W. Wara. 2012. LateMiocene decoupling of oceanicwarmth and atmospheric carbon dioxide forcing. Nature 486:97–100.

Leao, Z., U. Federal, R. Kikuchi, and U. Federal. 2003. Corals and coral reefs of Brazil.

Leão, Z. M. A. N., R. K. P. Kikuchi, B. P. Ferreira, E. G. Neves, H. H. Sovierzoski, M. D. M. Oliveira, M. Maida, M. D. Correia, and R. Jhonsson. 2016a. Brazilian coral reefs in a period of global change: A synthesis. Brazilian Journal of Oceanography 64:97–116.

Leão, Z. M. A. N., R. K. P. Kikuchi, B. P. Ferreira, E. G. Neves, H. H. Sovierzoski, M. D. M. Oliveira, M. Maida, M. D. Correia, and R. Johnsson. 2016b. Brazilian coral reefs in a period of global change: A synthesis.

Leão, Z. M. A. N., R. K. P. Kikuchi, and V. Testa. 2003. Corals and coral reefs of Brazil.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes,

R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lesser, M. I. P., M. Lattery, M. I. S. Tat, M. I. O. Jimi, and R. Ates. 2010. Photoacclimatization by the coral Montastraea cavernosa in the mesophotic zone : light , food , and genetics. Ecology 91:990–1003.

Lesser, M. P., M. Slattery, and J. J. Leichter. 2009. Ecology of mesophotic coral reefs. Journal of Experimental Marine Biology and Ecology 375:1–8.

Lewis, J. B. 2006. Biology and Ecology of the Hydrocoral Millepora on Coral Reefs. Advances in Marine Biology 50:1–55.

Liddell, W. D., and W. E. Avery. 2000. Temporal change in hard substrate communities 10-250 m, the Bahamas. Proceedings of the Ninth International Coral Reef Symposium. Volume 2 23–27 Octo:1053–1058.

Lins-De-Barros, M., and D. O. Pires. 2007. Comparison of the reproductive status of the scleractinian coral Siderastrea stellata throughout a gradient of 20 degrees of latitude. Brazilian Journal of Oceanography 55:67–69.

Loya, Y., G. Eyal, T. Treibitz, M. P. Lesser, and R. Appeldoorn. 2016. Theme section on mesophotic coral ecosystems: advances in knowledge and future perspectives. Coral Reefs 35:1–9.

Lueg, J. R., A. L. Moulding, V. N. Kosmynin, and D. S. Gilliam. 2012. Gametogenesis and Spawning of *Solenastrea bournoni* and *Stephanocoenia intersepta* in Southeast Florida, USA. Journal of Marine Biology 2012:1–13.

Luiz, O. J., J. S. Madin, D. R. Robertson, L. A. Rocha, P. Wirtz, and S. R. Floeter. 2012. Ecological traits influencing range expansion across large oceanic dispersal barriers : insights from tropical Atlantic reef fishes. Proc Roy Soc B. 279:1033–

1040.

Meirelles, P. M., G. M. Amado-Filho, G. H. Pereira-Filho, H. T. Pinheiro, R. L. De Moura, J. C. Joyeux, E. F. Mazzei, A. C. Bastos, R. A. Edwards, E. Dinsdale, R. Paranhos, E. O. Santos, T. Iida, K. Gotoh, S. Nakamura, T. Sawabe, C. E. Rezende, L. M. R. Gadelha, R. B. Francini-Filho, C. Thompson, and F. L. Thompson. 2015. Baseline assessment of mesophotic reefs of the Vitória-Trindade Seamount Chain based on water quality, microbial diversity, benthic cover and fish biomass data. PLoS ONE 10:1–22.

Moberg, F. F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29:215–233.

Van Moorsel, G. 1983. Reproductive strategies in two closely related stony corals (Agaricia, Scleractinia). Marine Ecology Progress Series 13:273–283.

Morgan, K. M., C. T. Perry, S. G. Smithers, J. A. Johnson, and J. J. Daniell. 2016. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. Scientific Reports 6:29616.

