Endangered Species Act

16 U.S.C. Sections 1531-1544

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Section 1531. Congressional findings and declaration of purposes and policy [ESA Section 2]

(a) Findings

The Congress finds and declares that -

(1) various species of fish, wildlife, and plants in the United States have been rendered extinct as a consequence of economic growth and development untempered by adequate concern and conservation;

(2) other species of fish, wildlife, and plants have been so depleted in numbers that they are in danger of or threatened with extinction;

(3) these species of fish, wildlife, and plants are of aesthetic, ecological, educational, historical, recreational, and scientific value to the Nation and its people;

(4) the United States has pledged itself as a sovereign state in the international community to conserve to the extent practicable the various species of fish or wildlife and plants facing extinction, pursuant to -

(A) migratory bird treaties with Canada and Mexico;

(B) the Migratory and Endangered Bird Treaty with Japan;

(C) the Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere;

(D) the International Convention for the Northwest Atlantic Fisheries;

(E) the International Convention for the High Seas Fisheries of the North Pacific Ocean;

(F) the Convention on International Trade in Endangered Species of Wild Fauna and Flora; and

(G) other international agreements; and

(5) encouraging the States and other interested parties, through Federal financial assistance and a system of incentives, to develop and maintain conservation programs which meet national and international standards is a key to meeting the Nation's international commitments and to better safeguarding, for the benefit of all citizens, the Nation's heritage in fish, wildlife, and plants.

(b) Purposes

The purposes of this chapter are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve the purposes of the treaties and conventions set forth in subsection (a) of this section.

(c) Policy

(1) It is further declared to be the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species and shall utilize their authorities in furtherance of the purposes of this chapter.

(2) It is further declared to be the policy of Congress that Federal agencies shall cooperate with State and local agencies to resolve water resource issues in concert with conservation of endangered species.

Section 1532. Definitions [ESA Section 3]

For the purposes of this chapter -

(1) The term "alternative courses of action" means all alternatives and thus is not limited to original project objectives and agency jurisdiction.

(2) The term "commercial activity" means all activities of industry and trade, including, but not limited to, the buying or selling of commodities and activities conducted for the purpose of facilitating such buying and selling: Provided, however, That it does not include exhibition of commodities by museums or similar cultural or historical organizations.

(3) The terms "conserve", "conserving", and "conservation" mean to use and the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this chapter are no longer necessary. Such methods and procedures include, but are not limited to, all activities associated with scientific resources management such as research, census, law enforcement, habitat acquisition and maintenance, propagation, live trapping, and transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, may include regulated taking.

(4) The term "Convention" means the Convention on International Trade in Endangered Species of Wild Fauna and Flora, signed on March 3, 1973, and the appendices thereto.

(5)(A) The term "critical habitat" for a threatened or endangered species means -

(i) the specific areas within the geographical area occupied by the species, at the time it is listed in accordance with the provisions of section 1533 of this title, on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and

(ii) specific areas outside the geographical area occupied by the species at the time it is listed in accordance with the provisions of section 1533 of this title, upon a determination by the Secretary that such areas are essential for the conservation of the species.

(B) Critical habitat may be established for those species now listed as threatened or endangered species for which no critical habitat has heretofore been established as set forth in subparagraph (A) of this paragraph.

(C) Except in those circumstances determined by the Secretary, critical habitat shall not include the entire geographical area which can be occupied by the threatened or endangered species.

(6) The term "endangered species" means any species which is in danger of extinction throughout all or a significant portion of its range other than a species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of this chapter would present an overwhelming and overriding risk to man.

(7) The term "Federal agency" means any department, agency, or instrumentality of the United States.

(8) The term "fish or wildlife" means any member of the animal kingdom, including without limitation any mammal, fish, bird (including any migratory, nonmigratory, or endangered bird for which protection is also afforded by treaty or other international agreement), amphibian, reptile, mollusk, crustacean, arthropod or other invertebrate, and includes any part, product, egg, or offspring thereof, or the dead body or parts thereof.

(9) The term "foreign commerce" includes, among other things, any transaction -

(A) between persons within one foreign country;

(B) between persons in two or more foreign countries;

(C) between a person within the United States and a person in a foreign country; or

(D) between persons within the United States, where the fish and wildlife in question are moving in any country or countries outside the United States.

(10) The term "import" means to land on, bring into, or introduce into, or attempt to land on, bring into, or introduce into, any place subject to the jurisdiction of the United States, whether or not such landing, bringing, or introduction constitutes an importation within the meaning of the customs laws of the United States.

(11) Repealed. Pub.L. 97-304, Section 4(b), Oct. 13, 1982, 96 Stat. 1420.

(12) The term "permit or license applicant" means, when used with respect to an action of a Federal agency for which exemption is sought under section 1536 of this title, any person whose application to such agency for a permit or license has been denied primarily because of the application of section 1536(a) of this title to such agency action.

(13) The term "person" means an individual, corporation, partnership, trust, association, or any other private entity; or any officer, employee, agent, department, or instrumentality of the Federal Government, of any State, municipality, or political subdivision of a State, or of any foreign government; any State, municipality, or political subdivision of a State; or any other entity subject to the jurisdiction of the United States.

(14) The term "plant" means any member of the plant kingdom, including seeds, roots and other parts thereof.

(15) The term "Secretary" means, except as otherwise herein provided, the Secretary of the Interior or the Secretary of Commerce as program responsibilities are vested pursuant to the provisions of Reorganization Plan Numbered 4 of 1970; except that with respect to the enforcement of the provisions of this chapter and the Convention which pertain to the importation or exportation of terrestrial plants, the term also means the Secretary of Agriculture.

(16) The term "species" includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.

(17) The term "State" means any of the several States, the District of Columbia, the Commonwealth of Puerto Rico, American Samoa, the Virgin Islands, Guam, and the Trust Territory of the Pacific Islands.

(18) The term "State agency" means any State agency, department, board, commission, or other governmental entity which is responsible for the management and conservation of fish, plant, or wildlife resources within a State.

(19) The term "take" means to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct.

(20) The term "threatened species" means any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

(21) The term "United States", when used in a geographical context, includes all States.

Section 1533. Determination of endangered species and threatened species [ESA Section 4]

(a) Generally

(1) The Secretary shall by regulation promulgated in accordance with subsection (b) of this section determine whether any species is an endangered species or a threatened species because of any of the following factors:

(A) the present or threatened destruction, modification, or curtailment of its habitat or range;

(B) overutilization for commercial, recreational, scientific, or educational purposes;

(C) disease or predation;

(D) the inadequacy of existing regulatory mechanisms; or

(E) other natural or manmade factors affecting its continued existence.

(2) With respect to any species over which program responsibilities have been vested in the Secretary of Commerce pursuant to Reorganization Plan Numbered 4 of 1970 -

(A) in any case in which the Secretary of Commerce determines that such species should -

(i) be listed as an endangered species or a threatened species, or

(ii) be changed in status from a threatened species to an endangered species, he shall so inform the Secretary of the Interior, who shall list such species in accordance with this section;

(B) in any case in which the Secretary of Commerce determines that such species should -

(i) be removed from any list published pursuant to subsection (c) of this section, or

(ii) be changed in status from an endangered species to a threatened species, he shall recommend such action to the Secretary of the Interior, and the Secretary of the Interior, if he concurs in the recommendation, shall implement such action; and

(C) the Secretary of the Interior may not list or remove from any list any such species, and may not change the status of any such species which are listed, without a prior favorable determination made pursuant to this section by the Secretary of Commerce.

(3) The Secretary, by regulation promulgated in accordance with subsection (b) of this section and to the maximum extent prudent and determinable -

(A) shall, concurrently with making a determination under paragraph (1) that a species is an endangered species or a threatened species, designate any habitat of such species which is then considered to be critical habitat; and

(B) may, from time-to-time thereafter as appropriate, revise such designation.

(b) Basis for determinations

(1)(A) The Secretary shall make determinations required by subsection (a) (1) of this section solely on the basis of the best scientific and commercial data available to him after conducting a review of the status of the species and after taking into account those efforts, if any, being made by any State or foreign nation, or any political subdivision of a State or foreign nation, to protect such species, whether by predator control, protection of habitat and food supply, or other conservation practices, within any area under its jurisdiction, or on the high seas.

(B) In carrying out this section, the Secretary shall give consideration to species which have been -

(i) designated as requiring protection from unrestricted commerce by any foreign nation, or pursuant to any international agreement; or

(ii) identified as in danger of extinction, or likely to become so within the foreseeable future, by any State agency or by any agency of a foreign nation that is responsible for the conservati on of fish or wildlife or plants.

(2) The Secretary shall designate critical habitat, and make revisions thereto, under subsection (a) (3) of this section on the basis of the best scientific data available and after taking into consideration the economic impact, and any other relevant impact, of specifying any particular area as critical habitat. The Secretary may exclude any area from critical habitat if he determines that the benefits of such exclusion outweigh the benefits of specifying such area as part of the critical habitat, unless he determines, based on the best scientific and commercial data available, that the failure to designate such area as critical habitat will result in the extinction of the species concerned.

(3)(A) To the maximum extent practicable, within 90 days after receiving the petition of an interested person under section 553(e) of Title 5 to add a species to, or to remove a species from, either of the lists published under subsection (c) of this section, the Secretary shall make a finding as to whether the petition presents substantial scientific or commercial information indicating that the petitioned action may be warranted. If such a petition is found to present such information, the Secretary shall promptly commence a review of the status of the species concerned. The Secretary shall promptly publish each finding made under this subparagraph in the Federal Register.

(B) Within 12 months after receiving a petition that is found under subparagraph (A) to present substantial information indicating that the petitioned action may be warranted, the Secretary shall make one of the following findings:

(i) The petitioned action is not warranted, in which case the Secretary shall promptly publish such finding in the Federal Register.

(ii) The petitioned action is warranted, in which case the Secretary shall promptly publish in the Federal Register a general notice and the complete text of a proposed regulation to implement such action in accordance with paragraph (5).

(iii) The petitioned action is warranted, but that -

(I) the immediate proposal and timely promulgation of a final regulation implementing the petitioned action in accordance with paragraphs (5) and (6) is precluded by pending proposals to determine whether any species is an endangered species or a threatened species, and

(II) expeditious progress is being made to add qualified species to either of the lists published under subsection (c) of this section and to remove from such lists species for which the protections of this chapter are no longer necessary, in which case the Secretary shall promptly publish such finding in the Federal Register, together with a description and evaluation of the reasons and data on which the finding is based.

(C) (i) A petition with respect to which a finding is made under subparagraph (B)(iii) shall be treated as a petition that is resubmitted to the Secretary under subparagraph (A) on the date of such finding and that presents substantial scientific or commercial information that the petitioned action may be warranted.

(ii) Any negative finding described in subparagraph (A) and any finding described in subparagraph (B) (i) or (iii) shall be subject to judicial review.

(iii) The Secretary shall implement a system to monitor effectively the status of all species with respect to which a finding is made under subparagraph (B)(iii) and shall make prompt use of the authority under paragraph 7 to prevent a significant risk to the well being of any such species.

(D) (i) To the maximum extent practicable, within 90 days after receiving the petition of an interested person under section 553(e) of Title 5, to revise a critical habitat designation, the Secretary shall make a finding as to whether the petition presents substantial scientific information indicating that the revision may be warranted. The Secretary shall promptly publish such finding in the Federal Register.

(ii) Within 12 months after receiving a petition that is found under clause (i) to present substantial information indicating that the requested revision may be warranted, the Secretary shall determine how he intends to proceed with the requested revision, and shall promptly publish notice of such intention in the Federal Register.

(4) Except as provided in paragraphs (5) and (6) of this subsection, the provisions of section 553 of Title 5 (relating to rulemaking procedures), shall apply to any regulation promulgated to carry out the purposes of this chapter.

(5) With respect to any regulation proposed by the Secretary to implement a determination, designation, or revision referred to in subsection (a) (1) or (3) of this section, the Secretary shall -

(A) not less than 90 days before the effective date of the regulation -

(i) publish a general notice and the complete text of the proposed regulation in the Federal Register, and

(ii) give actual notice of the proposed regulation (including the complete text of the regulation) to the State agency in each State in which the species is believed to occur, and to each county or equivalent jurisdiction in which the species is believed to occur, and invite the comment of such agency, and each such jurisdiction, thereon;

(B) insofar as practical, and in cooperation with the Secretary of State, give notice of the proposed regulation to each foreign nation in which the species is believed to occur or whose citizens harvest the species on the high seas, and invite the comment of such nation thereon;

(C) give notice of the proposed regulation to such professional scientific organizations as he deems appropriate;

(D) publish a summary of the proposed regulation in a newspaper of general circulation in each area of the United States in which the species is believed to occur; and

(E) promptly hold one public hearing on the proposed regulation if any person files a request for such a hearing within 45 days after the date of publication of general notice.

(6)(A) Within the one-year period beginning on the date on which general notice is published in accordance with paragraph (5) (A) (i) regarding a proposed regulation, the Secretary shall publish in the Federal Register -

(i) if a determination as to whether a species is an endangered species or a threatened species, or a revision of critical habitat, is involved, either -

(I) a final regulation to implement such determination,

(II) a final regulation to implement such revision or a finding that such revision should not be made,

(III) notice that such one-year period is being extended under subparagraph (B) (i), or

(IV) notice that the proposed regulation is being withdrawn under subparagraph (B) (ii), together with the finding on which such withdrawal is based; or

(ii) subject to subparagraph (C), if a designation of critical habitat is involved, either -

(I) a final regulation to implement such designation, or

(II) notice that such one-year period is being extended under such subparagraph.

(B) (i) If the Secretary finds with respect to a proposed regulation referred to in subparagraph (A) (i) that there is substantial disagreement regarding the sufficiency or accuracy of the available data relevant to the determination or revision concerned, the Secretary may extend the one-year period specified in subparagraph (A) for not more than six months for purposes of soliciting additional data.

(ii) If a proposed regulation referred to in subparagraph (A) (i) is not promulgated as a final regulation within such one-year period (or longer period if extension under clause (i) applies) because the Secretary finds that there is not sufficient evidence to justify the action proposed by the regulation, the Secretary shall immediately withdraw the regulation. The finding on which a withdrawal is based shall be subject to judicial review. The Secretary may not propose a regulation that has previously been withdrawn under this clause unless he determines that sufficient new information is available to warrant such proposal.

(iii) If the one-year period specified in subparagraph (A) is extended under clause (i) with respect to a proposed regulation, then before the close of such extended period the Secretary shall publish in the Federal Register either a final regulation to implement the determination or revision concerned, a finding that the revision should not be made, or a notice of withdrawal of the regulation under clause (ii), together with the finding on which the withdrawal is based.

(C) A final regulation designating critical habitat of an endangered species or a threatened species shall be published concurrently with the final regulation implementing the determination that such species is endangered or threatened, unless the Secretary deems that -

(i) it is essential to the conservation of such species that the regulation implementing such determination be promptly published; or

(ii) critical habitat of such species is not then determinable, in which case the Secretary, with respect to the proposed regulation to designate such habitat, may extend the one-year period specified in subparagraph (A) by not more than one additional year, but not later than the close of such additional year the Secretary must publish a final regulation, based on such data as may be available at that time, designating, to the maximum extent prudent, such habitat.

(7) Neither paragraph (4), (5), or (6) of this subsection nor section 553 of Title 5 shall apply to any regulation issued by the Secretary in regard to any emergency posing a significant risk to the well-being of any species of fish or wildlife or plants, but only if -

(A) at the time of publication of the regulation in the Federal Register the Secretary publishes therein detailed reasons why such regulation is necessary; and

(B) in the case such regulation applies to resident species of fish or wildlife, or plants, the Secretary gives actual notice of such regulation to the State agency in each State in which such species is believed to occur.

Such regulation shall, at the discretion of the Secretary, take effect immediately upon the publication of the regulation in the Federal Register. Any regulation promulgated under the authority of this paragraph shall cease to have force and effect at the close of the 240-day period following the date of publication unless, during such 240-day period, the rulemaking procedures which would apply to such regulation without regard to this paragraph are complied with. If at any time after issuing an emergency regulation the Secretary determines, on the basis of the best appropriate data available to him, that substantial evidence does not exist to warrant such regulation, he shall withdraw it.

(8) The publication in the Federal Register of any proposed or final regulation which is necessary or appropriate to carry out the purposes of this chapter shall include a summary by the Secretary of the data on which such regulation is based and shall show the relationship of such data to such regulation; and if such regulation designates or revises critical habitat, such summary shall, to the maximum extent practicable, also include a brief description and evaluation of those activities (whether public or private) which, in the opinion of the Secretary, if undertaken may adversely modify such habitat, or may be affected by such designation.

(c) Lists

(1) The Secretary of the Interior shall publish in the Federal Register a list of all species determined by him or the Secretary of Commerce to be endangered species and a list of all species determined by him or the Secretary of Commerce to be threatened species. Each list shall refer to the species contained therein by scientific and common name or names, if any, specify with respect to each such species over what portion of its range it is endangered or threatened, and specify any critical habitat within such range. The Secretary shall from time to time revise each list published under the authority of this subsection to reflect recent determinations, designations, and revisions made in accordance with subsections (a) and (b) of this section.

(2) The Secretary shall -

(A) conduct, at least once every five years, a review of all species included in a list which is published pursuant to paragraph (1) and which is in effect at the time of such review; and

(B) determine on the basis of such review whether any such species should -

(i) be removed from such list;

(ii) be changed in status from an endangered species to a threatened species; or

(iii) be changed in status from a threatened species to an endangered species.

Each determination under subparagraph (B) shall be made in accordance with the provisions of subsections (a) and (b) of this section.

(d) Protective regulations

Whenever any species is listed as a threatened species pursuant to subsection (c) of this section, the Secretary shall issue such regulations as he deems necessary and advisable to provide for the conservation of such species. The Secretary may by regulation prohibit with respect to any threatened species any act prohibited under section 1538(a) (1) of this title, in the case of fish or wildlife, or section 1538(a) (2) of this title, in the case of plants, with respect to endangered species; except that with respect to the taking of resident species of fish or wildlife, such regulations shall apply in any State which has entered into a cooperative agreement pursuant to section 1535(c) of this title only to the extent that such regulations have also been adopted by such State.

