Citation for final published version:

Simpfendorfer, Colin A., Heithaus, Michael R., Heupel, Michelle R., MacNeil, M. Aaron, Meekan, Mark, Harvey, Euan, Sherman, C. Samantha, Currey-Randall, Leanne M., Goetze, Jordan S., Kiszka, Jeremy J., Rees, Matthew J., Speed, Conrad W., Udyawer, Vinay, Bond, Mark E., Flowers, Kathryn I., Clementi, Gina M., Valentin-Albanese, Jasmine, Adam, M. Shiham, Ali, Khadeeja, Asher, Jacob, Aylagas, Eva, Beaufort, Océane, Benjamin, Cecilie, Bernard, Anthony T. F., Berumen, Michael L., Bierwagen, Stacy, Birrell, Chico, Bonnema, Erika, Bown, Rosalind M. K., Brooks, Edward J., Brown, J. Jed, Buddo, Dayne, Burke, Patrick J., Cáceres, Camila, Cambra, Marta, Cardeñosa, Diego, Carrier, Jeffrey C., Casareto, Sara, Caselle, Jennifer E., Charloo, Venkatesh, Cinner, Joshua E., Claverie, Thomas, Clua, Eric E. G., Cochran, Jesse E. M., Cook, Neil, Cramp, Jessica E., D'Alberto, Brooke M., de Graaf, Martin, Dornhege, Mareike C., Espinoza, Mario, Estep, Andy, Fanovich, Lanya, Farabaugh, Naomi F., Fernando, Daniel, Ferreira, Carlos E. L., Fields, Candace Y. A., Flam, Anna L., Floros, Camilla, Fourqurean, Virginia, Gajdzik, Laura, Barcia, Laura García, Garla, Ricardo, Gastrich, Kirk, George, Lachlan, Giarrizzo, Tommaso, Graham, Rory, Guttridge, Tristan L., Hagan, Valerie, Hardenstine, Royale S., Heck, Stephen M., Henderson, Aaron C., Heithaus, Patricia, Hertler, Heidi, Padilla, Mauricio Hoyos, Hueter, Robert E., Jabado, Rima W., Joyeux, Jean-Christophe, Jaiteh, Vanessa, Johnson, Mohini, Jupiter, Stacy D., Kaimuddin, Muslimin, Kasana, Devanshi, Kelley, Megan, Kessel, Steven T., Kiilu, Benedict, Kirata, Taratau, Kuguru, Baraka, Kyne, Fabian, Langlois, Tim, Lara, Frida, Lawe, Jaedon, Lédée, Elodie J. I., Lindfield, Steve, Luna-Acosta, Andrea, Maggs, Jade Q., Manjaji-Matsumoto, B. Mabel, Marshall, Andrea, Martin, Lucy, Mateos-Molina, Daniel, Matich, Philip, McCombs, Erin, McIvor, Ashlie, McLean, Dianne, Meggs, Llewelyn, Moore, Stephen, Mukherji, Sushmita, Murray, Ryan, Newman, Stephen J., Nogués, Josep, Obota, Clay, Ochavillo, Domingo, O'Shea, Owen, Osuka, Kennedy E., Papastamatiou, Yannis P., Perera, Nishan, Peterson, Bradley, Pimentel, Caio R., Pina-Amargós, Fabián, Pinheiro, Hudson T., Ponzo, Alessandro, Prasetyo, Andhika, Quamar, L. M. Sjamsul, Quinlan, Jessica R., Reis-Filho, José Amorim, Ruiz, Hector, Ruiz-Abierno, Alexei, Sala, Enric, de-León, Pelayo Salinas, Samoilys, Melita A., Sample, William R., Schärer-Umpierre, Michelle, Schlaff, Audrey M., Schmid, Kurt, Schoen, Sara N., Simpson, Nikola, Smith, Adam N. H., Spaet, Julia L. Y., Sparks, Lauren, Stoffers, Twan, Tanna, Akshay, Torres, Rubén, Travers, Michael J., van Zinnicq Bergmann, Maurits, Vigliola, Laurent, Ward, Juney, Warren, Joseph D., Watts, Alexandra M., Wen, Colin K., Whitman, Elizabeth R., Wirsing, Aaron J., Wothke, Aljoscha, Zarza-González, Esteban and Chapman, Demian D. 2023. Widespread diversity deficits of coral reef sharks and rays. Science 380 (6650) , pp. 1155-1160. 10.1126/science.ade4884

Publishers page: http://dx.doi.org/10.1126/science.ade4884

Title: Widespread diversity deficits of coral reef sharks and rays

Authors:

Colin A. Simpfendorfer[1,2], Michael R. Heithaus[3], Michelle R. Heupel[2,4], M. Aaron MacNeil[5], Mark Meekan[6], Euan Harvey[7], C. Samantha Sherman[8,1], Leanne M. Currey-Randall[4], Jordan S. Goetze[9,10], Jeremy J. Kiszka[3], Matthew J. Rees[6,11], Conrad W. Speed[6], Vinay Udyawer[12], Mark E. Bond[3], Kathryn I. Flowers[3], Gina M. Clementi[3], Jasmine Valentin-Albanese[13], M. Shiham Adam[14], Khadeeja Ali[15,3], Jacob Asher[16], Eva Aylagas[16], Océane Beaufort[17], Cecilie Benjamin[18], Anthony T.F. Bernard[19,20], Michael L. Berumen[21], Stacy Bierwagen[4], Chico Birrell[22], Erika Bonnema[3], Rosalind M.K. Bown[23], Edward J. Brooks[24], J. Jed Brown[25], Dayne Buddo[26], Patrick J. Burke[27,28], Camila Cáceres[3], Marta Cambra[29,30], Diego Cardeñosa[3], Jeffrey C. Carrier[31], Sara Casareto[3], Jennifer E. Caselle[32], Venkatesh Charloo[33], Joshua E. Cinner[34], Thomas Claverie[35,33], Eric E.G. Clua[36,37], Jesse E.M. Cochran[21], Neil Cook[38,39], Jessica E. Cramp[40,41], Brooke M. D'Alberto[1,42], Martin de Graaf[43], Mareike C. Dornhege[44], Mario Espinoza[29,30], Andy Estep[45], Lanya Fanovich[39], Naomi F. Farabaugh[3], Daniel Fernando[23], Carlos Eduardo Leite Ferreira[46], Candace Y.A. Fields[3,24], Anna L. Flam[47], Camilla Floros[48,49], Virginia Fourqurean[50,51], Laura Gajdzik[21,52], Laura García Barcia[3], Ricardo Garla[53,54], Kirk Gastrich[3], Lachlan George[2], Tommaso Giarrizzo[55,56], Rory Graham[57], Tristan L. Guttridge[58,59], Valerie Hagan[60], Royale S. Hardenstine[16], Stephen M. Heck[13], Aaron C. Henderson[61], Patricia Heithaus[3], Heidi Hertler[61], Mauricio Hoyos Padilla[62,63], Robert E. Hueter[64,65], Rima W. Jabado[66], Jean-Christophe Joyeux[67], Vanessa Jaiteh[68,69], Mohini Johnson[70], Stacy D. Jupiter[71], Muslimin Kaimuddin[72,70], Devanshi Kasana[3], Megan Kelley[3], Steven T. Kessel[73], Benedict Kiilu[74], Taratau Kirata[75], Baraka Kuguru[76], Fabian Kyne[77], Tim Langlois[78,79], Frida Lara[80,81], Jaedon Lawe[82], Elodie J.I. Lédée[1], Steve Lindfield[83], Andrea Luna-Acosta[84], Jade Q. Maggs[85], B. Mabel Manjaji-Matsumoto[86], Andrea Marshall[87], Lucy Martin[88], Daniel Mateos-Molina[89,90], Philip Matich[59], Erin McCombs[91], Ashlie McIvor[21,92], Dianne McLean[6,93], Llewelyn Meggs[82], Stephen Moore[1], Sushmita Mukherji[1,2], Ryan Murray[94], Stephen J. Newman[95], Josep Nogués[88], Clay Obota[96,97], Domingo Ochavillo[98], Owen O'Shea[99,100], Kennedy E. Osuka[101,96], Yannis P. Papastamatiou[3], Nishan Perera[23], Bradley Peterson[13], Caio R. Pimentel[67,102], Fabián Pina-Amargós[103,104], Hudson T. Pinheiro[105], Alessandro Ponzo[106], Andhika Prasetyo[107], L.M. Sjamsul Quamar[108], Jessica R. Quinlan[3], José Amorim Reis-Filho[109], Hector Ruiz[110], Alexei Ruiz-Abierno[104], Enric Sala[111], Pelayo Salinas-de-León[112,113], Melita A. Samoilys[96,114], William R. Sample[3], Michelle Schärer-Umpierre[110], Audrey M. Schlaff[1], Kurt Schmid[55,115], Sara N. Schoen[3], Nikola Simpson[116], Adam N.H. Smith[117], Julia L.Y. Spaet[118], Lauren Sparks[119], Twan Stoffers[120], Akshay Tanna[23], Rubén Torres[121], Michael J. Travers[95], Maurits van Zinnicq Bergmann[3,58], Laurent Vigliola[122], Juney Ward[123], Joseph D. Warren[13], Alexandra M. Watts[47,124], Colin K. Wen[125], Elizabeth R. Whitman[3], Aaron J. Wirsing[126], Aljoscha Wothke[39], Esteban Zarza-González[127,128], Demian D. Chapman[60,3]

Affiliations:

[1]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia
[2]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia
[3]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida, USA

[4]Australian Institute of Marine Science, Townsville, Queensland, Australia
[5]Ocean Frontier Institute, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada
[6]Australian Institute of Marine Science, Perth, Western Australia, Australia
[7]School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia, Australia
[8]Earth to Ocean Group, Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada
[9]School of Molecular and Life Sciences, Curtin University, Perth, Western Australia, Australia
[10]Marine Science Program, Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Perth, Western Australia, Australia
[11]Centre for Sustainable Ecosystems Solutions, School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, New South Wales, Australia
[12]Australian Institute of Marine Science, Darwin, Northern Territory, Australia
[13]School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, New York, USA
[14]International Pole and Line Foundation – Maldives, Malé, Republic of Maldives
[15]Maldives Marine Research Institute, Ministry of Fisheries, Marine Resources and Agriculture, Malé, Republic of Maldives
[16]The Red Sea Development Company, Department of Environmental Sustainability, AlRaidah Digital City, Riyadh, Saudi Arabia
[17]Kap Natirel NGO, Fort l'Olive, Guadeloupe, France
[18]Mahonia Na Dari Research and Conservation Centre, Kimbe, Papua New Guinea
[19]South African Institute for Aquatic Biodiversity, National Research Foundation, Makhanda, South Africa
[20]Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa
[21]Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia
[22]Marine Conservation, Madagascar Program, Wildlife Conservation Society, Antananarivo, Madagascar
[23]Blue Resources Trust, Colombo, Sri Lanka
[24]Cape Eleuthera Institute, Cape Eleuthera, Eleuthera, The Bahamas
[25]Center for Sustainable Development, College of Arts and Sciences, Qatar University, Doha, Qatar
[26]Georgia Aquarium - Research and Conservation, Atlanta, Georgia, USA
[27]School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia
[28]Bimini Biological Field Station, Bimini, Bahama
[29]Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San José, Costa Rica
[30]MigraMar, Olema, California, USA
[31]Department of Biology, Albion College, Albion, Michigan, USA
[32]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, USA
[33]MARBEC, Univ Montpellier, IFREMER IRD, Montpellier, France
[34]ARC Centre of Excellent in Coral Reef Studies, James Cook University, Townsville, Queensland, Australia
[35]Centre Universitaire de Formation et de Recherche de Mayotte, Dembeni, France
[36]Paris Sciences Lettres, Centre de Recherche Insulaire et Observatoire de l’Environnement, Opunohu Bay, Papetoai, French Polynesia

[37]LABEX CORAIL, Ecole Pratique des Hautes Etudes, Perpignan, France
[38]School of Biosciences, Cardiff University, Cardiff, UK
[39]Environmental Research Institute Charlotteville, Charlotteville, Trinidad and Tobago
[40]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia
[41]Sharks Pacific, Rarotonga, Cook Islands
[42]Oceans and Atmosphere, CSIRO, Hobart, Tasmania, Australia
[43]Wageningen Marine Research, Wageningen University & Research, IJmuiden, The Netherlands
[44]Graduate School for Global Environmental Studies, Sophia University, Tokyo, Japan
[45]Waitt Institute, La Jolla, California, USA
[46]Reef Systems Ecology and Conservation Lab, Departamento de Biologia Marinha, Universidade Federal Fluminense, Rio de Janeiro, Brazil
[47]Marine Megafauna Foundation, Truckee, California, USA
[48]Oceanographic Research Institute, Durban, South Africa
[49]TRAFFIC International, Cambridge, UK
[50]College of Arts, Science, and Education, Florida International University, North Miami, Florida, USA
[51]Science Department, Georgia Jones-Ayers Middle School, Miami, Florida, USA
[52]Division of Aquatic Resources, Department of Land and Natural Resources, Honolulu, Hawai`i, USA
[53]Centro de Biociências, Departmento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Brasil
[54]Beacon Development Company, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia
[55]Instituto de Ciencias do Mar, Universidade Federal do Ceará, Fortaleza, Brazil
[56]Grupo de Ecologia Aquática, Espaço Inovação do Parque de Ciência e Tecnologia Guamá, Guamá, Pará, Brazil
[57]Independent consultant, Hull, UK
[58]Bimini Biological Field Station Foundation, South Bimini, The Bahamas
[59]Saving the Blue, Cooper City, Florida, USA
[60]Sharks and Rays Conservation Program, Mote Marine Laboratory, Sarasota, Florida, USA
[61]The School for Field Studies, Center for Marine Resource Studies, South Caicos, Turks and Caicos Islands
[62]Pelagios Kakunjá, La Paz, Mexico
[63]Fins Attached, Colorado Springs, Colorado, USA
[64]Center for Shark Research, Mote Marine Laboratory, Sarasota, Florida, USA
[65]OCEARCH, Park City, Utah, USA
[66]Elasmo Project, Dubai, United Arab Emirates
[67]Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil
[68]Murdoch University, Murdoch, Western Australia, Australia
[69]Rights Lab, University of Nottingham, Nottingham, UK
[70]Operation Wallacea, Spilsby, Lincolnshire, UK
[71]Melanesia Program, Wildlife Conservation Society, Suva, Fiji
[72]Wasage Divers, Wakatobi & Buton, Southeast Sulawesi, Indonesia
[73]Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, Chicago, Illinois, USA