Moura, R. L., G. M. Amado-Filho, F. C. Moraes, P. S. Brasileiro, P. S. Salomon, M. M. Mahiques, A. C. Bastos, M. G. Almeida, J. M. Silva, B. F. Araujo, F. P. Brito, T. P. Rangel, B. C. V. Oliveira, R. G. Bahia, R. P. Paranhos, R. J. S. Dias, E. Siegle, A. G. Figueiredo, R. C. Pereira, C. V Leal, E. Hajdu, N. E. Asp, G. B. Gregoracci, S. Neumann-Leitao, P. L. Yager, R. B. Francini-Filho, A. Froes, M. Campeao, B. S. Silva, A. P. B. Moreira, L. Oliveira, A. C. Soares, L. Araujo, N. L. Oliveira, J. B. Teixeira, R. A. B. Valle, C. C. Thompson, C. E. Rezende, and F. L. Thompson. 2016. An extensive reef system at the Amazon River mouth. Science Advances 2:e1501252–e1501252.

Moura, R. L. De, N. A. Secchin, G. M. Amado-filho, R. Bastos, M. O. Freitas, C. V. Minte-vera, J. Batista, F. L. Thompson, A. Z. Guth, R. M. Lopes, and A. C. Bastos. 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Continental Shelf Research 70:109–117.

Neves, E. G., and D. O. Pires. 2002. Sexual reproduction of Brazilian coral Mussismilia hispida (Verrill, 1902). Coral Reefs 21:161–168.

Neves, E. G., F. L. Silveira, M. Pichon, and R. Johnsson. 2010. Cnidaria, Scleractinia, Siderastreidae, Siderastrea siderea (Ellis and Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical Southwestern Atlantic. Check List 6:505–510.

Nozawa, Y., M. Tokeshi, and S. Nojima. 2006. Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. Marine Biology 149:1047–1058.

Nunes, F., R. D. NorrisS, and N. Knowlton. 2009. Implications of isolation and low genetic diversity in peripheral populations of an amphi-Atlantic coral. Molecular Ecology 18:4283–4297.

de Oliveira Soares, M., M. Davis, C. C. de Paiva, and P. B. de Macêdo Carneiro. 2016. Mesophotic ecosystems: coral and fish assemblages in a tropical marginal reef (northeastern Brazil). Marine Biodiversity.

Van Oppen, M. J. H., P. Bongaerts, J. N. Underwood, L. M. Peplow, and T. F. Cooper. 2011. The role of deep reefs in shallow reef recovery : an assessment of vertical connectivity in a brooding coral from west and east Australia. Molecular Ecology 20:1647–1660.

De Putron, S. J., and S. R. Smith. 2011. Planula release and reproductive seasonality of the scleractinian coral porites astreoides in bermuda, a high-latitude reef. Bulletin of Marine Science 87:75–90.

Riegl, B., and W. E. Piller. 2003. Possible refugia for reefs in times of environmental stress. International Journal of Earth Sciences 92:520–531.

Safuan, M., H. B. Wee, Y.-S. Hii, H.-C. Liew, and Z. Bachok. 2015. Optimization of Coral Video Transect Technique for Coral Reef Survey : Comparison with Intercept Transect Technique. Open Journal of Marine Science 5:379–397.

Semmler, R. F., W. C. Hoot, and M. L. Reaka. 2017. Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs ? Coral Reefs 36:433–444.

Serrano, X. M., I. B. Baums, K. O'Reilly, T. B. Smith, R. J. Jones, T. L. Shearer, F. L. D. Nunes, and A. C. Baker. 2014. Geographic differences in vertical connectivity in the Caribbean coral Montastraea cavernosa despite high levels of horizontal connectivity at shallow depths. Molecular Ecology 23:4226–4240.

Smith, T. B., J. Gyory, M. E. Brandt, W. J. Miller, J. Jossart, and R. S. Nemeth. 2016. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Global Change Biology 22:2756–2765.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. Mcmanus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. BioScience 57:573.

Spalding, M. D., and A. M. Grenfell. 1997. New estimates of global and regional coral reef areas. Coral Reefs 16:225–230.

Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–53.

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164:853–860.

Underwood., J. N., L. D. Smith., M. J. Van Oppen., and J. P. Gilmour. 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Molecular Ecology 16:771–784.

Venn, A. A., F. K. Weber, J. E. Loram, and R. J. Jones. 2009. Deep zooxanthellate corals at the high latitude Bermuda Seamount. Coral Reefs 28:135.

Wagner, D., R. G. Waller, A. D. Montgomery, C. D. Kelley, and R. J. Toonen. 2012. Sexual reproduction of the Hawaiian black coral Antipathes griggi (Cnidaria: Antipatharia). Coral Reefs 31:795–806.