(e) Similarity of appearance cases

The Secretary may, by regulation of commerce or taking, and to the extent he deems advisable, treat any species as an endangered species or threatened species even though it is not listed pursuant to this section if he finds that -

(A) such species so closely resembles in appearance, at the point in question, a species which has been listed pursuant to such section that enforcement personnel would have substantial difficulty in attempting to differentiate between the listed and unlisted species;

(B) the effect of this substantial difficulty is an additional threat to an endangered or threatened species; and

(C) such treatment of an unlisted species will substantially facilitate the enforcement and further the policy of this chapter.

(f) Recovery plans

(1) The Secretary shall develop and implement plans (hereinafter in this subsection referred to as "recovery plans") for the conservation and survival of endangered species and threatened species listed pursuant to this section, unless he finds that such a plan will not promote the conservation of the species. The Secretary, in developing and implementing recovery plans, shall, to the maximum extent practicable -

(A) give priority to those endangered species or threatened species, without regard to taxonomic classification, that are most likely to benefit from such plans, particularly those species that are, or may be, in conflict with construction or other development projects or other forms of economic activity;

(B) incorporate in each plan -

(i) a description of such site-specific management actions as may be necessary to achieve the plan's goal for the conservation and survival of the species;

(ii) objective, measurable criteria which, when met, would result in a determination, in accordance with the provisions of this section, that the species be removed from the list; and

(iii) estimates of the time required and the cost to carry out those measures needed to achieve the plan's goal and to achieve intermediate steps toward that goal.

(2) The Secretary, in developing and implementing recovery plans, may procure the services of appropriate public and private agencies and institutions, and other qualified persons. Recovery teams appointed pursuant to this subsection shall not be subject to the Federal Advisory Committee Act.

(3) The Secretary shall report every two years to the Committee on Environment and Public Works of the Senate and the Committee on Merchant Marine and Fisheries of the House of Representatives on the status of efforts to

develop and implement recovery plans for all species listed pursuant to this section and on the status of all species for which such plans have been developed.

(4) The Secretary shall, prior to final approval of a new or revised recovery plan, provide public notice and an opportunity for public review and comment on such plan. The Secretary shall consider all information presented during the public comment period prior to approval of the plan.

(5) Each Federal agency shall, prior to implementation of a new or revised recovery plan, consider all information presented during the public comment period under paragraph (4).

(g) Monitoring

(1) The Secretary shall implement a system in cooperation with the States to monitor effectively for not less than five years the status of all species which have recovered to the point at which the measures provided pursuant to this chapter are no longer necessary and which, in accordance with the provisions of this section, have been removed from either of the lists published under subsection (c) of this section.

(2) The Secretary shall make prompt use of the authority under paragraph 7 of subsection (b) of this section to prevent a significant risk to the well being of any such recovered species.

(h) Agency guidelines; publication in Federal Register; scope; proposals and amendments: notice and opportunity for comments

The Secretary shall establish, and publish in the Federal Register, agency guidelines to insure that the purposes of this section are achieved efficiently and effectively. Such guidelines shall include, but are not limited to -

(1) procedures for recording the receipt and the disposition of petitions submitted under subsection (b)(3) of this section;

(2) criteria for making the findings required under such subsection with respect to petitions;

(3) a ranking system to assist in the identification of species that should receive priority review under subsection (a)(1) of this section; and

(4) a system for developing and implementing, on a priority basis, recovery plans under subsection (f) of this section.

The Secretary shall provide to the public notice of, and opportunity to submit written comments on, any guideline (including any amendment thereto) proposed to be established under this subsection.

(i) Submission to State agency of justification for regulations inconsistent with State agency's comments or petition

If, in the case of any regulation proposed by the Secretary under the authority of this section, a State agency to which notice thereof was given in accordance with subsection (b)(5)(A)(ii) of this section files comments disagreeing with all or part of the proposed regulation, and the Secretary issues a final regulation which is in conflict with such comments, or if the Secretary fails to adopt a regulation pursuant to an action petitioned by a State agency under subsection (b)(3) of this section, the Secretary shall submit to the State agency a written justification for his failure to adopt regulations consistent with the agency's comments or petition.

Section 1534 Land Acquisition [ESA Section 5] [omitted]

Section 1535. Cooperation with States [ESA Section 6]

(a) Generally

In carrying out the program authorized by this chapter, the Secretary shall cooperate to the maximum extent practicable with the StatesSecretary shall cooperate to the maximum extent practicable with the States. Such cooperation shall include consultation with the States concerned before acquiring any land or water, or interest therein, for the purpose of conserving any endangered species or threatened species.

Section 1536. Interagency cooperation [ESA Section 7]

(a) Federal agency actions and consultations

(1) The Secretary shall review other programs administered by him and utilize such programs in furtherance of the purposes of this chapter. All other Federal agencies shall, in consultation with and with the assistance of the Secretary, utilize their authorities in furtherance of the purposes of this chapter by carrying out programs for the conservation of endangered species and threatened species listed pursuant to section 1533 of this title.

(2) Each Federal agency shall, in consultation with and with the assistance of the Secretary, insure that any action authorized, funded, or carried out by such agency (hereinafter in this section referred to as an "agency action") is not likely to jeopardize the continued existence of any endangered species or threatened species or result in the destruction or adverse modification of habitat of such species which is determined by the Secretary, after consultation as appropriate with affected States, to be critical, unless such agency has been granted an exemption for such action by the Committee pursuant to subsection (h) of this section. In fulfilling the requirements of this paragraph each agency shall use the best scientific and commercial data available.

(3) Subject to such guidelines as the Secretary may establish, a Federal agency shall consult with the Secretary on any prospective agency action at the request of, and in cooperation with, the prospective permit or license applicant if the applicant has reason to believe that an endangered species or a threatened species may be present in the area affected by his project and that implementation of such action will likely affect such species.

(4) Each Federal agency shall confer with the Secretary onany agency action which is likely to jeopardize the continued existence of any species proposed to be listed under section 1533 of this title or result in the destruction or adverse modification of critical habitat proposed to be designated for such species. This paragraph does not require a limitation on the commitment of resources as described in subsection (d) of this section.

(b) Opinion of Secretary

(1)(A) Consultation under subsection (a) (2) of this section with respect to any agency action shall be concluded within the 90-day period beginning on the date on which initiated or, subject to subparagraph (B), within such other period of time as is mutually agreeable to the Secretary and the Federal agency.
(B) In the case of an agency action involving a permit or license applicant, the Secretary and the Federal agency may not mutually agree to conclude consultation within a period exceeding 90 days unless the Secretary, before the close of the 90th day referred to in subparagraph (A) -

> (i) if the consultation period proposed to be agreed to will end before the 150th day after the date on which consultation was initiated, submits to the applicant a written statement setting forth -

(I) the reasons why a longer period is required,
(II) the information that is required to complete the consultation, and
(III) the estimated date on which consultation will be completed; or

(ii) if the consultation period proposed to be agreed to will end 150 or more days after the date on which consultation was initiated, obtains the consent of the applicant to such period.

The Secretary and the Federal agency may mutually agree to extend a consultation period established under the preceding sentence if the Secretary, before the close of such period, obtains the consent of the applicant to the extension.

(2) Consultation under subsection (a) (3) of this section shall be concluded within such period as is agreeable to the Secretary, the Federal agency, and the applicant concerned.
(3)(A) Promptly after conclusion of consultation under paragraph (2) or (3) of subsection (a) of this section, the Secretary shall provide to the Federal agency and the applicant, if any, a written statement setting forth the Secretary's opinion, and a summary of the information on which the opinion is based, detailing how the agency action affects the species or its critical habitat. If jeopardy or adverse modification is found, the Secretary shall suggest those reasonable and prudent alternatives which he believes would not violate subsection (a) (2) of this section and can be taken by the Federal agency or applicant in implementing the agency action.
(B) Consultation under subsection (a) (3) of this section, and an opinion issued by the Secretary incident to such consultation, regarding an agency action shall be treated respectively as a consultation under subsection (a) (2) of this section, and as an opinion issued after consultation under such subsection, regarding that action if the Secretary reviews the action before it is commenced by the Federal agency and finds, and notifies such agency, that no significant changes have been made with respect to the action and that no significant change has occurred regarding the information used during the initial consultation.
(4) If after consultation under subsection (a)(2) of this section, the Secretary concludes that -
(A) the agency action will not violate such subsection, or offers reasonable and prudent alternatives which the Secretary believes would not violate such subsection;
(B) the taking of an endangered species or a threatened species incidental to the agency action will not violate such subsection; and
(C) if an endangered species or threatened species of a marine mammal is involved, the taking is authorized pursuant to section 1371(a)(5) of this title; the Secretary shall provide the Federal agency and the applicant concerned, if any, with a written statement that -

(i) specifies the impact of such incidental taking on the species,
(ii) specifies those reasonable and prudent measures that the Secretary considers necessary or appropriate to minimize such impact,
(iii) in the case of marine mammals, specifies those measures that are necessary to comply with section 1371(a)(5) of this title with regard to such taking, and
(iv) sets forth the terms and conditions (including, but not limited to, reporting requirements) that must be complied with by the Federal agency or applicant (if any), or both, to implement the measures specified under clauses (ii) and (iii).

(c) Biological assessment

(1) To facilitate compliance with the requirements of subsection (a) (2) of this section, each Federal agency shall, with respect to any agency action of such agency for which no contract for construction has been entered into and for which no construction has begun on November 10, 1978, request of the Secretary information whether any species which is listed or proposed to be listed may be present in the area of such proposed action. If the Secretary advises, based on the best scientific and commercial data available, that such species may be present, such agency shall conduct a biological assessment for the purpose of identifying any endangered species or threatened species which is likely to be affected by such action. Such assessment shall be completed within 180 days after the date on which initiated (or within such other period as is mutually agreed to by the Secretary and such agency, except that if a permit or license applicant is involved, the 180-day period may not be extended unless such agency provides the applicant, before the close of such period, with a written statement setting forth

the estimated length of the proposed extension and the reasons therefor) and, before any contract for construction is entered into and before construction is begun with respect to such action. Such assessment may be undertaken as part of a Federal agency's compliance with the requirements of section 102 of the National Environmental Policy Act of 1969 (42 U.S.C. 4332).
(2) Any person who may wish to apply for an exemption under subsection (g) of this section for that action may conduct a biological assessment to identify any endangered species or threatened species which is likely to be affected by such action. Any such biological assessment must, however, be conducted in cooperation with the Secretary and under the supervision of the appropriate Federal agency.

(d) Limitation on commitment of resources

After initiation of consultation required under subsection (a) (2) of this section, the Federal agency and the permit or license applicant shall not make any irreversible or irretrievable commitment of resources with respect to the agency action which has the effect of foreclosing the formulation or implementation of any reasonable and prudent alternative measures which would not violate subsection (a) (2) of this section.

(e) Endangered Species Committee

(1) There is established a committee to be known as the Endangered Species Committee (hereinafter in this section referred to as the "Committee").
(2) The Committee shall review any application submitted to it pursuant to this section and determine in accordance with subsection (h) of this section whether or not to grant an exemption from the requirements of subsection (a) (2) of this section for the action set forth in such application.
(3) The Committee shall be composed of seven members as follows:
(A) The Secretary of Agriculture.
(B) The Secretary of the Army.
(C) The Chairman of the Council of Economic Advisors.
(D) The Administrator of the Environmental Protection Agency.
(E) The Secretary of the Interior.
(F) The Administrator of the National Oceanic and Atmospheric Administration.
(G) The President, after consideration of any recommendations received pursuant to subsection (g) (2) (B) of this section shall appoint one individual from each affected State, as determined by the Secretary, to be a member of the Committee for the consideration of the application for exemption for an agency action with respect to which such recommendations are made, not later than 30 days after an application is submitted pursuant to this section.
(4)(A) Members of the Committee shall receive additional pay on account of their service on the Committee.
(B) While away from their homes or regular places of business in the performance of services for the Committee, members of the Committee shall be allowed travel expenses, including per diem in lieu of subsistence, in the same manner as persons employed intermittently in the Government service are allowed expenses under section 5703 of Title 5.
(5)(A) Five members of the Committee or their representatives shall constitute a quorum for the transaction of any function of the Committee, except that, in no case shall any representative be considered in determining the existence of a quorum for the transaction of any function of the Committee if that function involves a vote by the Committee on any matter before the Committee.
(B) The Secretary of the Interior shall be the Chairman of the Committee.
(C) The Committee shall meet at the call of the Chairman or five of its members.
(D) All meetings and records of the Committee shall be open to the public.
(6) Upon request of the Committee, the head of any Federal agency is authorized to detail, on a nonreimbursable basis, any of the personnel of such agency to the Committee to assist it in carrying out its duties under this section.
(7)(A) The Committee may for the purpose of carrying out its duties under this section hold such hearings, sit and act at such times and places, take such testimony, and receive such evidence, as the Committee deems advisable.

(B) When so authorized by the Committee, any member or agent of the Committee may take any action which the Committee is authorized to take by this paragraph.
(C) Subject to the Privacy Act [5 U.S.C.A. Section 552a], the Committee may secure directly from any Federal agency information necessary to enable it to carry out its duties under this section. Upon request of the Chairman of the Committee, the head of such Federal agency shall furnish such information to the Committee.
(D) The Committee may use the United States mails in the same manner and upon the same conditions as a Federal agency.
(E) The Administrator of General Services shall provide to the Committee on a reimbursable basis such administrative support services as the Committee may request.
(8) In carrying out its duties under this section, the Committee may promulgate and amend such rules, regulations, and procedures, and issue and amend such orders as it deems necessary.
(9) For the purpose of obtaining information necessary for the consideration of an application for an exemption under this section the Committee may issue subpoenas for the attendance and testimony of witnesses and the production of relevant papers, books, and documents.
(10) In no case shall any representative, including a representative of a member designated pursuant to paragraph (3) (G) of this subsection, be eligible to cast a vote on behalf of any member.

(f) Promulgation of regulations; form and contents of exemption application

Not later than 90 days after November 10, 1978, the Secretary shall promulgate regulations which set forth the form and manner in which applications for exemption shall be submitted to the Secretary and the information to be contained in such applications. Such regulations shall require that information submitted in an application by the head of any Federal agency with respect to any agency action include, but not be limited to -

(1) a description of the consultation process carried out pursuant to subsection (a) (2) of this section between the head of the Federal agency and the Secretary; and
(2) a statement describing why such action cannot be altered or modified to conform with the requirements of subsection (a) (2) of this section.

(g) Application for exemption; report to Committee

(1) A Federal agency, the Governor of the State in which an agency action will occur, if any, or a permit or license applicant may apply to the Secretary for an exemption for an agency action of such agency if, after consultation under subsection (a) (2) of this section, the Secretary's opinion under subsection (b) of this section indicates that the agency action would violate subsection (a) (2) of this section. An application for an exemption shall be considered initially by the Secretary in the manner provided for in this subsection, and shall be considered by the Committee for a final determination under subsection (h) of this section after a report is made pursuant to paragraph (5). The applicant for an exemption shall be referred to as the "exemption applicant" in this section.
(2)(A) An exemption applicant shall submit a written application to the Secretary, in a form prescribed under subsection (f) of this section, not later than 90 days after the completion of the consultation process; except that, in the case of any agency action involving a permit or license applicant, such application shall be submitted not later than 90 days after the date on which the Federal agency concerned takes final agency action with respect to the issuance of the permit or license. For purposes of the preceding sentence, the term "final agency action" mean

- (i) a disposition by an agency with respect to the issuance of a permit or license that is subject to administrative review, whether or not such disposition is subject to judicial review; or
- (ii) if administrative review is sought with respect to such disposition, the decision resulting after such review. Such application shall set forth the reasons why the exemption applicant considers that the agency action meets the requirements for an exemption under this subsection.

(B) Upon receipt of an application for exemption for an agency action under paragraph

(1), the Secretary shall promptly

(i) notify the Governor of each affected State, if any, as determined by the Secretary, and request the Governors so notified to recommend individuals to be appointed to the Endangered Species Committee for consideration of such application; and

(ii) publish notice of receipt of the application in the Federal Register, including a summary of the information contained in the application and a description of the agency action with respect to which the application for exemption has been filed.

(3) The Secretary shall within 20 days after the receipt of an application for exemption, or within such other period of time as is mutually agreeable to the exemption applicant and the Secretary -

(A) determine that the Federal agency concerned and the exemption applicant have -

(i) carried out the consultation responsibilities described in subsection (a) of this section in good faith and made a reasonable and responsible effort to develop and fairly consider modifications or reasonable and prudent alternatives to the proposed agency action which would not violate subsection (a) (2) of this section;

(ii) conducted any biological assessment required by subsection (c) of this section; and

(iii) to the extent determinable within the time provided herein, refrained from making any irreversible or irretrievable commitment of resources prohibited by subsection (d) of this section; or

(B) deny the application for exemption because the Federal agency concerned or the exemption applicant have not met the requirements set forth in subparagraph (A) (i), (ii), and (iii).

The denial of an application under subparagraph (B) shall be considered final agency action for purposes of chapter 7 of Title 5.

(4) If the Secretary determines that the Federal agency concerned and the exemption applicant have met the requirements set forth in paragraph (3) (A) (i), (ii), and (iii) he shall, in consultation with the Members of the Committee, hold a hearing on the application for exemption in accordance with sections 554, 555, and 556 (other than subsection (b)

(1) and (2) thereof) of Title 5 and prepare the report to be submitted pursuant to paragraph (5).

(5) Within 140 days after making the determinations under paragraph (3) or within such other period of time as is mutually agreeable to the exemption applicant and the Secretary, the Secretary shall submit to the Committee a report discussing -

(A) the availability of reasonable and prudent alternatives to the agency action, and the nature and extent of the benefits of the agency action and of alternative courses of action consistent with conserving the species or the critical habitat;

(B) a summary of the evidence concerning whether or not the agency action is in the public interest and is of national or regional significance;

(C) appropriate reasonable mitigation and enhancement measures which should be considered by the Committee; and

(D) whether the Federal agency concerned and the exemption applicant refrained from making any irreversible or irretrievable commitment of resources prohibited by subsection (d) of this section.