[74]Kenya Fisheries Service, Mombasa, Kenya
[75]Ministry of Fisheries and Marine Resources, Kiritimati, Kiribati
[76]Tanzania Fisheries Research Institute, Dar Es Salaam, Tanzania
[77]University of the West Indies, Kingston, Jamaica
[78]School of Biological Sciences, University of Western Australia, Perth, Western Australia, Australia
[79]The UWA Oceans Institute, University of Western Australia, Perth, Western Australia, Australia
[80]Departamento de Pesquerias, Centro Interdisciplinario de Ciencias Marinas del IPN, La Paz, Baja California Sur, Mexico
[81]Pelagios Kakunjá, La Paz, Baja California Sur, Mexico
[82]Yardie Environmental Conservationists Limited, Kingston, Jamaica
[83]Coral Reef Research Foundation, Koror, Palau
[84]Departamento de Ecología y Territorio, Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Bogotá, Colombia
[85]National Institute of Water and Atmospheric Research, Auckland, New Zealand
[86]Borneo Marine Research Institute, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia
[87]Marine Megafauna Foundation, West Palm, Florida, USA
[88]Island Conservation Society Seychelles, Victoria, Mahé, Seychelles
[89]Emirates Nature - World Wide Fund for Nature, Dubai, United Arab Emirates
[90]Depto. Ecología e Hidrología, Universidad de Murcia, Murcia, Spain
[91]Aquarium of the Pacific, Long Beach, California, USA
[92]Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação, Funchal, Madeira, Portugal
[93]Oceans Institute, University of Western Australia, Perth, Western Australia, Australia
[94]Inland Fisheries Ireland, Dublin, Ireland
[95]Western Australian Fisheries and Marine Research Laboratories, Department of Primary Industries and Regional Development, Government of Western Australia, Hillarys, Western Australia, Australia
[96]CORDIO East Africa, Mombasa, Kenya
[97]Blue Ventures, Mombasa, Kenya
[98]American Samoa Department of Marine and Wildlife Resources, Pago Pago, American Samoa
[99]The Centre for Ocean Research and Education, Gregory Town, Eleuthera, The Bahamas
[100]Department of Ocean Science, Memorial University, Newfoundland, Canada
[101]Department of Environment and Geography, University of York, York, UK
[102]Departamento de Ciências Agrárias e Biológicas, Universidade Federal do Espírito Santo, São Mateus, Espírito Santo, Brazil
[103]Blue Sanctuary-Avalon, Jardines de la Reina, Cuba
[104]Centro de Investigaciones Marinas, Universidad de La Habana, Habana, Cuba
[105]Center for Marine Biology, University of São Paulo, São Sebastião, São Paulo, Brazil
[106]Large Marine Vertebrates Research Institute Philippines, Puerto Princesa City, Palawan, Philippines
[107]Center for Fisheries Research, Ministry for Marine Affairs and Fisheries, Jakarta Utara, Indonesia
[108]Fisheries Department, Universitas Dayanu Ikhsanuddin, Bau Bau, Southeast Sulawesi, Indonesia
[109]Programa de Pós Graduação em Ecologia: Teoria, Aplicação e valores, Instituto de Biologia, Universidade 5 Federal da Bahia, Salvador, BA, Brazil

[110]HJR Reefscaping, Boquerón, Puerto Rico
[111]Pristine Seas, National Geographic Society, Washington DC, USA
[112]Charles Darwin Research Station, Charles Darwin Foundation, Puerto Ayora, Galapagos Islands, Ecuador
[113]Save Our Seas Foundation Shark Research Center and Guy Harvey Research Institute, Nova Southeastern University, Dania Beach, Florida, USA
[114]School of Pure and Applied Sciences, Pwani University, Kilifi, Kenya
[115]Thurgau Hunting and Fishing Administration, Frauenfeld, Switzerland
[116]SalvageBlue, Kingstown, Saint Vincent and the Grenadines
[117]School of Mathematical and Computational Sciences, Massey University, Auckland, New Zealand
[118]Evolutionary Ecology Group, Department of Zoology, University of Cambridge, Cambridge, UK
[119]Indo Ocean Project, Jln Toyapakeh DESA Toyapakeh, Nusa Penida, Bali, Indonesia
[120]Aquaculture & Fisheries Group, Wageningen University & Research, Wageningen, The Netherlands
[121]Reef Check Dominican Republic, Santo Domingo, Dominican Republic
[122]Institut de Recherche pour le Développement, UMR ENTROPIE (IRD-UR-UNC-CNRS-IFREMER), Nouméa, New Caledonia, France
[123]Secretariat of the Pacific Regional Environment Programme, Apia, Samoa
[124]Department of Natural Sciences, Faculty of Science Engineering, Manchester Metropolitan University, Manchester, UK
[125]Department of Life Science, Tunghai University, Taichung, Taiwan
[126]School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA
[127]GIBEAM Research Group, Universidad del Sinú, Cartagena, Colombia
[128]Corales del Rosario and San Bernardo National Natural Park, Colombia

*Corresponding author. Email: colin.simpfendorfer@jcu.edu.au

Abstract:

A global survey of coral reefs reveals overfishing is driving resident shark species towards extinction, causing diversity deficits in reef elasmobranch (shark and ray) assemblages. Our species-level analysis revealed global declines of 60-73% for five common resident reef shark species, and that individual shark species were not detected at 34-47% of surveyed reefs. As reefs become more shark-depleted, rays begin to dominate assemblages. Shark-dominated assemblages persist in wealthy nations with strong governance, and in highly protected areas; while poverty, weak governance and a lack of shark management are associated with depauperate assemblages mainly composed of rays. Without action to address these diversity deficits, loss of ecological function and ecosystem services will increasingly impact human communities.

One-Sentence Summary:

Overfishing is driving common coral reef sharks towards global extinction and shifting reefs to ray-dominated assemblages.

Main text:

Coral reef ecosystems are under increasing pressure from human activities, including intense fishing, degraded water quality, and climate change (*1, 2*), that threaten species supporting a wide range of ecosystem functions (*3*). Sharks and rays (hereafter "elasmobranchs") have diverse roles on coral reefs as predators and prey across multiple trophic levels, and in the cycling and movement of nutrients (*3-5*). Recent evidence indicates that overfishing has driven sharks towards functional extinction on many reefs. In a global survey sharks were not observed on nearly 20% of reefs surveyed (*6*). Yet until recently reef shark species were listed in lower risk extinction categories by the International Union for the Conservation of Nature (IUCN). With ~37% of all elasmobranch species threatened with extinction (*7*), a key question for coral reef ecosystems lies in understanding the global extent of species loss in elasmobranch assemblages. Here we characterize elasmobranch assemblage structure on coral reefs across a gradient of human pressures to estimate the local depletion and global extinction risk of the most common reef species, revealing the human and environmental factors that influence assemblage structure, and that lead to a deficit in predator diversity that could affect reef ecological functioning.

To understand the extent of the reef shark diversity deficit, we surveyed 391 coral reefs in 67 nations and territories using 22,756 Baited Remote Underwater Video Stations (BRUVS). We examined reef-level species richness, species composition of elasmobranch assemblages, and species relative abundance (MaxN- the maximum number of each species observed in a single frame of each 60 minute deployment, then averaged across all deployments on one reef) (*8*). We examined how elasmobranch species assemblages changed in response to human pressures using unweighted pair group with arithmetic mean (UPGMA) clustering to identify reefs with the most similar assemblages (*8*). We then compared these clusters to estimated depletion of key resident elasmobranch species at the reef level, and examined if socioeconomic, management or environmental factors could predict cluster membership using linear discriminant analysis. Reef level depletion was estimated by dividing the observed mean MaxN of a species at individual reefs by a model-estimated baseline abundance (i.e., without human pressures) for each sampling site (a small group of closely associated reefs), and subtracting this value from one. Baseline abundance (also expressed as MaxN) was estimated from a general linear model relating observed MaxN to sampling site, human pressure (represented by total market gravity – the size and travel time to human markets (*2*)) and marine protected area (MPA) status (closed to all fishing, open to fishing or restricted [some fishing but with restrictions]). The baseline was estimated by setting all parameters to those expected at a site with no human pressure (i.e. gravity to the minimum for an ocean basin and protection status to closed) (*8*).

Sampling identified 104 unique elasmobranch species or species complexes (Table S1), representing more than 77% of elasmobranch species known to occur on coral reefs at some point during their lives (*9*). More than half (n = 53) of the species were rarely observed, with 10 or less sightings. We estimated reef level depletion for the 9 most commonly occurring species of shark (n= 5; Caribbean reef [*Carcharhinus perezi*] and nurse [*Ginglymostoma cirratum*] sharks in the Atlantic; grey reef [*C. amblyrhynchos*], blacktip reef [*C. melanopterus*], and whitetip reef [*Triaenodon obesus*] sharks in the Indo-Pacific; and rays (n = 4; yellow [*Urobatis jamaicensis*] and southern [*Hypanus americanus*] stingrays in the Atlantic; blue spotted mask [*Neotrygon* spp.] and blue spotted ribbontail [*Taeniura lymma* and *T. lessoni*] rays in the Indo-

Pacific). The Galapagos shark was excluded from estimates of global depletion because sampling only covered a relatively small proportion of its range, but the results for this species were broadly similar. The 9 key resident species represented 77.7% of all elasmobranchs observed in the study and are those that serve important ecological roles (*10*), contribute the most to, and underpin, livelihoods through fishing (*11*) and dive tourism (*12*).

We found that mean depletion of five key resident reef sharks on individual reefs ranged from 100% depletion (none observed) to 0% (no depletion), averaging 62.8% (Fig 1A). Mean depletion of key resident reef sharks followed the overall decline in elasmobranch abundance as measured by MaxN (Fig 1B), decreased as the fraction of the elasmobranch assemblage comprised of sharks decreased (Fig 1C), and showed little change across a range of elasmobranch species richness (Fig 1D); and these patterns were generally consistent between ocean basins. Across the range of depletion, five main clusters of reefs were identified in the Atlantic and eight in the Indo-Pacific (Fig 2, 3), including at least one cluster in each ocean basin (Cluster 1 in the Atlantic, Cluster 2 in the Indo-Pacific) having shark populations in a relatively intact state, with low levels of depletion of the five main resident reef shark species (Caribbean reef and nurse sharks in the Atlantic; grey reef , blacktip reef, and whitetip reef sharks in the Indo-Pacific) (*8*). Remaining clusters represented assemblages with increasing depletion of resident shark species and greater proportions of the overall elasmobranch assemblage represented by rays (Fig 2C, 3B). Both ocean basins show a similar transition through these assemblages as key resident shark species are depleted. The four key ray species (yellow and southern stingrays in the Atlantic; blue spotted mask and blue spotted ribbontail rays in the Indo-Pacific) increased only with depletion of one or more resident reef shark species; with rays dominating in the most shark-depleted areas. These predictable changes in assemblage provide the ability to infer the status of reef shark populations, and the level of human pressure they are experiencing, in future surveys.

Elasmobranch species assemblage clusters on reefs in both basins were significantly related to certain socioeconomic and management factors, with Linear Discriminant Analysis (LDA) accounting for ~85% of between cluster variance (Tables S2, S3). Important socioeconomic factors included the Human Development Index (HDI, an index of a nation's level of education, life expectancy and standard of living) and Voice and Accountability (an index of the extent to which people in each nation can participate in governance, free expression, free media and free association). Important management factors were whether the reef occurred in a Marine Protected Area (MPA) or whether a reef was within a nation where all targeted shark fishing and trade is prohibited, known as a 'Shark Sanctuary'. Given Shark Sanctuaries have largely been implemented in nations in which fishing for sharks was limited for economic or cultural reasons (*6*) their effectiveness as tools for recovering reef shark populations remains an open question. Total market gravity was more important in the Indo-Pacific than the Atlantic, possibly because remote reefs (> 4 hours travel time from human settlements) are relatively rare in the Atlantic compared to the Indo-Pacific (Fig S1) (*13*). Environmental factors (coral cover and relief) had little influence in predicting cluster membership. Elasmobranch assemblage structure on coral reefs in both the Atlantic and Indo-Pacific are therefore mainly driven by management and socio-economic factors, with shark-dominated assemblages more likely to occur in wealthy, well-governed nations, and in highly protected areas or Shark Sanctuaries; while poverty, limited governance and a lack of shark protection are associated with assemblages mainly composed of rays.

To further characterize the diversity deficits that underpin these assemblage differences, we compared species observations in our BRUVS with their historical ranges drawn from published literature, including historical accounts, finding that sharks were not detected at 13.6% (19 Atlantic, 34 Indo-Pacific) of reefs while rays were not detected at 21.5% (10 Atlantic, 74 Indo-Pacific); both groups were not detected at 6.6% (5 Atlantic, 19 Indo-Pacific) of reefs surveyed. At the species level, absences were severe: based on their known historic distribution, deficits were 46.9% of reefs (112 of 246) for blacktip reef sharks; 41.3% (31 of 75) for Caribbean reef sharks; 40.8% (102 of 250) for grey reef sharks, 36.2% (89 of 246) for whitetip reef sharks, and 34.7% (n = 26 of 75) for nurse sharks (Fig S2). Among rays, deficits were even more stark: 78.9% (75 of 95) for yellow stingray; 62.8% (81 of 129) for blue spotted ribbontail rays; and 55.6% (79 of 142) for blue spotted maskrays. An exception was the southern stingray which was not detected at only 19.8% (n = 20 of 101) of expected reefs in the Atlantic. A failure to detect rays may not always indicate absence as they are often cryptic and therefore missed on BRUVS, especially when sharks are present (*14*). Collectively, these diversity deficits show that elasmobranch loss on coral reefs is more extensive than previously demonstrated, with widespread losses of key species across many of the world's coral reefs, especially in Asia, eastern Africa, continental South America, and the central-eastern Caribbean.

Previous estimates of the status of reef shark and ray species have been geographically limited, varying among surveyed reefs from very high abundances (*15*) to local extinction (*16*). This disparity has made it difficult to assess the global status of individual species. Therefore, we used our estimates of reef level depletion to estimate the global depletion and extinction risk of the most common reef resident sharks (5 spp.) and rays (4 spp.). Mean and standard error reef level depletion was calculated within jurisdictions (nations or remote territories) and used to produce confidence intervals for jurisdictional depletion levels. To estimate an overall global depletion level by species we weighted the jurisdictional depletion by the percentage of the world's coral reefs in their waters and produced a weighted global mean depletion (*8*). Extinction risk was estimated by comparing proportional global depletion to the criteria for the IUCN Red List A2 (population decline) category (*17*) assuming that the decline had occurred in the past 3 generations (29 – 90 years). In IUCN assessments prior to the availability of this global survey, all resident reef shark species were considered at lower risk of extinction (i.e., Near Threatened) (*18*). Grey reef shark had the highest level of global decline (69.8% ± 1 standard error [s.e.] 62.6 – 77.1), followed by nurse shark (68.6% ± 49.7 – 87.4), Caribbean reef shark (64.8% ± 42.0 – 87.5), blacktip reef shark (64.5% ± 58.7 – 70.4) and whitetip reef shark (60.4% ± 51.2 – 70.2) (Fig 4). The estimated declines of resident species of reef sharks met the IUCN Red List criteria for Endangered. Population changes of rays were more variable, with increasing populations in some nations, and declines in others (Fig S3), reflecting the compositional changes seen across our gradient of human pressures. When examined at the global level, no ray species examined met criteria for elevated extinction risk, consistent with current non-threatened status of these species on the Red List.

Our study of nations hosting ~90% of global reefs reveals that resident reef shark species are at much higher risk of extinction than previously thought. Local declines, shaped by human pressures that vary across ocean basins, have led to consistent changes in the structure of coral reef elasmobranch assemblages that may have profound effects on the broader ecosystem. The direct and indirect effects of fishing have driven shifts in species composition from shark-dominated to ray-dominated assemblages, and ultimately the complete loss of sharks and rays at a small proportion (~ 7%) of reefs surveyed. In addition to changes in the structure of assemblages, all major resident shark species have declined to levels such that they qualify as Endangered by the IUCN Red List Criteria. These changes wrought on coral reef elasmobranch assemblages demonstrate the pervasiveness of fishing on coral reefs (*19*) and the substantial risks to reef-dependent human communities of continued overfishing. Elasmobranch species vary widely in their economic value, with some fished for subsistence, others for local or export markets, and others are valued alive as tourism resources (*12, 20*). Thus, understanding threats and conservation options for rebuilding populations at a species level will assist in developing effective management of coral reef elasmobranchs as part of a sustainable social-ecological system.