Wilkinson, C. 2002. Status of Coral Reefs of the World. Australian Institute of Marine 2.

Wilkinson, C. 2008. Status of Coral Reefs of the World: 2008. Status of Coral Reefs of the World: 2008:5–19.

Zilberberg, C., D. P. Abrantes, J. A. Marques, L. F. Machado, and L. F. de B. Marangoni. 2016. Conhecendo os Recifes Brasileiros - Coral Vio.

Figure legends

Figure 1. Alpha diversity of rare (^{0}D), typical (^{1}D) and dominant (^{2}D) coral species in shallow (<30 m) and deep (>30 m) reefs of Northeast Brazil. The mean (solid line), median (thin line), 25th and 75th percentiles (boundaries of boxes), and 5th and 95th percentiles (whiskers above and below box plots) are indicated in the boxplots. No linear relationship or significant differences between the means of shallow and deep reefs were observed ($P > 0.05$).

Figure 2. Beta diversity of rare (q=0), typical (q=1) and dominant (q=2) coral species across communities in shallow (<30 m) and deep (>30 m) reefs of Northeast Brazil.

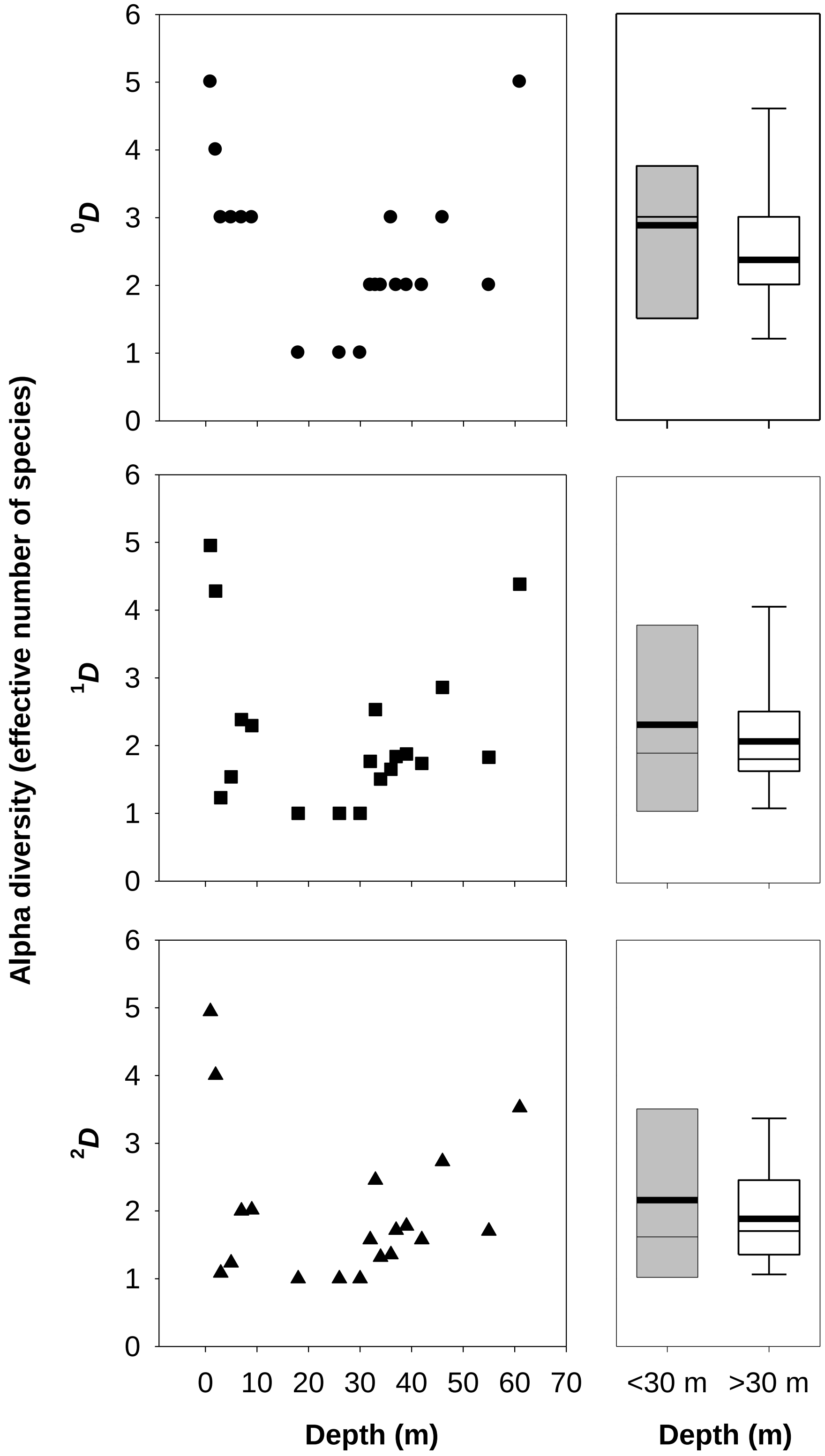

Alpha diversity (effective number of species)
^0D
^1D
^2D
0
1
2
3
4
5
6
0 10 20 30 40 50 60 70
Depth (m)
<30 m
>30 m
Depth (m)

Figure 1.

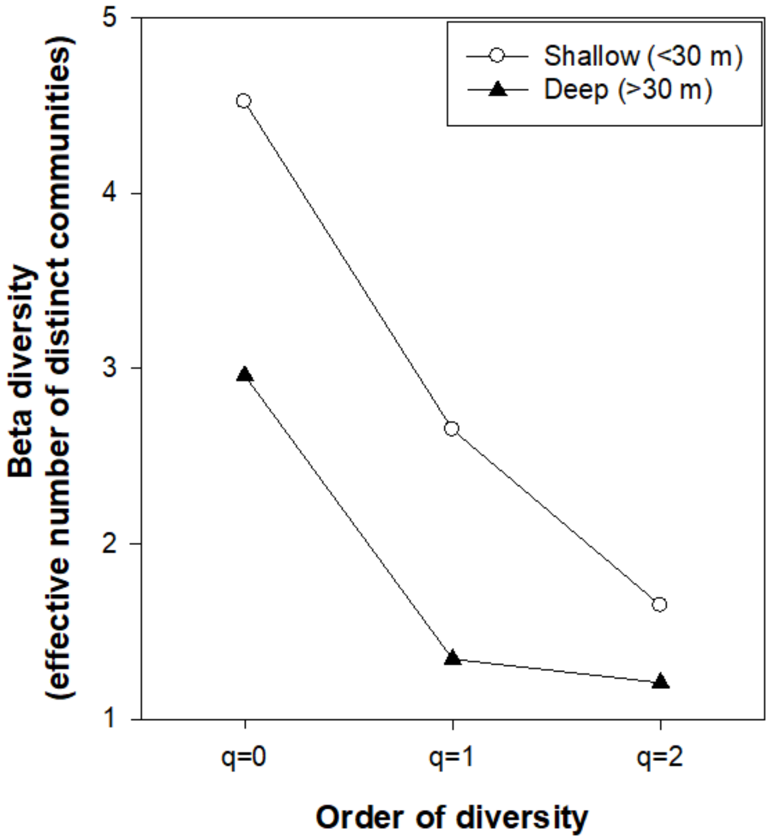
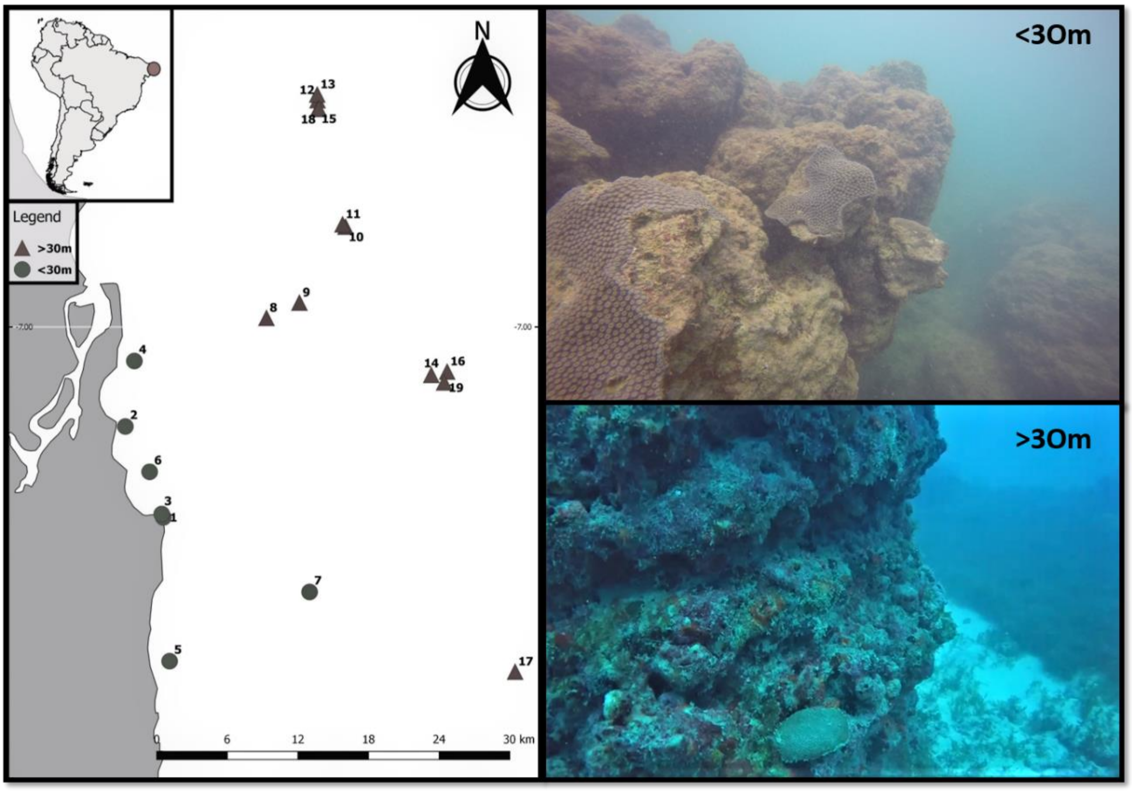