(6) To the extent practicable within the time required for action under subsection (g) of this section, and except to the extent inconsistent with the requirements of this section, the consideration of any application for an exemption under this section and the conduct of any hearing under this subsection shall be in accordance with sections 554, 555, and 556 (other than subsection (b) (3) of section 556) of Title 5.

(7) Upon request of the Secretary, the head of any Federal agency is authorized to detail, on a nonreimbursable basis, any of the personnel of such agency to the Secretary to assist him in carrying out his duties under this section.

(8) All meetings and records resulting from activities pursuant to this subsection shall be open to the public.

(h) Grant of exemption

(1) The Committee shall make a final determination whether or not to grant an exemption within 30 days after receiving the report of the Secretary pursuant to subsection (g) (5) of this section. The Committee shall grant an

exemption from the requirements of subsection (a) (2) of this section for an agency action if, by a vote of not less than five of its members voting in person -

(A) it determines on the record, based on the report of the Secretary, the record of the hearing held under subsection (g) (4) of this section and on such other testimony or evidence as it may receive, that -

  (i) there are no reasonable and prudent alternatives to the agency action;

  (ii) the benefits of such action clearly outweigh the benefits of alternative courses of action consistent with conserving the species or its critical habitat, and such action is in the public interest;

  (iii) the action is of regional or national significance; and

  (iv) neither the Federal agency concerned nor the exemption applicant made any irreversible or irretrievable commitment of resources prohibited by subsection (d) of this section; and

(B) it establishes such reasonable mitigation and enhancement measures, including, but not limited to, live propagation, transplantation, and habitat acquisition and improvement, as are necessary and appropriate to minimize the adverse effects of the agency action upon the endangered species, threatened species, or critical habitat concerned.

Any final determination by the Committee under this subsection shall be considered final agency action for purposes of chapter 7 of Title 5.

(2)(A) Except as provided in subparagraph (B), an exemption for an agency action granted under paragraph (1) shall constitute a permanent exemption with respect to all endangered or threatened species for the purposes of completing such agency action -

  (i) regardless whether the species was identified in the biological assessment; and

  (ii) only if a biological assessment has been conducted under subsection (c) of this section with respect to such agency action.

(B) An exemption shall be permanent under subparagraph (A) unless -

  (i) the Secretary finds, based on the best scientific and commercial data available, that such exemption would result in the extinction of a species that was not the subject of consultation under subsection (a) (2) of this section or was not identified in any biological assessment conducted under subsection (c) of this section, and

  (ii) the Committee determines within 60 days after the date of the Secretary's finding that the exemption should not be permanent.

  If the Secretary makes a finding described in clause (i), the Committee shall meet with respect to the matter within 30 days after the date of the finding.

(i) Review by Secretary of State; violation of international treaty or other international obligation of United States

Notwithstanding any other provision of this chapter, the Committee shall be prohibited from considering for exemption any application made to it, if the Secretary of State, after a review of the proposed agency action and its potential implications, and after hearing, certifies, in writing, to the Committee within 60 days of any application made under this section that the granting of any such exemption and the carrying out of such action would be in violation of an international treaty obligation or other international obligation of the United States. The Secretary of State shall, at the time of such certification, publish a copy thereof in the Federal Register.

(j) Exemption for national security reasons

Notwithstanding any other provision of this chapter, the Committee shall grant an exemption for any agency action if the Secretary of Defense finds that such exemption is necessary for reasons of national security.

(k) Exemption decision not considered major Federal action; environmental impact statement

An exemption decision by the Committee under this section shall not be a major Federal action for purposes of the National Environmental Policy Act of 1969 [42 U.S.C.A. Section 4321 et seq.]: Provided, That an environmental impact statement which discusses the impacts upon endangered species or threatened species or their critical habitats shall have been previously prepared with respect to any agency action exempted by such order.

(l) Committee order granting exemption; cost of mitigation and enhancement measures; report by applicant to Council on Environmental Quality

(1) If the Committee determines under subsection (h) of this section that an exemption should be granted with respect to any agency action, the Committee shall issue an order granting the exemption and specifying the mitigation and enhancement measures established pursuant to subsection (h) of this section which shall be carried out and paid for by the exemption applicant in implementing the agency action. All necessary mitigation and enhancement measures shall be authorized prior to the implementing of the agency action and funded concurrently with all other project features.

(2) The applicant receiving such exemption shall include the costs of such mitigation and enhancement measures within the overall costs of continuing the proposed action. Notwithstanding the preceding sentence the costs of such measures shall not be treated as project costs for the purpose of computing benefit-cost or other ratios for the proposed action. Any applicant may request the Secretary to carry out such mitigation and enhancement measures. The costs incurred by the Secretary in carrying out any such measures shall be paid by the applicant receiving the exemption. No later than one year after the granting of an exemption, the exemption applicant shall submit to the Council on Environmental Quality a report describing its compliance with the mitigation and enhancement measures prescribed by this section. Such a report shall be submitted annually until all such mitigation and enhancement measures have been completed. Notice of the public availability of such reports shall be published in the Federal Register by the Council on Environmental Quality.

(m) Notice requirement for citizen suits not applicable

The 60-day notice requirement of section 1540(g) of this title shall not apply with respect to review of any final determination of the Committee under subsection (h) of this section granting an exemption from the requirements of subsection (a) (2) of this section.

(n) Judicial review

Any person, as defined by section 1532(13) of this title, may obtain judicial review, under chapter 7 of Title 5, of any decision of the Endangered Species Committee under subsection (h) of this section in the United States Court of Appeals for (1) any circuit wherein the agency action concerned will be, or is being, carried out, or (2) in any case in which the agency action will be, or is being, carried out outside of any circuit, the District of Columbia, by filing in such court within 90 days after the date of issuance of the decision, a written petition for review. A copy of such petition shall be transmitted by the clerk of the court to the Committee and the Committee shall file in the court the record in the proceeding, as provided in section 2112, of Title 28. Attorneys designated by the Endangered Species Committee may appear for, and represent the Committee in any action for review under this subsection.

(o) Exemption as providing exception on taking of endangered species

Notwithstanding sections 1533(d) and 1538(a)(1)(B) and (C) of this title, sections 1371 and 1372 of this title, or any regulation promulgated to implement any such section -

(1) any action for which an exemption is granted under subsection (h) of this section shall not be considered to be a taking of any endangered species or threatened species with respect to any activity which is necessary to carry out such action; and

(2) any taking that is in compliance with the terms and conditions specified in a written statement provided under subsection (b)(4)(iv) of this section shall not be considered to be a prohibited taking of the species concerned.

(p) Exemptions in Presidentially declared disaster areas

In any area which has been declared by the President to be a major disaster area under the Disaster Relief and Emergency Assistance Act [42 U.S.C.A. Section 5121 et seq.], the President is authorized to make the determinations required by subsections (g) and (h) of this section for any project for the repair or replacement of a public facility substantially as it existed prior to the disaster under section 405 or 406 of the Disaster Relief and Emergency Assistance Act [42 U.S.C.A. ss 5171 or 5172], and which the President determines (1) is necessary to prevent the recurrence of such a natural disaster and to reduce the potential loss of human life, and (2) to involve an emergency situation which does not allow the ordinary procedures of this section to be followed. Notwithstanding any other provision of this section, the Committee shall accept the determinations of the President under this subsection.

Section 1537. International cooperation [ESA Section 8]

(a) Financial assistance

As a demonstration of the commitment of the United States to the worldwide protection of endangered species and threatened species, the President may, subject to the provisions of section 1306 of Title 31, use foreign currencies accruing to the United States Government under the Agricultural Trade Development and Assistance Act of 1954 [7 U.S.C.A. Section 1691 et seq.] or any other law to provide to any foreign country (with its consent) assistance in the development and management of programs in that country which the Secretary determines to be necessary or useful for the conservation of any endangered species or threatened species listed by the Secretary pursuant to section 1533 of this title. The President shall provide assistance (which includes, but is not limited to, the acquisition, by lease or otherwise, of lands, waters, or interests therein) to foreign countries under this section under such terms and conditions as he deems appropriate. Whenever foreign currencies are available for the provision of assistance under this section, such currencies shall be used in preference to funds appropriated under the authority of section 1542 of this title.

(b) Encouragement of foreign programs

In order to carry out further the provisions of this chapter, the Secretary, through the Secretary of State, shall encourage -

(1) foreign countries to provide for the conservation of fish or wildlife and plants including endangered species and threatened species listed pursuant to section 1533 of this title;

(2) the entering into of bilateral or multilateral agreements with foreign countries to provide for such conservation; and

(3) foreign persons who directly or indirectly take fish or wildlife or plants in foreign countries or on the high seas for importation into the United States for commercial or other purposes to develop and carry out with such assistance as he may provide, conservation practices designed to enhance such fish or wildlife or plants and their habitat.

Section 1537A. Convention implementation [ESA Section 8A]

(a) Management Authority and Scientific Authority

The Secretary of the Interior (hereinafter in this section referred to as the "Secretary") is designated as the Management Authority and the Scientific Authority for purposes of the Convention and the respective functions of each such Authority shall be carried out through the United States Fish and Wildlife Service.

(b) Management Authority functions

The Secretary shall do all things necessary and appropriate to carry out the functions of the Management Authority under the Convention.

(c) Scientific Authority functions; determinations

(1) The Secretary shall do all things necessary and appropriate to carry out the functions of the Scientific Authority under the Convention.

(2) The Secretary shall base the determinations and advice given by him under Article IV of the Convention with respect to wildlife upon the best available biological information derived from professionally accepted wildlife management practices; but is not required to make, or require any State to make, estimates of population size in making such determinations or giving such advice.

(d) Reservations by the United States under Convention

If the United States votes against including any species in Appendix I or II of the Convention and does not enter a reservation pursuant to paragraph (3) of Article XV of the Convention with respect to that species, the Secretary of State, before the 90th day after the last day on which such a reservation could be entered, shall submit to the Committee on Merchant Marine and Fisheries of the House of Representatives, and to the Committee on the Environment and Public Works of the Senate, a written report setting forth the reasons why such a reservation was not entered.

(e) Wildlife Preservation in Western Hemisphere

(1) The Secretary of the Interior (hereinafter in this subsection referred to as the "Secretary"), in cooperation with the Secretary of State, shall act on behalf of, and represent, the United States in all regards as required by the Convention on Nature Protection and Wildlife Preservation in the Western Hemisphere (56 Stat. 1354, T.S. 982, hereinafter in this subsection referred to as the "Western Convention"). In the discharge of these responsibilities, the Secretary and the Secretary of State shall consult with the Secretary of Agriculture, the

Secretary of Commerce, and the heads of other agencies with respect to matters relating to or affecting their areas of responsibility.

(2) The Secretary and the Secretary of State shall, in cooperation with the contracting parties to the Western Convention and, to the extent feasible and appropriate, with the participation of State agencies, take such steps as are necessary to implement the Western Convention. Such steps shall include, but not be limited to -

(A) cooperation with contracting parties and international organizations for the purpose of developing personnel resources and programs that will facilitate implementation of the Western Convention;

(B) identification of those species of birds that migrate between the United States and other contracting parties, and the habitats upon which those species depend, and the implementation of cooperative measures to ensure that such species will not become endangered or threatened; and

(C) identification of measures that are necessary and appropriate to implement those provisions of the Western Convention which address the protection of wild plants.

(3) No later than September 30, 1985, the Secretary and the Secretary of State shall submit a report to Congress describing those steps taken in accordance with the requirements of this subsection and identifying the principal remaining actions yet necessary for comprehensive and effective implementation of the Western Convention.

(4) The provisions of this subsection shall not be construed as affecting the authority, jurisdiction, or responsibility of the several States to manage, control, or regulate resident fish or wildlife under State law or regulations.

Section 1538. Prohibited acts [ESA Section 9]

(a) Generally

(1) Except as provided in sections 1535(g)(2) and 1539 of this title, with respect to any endangered species of fish or wildlife listed pursuant to section 1533 of this title it is unlawful for any person subject to the jurisdiction of the United States to -

(A) import any such species into, or export any such species from the United States;

(B) take any such species within the United States or the territorial sea of the United States;

(C) take any such species upon the high seas;

(D) possess, sell, deliver, carry, transport, or ship, by any means whatsoever, any such species taken in violation of subparagraphs (B) and (C);

(E) deliver, receive, carry, transport, or ship in interstate or foreign commerce, by any means whatsoever and in the course of a commercial activity, any such species;

(F) sell or offer for sale in interstate or foreign commerce any such species; or

(G) violate any regulation pertaining to such species or to any threatened species of fish or wildlife listed pursuant to section 1533 of this title and promulgated by the Secretary pursuant to authority provided by this chapter.

(2) Except as provided in sections 1535(g)(2) and 1539 of this title, with respect to any endangered species of plants listed pursuant to section 1533 of this title, it is unlawful for any person subject to the jurisdiction of the

United States to -

(A) import any such species into, or export any such species from, the United States;

(B) remove and reduce to possession any such species from areas under Federal jurisdiction; maliciously damage or destroy any such species on any such area; or remove, cut, dig up, or damage or destroy any such species on any other area in knowing violation of any law or regulation of any State or in the course of any violation of a State criminal trespass law;

(C) deliver, receive, carry, transport, or ship in interstate or foreign commerce, by any means whatsoever and in the course of a commercial activity, any such species;

(D) sell or offer for sale in interstate or foreign commerce any such species; or

(E) violate any regulation pertaining to such species or to any threatened species of plants listed pursuant to section 1533 of this title and promulgated by the Secretary pursuant to authority provided by this chapter.

(b) Species held in captivity or controlled environment

(1) The provisions of subsections (a) (1) (A) and (a) (1) (G) of this section shall not apply to any fish or wildlife which was held in captivity or in a controlled environment on (A) December 28, 1973, or (B) the date of the publication in the Federal Register of a final regulation adding such fish or wildlife species to any list published pursuant to subsection (c) of section 1533 of this title: Provided, That such holding and any subsequent holding or use of the fish or wildlife was not in the course of a commercial activity. With respect to any act prohibited by subsections (a) (1) (A) and (a) (1) (G) of this section which occurs after a period of 180 days from (i) December 28, 1973, or (ii) the date of publication in the Federal Register of a final regulation adding such fish or wildlife species to any list published pursuant to subsection (c) of section 1533 of this title, there shall be a rebuttable presumption that the fish or wildlife involved in such act is not entitled to the exemption contained in this subsection.

(2)(A) The provisions of subsection (a) (1) of this section shall not apply to -

(i) any raptor legally held in captivity or in a controlled environment on November 10, 1978; or

(ii) any progeny of any raptor described in clause (i); until such time as any such raptor or progeny is intentionally returned to a wild state.

(B) Any person holding any raptor or progeny described in subparagraph (A) must be able to demonstrate that the raptor or progeny does, in fact, qualify under the provisions of this paragraph, and shall maintain and submit to the Secretary, on request, such inventories, documentation, and records as the Secretary may by regulation require as being reasonably appropriate to carry out the purposes of this paragraph. Such requirements shall not unnecessarily duplicate the requirements of other rules and regulations promulgated by the Secretary.

(c) Violation of Convention

(1) It is unlawful for any person subject to the jurisdiction of the United States to engage in any trade in any specimens contrary to the provisions of the Convention, or to possess any specimens traded contrary to the provisions of the Convention, including the definitions of terms in article I thereof.

(2) Any importation into the United States of fish or wildlife shall, if -

(A) such fish or wildlife is not an endangered species listed pursuant to section 1533 of this title but is listed in Appendix II to the Convention,

(B) the taking and exportation of such fish or wildlife is not contrary to the provisions of the Convention and all other applicable requirements of the Convention have been satisfied,

(C) the applicable requirements of subsections (d), (e), and (f) of this section have been satisfied, and

(D) such importation is not made in the course of a commercial activity, be presumed to be an importation not in violation of any provision of this chapter or any regulation issued pursuant to this chapter.

(d) Imports and exports

(1) In general

It is unlawful for any person, without first having obtained permission from the Secretary, to engage in business -

(A) as an importer or exporter of fish or wildlife (other than shellfish and fishery products which (i) are not listed pursuant to section 1533 of this title as endangered species or threatened species, and (ii) are imported for purposes of human or animal consumption or taken in waters under the jurisdiction of the United States or on the high seas for recreational purposes) or plants; or

(B) as an importer or exporter of any amount of raw or worked African elephant ivory.

(2) Requirements

Any person required to obtain permission under paragraph (1) of this subsection shall -

(A) keep such records as will fully and correctly disclose each importation or exportation of fish, wildlife, plants, or African elephant ivory made by him and the subsequent disposition made by him with respect to such fish, wildlife, plants, or ivory;

(B) at all reasonable times upon notice by a duly authorized representative of the Secretary, afford such representative access to his place of business, an opportunity to examine his inventory of imported fish, wildlife, plants, or African elephant ivory and the records required to be kept under subparagraph (A) of this paragraph, and to copy such records; and

(C) file such reports as the Secretary may require.

(3) Regulations

The Secretary shall prescribe such regulations as are necessary and appropriate to carry out the purposes of this subsection.

(4) Restriction on consideration of value or amount of African elephant ivory imported or exported

In granting permission under this subsection for importation or exportation of African elephant ivory, the Secretary shall not vary the requirements for obtaining such permission on the basis of the value or amount of ivory imported or exported under such permission.

(e) Reports

It is unlawful for any person importing or exporting fish or wildlife (other than shellfish and fishery products which (1) are not listed pursuant to section 1533 of this title as endangered or threatened species, and (2) are imported for purposes of human or animal consumption or taken in waters under the jurisdiction of the United

States or on the high seas for recreational purposes) or plants to fail to file any declaration or report as the Secretary deems necessary to facilitate enforcement of this chapter or to meet the obligations of the Convention.