Although reef sharks are at considerable risk over broad spatial scales, our results show declines at one reef will have little effect on reefs tens to hundreds of kilometers distant. Thus, despite populations being functionally extinct at the reef level, the potential to rebuild abundances remains relatively high if there are protected areas or strong fisheries management within a region (*6*). These source populations are present among many small oceanic islands where low human populations and the high cultural value of sharks has resulted in fishing levels that are below those seen elsewhere (*21*). MPAs also provide the opportunity to act as source populations, however, their designation alone is insufficient to deliver benefits. As others have observed (*22*), high compliance is required. We show that there are reefs in regions with wide-spread depletion of reef shark species that had metrics indicating that they are in a relatively healthy state compared to those around them. These included Tubbataha (Philippines), Sipidan (Island Malaysia), Glover’s Reef and Lighthouse Reef (Belize) and Misool (Indonesia); in all of these locations there are programs to actively manage and enforce MPA regulations that are likely to account for these successes (*23-25*).

Multiple nations have strong management measures (e.g., spatial protections and/or fishing restrictions) in place that benefit reef species. This study builds the case that species-specific reef shark management provides the best way forward for conservation and rebuilding of reef sharks in places where they have declined, among nations with the desire and capacity to do so (7,8). Recent studies show that populations of reef sharks can rebound in under a decade if appropriate management strategies that reduce fishing pressure are in place (*26*). While direct management is critical, local and national socioeconomic factors that affect the ability of nations to develop, implement and enforce regulations, and the likelihood that fishers comply with regulations, will be critical to maintaining or rebuilding populations and diverse elasmobranch assemblages. If not addressed, pressures causing the shark and ray diversity deficits we outline will continue to result in a loss of species, ecological functions, and ecosystem services that support sustainable livelihoods for millions of people worldwide.

References and Notes

1. Terry P. Hughes, David R. Bellwood, Sean R. Connolly, Howard V. Cornell, Ronald H. Karlson, Double jeopardy and global extinction risk in corals and reef fishes. *Current Biology* **24**, 2946-2951 (2014).
2. J. E. Cinner *et al.*, Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences* **115**, E6116-E6125 (2018).
3. G. Roff *et al.*, The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution* **31**, 395-407 (2016).
4. K. I. Flowers, M. R. Heithaus, Y. P. Papastamatiou, Buried in the sand: Uncovering the ecological roles and importance of rays. *Fish and Fisheries* **22**, 105-127 (2021).
5. J. J. Williams, Y. P. Papastamatiou, J. E. Caselle, D. Bradley, D. M. P. Jacoby, Mobile marine predators: an understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B: Biological Sciences* **285**, (2018).
6. M. A. MacNeil *et al.*, Global status and conservation potential of reef sharks. *Nature* **583**, 801-806 (2020).
7. N. K. Dulvy *et al.*, Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology* **31**, 4773-4787 (2021).
8. Materials and methods are available as supplementary materials.
9. C. S. Sherman *et al.*, Half a century of rising extinction risk of coral reef sharks and rays. *Nature Communications*, (2023).
10. M. R. Heupel, Y. P. Papastamatiou, M. Espinoza, M. E. Green, C. A. Simpfendorfer, Reef shark science – Key questions and future directions. *Frontiers in Marine Science* **6**, (2019).
11. S. A. Appleyard, W. T. White, S. Vieira, B. Sabub, Artisanal shark fishing in Milne Bay Province, Papua New Guinea: biomass estimation from genetically identified shark and ray fins. *Scientific Reports* **8**, 6693 (2018).
12. A. M. Cisneros-Montemayor, M. Barnes-Mauthe, D. Al-Abdulrazzak, E. Navarro-Holm, U. R. Sumaila, Global economic value of shark ecotourism: implications for conservation. *Oryx* **47**, 381-388 (2013).
13. T. R. McClanahan, Wilderness and conservation policies needed to avoid a coral reef fisheries crisis. *Marine Policy* **119**, 104022 (2020).
14. C. S. Sherman, M. R. Heupel, S. K. Moore, A. Chin, C. A. Simpfendorfer, When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **641**, 145-157 (2020).
15. J. Mourier *et al.*, Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. *Current Biology* **26**, 2011-2016 (2016).
16. M. O. Nadon *et al.*, Re-creating missing population baselines for Pacific reef sharks. *Conservation Biology* **26**, 493-503 (2012).
17. IUCN, *IUCN Red List categories and criteria, version 3.1, second edition*. (IUCN, Gland, Switzerland and Cambridge, UK, 2012).
18. N. K. Dulvy *et al.*, Ghosts of the coast: global extinction risk and conservation of sawfishes. *Aquatic Conservation-Marine and Freshwater Ecosystems* **26**, 134-153 (2016).
19. T. D. Eddy *et al.*, Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* **4**, 1278-1285 (2021).

20. H. Booth, D. Squires, E. J. Milner-Gulland, The neglected complexities of shark fisheries, and priorities for holistic risk-based management. *Ocean & Coastal Management* **182**, 104994 (2019).
21. J. S. Goetze *et al.*, Drivers of reef shark abundance and biomass in the Solomon Islands. *PLOS ONE* **13**, e0200960 (2018).
22. G. J. Edgar *et al.*, Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216-220 (2014).
23. R. Murray *et al.*, Tubbataha Reefs Natural Park: the first comprehensive elasmobranch assessment reveals global hotspot for reef sharks. *Journal of Asia-Pacific Biodiversity* **12**, 49-56 (2019).
24. V. F. Jaiteh *et al.*, Higher abundance of marine predators and changes in fishers' behavior following spatial protection within the world's biggest shark fishery. *Frontiers in Marine Science* **3**, (2016).
25. G. Clementi *et al.*, Anthropogenic pressures on reef-associated sharks in jurisdictions with and without directed shark fishing. *Mar. Ecol. Prog. Ser.* **661**, 175-186 (2021).
26. C. W. Speed, M. Cappo, M. G. Meekan, Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biological Conservation* **220**, 308-319 (2018).
27. C. Simpfendorfer, Widespread diversity deficits of coral reef sharks and rays. Dryad, Dataset (2023) https://doi.org/10.5061/dryad.qbzkh18h0.
28. C. Simpfendorfer, Widespread diversity deficits of coral reef sharks and rays. Zenodo (2023) https://doi.org/10.5281/zenodo.7030578.
29. L. M. Currey-Randall, M. Cappo, C. A. Simpfendorfer, N. F. Farabaugh, M. R. Heupel, Optimal soak times for Baited Remote Underwater Video Station surveys of reef-associated elasmobranchs. PLOS ONE 15, e0231688 (2020).
30. C. S. Sherman, A. Chin, M. R. Heupel, C. A. Simpfendorfer, Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? Journal of Experimental Marine Biology and Ecology 503, 80-85 (2018).
31. D. A. Ebert, S. L. Fowler, L. J. V. Compagno, Sharks of the World. A Fully Illustrated Guide. (Wild Nature Press, Plymoth, 2013).
32. P. R. Last, J. D. Stevens, Sharks and Rays of Australia. (CSIRO Publishing, Melbourne, ed. 2nd, 2009), pp. 656.
33. P. R. Last et al., Rays of the World. (CSIRO Publishing, Melbourne, 2016).
34. J. E. Cinner et al., Gravity of human impacts mediates coral reef conservation gains. Proceedings of the National Academy of Sciences 115, E6116-E6125 (2018).
35. C. A. Ward-Paige, B. Worm, Global evaluation of shark sanctuaries. Global Environmental Change 47, 174-189 (2017).
36. C. S. Sherman, M. R. Heupel, S. K. Moore, A. Chin, C. A. Simpfendorfer, When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. Mar. Ecol. Prog. Ser. 641, 145-157 (2020).
37. M. D. Spalding, C. Ravilious, E. P. Green, World Atlas of Coral Reefs. (University of California Press, Berkeley, 2001).

38. F. Dent, S. C. Clarke, State of the global market for shark products. FAO Fisheries and Aquaculture Technical Paper 590, 1-187 (2015).

39. F. Ferretti, D. Curnick, K. Liu, E. V. Romanov, B. A. Block, Shark baselines and the conservation role of remote coral reef ecosystems. Science Advances 4, eaaq0333 (2018).

Acknowledgments: We thank our individual funders for country-specific deployments, whose contributions greatly enhanced the sampling coverage of the projects; all of the government permitting agencies that allowed us to work in their waters; and the Global FinPrint volunteers from Stony Brook University, Florida International University, James Cook University, the Aquarium of the Pacific and Shedd Aquarium who watched the BRUVS footage.

Funding: Provide complete funding information, including grant numbers, complete funding agency names, and recipient's initials. Each funding source should be listed in a separate paragraph.

Core funding for Global FinPrint was provided by the Paul G. Allen Family Foundation (to DDC, MH).

Author contributions:

Conceptualization: DDC, MH, CAS, MRH, MAM, MM, EH

Methodology: DDC, MH, CAS, MRH, MAM, MM, EH

Investigation: All authors

Visualization: CAS

Funding acquisition: DDC, MH

Project administration: DDC, MH, CAS, MRH, MAM, MM, EH

Writing – original draft: CAS, DDC, MH, MRH, MAM, MM, EH, CSS

Writing – review & editing: All authors

Competing interests: Authors declare that they have no competing interests

Data and materials availability:

Data files have been deposited in Dryad (*27*) and R script in Zenodo (*28*) are available at:

Data files: https://doi.org/10.5061/dryad.qbzkh18h0

R code: https://doi.org/10.5281/zenodo.7030578

Supplementary Materials

Materials and Methods

Figs. S1 to S8

Tables S1 to S9

References (*29–39)*

Figure captions:

Fig 1. The global decline of coral reef elasmobranchs. **A**, Reef scale estimates of depletion of resident coral reef shark species. Depletion is proportion of unfished population lost, represented as the measured MaxN as a proportion of MaxN in an unfished state (i.e. gravity = lowest in basin, and MPA status = closed; see Methods). Open circles indicate no sharks or rays were observed; grey circles indicate none of the resident shark species used to calculate mean depletion were present. **B**, relationship between depletion of resident shark species and MaxN by ocean basin. **C**, relationship between depletion of resident shark species and the proportion of elasmobranch MaxN comprised shark, demonstrating the transition from shark to ray dominated assemblages. **D**, relationship between depletion of resident shark species and species richness.

Fig 2. Structure of shark and ray assemblages on Atlantic coral reefs. **A-B**, clusters of reefs with similar species composition from UPGMA clustering of 106 reefs in the Atlantic basin based on a global set of 31 coral reef-associated species. Five main clusters, representing 87.0% of reefs, were identified. Their locations are indicated by colored triangles. Reefs with minor clusters are indicated by grey dots (n=7). Reefs where no elasmobranchs were observed are indicated by black dots (n=5). **C**, regime plot showing all species assemblage clusters as a function of the mean depletion of the resident reef shark species (Caribbean reef and nurse sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, colors indicate cluster identity as per panel A; minor clusters are indicated in grey. **D**, population level, relative to original levels, of four resident reef species in each of the five main clusters. (Note that proportion of original level = 1-depletion.) Horizontal line indicates mean, box indicates 25-75 percentile, and whiskers indicate 95% confidence interval.

Fig 3. Structure of shark and ray assemblages on Indo-Pacific coral reefs. **A**, clusters of reefs with similar species composition from UPGMA clustering of 285 reefs in the Indo-Pacific basin based on a global set of 31 coral reef-associated species. Eight main clusters, representing 82.1% of reefs, were identified. Their locations are indicated by colored triangles. Reefs with minor clusters are indicated by grey dots (n=30). Reefs where no elasmobranchs were observed are indicated by black dots (n=21). **B**, regime plot showing all species assemblage clusters as a function of the mean depletion of the resident species of reef shark (grey reef, blacktip reef, whitetip reef and Galapagos sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, colors indicate cluster identity as per panel A; minor clusters indicated in grey. **C**, population level relative to original levels, of five core shark and ray species in each of the eight main species assemblage clusters. (Note that proportion of original level = 1- depletion.) Horizontal line indicates mean, box indicates 25-75 percentile, and whiskers indicate 95% confidence interval.

Fig 4 Depletion of core coral reef shark species in the (A) Indo-Pacific and (B) Atlantic basins at national, or near-national, scale. Depletion was calculated by comparing reef level species MaxN values to unfished estimated using a linear model where market gravity (a measure of the human pressure from population and access to reefs) was set to the ocean basin minimum and reef protected status was “closed” (i.e. no take MPA) (see Supplementary Material for details). Reef level depletion scores were modeled by nation and used to estimate a global level of depletion (vertical dashed lines) ± 1 standard error (shaded area) calculated by weighting national level depletion by coral reef area (as a % of global total coral reef area that occurs within the range of each shark species).

Figure captions:

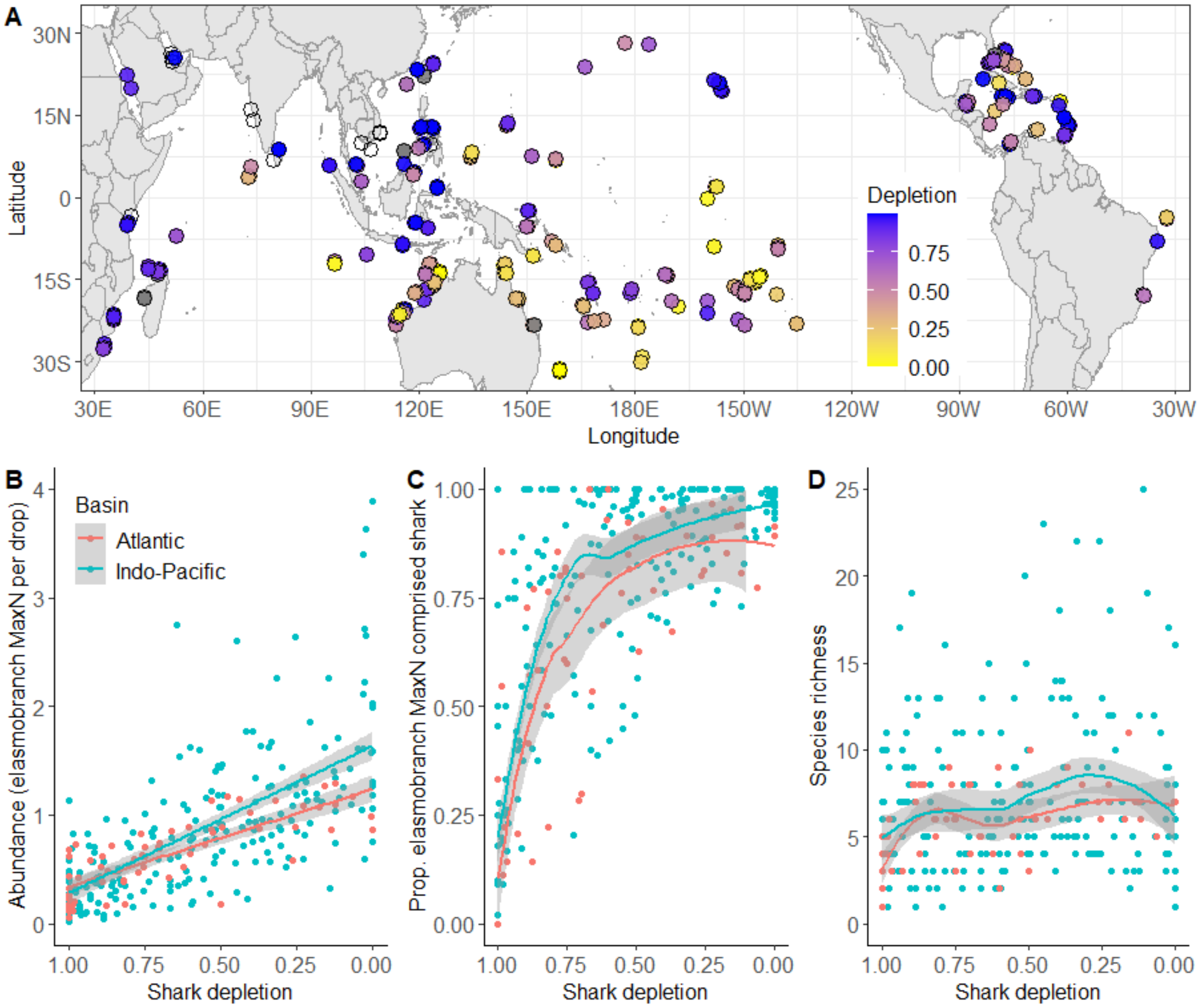

Fig 1. The global decline of coral reef elasmobranchs. **A**, Reef scale estimates of depletion of resident coral reef shark species. Depletion is proportion of unfished population lost, represented as the measured MaxN as a proportion of MaxN in an unfished state (i.e. gravity = lowest in basin, and MPA status = closed; see Methods). Open circles indicate no sharks or rays were observed; grey circles indicate none of the resident shark species used to calculate mean depletion were present. **B**, relationship between depletion of resident shark species and MaxN by ocean basin. **C**, relationship between depletion of resident shark species and the proportion of elasmobranch MaxN comprised shark, demonstrating the transition from shark to ray dominated assemblages. **D**, relationship between depletion of resident shark species and species richness.