Beta diversity
(effective number of distinct communities)
1
2
3
4
5
q=0
q=1
q=2
Order of diversity
Shallow (<30 m)
Deep (>30 m)

Figure 2.

Appendix S1. Study region in the coast of Paraíba, Northeast Brazil, showing an example of shallow (<30m depth) and deep reefs (> 30m depth).



Appendix S2. Estimation of sample completeness of the 19 coral communities sampled in the coast of Paraíba, Northeast Brazil.

We first calculated the inventory completeness for each reef using the coverage estimator recommended by Chao and Shen (2010), which is a less biased estimator of sample completeness:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species represented by one (singletons) and two (doubletons) colonies, respectively, and n is the total number of colonies in each reef.

Because species richness was low [1-5 species per feed; common in Southwestern Atlantic reefs (Leão et al. 2016b)] but colony abundance was relatively high (on average 45 colonies per reef), 11 of the 19 reefs presented no singleton or doubleton, with all species being represented by three or more colonies. In such cases sample completeness reached the maximum (1). The other 8 reefs with at least a singleton or a doubleton averaged 0.94, ranging from 0.83 to 1.00. This analysis ensured that our estimates of species diversity and its partitioning were not be biased by differences in sample completeness (Chao and Jost 2012). We calculated the estimator of sample coverage with the iNEXT software (Chao et al. 2016).

Literature cited

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

Chao, A., K. H. Ma, and T. C. Hsieh. 2016. iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User’s Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Chao, A., and T. J. Shen. 2010. Program SPADE: species prediction and diversity estimation. Program and user’s guide. CARE, Hsin-Chu, Taiwan.

Leão, Z. M. A. N., R. K. P. Kikuchi, B. P. Ferreira, E. G. Neves, H. H. Sovierzoski, M. D. M. Oliveira, M. Maida, M. D. Correia, and R. Johnsson. 2016. Brazilian coral reefs in a period of global change: A synthesis.

Appendix S3. Diversity calculation and partition of coral communities.

For S species, gamma (γ) diversity of order *q* was defined as:

$$ {}^{q}D_{\gamma} = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)} $$

where *S* is the number of species in the reef, p_i is the relative abundance of colonies of the *i*th species, and *q* is a parameter that controls the measure's sensitivity to species relative abundances (Jost 2007, Tuomisto 2010).

When $q = 0$, diversity represents the species richness, which is not sensitive to abundances and so gives disproportionate weight to rare species (Jost 2006, Tuomisto 2010). When $q = 1$, diversity is equivalent to the exponential of Shannon's entropy index and weights each species according to its abundance in the community, without favoring rare or abundant species (Jost 2007). The Hill number of order 1 can be therefore interpreted as the effective number of 'typical species' in the community (Chao and Jost 2012). When $q = 2$, diversity is equivalent to the inverse Simpson concentration and the abundant species are favoured in detriment of rare species. This diversity of order 2 is recognized as the number of 'very abundant' or 'dominant' species in the community (Jost 2010, Chao et al. 2012).