(f) Designation of ports

(1) It is unlawful for any person subject to the jurisdiction of the United States to import into or export from the United States any fish or wildlife (other than shellfish and fishery products which (A) are not listed pursuant to section 1533 of this title as endangered species or threatened species, and (B) are imported for purposes of human or animal consumption or taken in waters under the jurisdiction of the United States or on the high seas for recreational purposes) or plants, except at a port or ports designated by the Secretary of the Interior. For the purpose of facilitating enforcement of this chapter and reducing the costs thereof, the Secretary of the Interior, with approval of the Secretary of the Treasury and after notice and opportunity for public hearing, may, by regulation, designate ports and change such designations. The Secretary of the Interior, under such terms and conditions as he may prescribe, may permit the importation or exportation at nondesignated ports in the interest of the health or safety of the fish or wildlife or plants, or for other reasons if, in his discretion, he deems it appropriate and consistent with the purpose of this subsection.

(2) Any port designated by the Secretary of the Interior under the authority of section 668cc-4(d) of this title, shall, if such designation is in effect on December 27, 1973, be deemed to be a port designated by the Secretary under paragraph (1) of this subsection until such time as the Secretary otherwise provides.

(g) Violations

It is unlawful for any person subject to the jurisdiction of the United States to attempt to commit, solicit another to commit, or cause to be committed, any offense defined in this section.

Section 1539. Exceptions [ESA Section 10]

(a) Permits

(1) The Secretary may permit, under such terms and conditions as he shall prescribe -

(A) any act otherwise prohibited by section 1538 of this title for scientific purposes or to enhance the propagation or survival of the affected species, including, but not limited to, acts necessary for the establishment and maintenance of experimental populations pursuant to subsection (j) of this section; or

(B) any taking otherwise prohibited by section 1538(a) (1) (B) of this title if such taking is incidental to, and not the purpose of, the carrying out of an otherwise lawful activity.

(2)(A) No permit may be issued by the Secretary authorizing any taking referred to in paragraph (1) (B) unless the applicant therefor submits to the Secretary a conservation plan that specifies -

(i) the impact which will likely result from such taking;

(ii) what steps the applicant will take to minimize and mitigate such impacts, and the funding that will be available to implement such steps;

(iii) what alternative actions to such taking the applicant considered and the reasons why such alternatives are not being utilized; and

(iv) such other measures that the Secretary may require as being necessary or appropriate for purposes of the plan.

(B) If the Secretary finds, after opportunity for public comment, with respect to a permit application and the related conservation plan that -

(i) the taking will be incidental;

(ii) the applicant will, to the maximum extent practicable, minimize and mitigate the impacts of such taking;

(iii) the applicant will ensure that adequate funding for the plan will be provided;

(iv) the taking will not appreciably reduce the likelihood of the survival and recovery of the species in the wild; and

(v) the measures, if any, required under subparagraph (A) (iv) will be met; and he has received such other assurances as he may require that the plan will be implemented, the Secretary shall issue the permit. The permit shall contain such terms and conditions as the Secretary deems necessary or appropriate to carry out the purposes of this paragraph, including, but not limited to, such reporting requirements as the Secretary deems necessary for determining whether such terms and conditions are being complied with.

(C) The Secretary shall revoke a permit issued under this paragraph if he finds that the permittee is not complying with the terms and conditions of the permit.

(b) Hardship exemptions

(1) If any person enters into a contract with respect to a species of fish or wildlife or plant before the date of the publication in the Federal Register of notice of consideration of that species as an endangered species and the subsequent listing of that species as an endangered species pursuant to section 1533 of this title will cause undue economic hardship to such person under the contract, the Secretary, in order to minimize such hardship, may exempt such person from the application of section 1538(a) of this title to the extent the Secretary deems appropriate if such person applies to him for such exemption and includes with such application such information as the Secretary may require to prove such hardship; except that

(A) no such exemption shall be for a duration of more than one year from the date of publication in the Federal Register of notice of consideration of the species concerned, or shall apply to a quantity of fish or wildlife or plants in excess of that specified by the Secretary;

(B) the one-year period for those species of fish or wildlife listed by the Secretary as endangered prior to December 28, 1973 shall expire in accordance with the terms of section 668cc-3 of this title; and

(C) no such exemption may be granted for the importation or exportation of a specimen listed in Appendix I of the Convention which is to be used in a commercial activity.

(2) As used in this subsection, the term "undue economic hardship" shall include, but not be limited to:

(A) substantial economic loss resulting from inability caused by this chapter to perform contracts with respect to species of fish and wildlife entered into prior to the date of publication in the Federal Register of a notice of consideration of such species as an endangered species;

(B) substantial economic loss to persons who, for the year prior to the notice of consideration of such species as an endangered species, derived a substantial portion of their income from the lawful taking of any listed species, which taking would be made unlawful under this chapter; or

(C) curtailment of subsistence taking made unlawful under this chapter by persons (i) not reasonably able to secure other sources of subsistence; and (ii) dependent to a substantial extent upon hunting and fishing for subsistence; and (iii) who must engage in such curtailed taking for subsistence purposes.

(3) The Secretary may make further requirements for a showing of undue economic hardship as he deems fit. Exceptions granted under this section may be limited by the Secretary in his discretion as to time, area, or other factor of applicability.

(c) Notice and review

The Secretary shall publish notice in the Federal Register of each application for an exemption or permit which is made under this section. Each notice shall invite the submission from interested parties, within thirty days after the date of the notice, of written data, views, or arguments with respect to the application; except that such thirty-day period may be waived by the Secretary in an emergency situation where the health or life of an endangered animal is threatened and no reasonable alternative is available to the applicant, but notice of any such waiver shall be published by the Secretary in the Federal Register within ten days following the issuance of the exemption or permit. Information received by the Secretary as a part of any application shall be available to the public as a matter of public record at every stage of the proceeding.

(d) Permit and exemption policy

The Secretary may grant exceptions under subsections (a) (1) (A) and (b) of this section only if he finds and publishes his finding in the Federal Register that (1) such exceptions were applied for in good faith, (2) if granted and exercised will not operate to the disadvantage of such endangered species, and (3) will be consistent with the purposes and policy set forth in section 1531 of this title.

(e) Alaska natives [omitted]

(f) Pre-Act endangered species parts exemption; application and certification; regulation; validity of sales contract; separabili ty of provisions; renewal of exemption; expiration of renewal certification [omitted]

(g) Burden of proof

In connection with any action alleging a violation of section 1538 of this title, any person claiming the benefit of any exemption or permit under this chapter shall have the burden of proving that the exemption or permit is applicable, has been granted, and was valid and in force at the time of the alleged violation.

(h) Certain antique articles; importation; port designation; application for return of articles [omitted]

(i) Noncommercial transshipments [omitted]

(j) Experimental populations

(1) For purposes of this subsection, the term "experimental population" means any population (including any offspring arising solely therefrom) authorized by the Secretary for release under paragraph (2), but only when, and at such times as, the population is wholly separate geographically from nonexperimental populations of the same species.

(2)(A) The Secretary may authorize the release (and the related transportation) of any population (including eggs, propagules, or individuals) of an endangered species or a threatened species outside the current range of such species if the Secretary determines that such release will further the conservation of such species.

(B) Before authorizing the release of any population under subparagraph (A), the Secretary shall by regulation identify the population and determine, on the basis of the best available information, whether or not such population is essential to the continued existence of an endangered species or a threatened species.

(C) For the purposes of this chapter, each member of an experimental population shall be treated as a threatened species; except that -

(i) solely for purposes of section 1536 of this title (other than subsection (a) (1) thereof), an experimental population determined under subparagraph (B) to be not essential to the continued existence of a species shall be treated, except when it occurs in an area within the National Wildlife Refuge System or the National Park System, as a species proposed to be listed under section 1533 of this title; and

(ii) critical habitat shall not be designated under this chapter for any experimental population determined under subparagraph (B) to be not essential to the continued existence of a species.

(3) The Secretary, with respect to populations of endangered species or threatened species that the Secretary authorized, before October 13, 1982, for release in geographical areas separate from the other populations of such species, shall determine by regulation which of such populations are an experimental population for the purposes of this subsection and whether or not each is essential to the continued existence of an endangered species or a threatened species.

Section 1540. Penalties and enforcement [ESA Section11]

(a) Civil penalties

(1) Any person who knowingly violates, and any person engaged in business as an importer or exporter of fish, wildlife, or plants who violates, any provision of this chapter, or any provision of any permit or certificate issued hereunder, or of any regulation issued in order to implement subsection (a)(1)(A), (B), (C), (D), (E), or (F), (a)(2)(A), (B), (C), or (D), (c), (d) (other than regulation relating to recordkeeping or filing of reports), (f) or (g) of section 1538 of this title, may be assessed a civil penalty by the Secretary of not more than $25,000 for each violation. Any person who knowingly violates, and any person engaged in business as an importer or exporter of fish, wildlife, or plants who violates, any provision of any other regulation issued under this chapter may be assessed a civil penalty by the Secretary of not more than $12,000 for each such violation. Any person who otherwise violates any provision of this chapter, or any regulation, permit, or certificate issued hereunder, may be assessed a civil penalty by the Secretary of not more than $500 for each such violation. No penalty may be assessed under this subsection unless such person is given notice and opportunity for a hearing with respect to such violation. Each violation shall be a separate offense. Any such civil penalty may be remitted or mitigated by the Secretary. Upon any failure to pay a penalty assessed under this subsection, the Secretary may request the Attorney General to institute a civil action in a district court of the United States for any district in which such person is found, resides, or transacts business to collect the penalty and such court shall have jurisdiction to hear and decide any such action. The court shall hear such action on the record made before the Secretary and shall sustain his action if it is supported by substantial evidence on the record considered as a whole.

(2) Hearings held during proceedings for the assessment of civil penalties authorized by paragraph (1) of this subsection shall be conducted in accordance with section 554 of Title 5. The Secretary may issue subpoenas for the attendance and testimony of witnesses and the production of relevant papers, books, and documents, and administer oaths. Witnesses summoned shall be paid the same fees and mileage that are paid to witnesses in the courts of the United States. In case of contumacy or refusal to obey a subpena served upon any person pursuant to this paragraph, the district court of the United States for any district in which such person is found or resides or transacts business, upon application by the United States and after notice to such person, shall have jurisdiction to issue an order requiring such person to appear and give testimony before the Secretary or to appear and produce documents before the Secretary, or both, and any failure to obey such order of the court may be punished by such court as a contempt thereof.

(3) Notwithstanding any other provision of this chapter, no civil penalty shall be imposed if it can be shown by a preponderance of the evidence that the defendant committed an act based on a good faith belief that he was acting to protect himself or herself, a member of his or her family, or any other individual from bodily harm, from any endangered or threatened species.

(b) Criminal violations

(1) Any person who knowingly violates any provision of this chapter, of any permit or certificate issued hereunder, or of any regulation issued in order to implement subsection (a)(1)(A), (B), (C), (D), (E), or (F); (a)(2)(A), (B), (C), or (D), (c), (d) (other than a regulation relating to recordkeeping, or filing of reports), (f), or (g) of section 1538 of this title shall, upon conviction, be fined not more than $50,000 or imprisoned for not more than one year, or both. Any person who knowingly violates any provision of any other regulation issued under this chapter shall, upon conviction, be fined not more than $25,000 or imprisoned for not more than six months, or both.

(2) The head of any Federal agency which has issued a lease, license, permit, or other agreement authorizing a person to import or export fish, wildlife, or plants, or to operate a quarantine station for imported wildlife, or authorizing the use of Federal lands, including grazing of domestic livestock, to any person who is convicted of a criminal violation of this chapter or any regulation, permit, or certificate issued hereunder may immediately modify, suspend, or revoke each lease, license, permit, or other agreement. The Secretary shall also suspend for a period of up to one year, or cancel, any Federal hunting or fishing permits or stamps issued to any person who is convicted of a criminal violation of any provision of this chapter or any regulation, permit, or certificate issued hereunder. The United States shall not be liable for the payments of any compensation, reimbursement, or damages in connection with the modification, suspension, or revocation of any leases, licenses, permits, stamps, or other agreements pursuant to this section.

(3) Notwithstanding any other provision of this chapter, it shall be a defense to prosecution under this subsection if the defendant committed the offense based on a good faith belief that he was acting to protect himself or herself, a member of his or her family, or any other individual, from bodily harm from any endangered or threatened species.

(c) District court jurisdiction

The several district courts of the United States, including the courts enumerated in section 460 of Title 28, shall have jurisdiction over any actions arising under this chapter. For the purpose of this chapter, American Samoa shall be included within the judicial district of the District Court of the United States for the District of Hawaii.

(d) Rewards and certain incidental expenses

The Secretary or the Secretary of the Treasury shall pay, from sums received as penalties, fines, or forfeitures of property for any violation of this chapter or any regulation issued hereunder (1) a reward to any person who furnishes information which leads to an arrest, a criminal conviction, civil penalty assessment, or forfeiture of property for any violation of this chapter or any regulation issued hereunder, and (2) the reasonable and necessary costs incurred by any person in providing temporary care for any fish, wildlife, or plant pending the disposition of any civil or criminal proceeding alleging a violation of this chapter with respect to that fish, wildlife, or plant. The amount of the reward, if any, is to be designated by the Secretary or the Secretary of the Treasury, as appropriate. Any officer or employee of the United States or any State or local government who furnishes information or renders service in the performance of his official duties is ineligible for payment under this subsection. Whenever the balance of sums received under this section and section 3375(d) of this title, as penalties or fines, or from forfeitures of property, exceed $500,000, the Secretary of the Treasury shall deposit an amount equal to such excess balance in the cooperative endangered species conservation fund established under section 1535(i) of this title.

(e) Enforcement

(1) The provisions of this chapter and any regulations or permits issued pursuant thereto shall be enforced by the Secretary, the Secretary of the Treasury, or the Secretary of the Department in which the Coast Guard is operating, or all such Secretaries. Each such Secretary may utilize by agreement, with or without reimbursement, the personnel, services, and facilities of any other Federal agency or any State agency for purposes of enforcing this chapter.

(2) The judges of the district courts of the United States and the United States magistrates may, within their respective jurisdictions, upon proper oath or affirmation showing probable cause, issue such warrants or other process as may be required for enforcement of this chapter and any regulation issued thereunder.

(3) Any person authorized by the Secretary, the Secretary of the Treasury, or the Secretary of the Department in which the Coast Guard is operating, to enforce this chapter may detain for inspection and inspect any package, crate, or other container, including its contents, and all accompanying documents, upon importation or exportation. Such person may make arrests without a warrant for any violation of this chapter if he has reasonable grounds to believe that the person to be arrested is committing the violation in his presence or view, and may execute and serve any arrest warrant, search warrant, or other warrant or civil or criminal process issued by any officer or court of competent jurisdiction for enforcement of this chapter. Such person so authorized may search and seize, with or without a warrant, as authorized by law. Any fish, wildlife, property, or item so seized shall be held by any person authorized by the Secretary, the Secretary of the Treasury, or the Secretary of the Department in which the Coast Guard is operating pending disposition of civil or criminal proceedings, or the institution of an action in rem for forfeiture of such fish, wildlife, property, or item pursuant to paragraph (4) of this subsection; except that the Secretary may, in lieu of holding such fish, wildlife, property, or item, permit the owner or consignee to post a bond or other surety satisfactory to the Secretary, but upon forfeiture of any such property to the United States, or the abandonment or waiver of any claim to any such property, it shall be disposed of (other than by sale to the general public) by the Secretary in such a manner, consistent with the purposes of this chapter, as the Secretary shall by regulation prescribe.

(4)(A) All fish or wildlife or plants taken, possessed, sold, purchased, offered for sale or purchase, transported, delivered, received, carried, shipped, exported, or imported contrary to the provisions of this chapter, any regulation made pursuant thereto, or any permit or certificate issued hereunder shall be subject to forfeiture to the United States.

(B) All guns, traps, nets, and other equipment, vessels, vehicles, aircraft, and other means of transportation used to aid the taking, possessing, selling, purchasing, offering for sale or purchase, transporting, delivering, receiving, carrying, shipping, exporting, or importing of any fish or wildlife or plants in violation of this chapter, any regulation made pursuant thereto, or any permit or certificate issued thereunder shall be subject to forfeiture to the United States upon conviction of a criminal violation pursuant to subsection (b)(1) of this section.

(5) All provisions of law relating to the seizure, forfeiture, and condemnation of a vessel for violation of the customs laws, the disposition of such vessel or the proceeds from the sale thereof, and the remission or

mitigation of such forfeiture, shall apply to the seizures and forfeitures incurred, or alleged to have been incurred, under the provisions of this chapter, insofar as such provisions of law are applicable and not inconsistent with the provisions of this chapter; except that all powers, rights, and duties conferred or imposed by the customs laws upon any officer or employee of the Treasury Department shall, for the purposes of this chapter, be exercised or performed by the Secretary or by such persons as he may designate.

(6) The Attorney General of the United States may seek to enjoin any person who is alleged to be in violation of any provision of this chapter or regulation issued under authority thereof.

(f) Regulations

The Secretary, the Secretary of the Treasury, and the Secretary of the Department in which the Coast Guard is operating, are authorized to promulgate such regulations as may be appropriate to enforce this chapter, and charge reasonable fees for expenses to the Government connected with permits or certificates authorized by this chapter including processing applications and reasonable inspections, and with the transfer, board, handling, or storage of fish or wildlife or plants and evidentiary items seized and forfeited under this chapter. All such fees collected pursuant to this subsection shall be deposited in the Treasury to the credit of the appropriation which is current and chargeable for the cost of furnishing the services. Appropriated funds may be expended pending reimbursement from parties in interest.