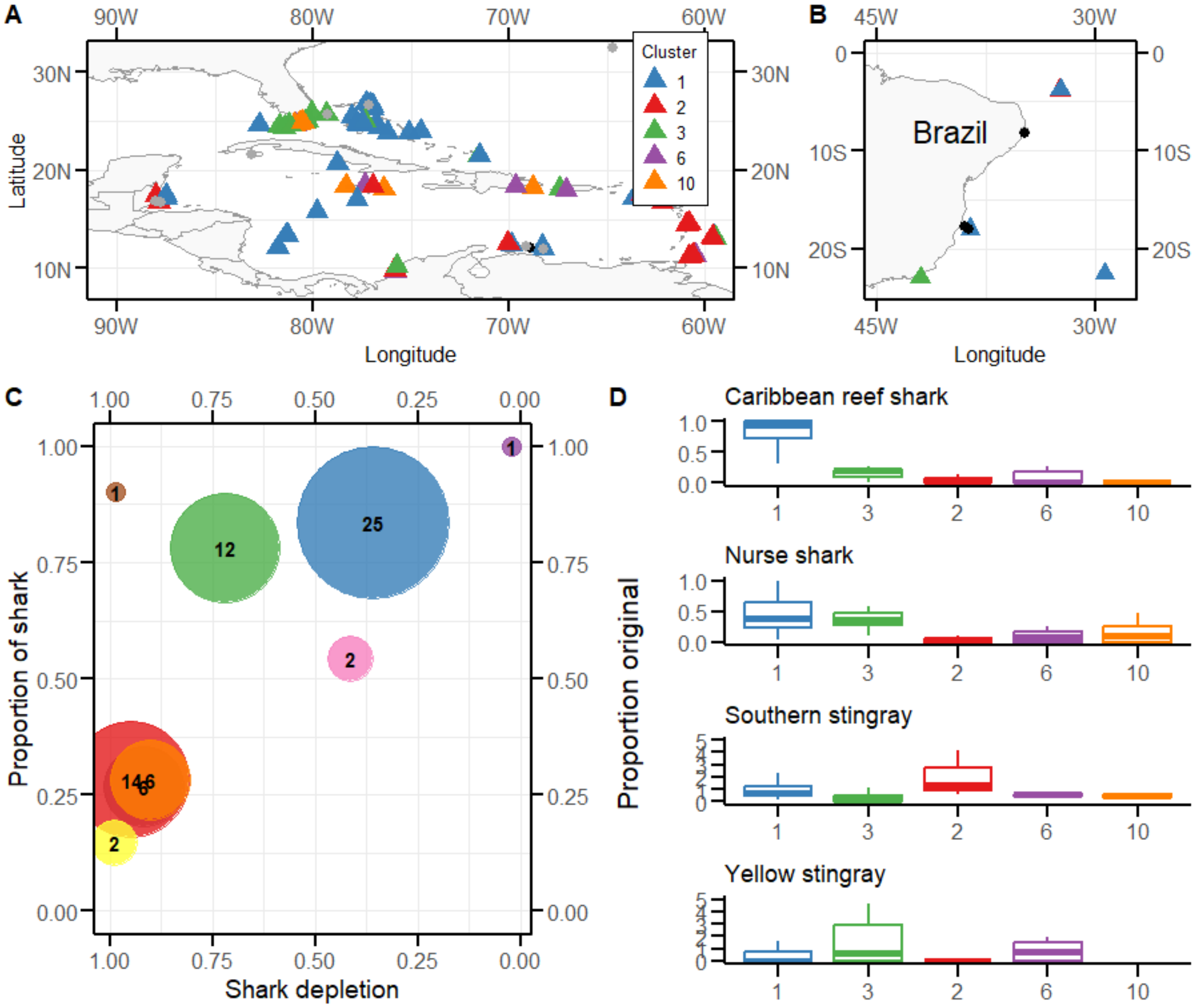

Fig 2. Structure of shark and ray assemblages on Atlantic coral reefs. **A-B**, clusters of reefs with similar species composition from UPGMA clustering of 106 reefs in the Atlantic basin based on a global set of 31 coral reef-associated species. Five main clusters, representing 87.0% of reefs, were identified. Their locations are indicated by colored triangles. Reefs with minor clusters are indicated by grey dots (n=7). Reefs where no elasmobranchs were observed are indicated by black dots (n=5). **C**, regime plot showing all species assemblage clusters as a function of the mean depletion of the resident reef shark species (Caribbean reef and nurse sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, colors indicate cluster identity as per panel A; minor clusters are indicated in grey. **D**, population level, relative to original levels, of four resident reef species in each of the five main clusters. (Note that proportion of original level = 1- depletion.) Horizontal line indicates mean, box indicates 25-75 percentile, and whiskers indicate 95% confidence interval.

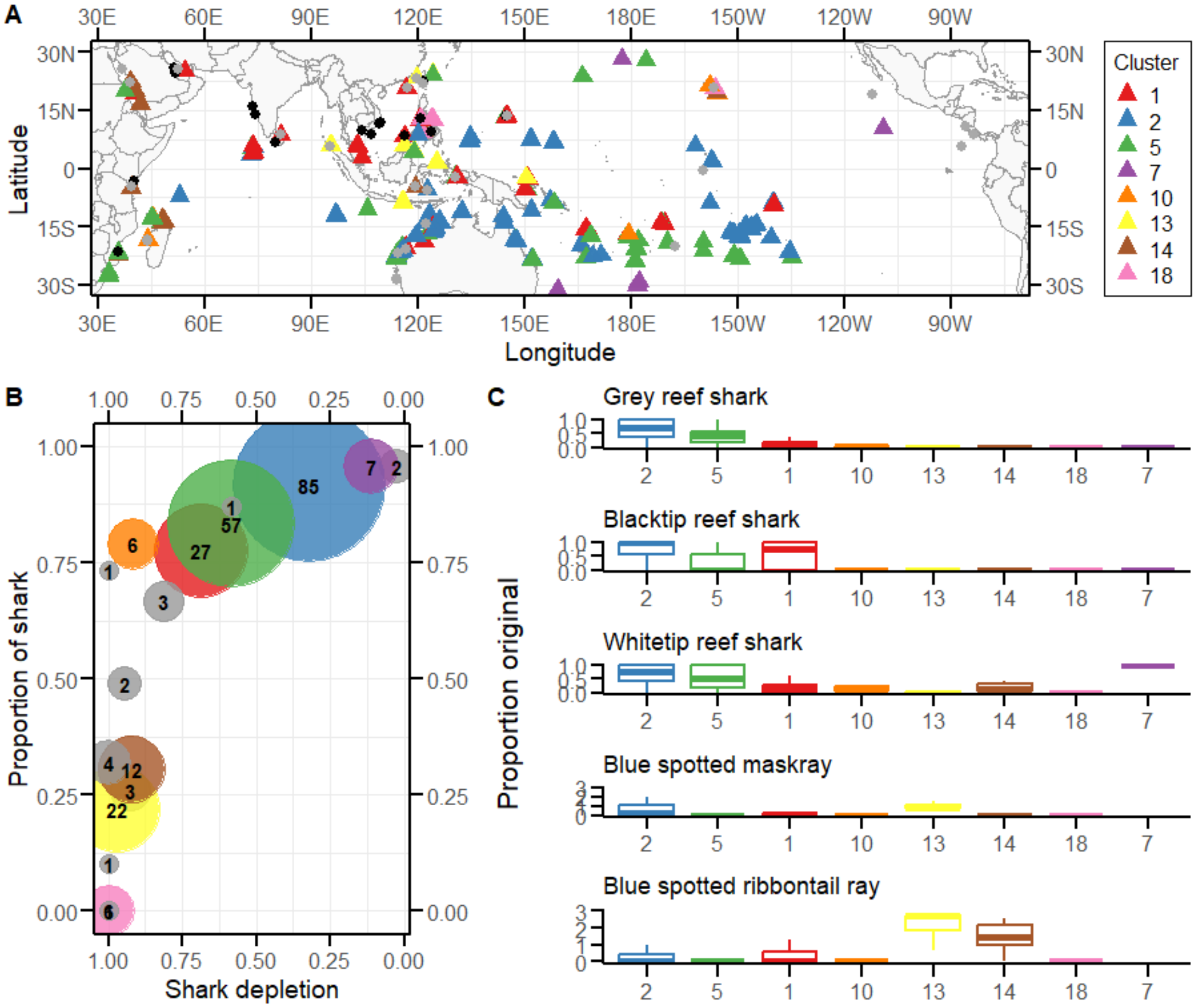

Fig 3. Structure of shark and ray assemblages on Indo-Pacific coral reefs. **A**, clusters of reefs with similar species composition from UPGMA clustering of 285 reefs in the Indo-Pacific basin based on a global set of 31 coral reef-associated species. Eight main clusters, representing 82.1% of reefs, were identified. Their locations are indicated by colored triangles. Reefs with minor clusters are indicated by grey dots (n=30). Reefs where no elasmobranchs were observed are indicated by black dots (n=21). **B**, regime plot showing all species assemblage clusters as a function of the mean depletion of the resident species of reef shark (grey reef, blacktip reef, whitetip reef and Galapagos sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, colors indicate cluster identity as per panel A; minor clusters indicated in grey. **C**, population level relative to original levels, of five core shark and ray species in each of the eight main species assemblage clusters. (Note that proportion of original level = 1- depletion.) Horizontal line indicates mean, box indicates 25-75 percentile, and whiskers indicate 95% confidence interval.

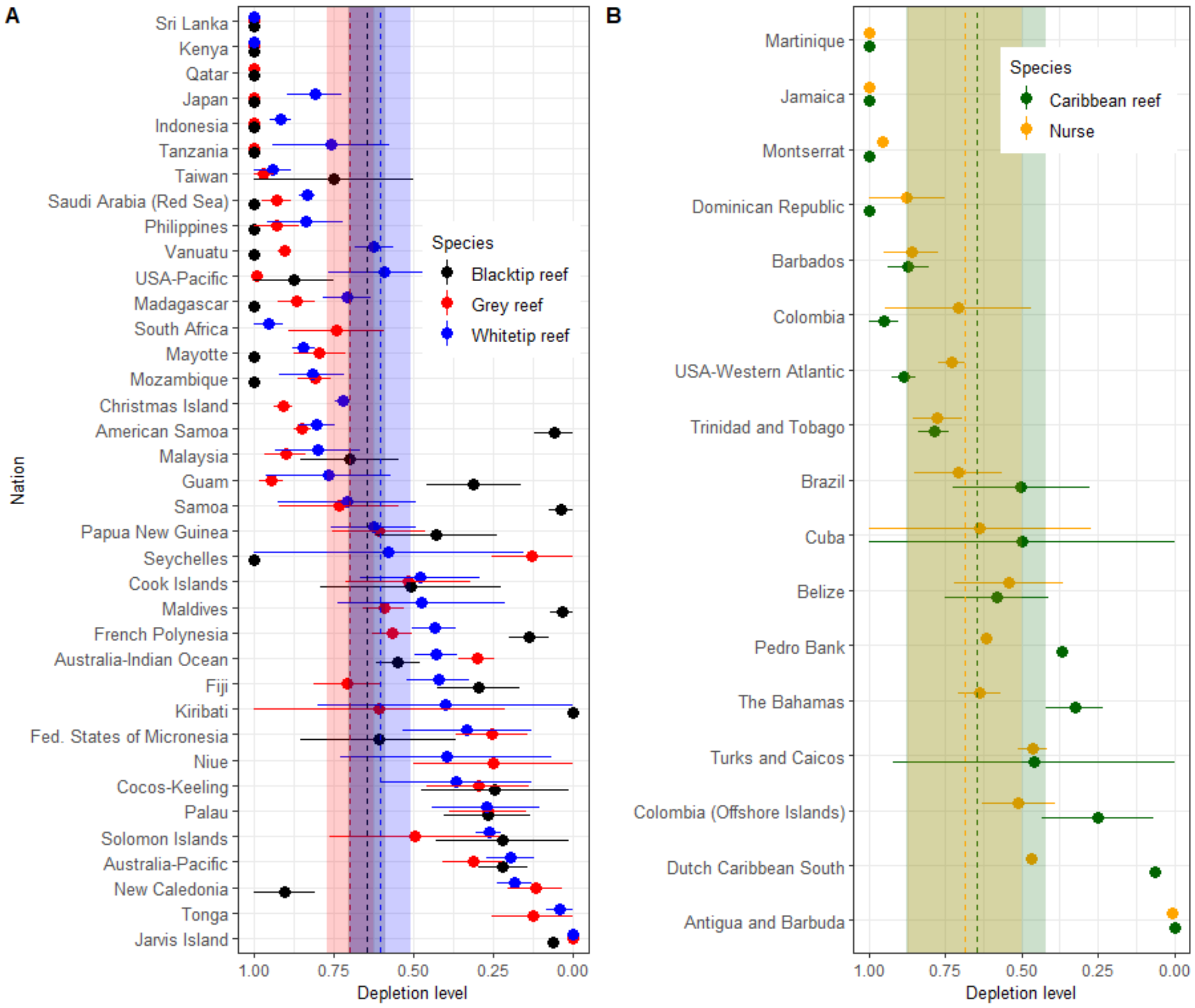

Fig 4 Depletion of core coral reef shark species in the (A) Indo-Pacific and (B) Atlantic basins at national, or near-national, scale. Depletion was calculated by comparing reef level species MaxN values to unfished estimated using a linear model where market gravity (a measure of the human pressure from population and access to reefs) was set to the ocean basin minimum and reef protected status was “closed” (i.e. no take MPA) (see Supplementary Material for details). Reef level depletion scores were modeled by nation and used to estimate a global level of depletion (vertical dashed lines) ± 1 standard error (shaded area) calculated by weighting national level depletion by coral reef area (as a % of global total coral reef area that occurs within the range of each shark species).