Following the same rationale, the alpha (α) component of diversity was defined as:

$$ {}^{q}D_{\alpha} = \left(\frac{1}{N} \sum_{i=1}^{S} p_{i1}^q + \frac{1}{N} \sum_{i=1}^{S} p_{i2}^q + \ldots \right)^{1/(1-q)} $$

where *Pi* denotes the relative abundance of the *i*th species in each of the N communities (Jost 2007).

To calculate the beta (β) diversity of coral communities, we adopted the multiplicative diversity partition (Jost 2007, 2010) defined as:

$$^{q}D_{\beta} = \frac{^{q}D_{\gamma}}{^{q}D_{\alpha}}$$

This metric expresses the 'effective number of completely distinct communities' (Jost 2007), as it ranges between 1 (when all communities are identical) and N (when all communities are completely different from each other). Because we sampled 19 communities, values of beta diversity could vary between 1 and 19.

We used Mantel tests to assess whether coral beta diversity was related to reef location in the seascape (i.e. log-transformed geographical distances between sampled patches) and/or to differences in reef depth. We calculated the *P*-values using the distribution of the Rho coefficients obtained from 10 000 permutations. We observed no distance decay in beta diversity (Rho = 0.105; $P = 0.192$) and a significant but weak effect of depth on beta diversity (Rho = 0.298; $P = 0.004$). This indicates that closer communities are not necessarily more similar than distant communities, but communities at similar depths may be a bit more similar to each other than communities at different depths. We performed all analyses in R v. 2.15.2 (R Development Core Team, Vienna, Austria).

Literature cited

Chao, A., C. Chiu, and T. C. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93:2037–2051.

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88:2427–2439.

Jost, L. 2010. Independence of alpha and beta diversities. Ecology 91:1969–1974.

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164:853–860.

Appendix S4. List of the 17 species recorded in shallow and deep reefs of Paraiba, Northeast Brazil. Reproduction; B = Brooding, S = Broadcast spawning. Reef building and zooxanthellate Y = Yes, N = No. IUCN; DD = Data Deficient, LC = Least Concern. Sexual pattern; H = Hermaphrodite, G = Gonochoric

	Depth	**IUCN**	**Reproductive mode**	**Reef building**	**Zooxanthellate**	**Sexual pattern**	**Reference**
Scleractinia							
Siderastrea stellata	S,D	DD	B	Y	Y	G	(Barros et al. 2003, Lins-De-Barros and Pires 2007),
Montastrea cavernosa	S,D		S	Y	Y	G	(Szmant 1986, Zilberberg et al. 2016)
Mussismilia hispida	S,D	DD	S	Y	Y	H	(Neves and Pires 2002)
Mussismilia harttii	S	DD	S	Y	Y	H	(Zilberberg et al. 2016)
Porites astreoides	S	LC	B	Y	Y	H	(De Putron and Smith 2011, Zilberberg et al. 2016)
Favia gravida	S		B	Y	Y	H	(Hoeksema 2012, Zilberberg et al. 2016)
Stephanocoenia michelini	D		S	Y	Y		(Venn et al. 2009, Bongaerts et al. 2010, Lueg et al. 2012)
Agaricia fragilis	D	DD	B	Y	Y		(Kühlmann 1983, Culter et al. 2006)
Agaricia agaricites	S	LC	B	Y	Y		(Van Moorsel 1983)
Madracis decactis	D	LC	B	Y	Y	H	(Venn et al. 2009)
Meandrina braziliensis	S	DD	B	Y	Y		(Kühlmann 1983)
Octacorallia							
Muriceopsis sp.	S		S	N	Y		(Castro et al. 2010, Kahng et al. 2011)
Anthipatharia							
Cirrhipathes sp.	D		S	N	N	H	(Wagner et al. 2012)
Zoanthidae							
Protopalythoa variabilis	S		S	N	Y	H, G	(Boscolo and Silveira 2005)
Palythoa caribaeroum	S		S	N	Y	H, G	(Boscolo and Silveira 2005)
Zoanthus sociatus	S		S	N	Y		(Karlson 1981)
Hydrozoa							
Millepora alcicornis	S		S	Y	Y	H	(Lewis 2006)

Literature cited

Barros, M. M. L. de, D. de O. Pires, and C. B. Castro. 2003. Sexual Reproduction of the Brazilian Reef Coral Siderastrea Stellataverrill 1868 (Anthozoa , Scleractinia). Bulletin of Marine Science 73:713–724.