(g) Citizen suits

(1) Except as provided in paragraph (2) of this subsection any person may commence a civil suit on his own behalf -

(A) to enjoin any person, including the United States and any other governmental instrumentality or agency (to the extent permitted by the eleventh amendment to the Constitution), who is alleged to be in violation of any provision of this chapter or regulation issued under the authority thereof; or

(B) to compel the Secretary to apply, pursuant to section 1535(g) (2) (B) (ii) of this title, the prohibitions set forth in or authorized pursuant to section 1533(d) or 1538(a) (1) (B) of this title with respect to the taking of any resident endangered species or threatened species within any State; or

(C) against the Secretary where there is alleged a failure of the Secretary to perform any act or duty under section 1533 of this title which is not discretionary with the Secretary.

The district courts shall have jurisdiction, without regard to the amount in controversy or the citizenship of the parties, to enforce any such provision or regulation, or to order the Secretary to perform such act or duty, as the case may be. In any civil suit commenced under subparagraph (B) the district court shall compel the Secretary to apply the prohibition sought if the court finds that the allegation that an emergency exists is supported by substantial evidence.

(2)(A) No action may be commenced under subparagraph (1)(A) of this section -

(i) prior to sixty days after written notice of the violation has been given to the Secretary, and to any alleged violator of any such provision or regulation;

(ii) if the Secretary has commenced action to impose a penalty pursuant to subsection (a) of this section; or

(iii) if the United States has commenced and is diligently prosecuting a criminal action in a court of the United States or a State to redress a violation of any such provision or regulation.

(B) No action may be commenced under subparagraph (1)(B) of this section -

(i) prior to sixty days after written notice has been given to the Secretary setting forth the reasons why an emergency is thought to exist with respect to an endangered species or a threatened species in the State concerned; or

(ii) if the Secretary has commenced and is diligently prosecuting action under section 1535(g)(2)(B)(ii) of this title to determine whether any such emergency exists.

(C) No action may be commenced under subparagraph (1) (C) of this section prior to sixty days after written notice has been given to the Secretary; except that such action may be brought immediately after such notification in the case of an action under this section respecting an emergency posing a significant risk to the well-being of any species of fish or wildlife or plants.

(3)(A) Any suit under this subsection may be brought in the judicial district in which the violation occurs.

(B) In any such suit under this subsection in which the United States is not a party, the Attorney General, at the request of the Secretary, may intervene on behalf of the United States as a matter of right.

(4) The court, in issuing any final order in any suit brought pursuant to paragraph (1) of this subsection, may award costs of litigation (including reasonable attorney and expert witness fees) to any party, whenever the court determines such award is appropriate.

(5) The injunctive relief provided by this subsection shall not restrict any right which any person (or class of persons) may have under any statute or common law to seek enforcement of any standard or limitation or to seek any other relief (including relief against the Secretary or a State agency).

(h) Coordination with other laws

The Secretary of Agriculture and the Secretary shall provide for appropriate coordination of the administration of this chapter with the administration of the animal quarantine laws (21 U.S.C. 101-105, 111-135b, and 612-614) and section 306 of the Tariff Act of 1930 (19 U.S.C. 1306). Nothing in this chapter or any amendment made by this Act shall be construed as superseding or limiting in any manner the functions of the Secretary of Agriculture under any other law relating to prohibited or restricted importations or possession of animals and other articles and no proceeding or determination under this chapter shall preclude any proceeding or be considered determinative of any issue of fact or law in any proceeding under any Act administered by the Secretary of Agriculture. Nothing in this chapter shall be construed as superseding or limiting in any manner the functions and responsibilities of the Secretary of the Treasury under the Tariff Act of 1930 [19 U.S.C.A. Section 1202 et seq.], including, without limitation, section 527 of that Act (19 U.S.C. 1527), relating to the importation of wildlife taken, killed, possessed, or exported to the United States in violation of the laws or regulations of a foreign country.

allow effective conservation and management of the species consistent with the requirements of the Act and this part.

(c) When revocation of a management authority pursuant to paragraph (a) of this section becomes final, or when a state returns management pursuant to paragraph (b) of this section, the Service shall resume such management authority and provide for the conservation of the species within the state in accordance with the provisions of the Act.

§403.08 List of States to which management has been transferred.

The following states have received management authority pursuant to this part for the species listed and, where appropriate, cooperative allocation agreements pursuant to §403.05(c) are in force: [Reserved].

PART 424—LISTING ENDANGERED AND THREATENED SPECIES AND DESIGNATING CRITICAL HABITAT

AUTHORITY: Pub. L. 93–205, 87 Stat. 884; Pub. L. 95–632, 92 Stat. 3751; Pub. L. 96–159, 93 Stat. 1225; Pub. L. 97–304, 96 Stat. 1411 (16 U.S.C. 1531 *et seq.*).

SOURCE: 49 FR 38908, Oct. 1, 1984, unless otherwise noted.

Subpart A—General Provisions

§424.01 Scope and purpose.

(a) Part 424 provides rules for revising the Lists of Endangered and Threatened Wildlife and Plants and, where appropriate, designating or revising their critical habitats. Criteria are provided for determining species to be endangered or threatened and for designating critical habitats. Procedures for receiving and considering petitions to revise the lists and for conducting periodic reviews of listed species also are established.

(b) The purpose of these rules is to interpret and implement those portions of the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 *et seq.*), that pertain to the listing of species and the determination of critical habitats.

§424.02 Definitions.

(a) The definitions of terms in 50 CFR 402.02 shall apply to this part 424, except as otherwise stated.

(b) *Candidate* means any species being considered by the Secretary for listing as an endangered or a threatened species, but not yet the subject of a proposed rule.

(c) *Conservation, conserve,* and *conserving* mean to use and the use of all methods and procedures that are necessary to bring any endangered or threatened species to the point at which the measures provided pursuant to the Act are no longer necessary. Such methods and procedures include, but are not limited to, all activities associated with scientific resources management such as research, census, law enforcement, habitat acquisition and maintenance, propagation, live trapping, and transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, may include regulated taking.

(d) *Critical habitat* means (1) the specific areas within the geographical area currently occupied by a species, at the time it is listed in accordance with the Act, on which are found those physical or biological features (i) essential to the conservation of the species and (ii) that may require special management considerations or protection, and

(2) specific areas outside the geographical area occupied by a species at the time it is listed upon a determination by the Secretary that such areas are essential for the conservation of the species.

(e) *Endangered species* means a species that is in danger of extinction throughout all or a significant portion of its range.

(f) *List* or *lists* means the Lists of Endangered and Threatened Wildlife and Plants found at 50 CFR 17.11(h) or 17.12(h).

(g) *Plant* means any member of the plant kingdom, including, without limitation, seeds, roots, and other parts thereof.

(h) *Public hearing* means an informal hearing to provide the public with the opportunity to give comments and to permit an exchange of information and opinion on a proposed rule.

(i) *Secretary* means the Secretary of the Interior or the Secretary of Commerce, as appropriate, or their authorized representatives.

(j) *Special management considerations or protection* means any methods or procedures useful in protecting physical and biological features of the environment for the conservation of listed species.

(k) *Species* includes any species or subspecies of fish, wildlife, or plant, and any distinct population segment of any vertebrate species that interbreeds when mature. Excluded is any species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of the Act would present an overwhelming and overriding risk to man.

(l) *State agency* means any State agency, department, board, commission, or other governmental entity that is responsible for the management and conservation of fish, plant, or wildlife resources within a State.

(m) *Threatened species* means any species that is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

(n) *Wildlife* or *fish and wildlife* means any member of the animal kingdom, including without limitation, any vertebrate, mollusk, crustacean, arthropod, or other invertebrate, and includes any part, product, egg, or offspring thereof, or the dead body or parts thereof.

Subpart B—Revision of the Lists

§ 424.10 General.

The Secretary may add a species to the lists or designate critical habitat, delete a species or critical habitat, change the listed status of a species, revise the boundary of an area designated as critical habitat, or adopt or modify special rules (see 50 CFR 17.40–17.48 and parts 222 and 227) applied to a threatened species only in accordance with the procedures of this part.

§ 424.11 Factors for listing, delisting, or reclassifying species.

(a) Any species or taxonomic group of species (e.g., genus, subgenus) as defined in § 424.02(k) is eligible for listing under the Act. A taxon of higher rank than species may be listed only if all included species are individually found to be endangered or threatened. In determining whether a particular taxon or population is a species for the purposes of the Act, the Secretary shall rely on standard taxonomic distinctions and the biological expertise of the Department and the scientific community concerning the relevant taxonomic group.

(b) The Secretary shall make any determination required by paragraphs (c) and (d) of this section *solely* on the basis of the best available scientific and commercial information regarding a species' status, without reference to possible economic or other impacts of such determination.

(c) A species shall be listed or reclassified if the Secretary determines, on the basis of the best scientific and commercial data available after conducting a review of the species' status, that the species is endangered or threatened because of any one or a combination of the following factors:

(1) The present or threatened destruction, modification, or curtailment of its habitat or range;

(2) Over utilization for commercial, recreational, scientific, or educational purposes;

(3) Disease or predation;

LETTER

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Reversal of ocean acidification enhances net coral reef calcification

Rebecca Albright[1], Lilian Caldeira[1], Jessica Hosfelt[2], Lester Kwiatkowski[1], Jana K. Maclaren[1,3], Benjamin M. Mason[4], Yana Nebuchina[1], Aaron Ninokawa[2], Julia Pongratz[1,5], Katharine L. Ricke[1,6], Tanya Rivlin[7,8], Kenneth Schneider[1,9], Marine Sesboüé[1], Kathryn Shamberger[10,11], Jacob Silverman[12], Kennedy Wolfe[13], Kai Zhu[1,14,15] & Ken Caldeira[1]

Approximately one-quarter of the anthropogenic carbon dioxide released into the atmosphere each year is absorbed by the global oceans, causing measurable declines in surface ocean pH, carbonate ion concentration ($[\mathrm{CO_3}^{2-}]$), and saturation state of carbonate minerals (Ω)[1]. This process, referred to as ocean acidification, represents a major threat to marine ecosystems, in particular marine calcifiers such as oysters, crabs, and corals. Laboratory and field studies[2,3] have shown that calcification rates of many organisms decrease with declining pH, $[\mathrm{CO_3}^{2-}]$, and Ω. Coral reefs are widely regarded as one of the most vulnerable marine ecosystems to ocean acidification, in part because the very architecture of the ecosystem is reliant on carbonate-secreting organisms[4]. Acidification-induced reductions in calcification are projected to shift coral reefs from a state of net accretion to one of net dissolution this century[5]. While retrospective studies show large-scale declines in coral, and community, calcification over recent decades[6–12], determining the contribution of ocean acidification to these changes is difficult, if not impossible, owing to the confounding effects of other environmental factors such as temperature. Here we quantify the net calcification response of a coral reef flat to alkalinity enrichment, and show that, when ocean chemistry is restored closer to pre-industrial conditions, net community calcification increases. In providing results from the first seawater chemistry manipulation experiment of a natural coral reef community, we provide evidence that net community calcification is depressed compared with values expected for pre-industrial conditions, indicating that ocean acidification may already be impairing coral reef growth.

The aragonite saturation state (Ω_{arag}) of tropical surface waters has decreased from about 4.5 in pre-industrial time[13] to approximately 3.8 by 1995 (ref. 14). In this study, sodium hydroxide (NaOH) was used to increase the total alkalinity of seawater flowing over a reef flat, with the aim of increasing $[\mathrm{CO_3}^{2-}]$ and Ω_{arag} closer to values that would have been attained under pre-industrial levels of atmospheric $\mathrm{CO_2}$ partial pressure ($p_{\mathrm{CO_2}}$). We used a dual tracer regression method to estimate changes in alkalinity uptake (that is, net community calcification) in response to alkalinity addition. This approach uses the change in ratios between an active tracer (alkalinity) and a passive tracer (a non-reactive dye, Rhodamine WT) to assess the fraction of added alkalinity taken up by the reef. Changes in the active tracer (alkalinity) result from mixing, dilution, and biological activity (that is, calcification), whereas changes in the passive tracer (hereafter referred to as the 'dye') are due solely to mixing and dilution. By comparing the alkalinity to dye ratios before (upstream of the study site) and after (downstream) the water mass interacts with the reef, we were able to isolate the change in alkalinity that is due to an induced increase in net calcification (Extended Data Fig. 1).

Our study was conducted on One Tree Reef (23° 30′ S, 152° 06′ E), a pseudo-atoll in the southern Great Barrier Reef (Fig. 1a). One Tree Reef encloses three lagoons, two of which are hydrologically distinct (that is, separated by reef walls). At low tide, the water level drops below the outer reef crest, and the lagoons are effectively isolated from the ocean (Fig. 1c). Because First Lagoon sits approximately 30 cm higher than Third Lagoon, gravity-driven, unidirectional flow results from First Lagoon, over the reef flat separating the two lagoons, and into Third Lagoon. Our study site was situated along a section of the reef wall separating First and Third Lagoons. Unidirectional flow across this area of the reef flat persists for approximately 60 min following peak low tide, enabling an experimental setup depicted in Fig. 1d. This section of the reef flat is a well-developed, mixed reef community characterized by ~17% live coral (Extended Data Fig. 2).

Our study was conducted once per day, over 22 days between the dates of 16 September 2014 and 10 October 2014. Dates, times, light data, and predicted heights of low tides are provided in Extended Data Table 1. Before low tide each day, a 15 $\mathrm{m^3}$ tank was deployed in First Lagoon, adjacent to the study site. On all 22 days, 4 g Rhodamine WT were mixed with ambient seawater inside the tank. On 15 of those days (hereafter referred to as 'experiment' days), 15 mol (600 g) of NaOH was also introduced into the tank. The resulting solution was pumped onto the reef flat at a constant rate of $\sim 2\,\mathrm{l\,s^{-1}}$ for 60 min starting at the predicted time of low tide. The resulting plume flowed over the reef flat as described in the Methods. Following the 60 min pumping period, discrete water samples were taken at pre-defined sampling locations along the length of two parallel transects that defined the borders of the study area (along the upstream and downstream edges of the reef flat; Fig. 1d and Extended Data Fig. 3). Samples were analysed for total alkalinity, rhodamine, pH, dissolved inorganic carbon, and nutrients, as described in the Methods (Supplementary Table 1). On 7 days, observations were made when dye, but no alkalinity, was added (hereafter referred to as 'control days'), to test whether the dye addition had unexpected effects, and to characterize background variability in the study area. Mean chemical conditions for control and experimental days are provided in Fig. 2 and Extended Data Fig. 4. On experiment days, the mean concentration of added alkalinity in the central part of the plume (containing 50% of the dye), was $50.2 \pm 2.7\,\mu\mathrm{mol\,kg^{-1}}$, resulting in an average elevation of Ω_{arag} in this part of the plume by 0.6 units. Mean temperatures, salinities, nutrient concentrations,

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[1]Department of Global Ecology, Carnegie Institution for Science, Stanford, California 94305, USA. [2]Bodega Marine Laboratory, University of California, Davis, Bodega Bay, California 94923, USA. [3]Stanford Nano Shared Facilities, Stanford University, Stanford, California 94305, USA. [4]Department of Genetics, Stanford University School of Medicine, Stanford, California 94305, USA. [5]Max Planck Institute for Meteorology, Bundesstraße 53, 20146 Hamburg, Germany. [6]Sibley School of Mechanical and Aerospace Engineering, Cornell University, Ithaca, New York 14853, USA. [7]The Interuniversity Institute for Marine Sciences, The H. Steinitz Marine Biology Laboratory, The Hebrew University of Jerusalem, Eilat, Israel. [8]The Fredy and Nadine Herrman Institute of Earth Sciences, The Hebrew University of Jerusalem, Edmond J. Safra Campus, Jerusalem, Israel. [9]Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot, Israel. [10]Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA. [11]Texas A&M University, College Station, Texas 77843, USA. [12]Institute for Oceanographic and Limnological Research, Haifa, Israel. [13]School of Medical Sciences, The University of Sydney, Sydney, New South Wales 2006, Australia. [14]Department of Biology, Stanford University, Stanford, California 94305, USA. [15]Department of BioSciences, Rice University, Houston, Texas 77005, USA.

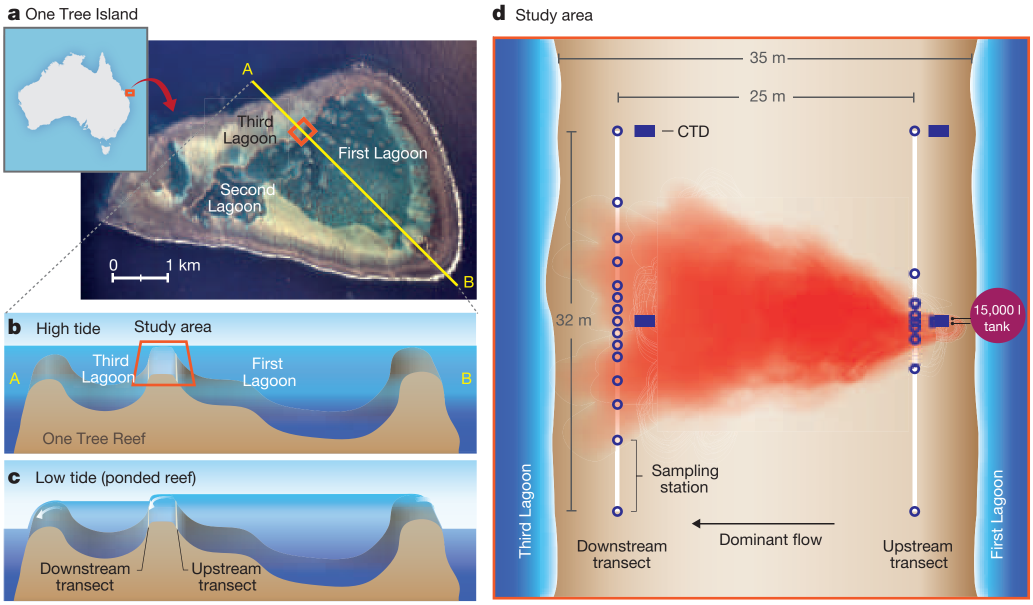

Figure 1 | Study site and experimental design. **a**, Map of Australia and aerial photograph of One Tree Reef with the study area denoted by an orange square. The map, sourced under Creative Commons CC0, is freely available for commercial use. Use of the photograph was permitted under an Educational license from the University of Sydney. **b**, **c**, Cross-sections of the reef along the yellow line are shown for high (**b**) and low (**c**) tides, demonstrating the unidirectional flow from the upper lagoon (First Lagoon), over the reef flat study area, and into the lower lagoon (Third Lagoon) during low tide. **d**, Schematic of the study area (to scale) indicating the positioning of the transects and sampling locations (blue circles).

and dissolved oxygen concentrations are provided in Extended Data Table 2.