Science
AAAS

Supplementary Materials for

Widespread diversity deficits of coral reef sharks and rays

Colin A. Simpfendorfer[1,2], Michael R. Heithaus[3], Michelle R. Heupel[2,4], M. Aaron MacNeil[5], Mark Meekan[6], Euan Harvey[7], C. Samantha Sherman[8,1], Leanne M. Currey-Randall[4], Jordan S. Goetze[9,10], Jeremy J. Kiszka[3], Matthew J. Rees[6,11], Conrad W. Speed[6], Vinay Udyawer[12], Mark E. Bond[3], Kathryn I. Flowers[3], Gina M. Clementi[3], Jasmine Valentin-Albanese[13], M. Shiham Adam[14], Khadeeja Ali[15,3], Jacob Asher[16], Eva Aylagas[16], Océane Beaufort[17], Cecilie Benjamin[18], Anthony T.F. Bernard[19,20], Michael L. Berumen[21], Stacy Bierwagen[4], Chico Birrell[22], Erika Bonnema[3], Rosalind M.K. Bown[23], Edward J. Brooks[24], J. Jed Brown[25], Dayne Buddo[26], Patrick J. Burke[27,28], Camila Cáceres[3], Marta Cambra[29,30], Diego Cardeñosa[3], Jeffrey C. Carrier[31], Sara Casareto[3], Jennifer E. Caselle[32], Venkatesh Charloo[33], Joshua E. Cinner[34], Thomas Claverie[35,33], Eric E.G. Clua[36,37], Jesse E.M. Cochran[21], Neil Cook[38,39], Jessica E. Cramp[40,41], Brooke M. D'Alberto[1,42], Martin de Graaf[43], Mareike C. Dornhege[44], Mario Espinoza[29,30], Andy Estep[45], Lanya Fanovich[39], Naomi F. Farabaugh[3], Daniel Fernando[23], Carlos Eduardo Leite Ferreira[46], Candace Y.A. Fields[3,24], Anna L. Flam[47], Camilla Floros[48,49], Virginia Fourqurean[50,51], Laura Gajdzik[21,52], Laura García Barcia[3], Ricardo Garla[53,54], Kirk Gastrich[3], Lachlan George[2], Tommaso Giarrizzo[55,56], Rory Graham[57], Tristan L. Guttridge[58,59], Valerie Hagan[60], Royale S. Hardenstine[16], Stephen M. Heck[13], Aaron C. Henderson[61], Patricia Heithaus[3], Heidi Hertler[61], Mauricio Hoyos Padilla[62,63], Robert E. Hueter[64,65], Rima W. Jabado[66], Jean-Christophe Joyeux[67], Vanessa Jaiteh[68,69], Mohini Johnson[70], Stacy D. Jupiter[71], Muslimin Kaimuddin[72,70], Devanshi Kasana[3], Megan Kelley[3], Steven T. Kessel[73], Benedict Kiilu[74], Taratau Kirata[75], Baraka Kuguru[76], Fabian Kyne[77], Tim Langlois[78,79], Frida Lara[80,81], Jaedon Lawe[82], Elodie J.I. Lédée[1], Steve Lindfield[83], Andrea Luna-Acosta[84], Jade Q. Maggs[85], B. Mabel Manjaji-Matsumoto[86], Andrea Marshall[87], Lucy Martin[88], Daniel Mateos-Molina[89,90], Philip Matich[59], Erin McCombs[91], Ashlie McIvor[21,92], Dianne McLean[6,93], Llewelyn Meggs[82], Stephen Moore[1], Sushmita Mukherji[1,2], Ryan Murray[94], Stephen J. Newman[95], Josep Nogués[88], Clay Obota[96,97], Domingo Ochavillo[98], Owen O'Shea[99,100], Kennedy E. Osuka[101,96], Yannis P. Papastamatiou[3], Nishan Perera[23], Bradley Peterson[13], Caio R. Pimentel[67,102], Fabián Pina-Amargós[103,104], Hudson T. Pinheiro[105], Alessandro Ponzo[106], Andhika Prasetyo[107], L.M. Sjamsul Quamar[108], Jessica R. Quinlan[3], José Amorim Reis-Filho[109], Hector Ruiz[110], Alexei Ruiz-Abierno[104], Enric Sala[111], Pelayo Salinas-de-León[112,113], Melita A. Samoilys[96,114], William R. Sample[3], Michelle Schärer-Umpierre[110], Audrey M. Schlaff[1], Kurt Schmid[55,115], Sara N. Schoen[3], Nikola Simpson[116], Adam N.H. Smith[117], Julia L.Y. Spaet[118], Lauren Sparks[119], Twan Stoffers[120], Akshay Tanna[23], Rubén Torres[121], Michael J. Travers[95], Maurits van Zinnicq Bergmann[3,58], Laurent Vigliola[122], Juney Ward[123], Joseph D. Warren[13], Alexandra M. Watts[47,124], Colin K. Wen[125], Elizabeth R.

Whitman[3], Aaron J. Wirsing[126], Aljoscha Wothke[39], Esteban Zarza-González[127,128], Demian D. Chapman[60,3]

Correspondence to: colin.simpfendorfer@jcu.edu.au

This PDF file includes:

Materials and Methods
Supplementary text
Figs. S1 to S8
Tables S1 to S9

Materials and Methods

General BRUVS methods

FinPrint sampling of coral reefs used Baited Remote Underwater Video Systems (BRUVS). BRUVS consisted of a weighted metal frame holding a compact high resolution video camera (typically a GoPro) and a 1 m arm holding a bait bag containing 1 kg of crushed oily fish in front of the camera. Where possible, at least 50 BRUVS were deployed at a reef (defined as a single isolated reef, or a patch of a large reef ~10 km^2). Four to eight BRUVS were deployed simultaneously in each reef, with all BRUVS set at least 500 m from each other. BRUVS were deployed between 0-40 m depth and for a minimum of 60 minutes. This deployment time was sufficient to adequately sample the core coral reef shark and ray species (*29*). At each BRUVS deployment the date, depth, time of deployment and retrieval, GPS coordinates, sea conditions, and weather conditions were collected.

All videos were read by trained annotators using either Event Measure (https://www.seagis.com.au/event.html) or FinPrint Annotator (https://github.com/GlobalFinPrint/Finprint-Annotator). BRUVS that landed with a severely obstructed view were not annotated and were removed from further analyses. All sharks and rays observed were identified to the lowest possible taxon (mostly to species), and the time they entered the video frame and the maximum number of each species in a single frame (MaxN) in each video were recorded. MaxN is a conservative measure of relative abundance that ensures individuals are not double counted (*30*). Species identifications were verified by a senior annotator. Each deployed BRUVS thus had a MaxN for each sighted species, which could then be summed across all deployments and averaged across the reef. Elasmobranch sightings that could not be identified to species were excluded from species level analyses. Information on deployments and the results of the video annotations as part of the FinPrint project were entered into a central database.

Among all species identified (Table S1), half (n=52) were rare and sighted less than 10 times each. Species observed included many that complete all (‘reef residents’) or a large part (‘partial residents’) of their life cycle on coral reefs and a smaller number of transient species, including wide-ranging apex predators and mesopredators that are also common in off-reef habitats (Fig S4). Only eight species were observed in both the Atlantic and Indo-Pacific basins, with each basin having a unique assemblage of sharks and rays that were conserved across most locations (Fig S2). We observed a greater total number of species on Indo-Pacific reefs (92 species) than on Atlantic reefs (26 species). Except for a small number of reefs with very high diversity in northern Australia and South Africa, and reefs where elasmobranchs were absent, species richness was remarkably consistent across sampled reefs (mean = 5.98 species, standard deviation = 4.19).

In addition to data included in the FinPrint database, we gathered data from regions in which the FinPrint project had been unable to collect data, or where data were not included in the FinPrint database. This data set included 36 reefs, including those from the eastern tropical Pacific (Costa Rica 3 reefs, Mexico 1 reef, Clipperton Island 1 reef), Fiji (3 reefs), Indonesia (3 reefs), Red Sea (Saudi Arabia 5 reefs, Sudan 1 reef), United Arab Emirates (1 reef), Maldives (5 reefs), Madagascar (2 reefs), Australia (2 reefs), Brazil (2 reefs), USA (1 reef), Puerto Rico (2 reefs) and Colombia (Seaflower Biosphere Reserve 3 reefs). These reefs were used only in the assemblage analysis, and not in the estimation of population depletion.

We also corrected an error in the FinPrint database previously used in (*6*). There was a data upload error in the 'Dutch Caribbean Windward' reefs that reduced the MaxN of all elasmobranchs. The correct data was re-entered for the current work.

Habitat determination

A screenshot from all deployments was taken once the BRUVS settled on the benthos and analysed using BenthoBox software (www.benthobox.com). Relief and habitat were determined for each deployment. A 20 square grid (five across, four up) was overlayed on the screenshot from each deployment. All squares containing benthos were categorised into one of six relief scores ranging from 0 (flat) to 5 (complex). The average relief score for all squares containing benthos was then calculated for each deployment. Habitat was similarly assessed. The most abundant habitat type within each square containing habitat was identified based on a predetermined list: hard coral, soft coral, bleached coral, unconsolidated (sand/rubble), consolidated (rock), seagrass, turf algae, macroalgae, and other (cnidarians, sponges, etc.). The percent cover of each habitat type was then calculated by the number of squares with that as the most abundant habitat type over the total number of squares containing benthos. For example, in a video where 13 squares contained benthos and five had hard coral as the most abundant habitat type, hard coral was considered to account for 38.5% of benthic cover for the deployment.

Data selection

We excluded locations from the FinPrint database that had low sample sizes (<20 drops per reef) or that did not sample fully formed coral reefs. The majority of reefs excluded came from the Western Australian coast or the Hawaiian Islands.

Species data

For each reef sampled we calculated the species richness (number of unique species). Each species was allocated *a priori* to one of three groups based on its level of association with coral reefs: reef resident, part reef resident and transient. Reef residents are those species rarely found in non-coral reef habitats and that complete their life cycle on coral reefs. Part reef residents are those species that complete part of their life cycle in coral reef habitat but normally use non- reef habitat(s) for part of their life cycle; individuals or life-stages can be residents of coral reef habitat but periodically and/or ontogenetically move away from it. Transient species are those species that use coral reef habitat occasionally and temporarily while using other habitats as frequently or more often. Allocations were based on habitat use information in the literature, or where data was lacking, on expert opinion from the author group.

Species distribution data from published literature (*31-33*) was used to determine which of the sampled reefs each species observed would have been expected to have been found (i.e. if it should have been expected to be observed). This produced an expected species-by-reef matrix. We calculated the proportion of reefs at which a species was absent, but would have been expected to occur, by comparing the matrix of observed counts by reef and species to the expected occurrence matrix.

Assemblage analysis

To compare species composition between reefs we selected the 31 most commonly occurring species in the data set. The remaining species were observed in small numbers and at very few reefs. Preliminary analysis using all species produced results very similar to the reduced dataset, however, the drivers of variation would be more difficult to parse with the larger species list, thus the truncated list was used. We used nMDS to examine the degree to which species composition varied with ocean basin, basin subregion (in the Indo-Pacific) and proportion of total elasmobranch MaxN that was sharks (=proportion shark) affected species composition. Species composition was significantly different between ocean basins, but not sub-region (Figure S5), indicating that reefs in the Indo-Pacific and Atlantic had unique communities of species, but that subregions within the Indo-Pacific did not. As a result, we examined species composition at the reef level for ocean basins separately. For each ocean basin a matrix of sum of MaxN by species and reef was used in UPGMA clustering with Bray-Curtis similarity that determined the reefs that were most similar. The numbers of clusters identified differed between ocean basin, but in both cases the numbers of clusters were increased until the group of reefs that had the lowest levels of decline of the main reef shark species was split at least once. For each cluster the mean and standard error of the reef level decline of the most common shark and ray species were calculated to identify how populations had changed for each cluster. To examine how changes in shark abundance related to the clusters identified, the mean decline of the most common species of reef sharks in each basin was also calculated and clusters located on a scatterplot of mean shark decline and the proportion shark with points scaled by the number of reefs in each cluster. The spatial distributions of clusters were examined by plotting cluster number on global maps.

To examine the influence of socioeconomic, fisheries, management and environmental factors on membership of clusters in each of the basins we used linear discriminant analysis. We included four national scale socioeconomic factors: (1) human development index (HDI), an index of life expectancy, level of education and standard of living developed by the UN Development Programme (http://hdr.undp.org/en/content/human-development-index-hdi); (2) voice and accountability, and index of the extent to which people in each nation are able to participate in governance, free expression, free media and free association developed by the World Bank (https://info.worldbank.org/governance/wgi/pdf/va.pdf); (3) gross domestic product; and (4) national fisheries catch (https://www.seaaroundus.org/). We also included two reef scale socioeconomic variables: (1) human population size within 50 km of the sampled reefs (https://sedac.ciesin.columbia.edu/data/collection/gpw-v4/sets/browse); and (2) total market gravity, the nearest market, equal to the population of the nearest market (defined as a port, provincial capital or major city) divided by the squared travel time between the reef site and the market (*34*). We included three management factors – whether a sampled reef was within a national shark sanctuary with a list of sanctuaries developed from (*35*), whether the reef was within a closed area (i.e., a no-take marine reserve) or an area where shark fishing was otherwise restricted (e.g., where there were shark catch limits or gear restrictions). Two environmental factors from our habitat characterization of each BRUVS drop were included: (1) mean hard coral cover; and (2) mean reef level habitat relief.

Species depletion and extinction risk

Changes in species abundance relative to unfished levels were estimated for the five most common shark species (Caribbean reef shark, grey reef shark, blacktip reef shark, whitetip reef shark and nurse shark) and four most common stingray species (southern stingray [a species complex, with at least one cryptic species recently described in Brazil (*Hypanus berthalutzae*) but here treated as a single species (*Hypanus americana*) for assessment purposes], yellow stingray, blue spotted ribbontail ray [a complex of 2 species – *Taeniura lymma* and *T. lessoni*] and blue spotted mask ray [a species complex treated as a single species here for assessment purposes]). We estimated depletion using MaxN data from all sampled reefs at which a species was historically known to occur, or still occurs. This involved searching published information on the species, including historic accounts. We consulted with local experts where questions remained about the historic occurrence of the species at individual reefs. For each reef within the species' known range, the observed mean MaxN value was calculated. The effect of total market gravity, protection status and site on MaxN was modelled using a generalised linear model. The goodness of fit of models to the data was calculated using McFadden's pseudo R^2. The fits of the model to total market gravity and protection status, and goodness of fit metrics are shown in Fig S6. The model was then used to predict site level MaxN when the protection status was "closed", and gravity was at the lowest value observed for the basin (IndoPacific or Atlantic). The estimates of site-level base-line MaxN, and the observed values of reefs within sites are shown in Fig S7 (IndoPacific species) and FigS8 (Atlantic species). These predicted values were assumed to represent the pre-exploitation MaxN and the level of depletion at each reef was calculated as:

$$depletion = 1 - \left(\frac{observed\ reef\ MaxN}{unfished\ site\ MaxN}\right)$$

For rays it has been demonstrated that abundance can increase at reefs with low levels of shark abundance (*36*), so we accounted for possible increases in abundance by selecting reefs with known healthy populations of Caribbean reef sharks (Atlantic species - Bahamas, Turks and Caicos, Pedro Bank (Jamaica) and the Colombian Islands) or grey reef sharks (Indo-Pacific species – Australia and PNG) as a reference for natural ray populations. The population level of rays relative to the no depletion reference level for each reef was calculated as: reef MaxN/(reference MaxN for reefs with undepleted reef shark populations). Ray population levels greater than one indicated increases, while those level or less than one indicated depletion.

Depletion levels by jurisdiction were calculated by taking the mean of all reefs within that jurisdiction. Jurisdictions were typically nations, but in some instances were remote territories considered separately (e.g. Dutch territories in the outer Caribbean islands and southern Caribbean were analysed separately, Colombian Islands in the Caribbean off Central America were analysed separately from mainland Colombian reefs) to account for spatial variation. Standard error of the means was also calculated and used to produce confidence intervals for depletion levels. Population change for rays by jurisdiction were calculated by taking the mean of all reefs within that jurisdiction. Standard error of the means was also calculated and used to produce confidence intervals. To estimate an overall global depletion level by species we weighted the jurisdictional values by the percentage of the world's coral reefs in their waters and produced a weighted mean depletion. Percentages of coral reefs by jurisdiction were taken from the "World Atlas of Coral Reefs"(*37*).