Bongaerts, P., T. Ridgway, E. M. Sampayo, and O. Hoegh-Guldberg. 2010. Assessing the “deep reef refugia” hypothesis: focus on Caribbean reefs. Coral Reefs 29:309–327.

Boscolo, H. K., and F. L. Silveira. 2005. Reproductive biology of Palythoa caribaeorum and Protopalythoa variabilis (Cnidaria, Anthozoa, Zoanthidea) from the southeastern coast of Brazil. Brazilian Journal of Biology 65:29–41.

Castro, C. B., M. S. Medeiros, and L. L. Loiola. 2010. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. Journal of Natural History 44:763–827.

Culter, J. K., K. B. Ritchie, S. A. Earle, D. E. Guggenheim, R. B. Halley, K. T. Ciembronowicz, A. C. Hine, B. D. Jarrett, S. D. Locker, and W. C. Jaap. 2006. Pulley reef: A deep photosynthetic coral reef on the West Florida Shelf, USA. Coral Reefs 25:228.

Hoeksema, B. W. 2012. Extreme morphological plasticity enables a free mode of life in Favia gravida at Ascension Island (South Atlantic). Marine Biodiversity 42:289–295.

Kahng, S. E., Y. Benayahu, and H. R. Lasker. 2011. Sexual reproduction in octocorals. Marine Ecology Progress Series 443:265–283.

Karlson, R. H. 1981. Reproductive patterns in Zoanthus spp. from Discovery Bay, Jamaica.

Kühlmann, D. H. H. 1983. Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36:183–204.

Lewis, J. B. 2006. Biology and Ecology of the Hydrocoral Millepora on Coral Reefs. Advances in Marine Biology 50:1–55.

Lins-De-Barros, M., and D. O. Pires. 2007. Comparison of the reproductive status of the scleractinian coral Siderastrea stellata throughout a gradient of 20 degrees of latitude. Brazilian Journal of Oceanography 55:67–69.

Lueg, J. R., A. L. Moulding, V. N. Kosmynin, and D. S. Gilliam. 2012. Gametogenesis and Spawning of Solenastrea bournoni and Stephanocoenia intersepta in Southeast Florida, USA. Journal of Marine Biology 2012:1–13.

Van Moorsel, G. 1983. Reproductive strategies in two closely related stony corals (Agaricia, Scleractinia). Marine Ecology Progress Series 13:273–283.

Neves, E. G., and D. O. Pires. 2002. Sexual reproduction of Brazilian coral Mussismilia hispida (Verrill, 1902). Coral Reefs 21:161–168.

De Putron, S. J., and S. R. Smith. 2011. Planula release and reproductive seasonality of the scleractinian coral porites astreoides in bermuda, a high-latitude reef. Bulletin of Marine Science 87:75–90.