Plots of the alkalinity and dye concentrations along the upstream and downstream transects illustrate the spatial distribution of the plume within the study area (Fig. 3a–d). On control days, when dye but no alkalinity was added, these parameters were not correlated, and the mean alkalinity–dye slopes did not differ from zero (Fig. 3e). On these days, the difference in alkalinity between the upstream and downstream transects was due to background reef calcification and is represented by the difference in y intercepts. On experiment days, when alkalinity and dye were jointly introduced to the study site, these parameters were well correlated, resulting in positive, significantly non-zero alkalinity–dye slopes both for the upstream and for the downstream transects (Fig. 3f). On these days, background reef calcification is represented by the difference in y intercepts (same as control days), and the fraction of added alkalinity taken up by the reef flat, f_{uptake}, was calculated as the difference between the upstream and downstream alkalinity–dye slopes:

$$f_{\mathrm{uptake}} = 1 - (r_{\mathrm{down}}/r_{\mathrm{up}}) \tag{1}$$

where r_{up} and r_{down} are the ratios (slopes) of alkalinity to dye for the upstream and downstream transects, respectively, in $\mu\mathrm{mol\,kg^{-1}\,ppb^{-1}}$ or $\mathrm{mmol\,g^{-1}}$. At a fixed rate of alkalinity and dye addition, r_{up} indicates the amount of added alkalinity entering our study site, while r_{down} indicates the amount of added alkalinity leaving our study site. The difference in these two values indicates the amount of added alkalinity taken up by the reef community and was used to calculate the percentage increase in net calcification according to equations (2)–(4).

Data from all days were analysed using a multivariate regression approach to calculate alkalinity–dye ratios (slopes) and mean background alkalinities (y intercepts) of the upstream and downstream transects, while simultaneously accounting for natural spatial and temporal variability (see Supplementary Information and Extended Data Figs 5–7). Mean alkalinity–dye slopes are presented in Fig. 4a. Results of a mixed-effects model indicate that upstream and downstream slopes are significantly different on experiment days but not control days, rejecting the null hypothesis that net community calcification did not respond to alkalinization (see Supplementary Information).

The fractional uptake of added alkalinity was calculated according to equation (1) and averaged for all control and experimental days. Using this method, we estimate that an average of 17.3% ± 2.3% (1 s.e.m.) of the experimentally added alkalinity was taken up by the reef community.

The percentage increase in net calcification, ΔG, resulting from alkalinity addition was calculated as:

$$\Delta G = G_{\mathrm{increase}}/G_{\mathrm{background}} \tag{2}$$

where G_{increase} is the additional calcification resulting from alkalinity addition in $\mathrm{mmol\,s^{-1}}$, and $G_{\mathrm{background}}$ is the background calcification in $\mathrm{mmol\,s^{-1}}$ (that is, the calcification rate without added alkalinity). G_{increase} and $G_{\mathrm{background}}$ were calculated as

$$G_{\mathrm{increase}} = P_{\mathrm{dye}}(r_{\mathrm{up}} - r_{\mathrm{down}}) \tag{3}$$

$$G_{\mathrm{background}} = F(Alk_{\mathrm{up}} - Alk_{\mathrm{down}}) \tag{4}$$

where P_{dye} is the pumping rate of the dye in $\mathrm{g\,s^{-1}}$, F is the volumetric flow rate in $\mathrm{m^3\,s^{-1}}$, and Alk_{up} and Alk_{down} are the mean background alkalinities (that is, the y intercepts) of the upstream and downstream transects, respectively, in $\mathrm{mmol\,m^{-3}}$ (see Supplementary Information). Using these equations, we estimate net community calcification increased by an average of 6.9% ± 0.9% (Fig. 4b). A one-tailed, unpaired t-test indicates that the change in calcification on experiment days was significantly greater than control days ($t_{20} = 1.981$, $P < 0.05$). On the basis of laboratory and mesocosm studies[15], the mean response of coral calcification to a unit change in Ω_{arag} is approximately 15%. Throughout the entire study area (inside and outside the plume), Ω_{arag} was elevated by an average of 0.4 units, indicating a theoretical increase in coral calcification of 6%, which agrees closely with the observed increase of 6.9%. Caution must be applied, however, when comparing calcification relationships derived from coral studies[15] to mixed-reef communities such as that of our study site.

The hypothesis that Ω_{arag} exerts strong control over coral reef calcification is supported by laboratory experiments and models[16,17] (but see ref. 18); however, isolating this control in a natural setting is complicated by the multiple drivers of calcification, which are often highly

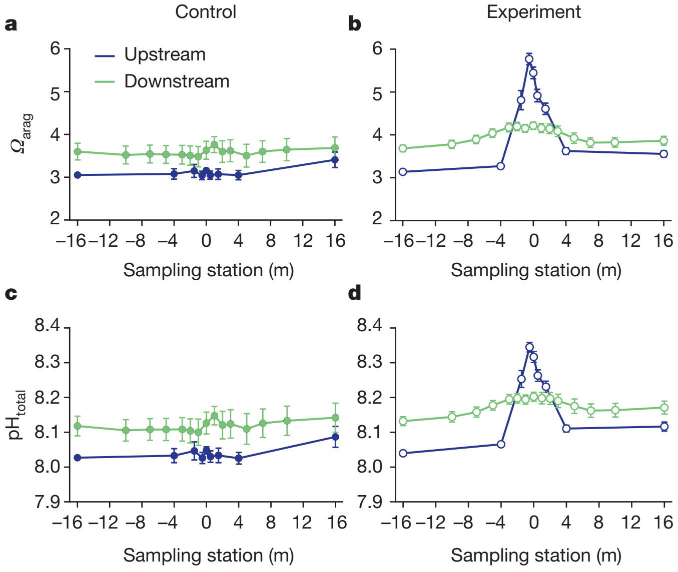

Figure 2 | Chemical conditions for control ($N = 7$) and experiment ($N = 15$) days (mean ± 1 s.e.m.). a, **b**, Aragonite saturation states (Ω_{arag}); **c**, **d**, pH. Error bars are indicative of day-to-day and hour-to-hour variability (not measurement error); estimated measurement errors are smaller than line thickness and are provided in the Methods. Experimental day standard errors are smaller than control day standard errors primarily because of the larger N.

correlated (for example, production, Ω_{arag}, light, temperature)[6,12,19–24]. Previous attempts to manipulate seawater chemistry in the natural environment were unable to demonstrate a causal relationship between seawater chemistry and reef calcification[25]. Further, retrospective studies documenting declines in coral reef calcification over the past several decades were unable to isolate the influences of various causal factors (for example, ocean warming, acidification, water quality, fishing pressure) owing to the confounding influence of co-varying parameters and a lack of reliable long-term carbonate chemistry observations[7,26]. Our experimental approach demonstrates the influence of alkalinity (and Ω_{arag}) on net community calcification in a natural setting by uncoupling Ω_{arag} from otherwise co-varying confounding environmental factors (where 'uncouple' is used in the technical sense of 'lack of correlation'). We demonstrate that restoring $[\mathrm{CO_3}^{2-}]$ and Ω_{arag} closer to pre-industrial values enhances net community calcification, providing evidence that ocean acidification may have contributed to the documented declines in coral reef calcification[6–12] in the industrial era.

Notably, ocean acidification is one of many stressors acting on coral reef calcification. Simultaneously to decreasing Ω_{arag}, sea surface temperatures have warmed by an estimated 0.4–0.8 °C (varying by region) since the early 1800s (ref. 27) which is posited to have increased calcification rates until a recent 'tipping point'[28]. Identifying the relative contributions of various environmental factors, and how they interact, to the documented declines in coral reef calcification is complex yet essential to understanding how calcification will probably change in the coming decades. Further work, using methods developed here, could examine how coral reef response is affected by a variety of stressors (in isolation and combination) and duration of exposure, and help to assess geographic variability in sensitivity to ongoing ocean acidification.

The Ω_{arag} of the tropical oceans is expected to continue declining from 3.8 to approximately 3.0 by the middle of the century and 2.3 by the end of the century[14]. Deliberate alkalinization has been proposed as a geoengineering technique to offset ocean acidification impacts on coral reefs and other shallow marine ecosystems[29]. Our results indicate that this approach could, in principle, help protect coral reefs from ocean acidification; however, the technical challenges associated with implementation would probably make it infeasible at anything but highly localized scales (for example, protected bays, lagoons). Large-scale and long-term protection of marine ecosystems from the threat of ocean acidification depends on deep and rapid reductions in anthropogenic emissions of carbon dioxide[30].

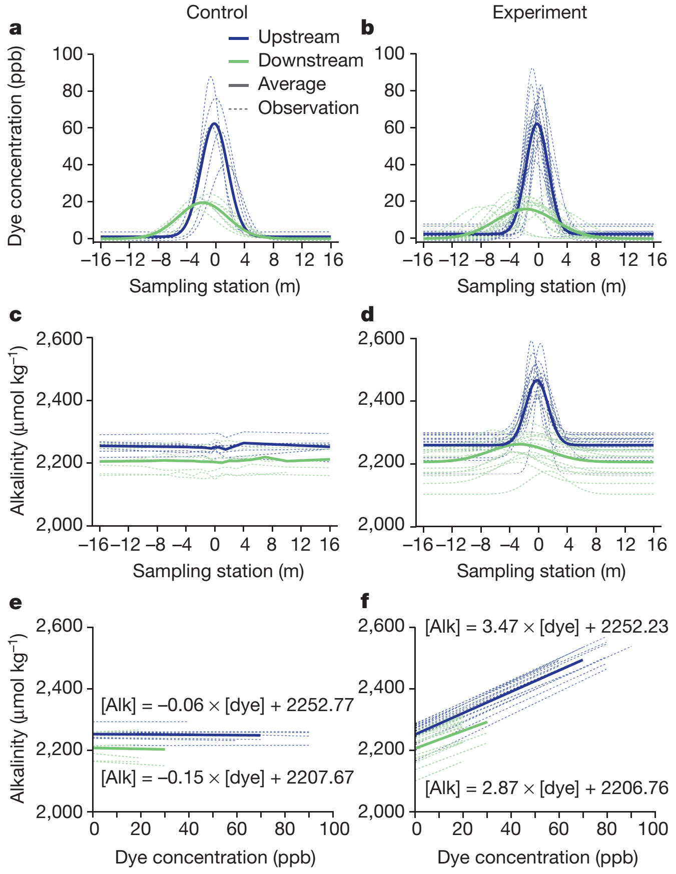

Figure 3 | Relationships between alkalinity and dye for control ($N = 7$) and experiment ($N = 15$) days. a, **b**, Dye concentrations; **c**, **d**, alkalinities; **e**, **f**, alkalinity–dye slopes. **e**, On control days, when dye, but no NaOH, was added to the study site, these parameters are not correlated, and the resulting alkalinity–dye slopes are not significantly different from zero. **f**, On experimental days, dye and NaOH were jointly added to the study site, and the correlation between these parameters results in a positive, significantly non-zero slope. Mean alkalinity–dye slopes for control and experiment days are shown in Fig. 4a.

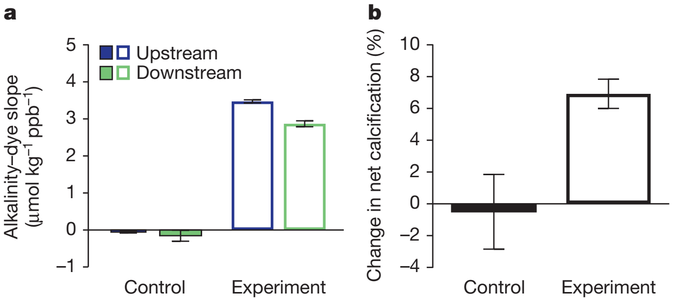

Figure 4 | Alkalinity–dye slopes and percentage change in net calcification for control ($N = 7$) and experiment ($N = 15$) days (mean ± 1 s.e.m.). a, **b**, The difference between upstream and downstream slopes (**a**) was used to calculate the uptake of added alkalinity (equation (1)) and the percentage change in net calcification (**b**) (equations (2)–(4)). The reef community took up an average of 17.3% ± 2.3% of the added alkalinity, implying a 6.9 ± 0.9% increase in net calcification. The percentage change in calcification on experiment days was significantly greater than control days (one-tailed, unpaired t-test, $t_{20} = 1.981$, $P < 0.05$). Results by day are presented in Extended Data Fig. 7.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions R.A., J.K.M., K.Sc., J.S., and K.C. conceived and designed the project. J.K.M., K.Sc., J.S., J.P., K.L.R., and K.Sh. conducted pilot studies and collected preliminary data. R.A., L.K., L.C., B.M.M., Y.N., T.R., M.S., K.W., A.N., J.H., and K.C. performed the experiments. R.A. and K.C. performed the computational analyses. K.Z. assisted with statistical analyses. R.A. wrote the manuscript with input from K.C. All co-authors reviewed and approved the final manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to R.A. (ralbright@carnegiescience.edu).

METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized. The investigators were not blinded to allocation during experiments and outcome assessment.

Concept. The dual tracer regression method developed here is an extension of ref. 31 and may have applications in other areas of research, such as nutrient or pollution assessments, uptake of industrial or agricultural waste, etc. The primary experimental criteria are that the active and passive tracers are added in a fixed ratio and at a fixed rate. The methods described here apply to situations where there is a dominant flow direction, dispersion or dilution, and a need to measure the effect of a reagent on community flux.

Experimental setup. Before low tide each day, a 15 m^3 floating 'header' tank was partly submerged in First Lagoon, adjacent to the reef flat study site. The tank was gravity-fed with ambient seawater from the lagoon, and when necessary, a submersible pump was used to completely fill the tank. Two marine grade bilge pumps (3,000 gallons per hour, Five Oceans) were secured inside the tank for mixing during chemical addition and to deliver the solution to the study site. On 22 days, 4 g Rhodamine WT (20 g of a 20% solution, Turner Designs 10–108), dissolved in 0.5 l reverse osmosis (RO) water, was manually added to the tank over the course of ~30 min and mixed. On 15 of those days, 600 g (~15 mol) of NaOH, dissolved in 1.5 l RO water, was also introduced into the tank. The solution inside the tank was subsequently mixed for an additional 30–45 min to ensure homogeneity. When a strong source of alkalinity is added to seawater, brucite forms as a solid precipitate. However, for pH levels below ~9, brucite dissolves. On the basis of visual inspection and associated laboratory experiments, we estimated brucite dissolution to occur on the timescale of ~100 s. Therefore, a mixing time of 30–45 min was sufficient to ensure complete dissolution of brucite; during this time, a handheld pH probe (Oakton) was used to manually check that the pH of the tank solution did not exceed 9.0. The tank was covered to avoid equilibration with the atmosphere, but given that the tank was emptied over a period of 60 min, it is possible that air–sea fluxes were not completely avoided. While acid/base manipulations of seawater carbonate chemistry are not directly equivalent to the addition/removal of dissolved inorganic carbon (C_T), the differences in carbon speciation between acid/base manipulations and CO_2 gas manipulations are minor if seawater is not allowed to equilibrate with the atmosphere (that is, in closed or continuous-flow systems). Further, it is infeasible to remove CO_2 from large volumes of seawater (>10,000 l) under field conditions. Therefore, acid/base manipulations are considered justified techniques to alter seawater carbonate chemistry in circumstances where large volumes of seawater are being manipulated, such as mimicking natural flow on coral reefs, particularly if the system is not allowed to equilibrate with the atmosphere[32].

The seawater solution from the tank (control days: seawater + dye; experiment days: seawater + NaOH + dye) was pumped onto the reef flat for a period of 60 min starting at the predicted time of low tide (Extended Data Table 1) at a constant rate (~21 s^{-1}). The solution was introduced to the study site via the two bilge pumps that were submerged in the tank, connected to two lengths of (1.5-inch inner diameter) vinyl tubing that were secured to a cinder block located ~2 m upstream from the centre of the study site. Throughout the addition, the ratio of alkalinity to dye being added to the study site was assumed to be constant, and flow within the study site was considered to be in steady-state. On 30 September 2014 (a control day), dye was added using a peristaltic pump instead of the above configuration; this was because low tide occurred at 5:32, and assembly of the tank configuration was not possible in low-light conditions.

Following a pumping period of 60 min, discrete water samples were taken at defined sampling locations along the length of two parallel transects that defined the borders of the study area: one along the upstream edge (adjacent to First Lagoon) and the other along the downstream edge (adjacent to Third Lagoon, see Extended Data Fig. 3). The total width of the reef flat in this area is approximately 35 m, and the upstream and downstream transects were separated by ~25 m. The length of each transect was 32 m. Thus, the study area consisted of an approximate 25 m × 32 m rectangle (800 m^2). The upstream transect consisted of 9 sampling stations spanning the width of 32 m, and the downstream transect consisted of 15 sampling stations spanning the width of 32 m. Sample locations were strategically assigned with a higher density near the centre of the study area to accurately characterize the shape of the resulting alkalinity and dye plume/curve. Spacing of the station locations is depicted in Extended Data Fig. 3.