The extinction risk for each reef shark species at the global level was assessed by applying Criteria A (population size reduction) of the IUCN Red List Categories over the past three generation lengths. The depletion estimates did not provide timeframes, however, pressure on most shark and ray populations increased from approximately 1980 when demand for shark fins increased (*38*). For example, Ferretti et al (*39*) showed that catches of coral reef species in the British Indian Ocean Territories increased dramatically from the mid-1970s to the early 1980s, and these are some of the more remote reefs in the world. Thus, we assumed that all, or the vast majority, of the declines described here have occurred during the past three generation lengths of each species.

To examine factors that effected the level of decline of each main reef shark species we used a linear model of reef level depletion with the factors Shark Sanctuary (y/n), MPA protection (open, restricted, closed), hard coral cover (log (x+1) transformed), and relief., Human Development Index, and Voice and Accountability. Variable importance was estimated for each factor in each species model using the r package *vip* (https://cran.r-project.org/web/packages/vip/vip.pdf). Variable importance values were converted to relative values (individual values divided by sum of all values for each species separately) to allow comparison between species. Results of models are shown in Tables S5 – S9. The effect of site, gravity and MPA protection status were not assessed in this model because they were previously used to estimate the depletion of the shark species.

Supplementary text

Additional acknowledgements

DDC was supported by the Roe Foundation and additional sampling for the Chapman lab was funded by the Moore Bahamas Foundation (Bahamas) and Earthwatch International (Belize). JSG was supported by a Niarchos Fellowship through the Wildlife Conservation Society (WCS). Additional support for data collection in Solomon Islands was provided by grants to WCS from the John D. and Catherine T. MacArthur Foundation (grant #13- 105118-000-INP) and by the National Science Foundation (grant #EF-1427453). Additional support for sampling in Indonesia was provide by Operation Wallacea and Wasage Divers. Additional support for sampling in Malaysia was provided by Scuba Junkie SEAS. Additional support for sampling in Mexico was provided by Alianza WWF/Fundación Carlos Slim and Ocean Blue Three Foundation. Additional support for sampling in Brazil was provided by Conselho Nacional de Desenvolvimento Científico e Tecnológicov(CNPq) through the scientific programs LTER [PELD-ILOC grant 441327/2020-6 and PELD-HCES grant 441243/2016-9; the latter with additional funding from Fundação Estadual de Amparo à Pesquisa do Estado do Espírito Santo (FAPES) and CNPq/PROTRINDADE (grant 405426/2012-7)]. Study in Brasil was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior–Brasil, CAPES finance code 001. CRP thanks the FAPES for the PhD scholarship and CAPES finance code 001 for the PDSE fellowship. Research in Brasil was in part funded by funding from Fundação Grupo O Boticário de Proteção à Natureza (grant 1141_20182 to HTP), and Fundação de Amparo à Pesquisa do Estado de São Paulo (grant 2019/24215-2 and 2021/07039-6 to HTP)

We thank Cat and David McCann for their assistance in Sabah, Malaysia. This research was carried out under permits from the Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (DGOPA.06668.150612.1691) and Comisión Nacional de Areas Naturales Protegidas (F00.DRPBCPN-APFFCSL.REBIARRE-102/13) of Mexico. We thank to authorities for granting the research permit in KKP-TWP Nusa Penida, Bali, Indonesia (No. 532/194/DPPK) and TWP Kapoposang, South Sulawesi, Indonesia (No. B.49.4/BKKPN/III/2016). In Sri Lanka we acknowledge the Department of Wildlife Conservation for facilitating this research project under permit number WL/3/2/23/17. Emirates Nature - WWF provided the funding for the study in United Arab Emirates. We thank the Brazilian Navy and SECIRM for the fundamental logistic support. We thank the Department of Natural Resources and Forestry of the Tobago House of Assembly for their endorsement and granting of research project and the necessary research permit. We thank the fishers of Tintipán, Colombia for assistance with the project.

Fig. S1.

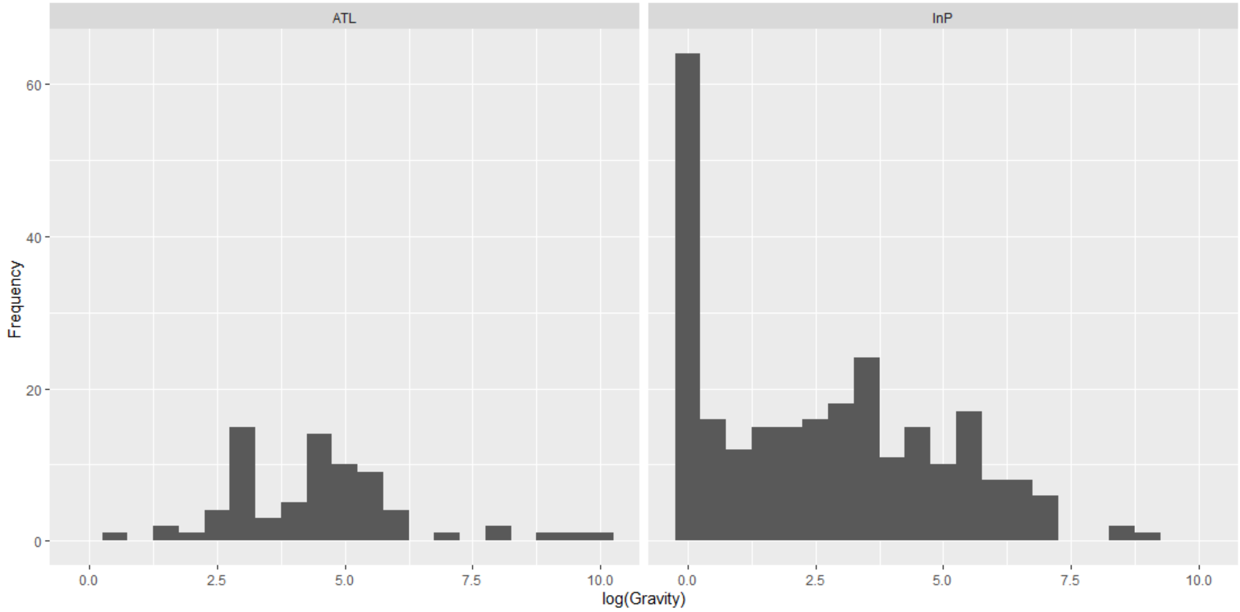

Fig. S1. Gravity of reefs sampled in the Atlantic Ocean were generally higher than in the Indo-Pacific where there where many reefs sampled with values less than 1000 (i.e., 10^3). Mean log(gravity) was significantly lower in the Indo-Pacific (2.617) compared to the Atlantic (4.548) (Welch's two sample, $t = 8.088$, $df = 165.0$, $p < 0.00001$).

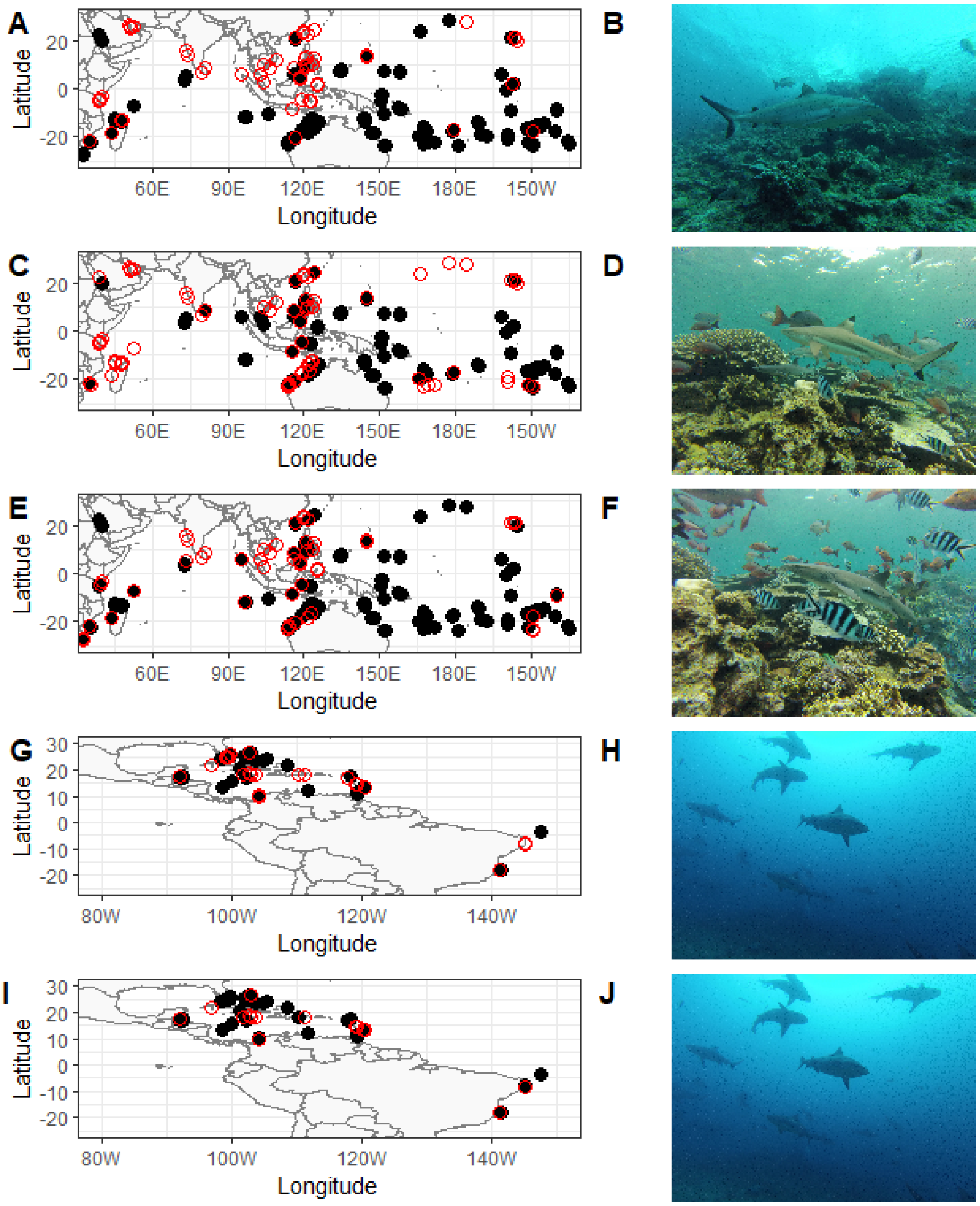

Fig S2. Locations of surveyed reefs where five key reef shark species were observed (black dots) and not observed (red circles): grey reef shark (A,B), blacktip reef shark (C,D), whitetip reef shark (E,F), Caribbean reef shark (G,H) and nurse shark (I,J).

Fig. S3.

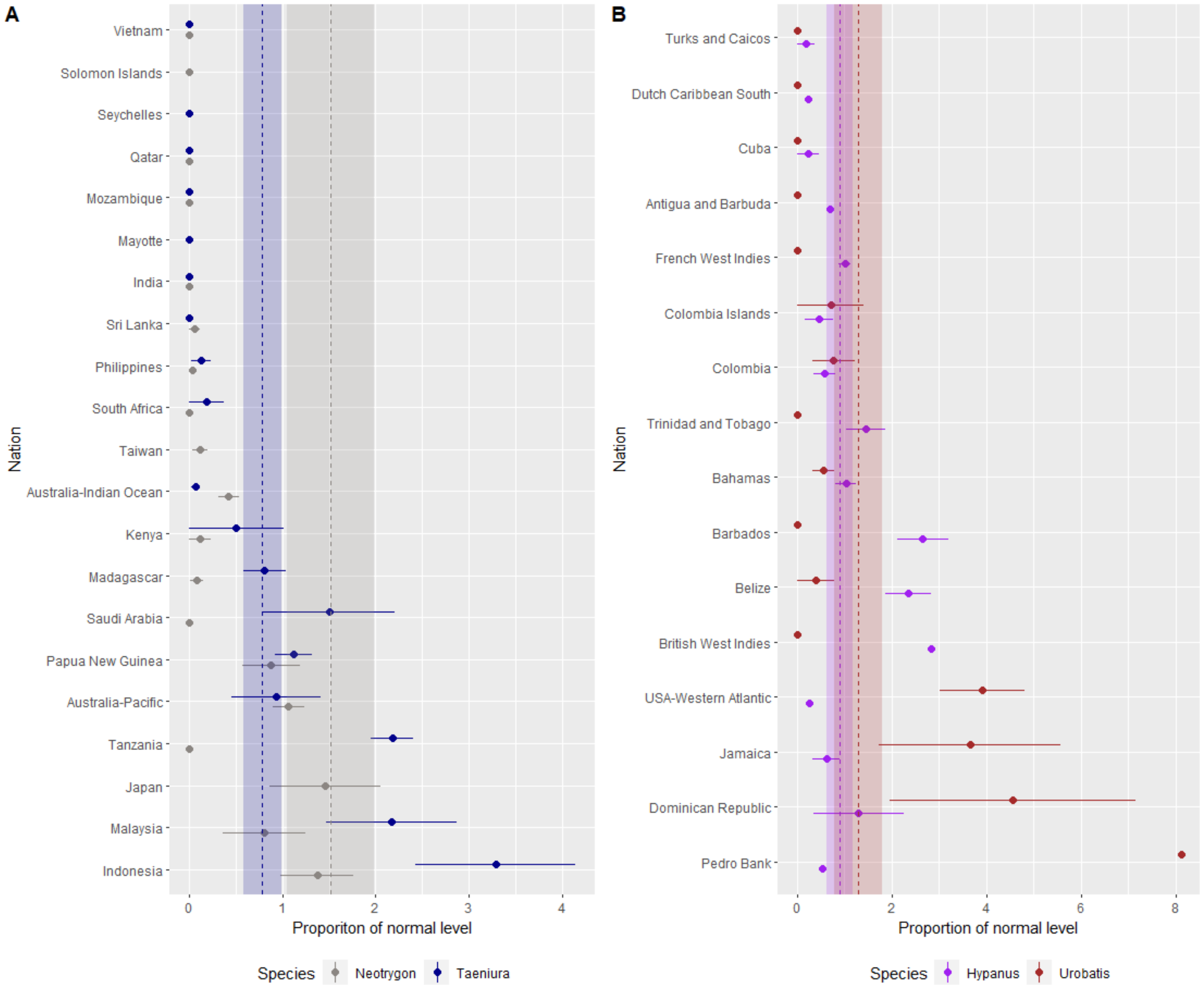

Fig. S3 – **Changes in abundance (relative to reefs with unfished shark populations) of key coral reef ray species in (A) the Indo-Pacific and (B) Atlantic basins at national, or near-national, scale.** Population level (proportion of normal level) was calculated by comparing reef level species MaxN values to levels assumed to represent no depletion (i.e., unfished reefs). Reef level depletion scores were modeled by nation and a global level of depletion (vertical dashed lines) and standard error (shaded area) calculated by weighting national level population level by coral reef area (as a % of global total coral reef area that occurs within the range of each shark species). Reef area-weighted global level relative population estimates were compared to IUCN Red List criteria to estimate species level extinction risk and Red List category. None of the species met criteria for listing in a threatened category.