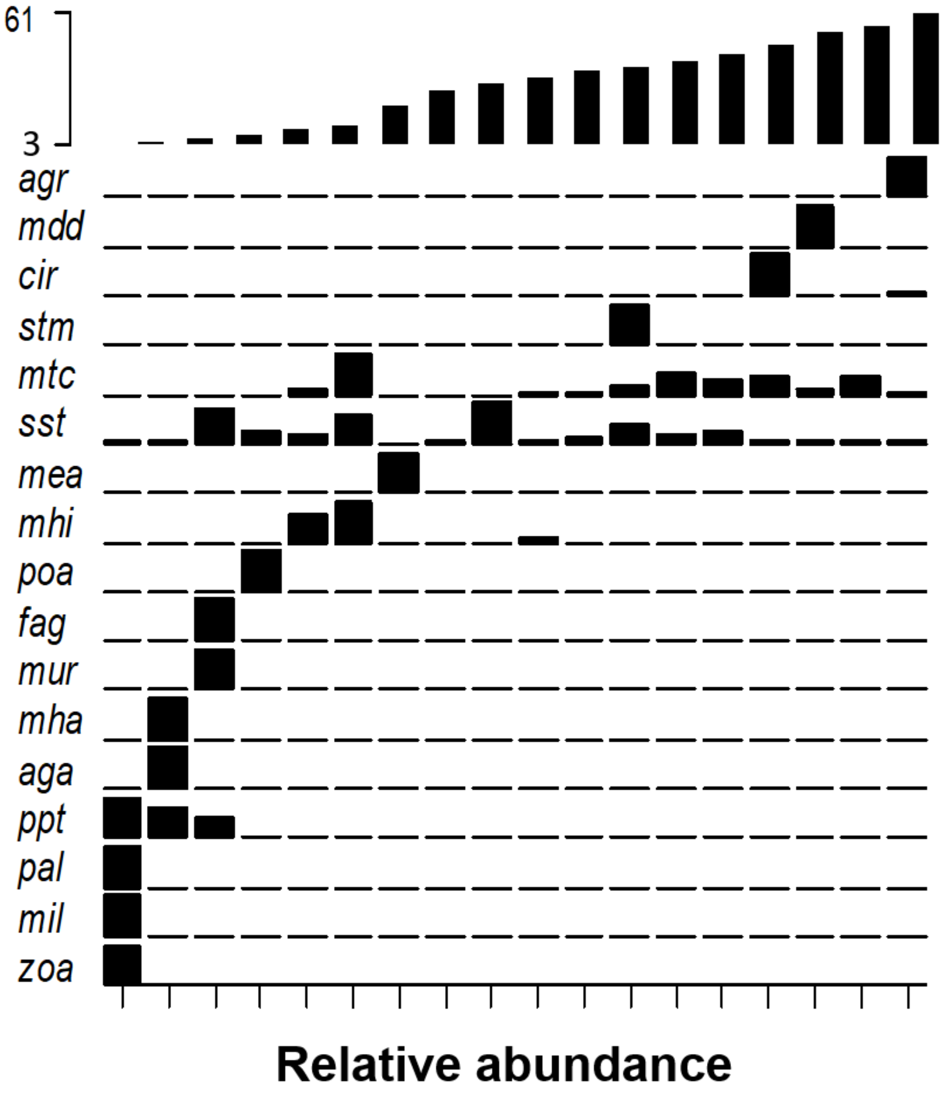
Szmant, A. M. 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5:43–53.

Venn, A. A., F. K. Weber, J. E. Loram, and R. J. Jones. 2009. Deep zooxanthellate corals at the high latitude Bermuda Seamount. Coral Reefs 28:135.

Wagner, D., R. G. Waller, A. D. Montgomery, C. D. Kelley, and R. J. Toonen. 2012. Sexual reproduction of the Hawaiian black coral Antipathes griggi (Cnidaria: Antipatharia). Coral Reefs 31:795–806.

Zilberberg, C., D. P. Abrantes, J. A. Marques, L. F. Machado, and L. F. de B. Marangoni. 2016. Conhecendo os Recifes Brasileiros - Coral Vivo. Rio de Janeiro, Museu Nacional, UFRJ.

Appendix S5. Relationship between depth (3-61 m) and the relative abundance of coral colonies. Species acronyms - **agr**: *Agaricia agaricites*; **mdd**: *Madracis decactis*; **cir**: *Cirrhipathes* sp; **stm**: *Stephanocoenia michelini*; **mtc**: *Montastrea cavernosa*; **sst**: *Siderastrea stellata*; **mea**: *Meandrina braziliensis*; **mhi**: *Mussismilia hispida*; **poa**: *Porites astreoides*; **fag**: *Favia gravida*; **mur**: *Muriceopsis* sp; **mha**: *Mussismilia harttii*; **aga**: *Agaricia fragilis*; **ppt**: *Protopalythoa variabilis*; **pal**: *Palythoa caribaeroum*; **mil**: *Millepora alcicornis*; **zoa**: *Zoanthus sociatus*



CONCLUSÃO GERAL

Com base na revisão da literatura, concluo que os corais são extremamente sensíveis as mudanças antropogênicas, e existe uma escassez de informações sobre as respostas dos corais à poluição, ao turismo, à sobrepesca e à acidificação, particularmente nos ecossistemas mesofóticos (> 30 m de profundidade) e em ecorregiões fora do Indo-Pacífico e do Caribe.

Concluo também que existe pouco suporte para a hipótese de que os recifes profundos funcionam como refúgios para corais, sendo as áreas rasas e profundas complementares e igualmente importantes para o funcionamento dos ecossistemas recifais da região e para a conservação da diversidade regional de corais.