Following the 60 min pumping period, discrete samples were collected at each of the 24 sample locations by pumping reef water into 500 ml borosilicate glass bottles (Corning, 1500-500 Pyrex glass reagent bottle) using battery-operated liquid transfer pumps (Sierra Tools, model JB5684). To minimize chemical variation due to minor changes in sampling depth and/or location, precise sample locations were marked with plastic discs, nailed to the reef substrate. Samples were collected along the upstream and downstream transects simultaneously by five individuals, with each person sampling four or five locations. All samples were typically collected in less than 3 minutes, and it was assumed that the study site was in steady state during this time (that is, all fluxes and flows did not change during the 3-minute sampling interval). Samples were immediately returned to the One Tree Island Research Station, where they were subsampled and analysed for pH, total alkalinity (A_T), dissolved inorganic carbon (C_T), and rhodamine (see 'Chemical Analyses' section). For three upstream stations (−U16, U0, U16) and three downstream stations (−D16, D0, D16), nitrate and ammonia concentrations were also determined. See Extended Data Fig. 3 for station locations.

CTD (conductivity–temperature–depth) devices (YSI models 6600, 6920) were deployed at four sampling locations, two upstream (−U16, U0) and two downstream (−D16, D0) for continuous measurements of seawater temperature, salinity, depth, and dissolved oxygen concentration. These instruments logged continuously at 2-minute intervals over the 22 study days. Discrete water samples (Corning, 1500-250 Pyrex glass reagent bottle) were collected each day at each of the four CTD locations, and the dissolved oxygen concentration was measured using an automated potentiometric Winkler titration technique[33]. These values were used to verify CTD measurements.

Alkalinity–dye slopes, r, and mean background alkalinities, $\hat{a}$, for each day were calculated using paired alkalinity and dye measurements that were collected across all sampling stations, transects, and days (see Supplementary Information). Over a 4-week period, we conducted our experimental protocol 23 times: 8 control days and 15 experimental days. One control day was omitted from subsequent analyses owing to intense rain that heavily influenced alkalinity measurements, resulting in 7 control days and 22 total days. This resulted in a total of 526 paired alkalinity and dye measurements that were used in the fitting procedure described in the Supplementary Information. Two previous expeditions to One Tree Island (September/October 2012 and March 2013) characterized site variability and allowed testing of the methods presented here. Preliminary data generated in these expeditions indicated that demonstrating statistical significance was dependent on maximizing signal (uptake of experimentally added alkalinity) to noise (natural/background uptake of alkalinity).

On experiment days, the difference between the upstream and downstream alkalinity–dye slopes indicates the fraction of experimentally added alkalinity that was taken up by the reef (equation (1) of the main text). We analysed the difference between slopes using a mixed-effects model in R (see Supplementary Information). Comparison of confidence intervals indicates that upstream and downstream slopes are significantly different on experiment days but not on control days. Shapiro–Wilk W-tests were used to verify the underlying assumptions of normality ($P > 0.05$). The purpose of control days was to demonstrate that significant changes in alkalinity–dye slopes do not occur when NaOH is not added, and to characterize natural spatial and temporal variability in the study site. Further, with this study methodology, effectively, within experimental days, the part of the study site that is not affected by the alkalinity-rich plume serves as additional control for the part of the study site that is affected by the plume.

While reef processes other than calcification can alter seawater alkalinity (for example, changes in nutrients, salinity), a previous study showed that changes in salinity and nutrients had a negligible effect on changes in alkalinity in coral reefs[34]. Salinity and nutrient data from our study are provided in Extended Data Table 2.

Code availability. The Mathematica routine used to calculate alkalinity-to-dye ratios (slopes) and dye-free mean alkalinity estimates (y intercepts) for each day is provided in the Supplementary Information.

Chemical analyses. Discrete samples were immediately returned to the laboratory on One Tree Island where they were analysed for pH_{total}, total alkalinity (A_T), and rhodamine, and subsampled for the later determination of total dissolved inorganic carbon (C_T), and nutrients (NH_4^+, NO_2, and NO_3). All measurements and calculations were consistent with 'best practices' recommendations[35]. For 99.6% of station–day combinations (24 stations × 22 days = 528 bottles), we successfully measured pH_{total}, A_T, rhodamine, and C_T, resulting in 526 paired measurements.

Aragonite saturation state (Ω_{arag}), carbonate ion concentration ($[CO_3^{2-}]$), and p_{CO_2} were calculated as a function of A_T, pH_{total}, and *in situ* salinity and temperature using the program CO2SYS[36]; dissociation constants for carbonate and boric acid were determined as in ref. 37 and as refitted in ref. 38, and the dissociation constant for boric acid was determined as in ref. 39.

Parameters that were measured at a subset of sampling stations (that is, temperature, salinity, and dissolved oxygen measured at -U16, U0, -D16, D0; nutrients measured at –U16, U0, U16, -D16, D0, D16) are presented in Extended Data Table 2. Parameters that were measured (or calculated) across all sampling stations are presented in Fig. 2 (Ω_{arag} and pH) and Extended Data Fig. 4 (CO_3^{2-}, p_{CO_2}, and C_T). All chemistry data are included in Supplementary Table 1.

Total alkalinity, A_T. Samples for A_T were pre-filtered using GF/F filters (Whatman) and analysed in triplicate using a Metrohm 855 Robotic Titrosampler (Metrohm

USA) using certified 0.1 N HCl (Fisher Chemical) diluted to a nominal concentration of 0.0125 N. Acid was calibrated by analysing certified reference material (CRM, batch 138) from A. Dickson's laboratory before each titration session (twice daily). A_T by volume (μmol l^{-1}) was converted to A_T by mass (μmol kg^{-1}) by applying a density correction using *in situ* salinities and temperatures. For each set of triplicate analyses, data points that were $>10\,\mu$mol kg^{-1} away from the median were removed from the analysis; these outliers resulted from drop scale variability in sample delivery. The resulting mean and standard error were calculated for each sample location on each day. Instrumental precision from 55 analyses of CRM (batch 138) over the course of the study was $<2\,\mu$mol kg^{-1} (1 s.d.). Alkalinities were normalized to the mean salinity of 35.75; salinity-normalized alkalinities were used for subsequent analyses.

pH. Seawater pH$_{\text{total}}$ was determined using an Ocean Optics spectrophotometer with 10 cm path length optical cells and *m*-cresol purple dye (Sigma Aldrich), following the methods of ref. 41. Water samples were kept in a temperature-controlled water bath (Thermo Scientific, Precision Microprocessor Controlled 280 Series) at 25 °C before analysis to minimize temperature-induced errors in absorbance measurements. The temperature of each sample was recorded immediately after analysis using a digital thermometer accurate to ±0.05 °C (VWR, Traceable Platinum Ultra-Accurate Digital Thermometer). CO2SYS[36] was used to calculate *in situ* pH values using *in situ* salinity and temperature measurements. Average precision from triplicate measurements for this system was less than 0.010 units (1 s.d.). CRM analyses (TRIS buffer, batch 22, A. Dickson) revealed that the system was accurate to within 0.005 pH units.

Rhodamine WT. Rhodamine WT concentration was measured fluorometrically using a Turner 10AU fluorometer and 25 ml cuvettes. A series of eight standards was made by mass-diluting a 400 ppb (Parts per 10^9) Rhodamine WT standard (Turner Designs) to 0, 0.5, 1, 2, 4, 16, 32, and 64 ppb. The standard curve was measured at the beginning, middle, and end of each measuring day to check for drift. Water samples were kept in a temperature-controlled water bath (Thermo Scientific, Precision Microprocessor Controlled 280 Series) at 25 °C before analysis to minimize temperature-induced errors in fluorescence. The temperature of each sample was recorded immediately after analysis using a digital thermometer accurate to ±0.05 °C (VWR, Traceable Platinum Ultra-Accurate Digital Thermometer). Rhodamine concentrations were temperature-corrected using the formula $F_r = F_s\exp(k(T_s - T_r))$, where F_r and F_s are the fluorescence at the reference and sample temperatures, T_r and T_s, and $k = 0.026$/K, equating to a 2.6% correction per kelvin (ref. 40). Temperature corrections were applied before normalizing values to the standard curve. Dye concentrations were then normalized to the mean salinity of 35.75; salinity-normalized concentrations were used for subsequent analyses. Instrumental precision from triplicate measurements for this system was less than 0.1 ppb.

Dissolved inorganic carbon (C_T). C_T samples were subsampled into 30 ml glass serum bottles (Wheaton, 223743), poisoned with 15 μl saturated $HgCl_2$ (0.05% by volume to inhibit biological activity[41]), sealed with rubber stoppers, crimped closed with aluminium caps, and transported to Stanford University for analysis. Samples were analysed approximately 3 months after sampling. C_T was extracted from samples by acidifying them with phosphoric acid (H_3PO_4, 5%) using a custom-built, automated acidification and delivery system (D. Mucciarone) using high-grade nitrogen as a carrier gas connected to an infrared gas analyser (Licor 7000). All samples were analysed in duplicate. The instrument was calibrated daily using CRM (Batches 141, 138), provided by A. Dickson. Immediate duplicate analyses of samples usually yielded instrumental precision of 1–2 μmol kg^{-1}.

Nutrients. Nutrient samples were subsampled into 15 ml conical centrifuge tubes (Falcon). Ammonia samples were immediately frozen, and total ammonium concentrations ($NH_{3\text{-tot}} = NH_3 + NH_4^{1+}$) were later determined using a modified fluorometric method[42]. Nitrate samples were preserved with 0.1 ml 1 N HCl, closed, shaken, and left in the dark at room temperature (~22 °C) until transport to Eilat, Israel. Nitrite (NO_2^{1-}) was measured using a colorimetric method[43], with a Flow Injection Autoanalyzer (Lachat Instruments model QuickChem 8500). Nitrate (NO_3^{1-}) was measured by reducing it to nitrite using a copperized cadmium column. Precision of ammonia, nitrite, and nitrate measurements was ~ 0.05 μmol l^{-1}. Nitrite and nitrate in this study are reported as total oxidized nitrogen ($\text{TON} = NO_2^{1-} + NO_3^{1-}$). Results are provided in Extended Data Table 2.

Salinity. Following the first 5 days of observations, it became evident that conductivity measurements from three of the four CTDs proved unreliable; we believed this to be from the formation of oxygen bubbles on the sensors (resulting from high productivity on the reef flat). Therefore, starting on day six, discrete water samples were taken each day at each of the four CTD locations. Samples were stored in an air-conditioned, shaded room until transport to the Australian Institute of Marine Science for analysis on a Guildline Portasal Salinometer (model 8410A), with a precision of ±0.0001 units. Accuracy was verified using CRM (OSIL, IAPSO Standard Seawater, batch P155). For days without discrete salinity measurements ($N = 5$), salinity values were calculated for the upstream transect by developing a linear relationship between the salinometer values and the reliable CTD. Salinities for the downstream transect were calculated from upstream values by applying an offset of 0.08 parts per thousand: this offset represents the mean increase in salinity between the upstream and downstream transects as a result of evaporation (Extended Data Table 2).

Benthic community structure. Benthic surveys were conducted to characterize the underlying community structure of the study area. Five 25 m transects were laid on the reef flat perpendicular to the reef front, spaced approximately 8 m apart. Photographs were taken of 0.25 m^2 quadrats at 5 m intervals. Photographs were analysed with Coral Point Count software with Excel extensions (CPCe) using 25 random points per quadrat. The benthos was assigned to one of six categories: (1) live coral; (2) macroalgae; (3) turf algae; (4) *Halimeda*; (5) crustose coralline algae (CCA); and (6) sand/rubble. Where morphological forms of $CaCO_3$ (for example, rubble, $CaCO_3$ rock) were covered with biologically active groups (for example, turf, CCA), the biologically active group was scored. Results are provided in Extended Data Fig. 2.

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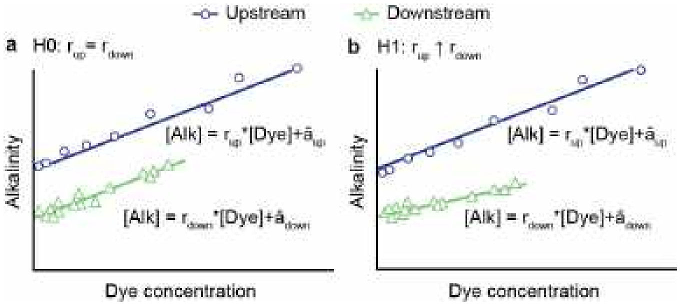
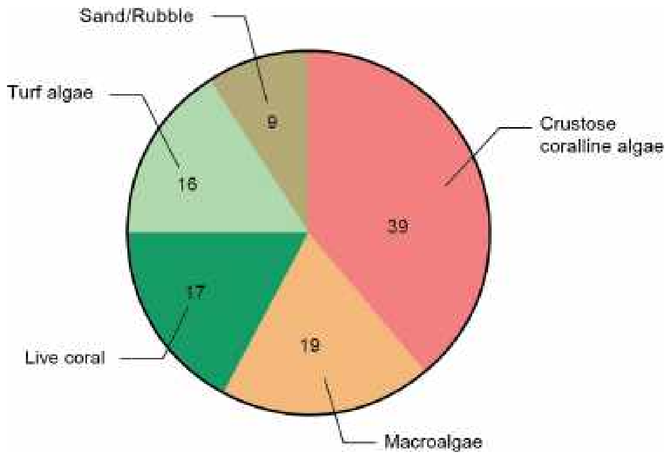
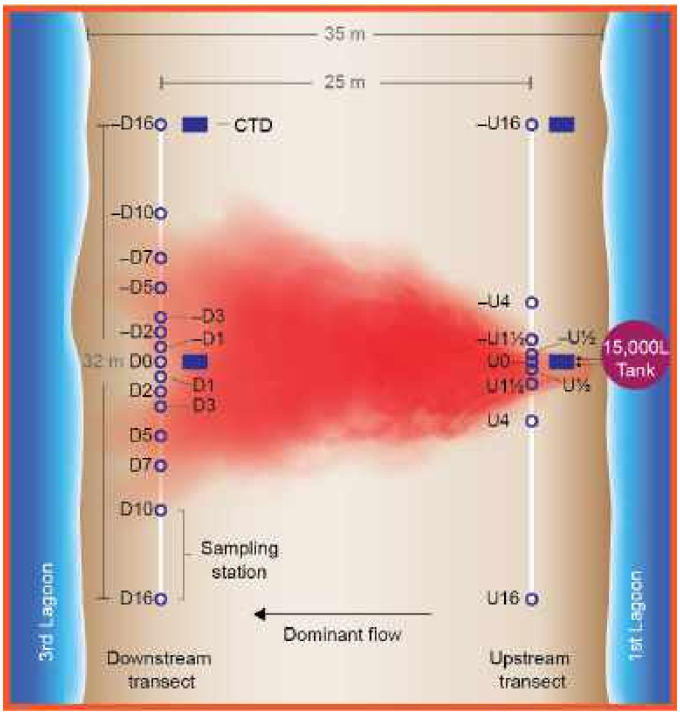


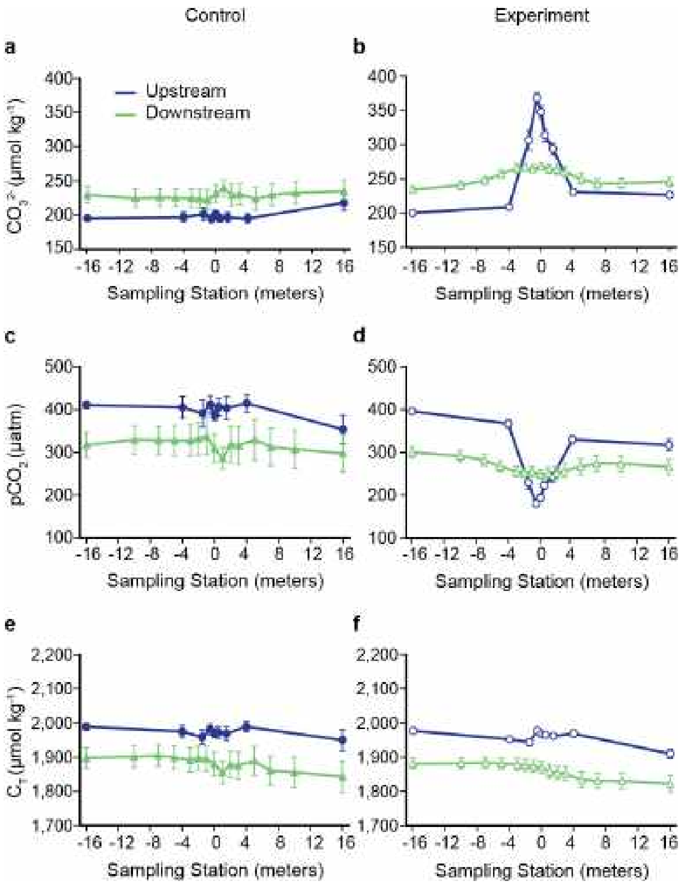
Extended Data Figure 1 | Theoretical representations of the null, H0, and alternative, H1, hypotheses. a, In H0, the reef does not take up added alkalinity; here, the change in alkalinity between the upstream and downstream transects would not be systematically related to the dye concentration, and the ratio of the alkalinity–dye relationship, *r*, would not be expected to change between the upstream and downstream locations (that is, $r_{up} = r_{down}$). **b**, In H1, reef uptake of added alkalinity occurs; here, areas with more alkalinity (and more dye) change at a different rate than areas with less alkalinity (and less dye), resulting in a change in the alkalinity–dye slope (that is, $r_{up} > r_{down}$).



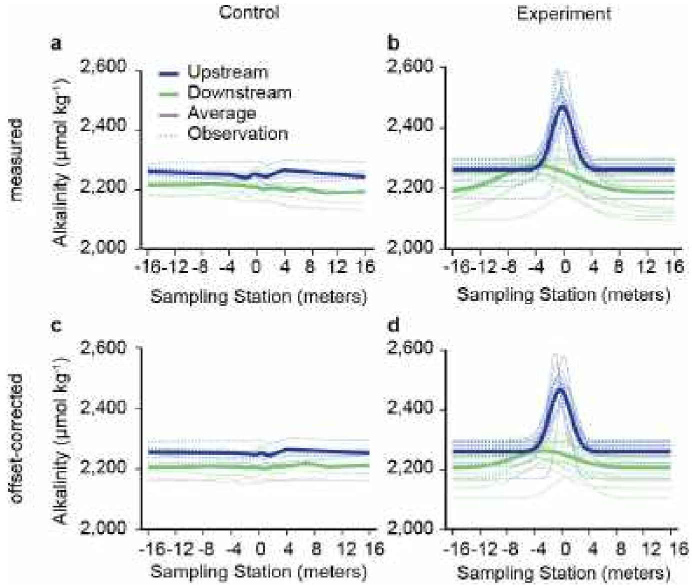
Extended Data Figure 2 | Community composition of the reef flat study area. Percentage cover by benthic type is as follows: crustose coralline algae (39%), live coral (17%), turf algae (16%), macroalgae (19%), sand/rubble (9%), and *Halimeda* (5%).