Fig S4

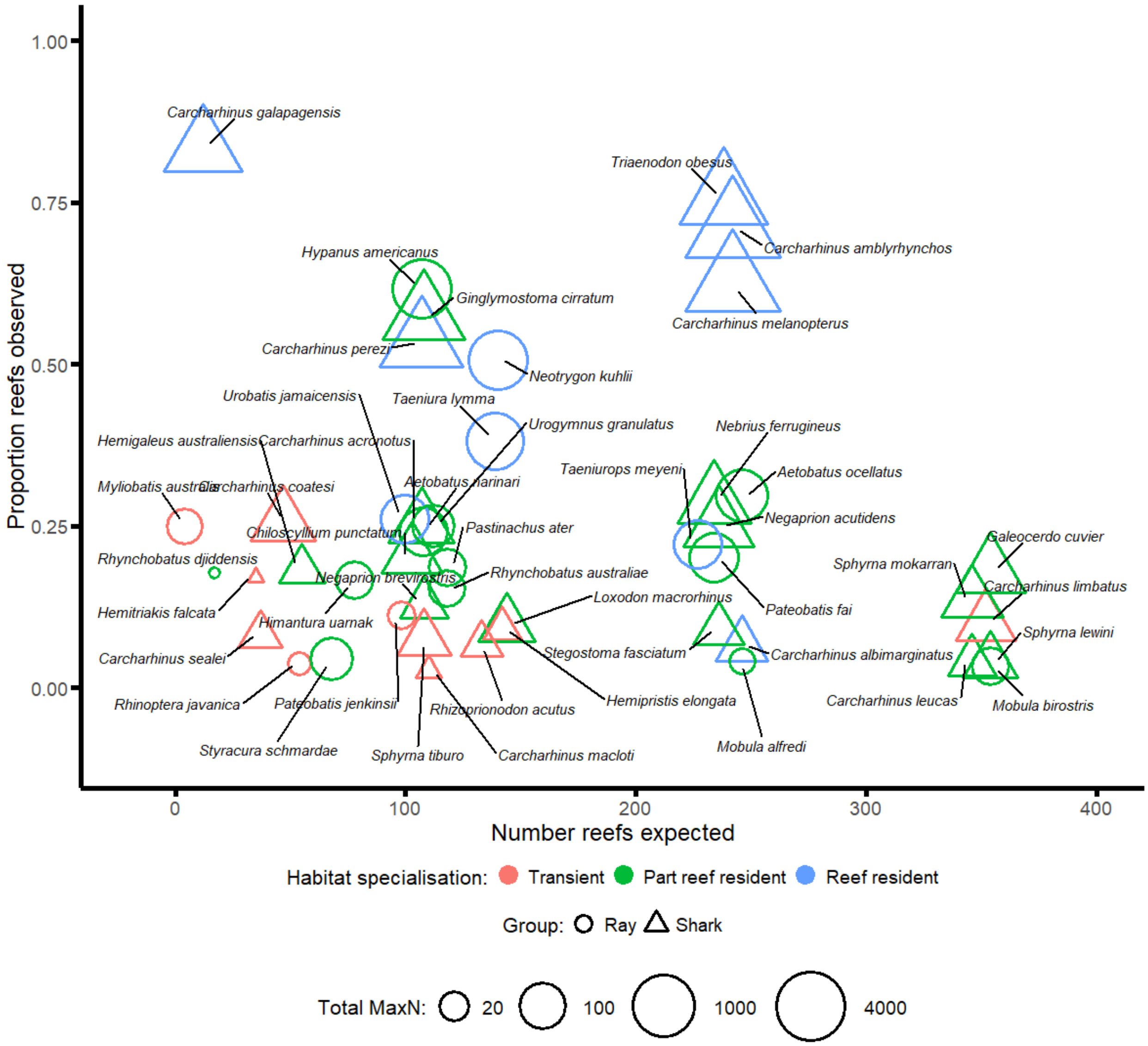

Fig. S4. Composition of shark and ray faunal assemblages on coral reefs globally. At least 104 species were recorded on 22,756 BRUVS at 391 reefs in 67 nations or territories. Species that were observed more than 10 times (i.e. total MaxN > 10) are shown in the figure, along with the proportion of expected reefs that they were observed on, their total MaxN, whether they are a shark or ray, and their degree of habitat specialization. Reef residents are those species rarely found in non-coral reef habitats and that complete their life cycle on coral reefs. Part reef residents are those species that complete part of their life cycle in coral reef habitat but normally use other near reef habitat(s) for part of the life-cycle; individuals or particular life-stages can be residents of coral reef habitat but periodically and/or ontogenetically move away from it. Transient species are those species that use coral reef habitat occasionally and temporarily while using other habitats as frequently or more often.

Fig. S5.

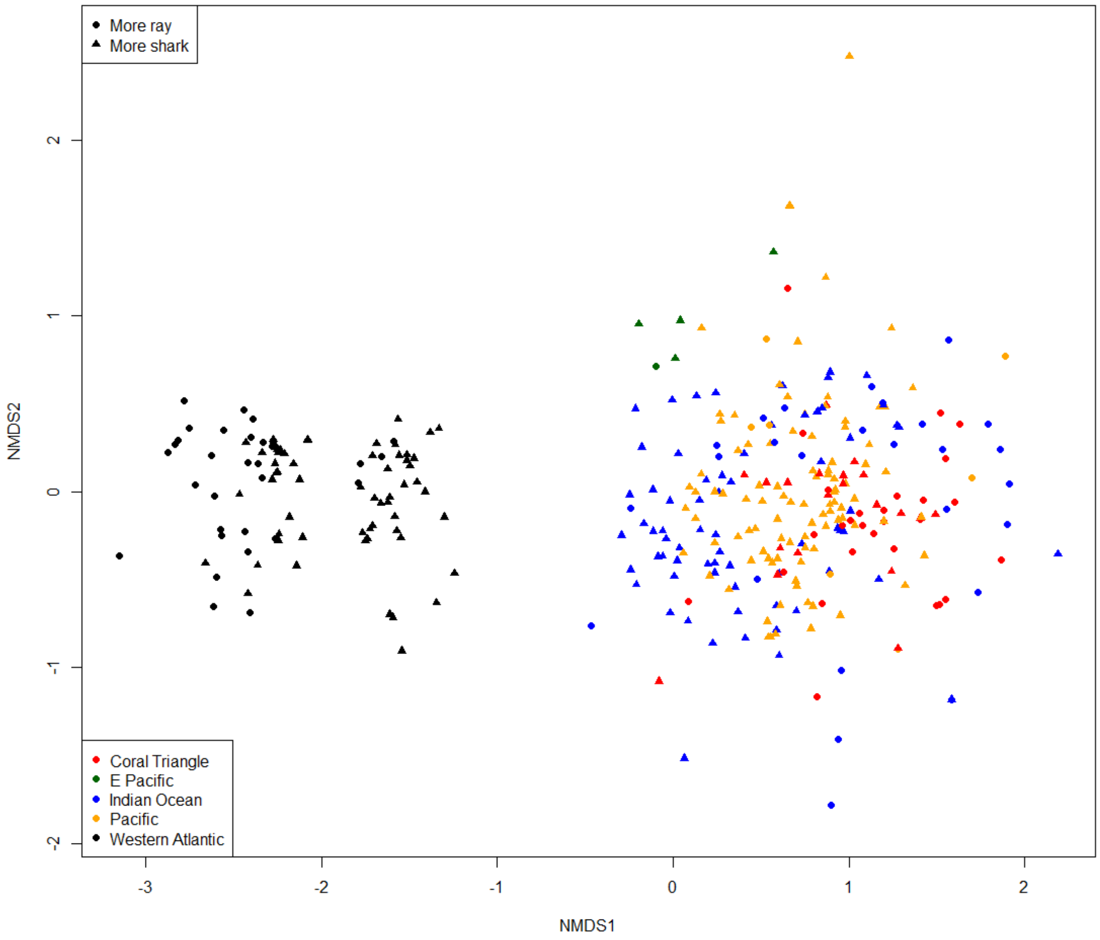

Fig. S5. Comparison of species composition between regions from BRUVS deployed on coral reefs using nMDS. Reefs with total MaxN of sharks> total MaxN rays were labelled "more shark"; reefs with total MaxN of rays> total MaxN sharks were labelled "more ray".

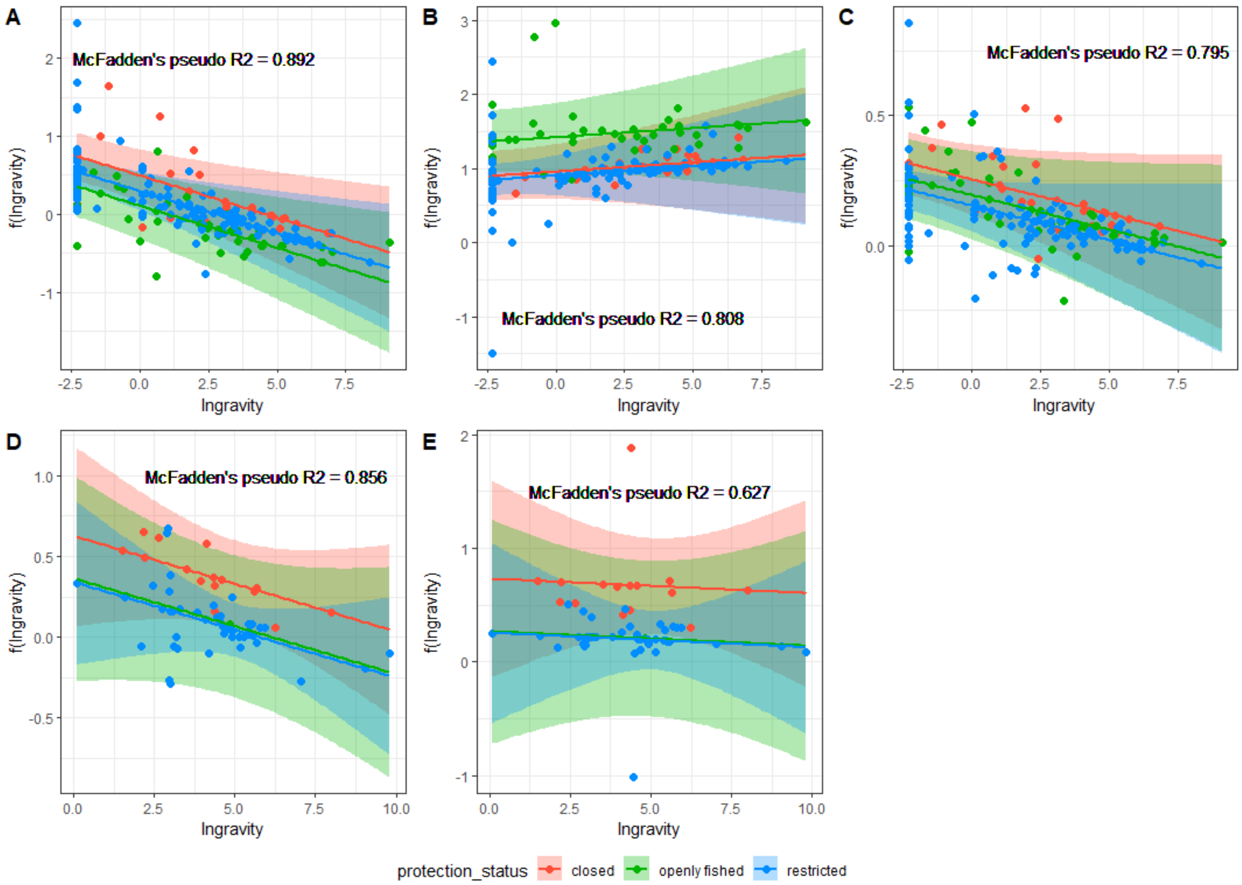

Fig S6. Fits of generalised linear models to observed data for five key reef shark species: grey reef shark (A), blacktip reef shark (B), whitetip reef shark (C), Caribbean reef shark (D) and nurse shark (E). Goodness of fit given by McFadden’s pseudo R^2.

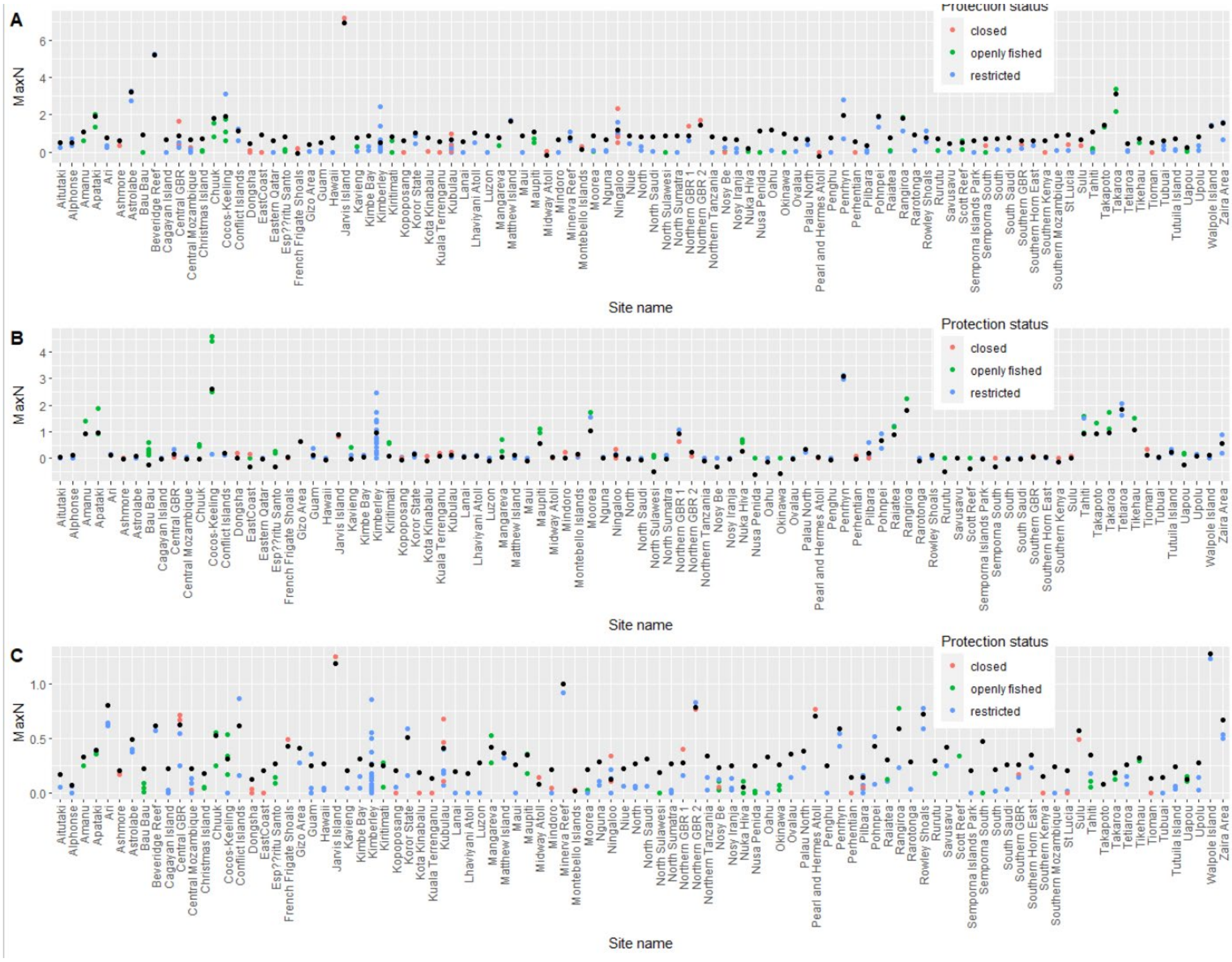

Fig S7. Estimated base-line MaxN of sampling sites (black dots) and observed values of reefs within sampling sites by MPA status (colored dots) for IndoPacific species: grey reef shark (A), blacktip reef shark (B) and whitetip reef shark (C).

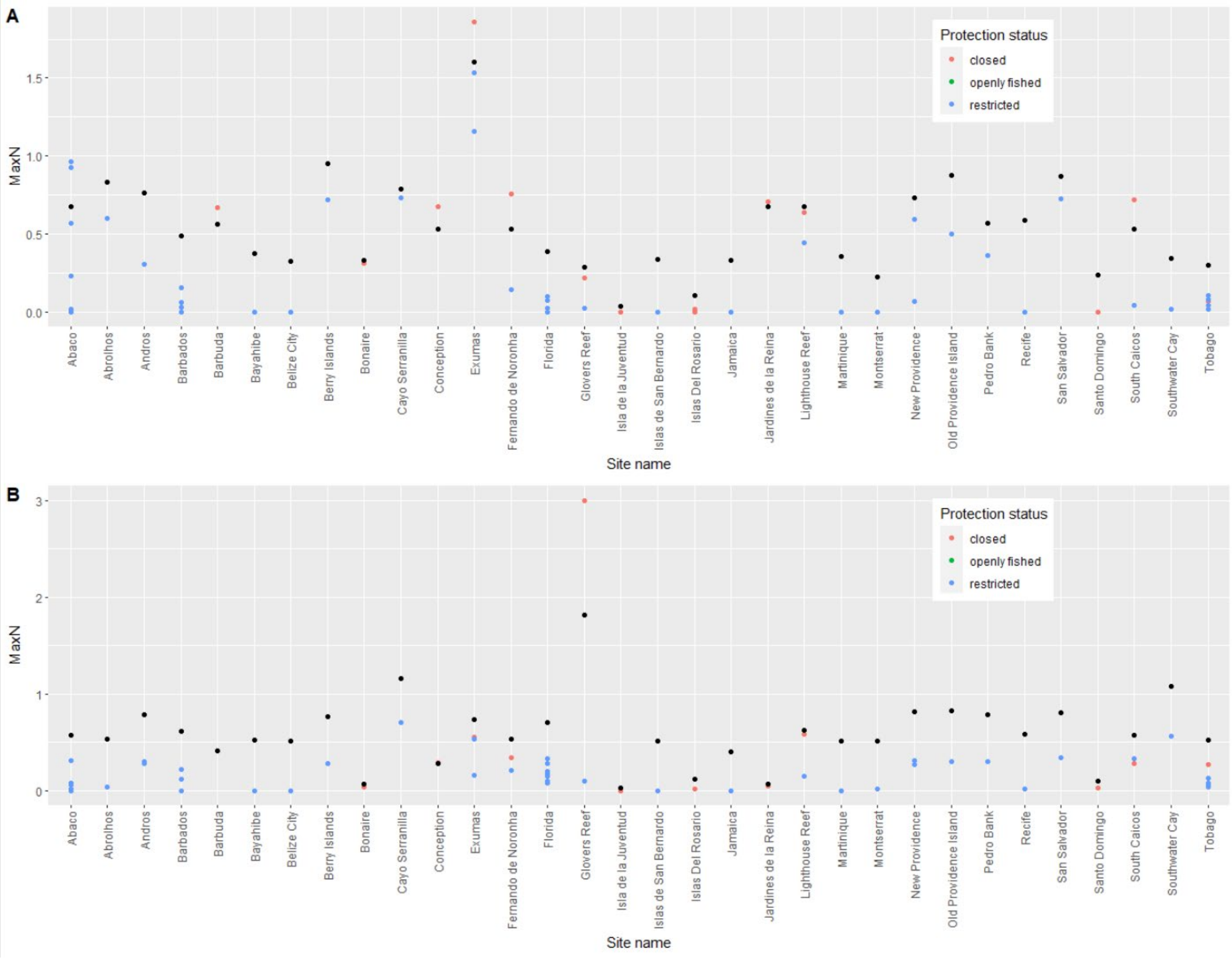

Fig S8. Estimated base-line MaxN of sampling sites (black dots) and observed values of reefs within sampling sites by MPA status (colored dots) for Atlantic species: Caribbean reef shark (A) and nurse shark (B).

Table S1.

Species name	**Indo-Pacific**	**Atlantic**	**Total**
Rays			
Acroteriobatus leucospilus	1		1
*Aetobatus ocellatus**	209		209
*Aetobatus narinari**		80	80
Aetobatus sp.*	162		162
Aetomylaeus vespertilio	3		3
Bathytoshia brevicaudata	2		2
Bathytoshia lata	6		6
Dasyatis thetidis	3		3
Glaucostegus typus	2		2
Himantura australis	1		1
Himantura leoparda	4		4
Himantura sp.	7		7
Himantura uarnak	38		38
*Hypanus americanus**		407	407
Hypanus berthalutzae		29	29
Hypanus marianae		1	1
Hypanus sp.		10	10
Megatrygon microps	1		1
Mobula alfredi	14		14
Mobula birostris	31		31
Mobula japanica	1		1
Mobula kuhlii	3		3
Mobula sp.	125	1	126
Myliobatis australis	32		32
Narcine bancroftii		2	2
Narcine sp.	1		1
Neotrygon annotata	1		1
*Neotrygon kuhlii**	664		664
Pastinachus ater	37		37
*Pateobatis fai**	148		148
Pateobatis jenkinsii	16		16
Pristis zijsron	1		1
Pseudobatos lentiginosus		2	2
Pseudobatos sp.		2	2

Rhina ancylostoma	3		3
Rhinobatos annulatus	1		1
Rhinobatos hynnicephalus	1		1
Rhinobatos sp.	1		1
Rhinoptera javanica	14		14
Rhynchobatus australiae	34		34
Rhynchobatus djiddensis	11		11
Rhynchobatus sp.	39		39
Styracura schmardae		7	7
Taeniura lessoni	1		1
*Taeniura lymma**	470		470
*Taeniurops meyeni**	116		116
Trygonoptera ovalis	1		1
*Urobatis jamaicensis**		135	135
Urogymnus asperrimus	4		4
*Urogymnus granulatus**	55		55
Urolophus westraliensis	1		1
Sharks			
Alopias sp.	3		3
Atelomycterus fasciatus	1		1
*Carcharhinus acronotus**		122	122
*Carcharhinus albimarginatus**	40		40
*Carcharhinus amblyrhynchos**	4697		4697
Carcharhinus amboinensis	5		5
Carcharhinus brachyurus	1		1
Carcharhinus coatesi	111		111
Carcharhinus falciformis	1		1
*Carcharhinus galapagensis**	452	1	453
*Carcharhinus leucas**	21	9	30
*Carcharhinus limbatus**	64	2	66
Carcharhinus longimanus	1		1
Carcharhinus macloti	12		12
*Carcharhinus melanopterus**	4507		4507
*Carcharhinus perezi**		867	867
Carcharhinus plumbeus	9		9
Carcharhinus sealei	23		23
Carcharhinus sorrah	3		3
Carcharhinus tilstoni/limbatus	15		15
Carcharhinus sp.	39	11	50
Carcharodon carcharias	1		1

_Chiloscyllium punctatum_*	76		76
Eucrossorhinus dasypogon	3		3
Furgaleus macki	1		1
_Galeocerdo cuvier_*	149	25	174
_Ginglymostoma cirratum_*		656	656
Hemigaleus australiensis	26		26
Hemigaleus microstoma	1		1
Hemipristis elongata	18		18
Hemiscyllium ocellatum	3		3
Hemiscyllium trispeculare	5		5
Hemitriakis abdita	7		7
Hemitriakis falcata	11		11
Hemitriakis sp.	2		2
Heterodontus portusjacksoni	1		1
Loxodon macrorhinus	53		53
Mustelus canis		5	5
Mustelus sp.	1		1
_Nebrius ferrugineus_*	273		273
_Negaprion acutidens_*	193		193
_Negaprion brevirostris_*		32	32
Orectolobus japonicus	1		1
Orectolobus ornatus	1		1
Rhincodon typus	6		6
Rhizoprionodon acutus	21		21
Rhizoprionodon taylori/acutus	9		9
Rhizoprionodon sp.		132	132
_Sphyrna lewini_*	45	1	46
_Sphyrna mokarran_*	54	27	81
Sphyrna tiburo		44	44
Sphyrna zygaena	1		1
Sphyrna sp.	5	5	10
Stegostoma tigrinum	34		34
_Triaenodon obesus_*	1769		1769
Unknown sp.	468	106	574
Total	15508	2721	18229

Table S1. Species composition of all BRUVS deployments used in the analysis of abundance and depletion. Groups identified as sp. could only be identified to genus level, and some may have included more than one species. Species indicated with * are the key species used in cluster analysis. Three additional species from the tropical Eastern Pacific were used in the cluster analysis: *Ginglymostoma unami*, *Urobatis halleri* and *Hypanus longus* but are not displayed here.

Table S2.

Factor	LD1	LD2	LD3
Proportion variance explained	0.5180	0.2541	0.1024
Human development index	43.088	0.1059	-2.7714
Voice and Accountability	0.0906	-0.8012	-0.4447
Gross Domestic Product	-0.0002	<-0.0001	<0.0001
Population size within 50km	0.2948	-0.1754	-0.1761
Market gravity	-0.3145	-0.4311	0.1151
National fisheries catch	0.4930	0.1852	0.3364
Shark sanctuary present	2.2841	-1.1239	0.3418
Spatial protection present	0.0234	0.2290	-0.4030
Hard coral cover	-0.2364	-0.0717	-0.0340
Habitat relief	-0.0706	0.2290	-0.4030

Table S2. Results of linear discriminant analysis of Atlantic clusters using a range of socioeconomic, management and habitat factors. The first three linear discriminants accounted for 87.45% of the between cluster variance. Top three weighted factors in each linear discriminant are shaded by color intensity.

Table S3.

Factor	LD1	LD2	LD3
Proportion variance explained	0.4987	0.3262	0.0214
Human development index	-2.2172	-5.2239	-1.6329
Voice and Accountability	0.4662	-1.0405	-1.9238
Gross Domestic Product	<-0.0001	<-0.0001	<0.0001
Population size within 50km	-0.0778	0.0865	-0.1313
Market gravity	-0.5279	0.0165	-0.0410
National fisheries catch	-0.1099	-0.5015	0.1326
Shark sanctuary present	1.3873	-0.1328	2.0148
Spatial Protection present	-0.1700	-0.1013	0.0811
Hard coral cover	0.2684	-0.0928	0.0629
Habitat relief	-0.3044	0.3071	-0.2552

Table S3. Results of linear discriminant analysis of Indo-Pacific clusters using a range of socioeconomic, management and habitat factors. The first three linear discriminants accounted for 84.63% of the between cluster variance. Top three weighted factors in each linear discriminant are shaded by color intensity.

Table S4.

Species	Factor	Chi sq.	df	p
Grey reef shark	site	681.14	98	**<0.0001**
	gravity	9.03	1	**0.0027**
	protection	4.8	2	0.0910
Blacktip reef shark	site	359.13	92	**<0.0001**
	gravity	0.39	1	0.5313
	protection	7.61	2	**0.0223**
Whitetip reef shark	site	299.48	97	**<0.0001**
	gravity	3.431	1	0.0639
	protection	4.573	2	0.1016
Caribbean reef shark	site	93.292	31	**<0.0001**
	gravity	1.459	1	0.2272
	protection	6.833	2	**0.0328**
Nurse shark	site	42.111	31	0.0878
	gravity	0.028	1	0.8662
	protection	7.822	2	**0.0200**

Table S4. Generalised linear model results for models used to estimate base-line abundance of five key resident reef shark species.

Factor	LR Chisq	DF	P
type (oceanic, coastal)	0.4320	1	0.5110
relief	1.4944	1	0.2215
ln(hard coral)	0.0463	1	0.8296
shark sanctuary (yes/no)	2.7623	1	0.0965
Human development index	0.3194	1	0.5720
Voice and accountability	11.776	1	0.0006

Table S5. Generalized linear model results for grey reef shark abundance by reef.

Factor	LR Chisq	DF	P
type (oceanic, coastal)	0. 0729	1	0.7871
relief	0.0141	1	0.9053
ln(hard coral)	0. 2217	1	0.6377
shark sanctuary (yes/no)	1.1060	1	0.2929
Human development index	0.0907	1	0.7633
Voice and accountability	5.8239	1	0.0158

Table S6. Generalized linear model results for blacktip reef shark abundance by reef.

Factor	LR Chisq	DF	P
type (oceanic, coastal)	2.6355	1	0.1045
relief	1.2912	1	0.2558
ln(hard coral)	1.5228	1	0.2171
shark sanctuary (yes/no)	0.2864	1	0.5925
Human development index	0.2864	1	0.7066
Voice and accountability	5.2340	1	0.0221

Table S7. Generalized linear model results for whitetip reef shark abundance by reef.

Factor	LR Chisq	DF	P
type (oceanic, coastal)	0.8473	1	0.3573
relief	0.0647	1	0.7991
ln(hard coral)	2.7601	1	0.0966
shark sanctuary (yes/no)	5.1128	1	0.0237
Human development index	0.0006	1	0.9804
Voice and accountability	0.8388	1	0.3597

Table S8. Generalized linear model results for Caribbean reef shark abundance by reef.

Factor	LR Chisq	DF	P
type (oceanic, coastal)	0.1273	1	0.7212
relief	0.1559	1	0.6929
ln(hard coral)	0.9583	1	0.3276
shark sanctuary (yes/no)	0.1860	1	0.6662
Human development index	0.0005	1	0.9811
Voice and accountability	0.1118	1	0.7380

Table S9. Generalized linear model results for nurse shark abundance by reef.

References

29. L. M. Currey-Randall, M. Cappo, C. A. Simpfendorfer, N. F. Farabaugh, M. R. Heupel, Optimal soak times for Baited Remote Underwater Video Station surveys of reef-associated elasmobranchs. *PLOS ONE* **15**, e0231688 (2020).
30. C. S. Sherman, A. Chin, M. R. Heupel, C. A. Simpfendorfer, Are we underestimating elasmobranch abundances on baited remote underwater video systems (BRUVS) using traditional metrics? *Journal of Experimental Marine Biology and Ecology* **503**, 80-85 (2018).
31. D. A. Ebert, S. L. Fowler, L. J. V. Compagno, *Sharks of the World. A Fully Illustrated Guide*. (Wild Nature Press, Plymoth, 2013).
32. P. R. Last, J. D. Stevens, *Sharks and Rays of Australia*. (CSIRO Publishing, Melbourne, ed. 2nd, 2009), pp. 656.
33. P. R. Last *et al.*, *Rays of the World*. (CSIRO Publishing, Melbourne, 2016).
34. J. E. Cinner *et al.*, Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences* **115**, E6116-E6125 (2018).
35. C. A. Ward-Paige, B. Worm, Global evaluation of shark sanctuaries. *Global Environmental Change* **47**, 174-189 (2017).
36. C. S. Sherman, M. R. Heupel, S. K. Moore, A. Chin, C. A. Simpfendorfer, When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **641**, 145-157 (2020).
37. M. D. Spalding, C. Ravilious, E. P. Green, *World Atlas of Coral Reefs*. (University of California Press, Berkeley, 2001).
38. F. Dent, S. C. Clarke, State of the global market for shark products. *FAO Fisheries and Aquaculture Technical Paper* **590**, 1-187 (2015).
39. F. Ferretti, D. Curnick, K. Liu, E. V. Romanov, B. A. Block, Shark baselines and the conservation role of remote coral reef ecosystems. *Science Advances* **4**, eaaq0333 (2018).