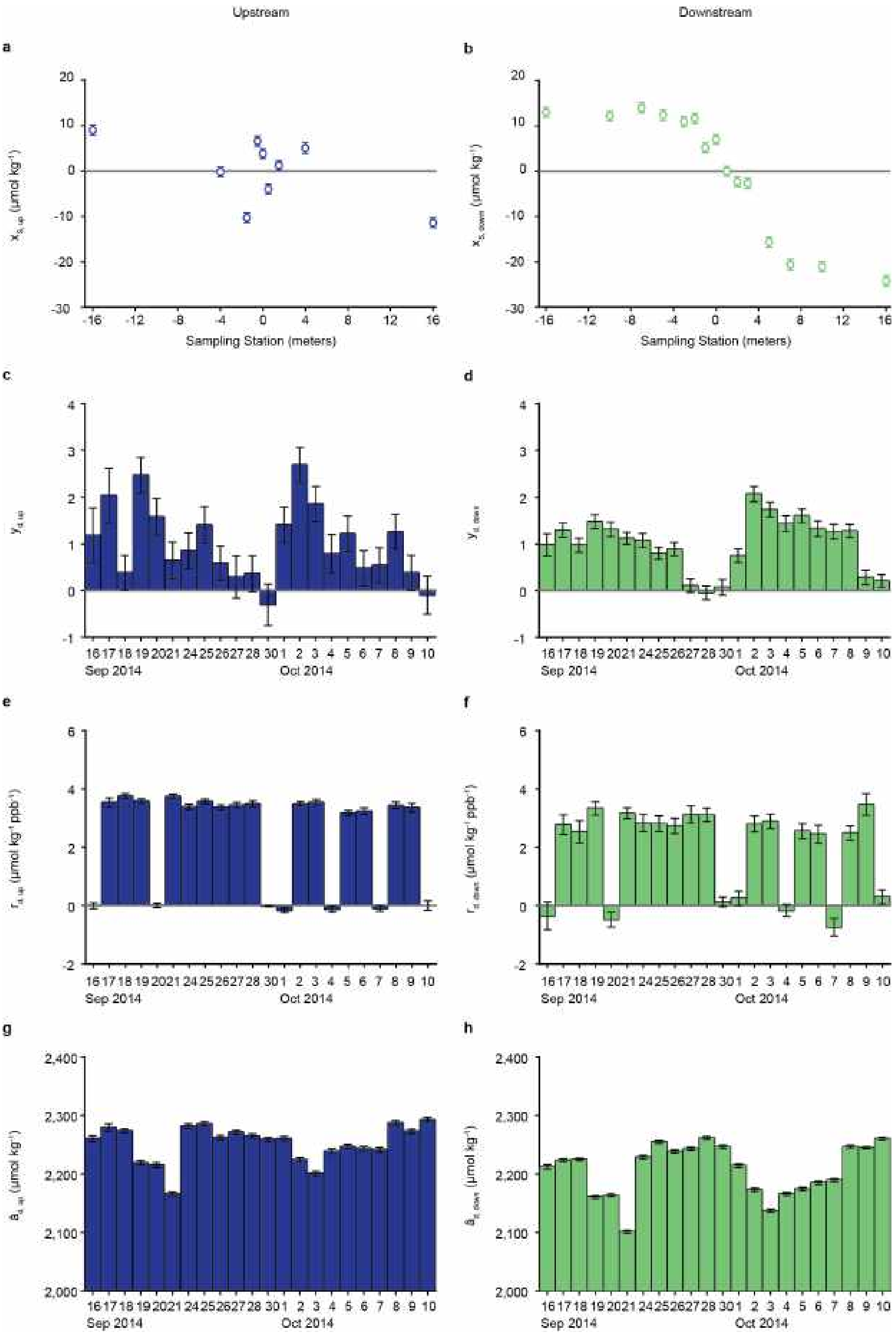
Extended Data Figure 3 | Schematic of study area showing meter-spacing of station locations for the 9 upstream (U) stations and 15 downstream (D) transects. Numbers indicate the metre-spacing from the centre of the study area, denoted as U0 for the upstream transect and D0 for the downstream transect. The outermost sampling locations for the upstream (−U16, U16) and downstream (−D16, D16) transects define the four outermost corners of the study area and were strategically positioned to lie outside the alkalinity–dye plume, rendering zero dye concentrations and added alkalinity.



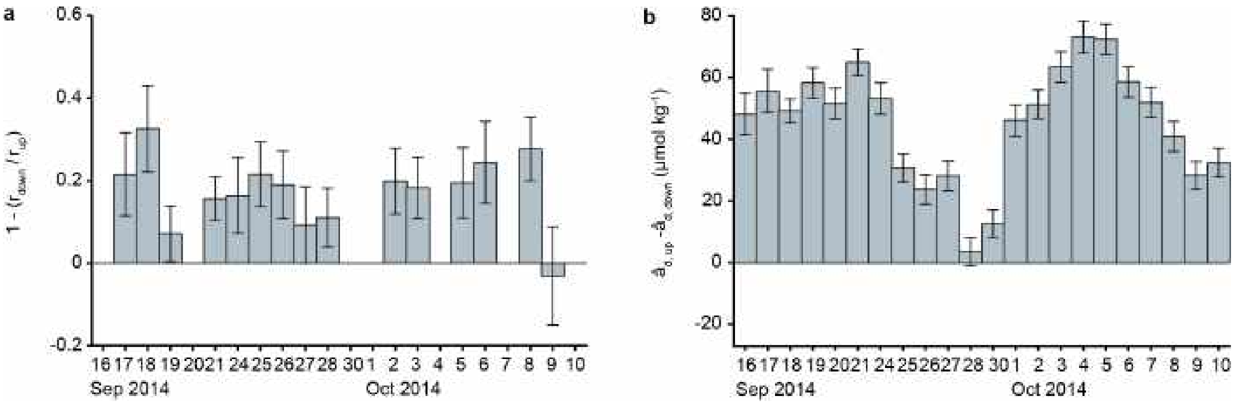
Extended Data Figure 4 | Mean chemical conditions for control ($N=7$) and experiment ($N=15$) days. a, **b**, Carbonate ion concentrations ([CO$_3^{2-}$]); **c**, **d**, p_{CO_2}; **e**, **f**, dissolved inorganic carbon concentrations (C_T) for upstream and downstream transects. Error bars, which represent standard errors, are indicative of day-to-day and hour-to-hour variability (not measurement error); estimates of measurement error are provided in the Methods. Total alkalinity (A_T), dye concentration, aragonite saturation state (Ω_{arag}), and total pH (pH$_T$) are provided in Figs 2 and 3.



Extended Data Figure 5 | Comparison of alkalinity values before and after 'offset-corrections' used in the multivariate regression analysis. **a**, **b**, Measured (that is, 'raw') alkalinity values. **c**, **d**, 'Offset-corrected' alkalinity values. Bold lines represent average conditions; dashed lines show results by day. See Supplementary Information.



Extended Data Figure 6 | Results of the multivariate regression analysis. **a**, **b**, Unique offsets by station, x_s, for the upstream and downstream transects. **c**, **d**, Magnitude of offsets by day, y_d, for upstream and downstream transects. **e**, **f**, Alkalinity–dye ratios by day, r_d, for upstream and downstream transects. **g**, **h**, Mean background alkalinities by day, $\hat{a}_d$, for upstream and downstream transects. Error bars represent standard errors. See Supplementary Information.



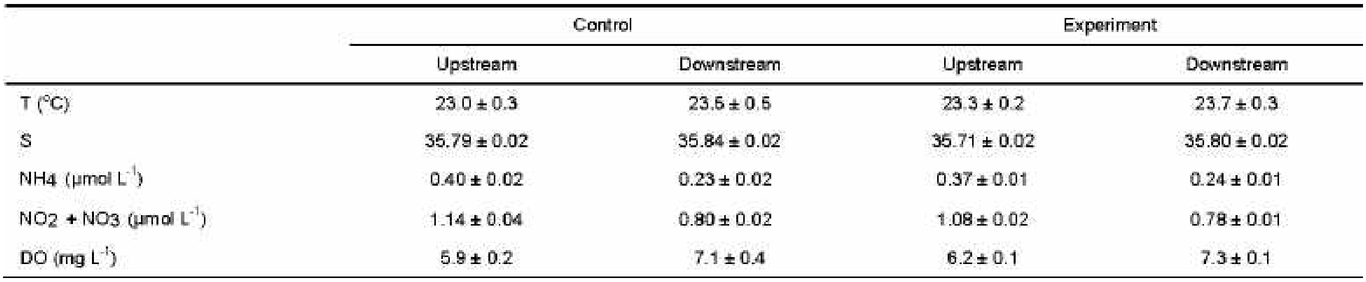
Extended Data Figure 7 | Results of the multivariate regression were used to calculate the additional alkalinity uptake (that is, G_{increase}) and background alkalinity uptake (that is, $G_{\mathrm{background}}$) by day. a, Fraction of added alkalinity taken up by the reef by day, given by (1 − ($r_{\mathrm{down}}/r_{\mathrm{up}}$), equation (1) of main text). **b**, Background reef uptake by day, given by ($\hat{a}_{d,\,\mathrm{up}} - \hat{a}_{d,\,\mathrm{down}}$). Error bars represent standard errors. See Supplementary Information.

Extended Data Table 1 | Schedule for control and experiment days, including date, time, predicted height of low tide, and mean photosynthetically active radiation (PAR) for the 1 h study period

Date	Low Tide (HHMM)	Water Depth (m)	PAR (μmol m^{-2} s^{-1})	Type of Study
16 Sept	0737	0.88	1146	Control
17 Sept	0907	0.93	1626	Experiment
18 Sept	1026	0.85	1797	Experiment
19 Sept	1125	0.72	1800	Experiment
20 Sept	1210	0.59	1715	Control
21 Sept	1249	0.47	1215	Experiment
24 Sept	1425	0.29	931	Experiment
25 Sept	1455	0.30	675	Experiment
26 Sept	1528	0.35	551	Experiment
27 Sept	1604	0.44	297	Experiment
28 Sept	1647	0.58	25	Experiment
30 Sept	0532	0.57	277	Control
01 Oct	0639	0.75	866	Control
02 Oct	0809	0.84	1459	Experiment
03 Oct	0940	0.80	1055	Experiment
04 Oct	1051	0.65	1916	Control
05 Oct	1150	0.46	1636	Experiment
06 Oct	1240	0.30	1707	Experiment
07 Oct	1327	0.19	1453	Control
08 Oct	1411	0.15	1179	Experiment
09 Oct	1455	0.19	787	Experiment
10 Oct	1539	0.29	513	Control

Tides were provided courtesy of One Tree Research Station. The low-tide time represents the time at which pumping onto the reef started; sampling occurred 60 min afterwards. Data for photosynthetically active radiation were obtained from the Australian Institute of Marine Science weather station at One Tree Island (http://data.aims.gov.au/aimsrtds/station.xhtml?station=131). There was no significant difference between mean light levels for control (1,166 ± 217 μmol m^{-2} s^{-1}, mean ± s.e.m.) and experiment (1,098 ± 150 μmol m^{-2} s^{-1}) days.

Extended Data Table 2 | Mean (±1 s.e.m.) values for temperature (*T*), salinity (*S*), ammonium (NH_4), nitrite and nitrate ($NO_2 + NO_3$), and dissolved oxygen (DO) during the 22-day study period



	Control		Experiment	
	Upstream	Downstream	Upstream	Downstream
T (°C)	23.0 ± 0.3	23.5 ± 0.5	23.3 ± 0.2	23.7 ± 0.3
S	35.79 ± 0.02	35.84 ± 0.02	35.71 ± 0.02	35.80 ± 0.02
NH_4 (μmol L^{-1})	0.40 ± 0.02	0.23 ± 0.02	0.37 ± 0.01	0.24 ± 0.01
$NO_2 + NO_3$ (μmol L^{-1})	1.14 ± 0.04	0.80 ± 0.02	1.08 ± 0.02	0.78 ± 0.01
DO (mg L^{-1})	5.9 ± 0.2	7.1 ± 0.4	6.2 ± 0.1	7.3 ± 0.1

Note that underlying natural variability (that is, day-to-day, hour-to-hour) contributes to standard errors; measurement errors for each parameter are indicated in the Methods.

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RESEARCH REVIEW

Operationalizing resilience for adaptive coral reef management under global environmental change

KENNETH R.N. ANTHONY[1], PAUL A. MARSHALL[2], AMEER ABDULLA[3], ROGER BEEDEN[2], CHRIS BERGH[4], RYAN BLACK[5], C. MARK EAKIN[6], EDWARD T. GAME[7], MARGARET GOOCH[2], NICHOLAS A.J. GRAHAM[8], ALISON GREEN[7], SCOTT F. HERON[9], RUBEN VAN HOOIDONK[10], CHERYL KNOWLAND[11], SANGEETA MANGUBHAI[12], NADINE MARSHALL[13], JEFFREY A. MAYNARD[14], PETER MCGINNITY[2], ELIZABETH MCLEOD[15], PETER. J. MUMBY[11], MAGNUS NYSTRÖM[16], DAVID OBURA[17], JAMIE OLIVER[1], HUGH P. POSSINGHAM[18], ROBERT L. PRESSEY[8], GWILYM P. ROWLANDS[19], JERKER TAMELANDER[20], DAVID WACHENFELD[2] and STEPHANIE WEAR[21]

[1]Australian Institute of Marine Science, PMB3, Townsville, Qld 4810, Australia, [2]Great Barrier Reef Marine Park Authority, PO Box 1379, Townsville, Qld 4810, Australia, [3]International Union for the Conservation of Nature, Gland Switzerland and University of Queensland, Brisbane, Qld, Australia, [4]The Nature Conservancy, Big Pine Key, FL, USA, [5]Department of the Environment, Great Barrier Reef Taskforce, Allara St, Canberra, ACT, Australia, [6]Coral Reef Watch, US National Oceanic and Atmospheric Administration, College Park, MD, USA, [7]The Nature Conservancy, West End, Qld 4101, Australia, [8]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, Australia, [9]Coral Reef Watch, National Oceanographic and Atmospheric Administration and School of Engineering and Physical Sciences, James Cook University, Townsville, Qld, Australia, [10]Atlantic Oceanographic and Meteorological Laboratory, National Oceanographic and Atmospheric Administration, Miami, FL, USA, [11]Spatial Ecology Lab, University of Queensland, St Lucia, Qld 4072, Australia, [12]Fiji Country Program, Wildlife Conservation Society, 11 Ma'afu Street, Suva, Fiji, [13]CSIRO Ecosystem Sciences, PMB, Aitkenvale, Qld 4810, Australia, [14]USR 3278 CNRS-EPHE, CRIOBE, BP 1013 Papetoai, Moorea 98729, Polynesie Francaise, [15]The Nature Conservancy, Austin, TX, USA, [16]Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, Stockholm SE-104 05, Sweden, [17]CORDIO East Africa, P.O.Box 10135-80101, Mombasa, Kenya, [18]Australian Research Council Centre of Excellence for Environmental Decisions, University of Queensland, St Lucia, Qld, Australia, [19]National Coral Reef Institute, Nova Southeastern University, Dania Beach, FL, USA, [20]UN, United Nations Environment Programme, Rajdamnern Nok Av., Bangkok 10200, Thailand, [21]The Nature Conservancy, Department of Biology, University of Florida, Gainesville, FL, USA

Abstract

Cumulative pressures from global climate and ocean change combined with multiple regional and local-scale stressors pose fundamental challenges to coral reef managers worldwide. Understanding how cumulative stressors affect coral reef vulnerability is critical for successful reef conservation now and in the future. In this review, we present the case that strategically managing for increased ecological resilience (capacity for stress resistance and recovery) can reduce coral reef vulnerability (risk of net decline) up to a point. Specifically, we propose an operational framework for identifying effective management levers to enhance resilience and support management decisions that reduce reef vulnerability. Building on a system understanding of biological and ecological processes that drive resilience of coral reefs in different environmental and socio-economic settings, we present an Adaptive Resilience-Based management (ARBM) framework and suggest a set of guidelines for how and where resilience can be enhanced via management interventions. We argue that press-type stressors (pollution, sedimentation, overfishing, ocean warming and acidification) are key threats to coral reef resilience by affecting processes underpinning resistance and recovery, while pulse-type (acute) stressors (e.g. storms, bleaching events, crown-of-thorns starfish outbreaks) increase the demand for resilience. We apply the framework to a set of example problems for Caribbean and Indo-Pacific reefs. A combined strategy of active risk reduction and resilience support is needed, informed by key management objectives, knowledge of reef ecosystem processes and consideration of environmental and social drivers. As climate change and ocean acidification erode the resilience and increase the vulnerability of coral reefs globally, successful adaptive management of coral reefs will become increasingly difficult. Given limited resources, on-the-ground solutions are likely to focus increasingly on actions that support resilience at finer spatial scales, and that are tightly linked to ecosystem goods and services.

Keywords: climate change, coral reefs, ecosystem vulnerability, environmental management, ocean acidification, social-ecological system, structured decision-making

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Introduction

The need for adaptive resilience-based management of coral reefs

Natural resource managers are facing growing challenges from multiple and cumulative stressors that are increasing the vulnerability of ecosystems and societies that depend on their goods and services (Chapin *et al.*, 2000). Coral reefs are vulnerable to the global pressures of climate change and ocean acidification (Hoegh-Guldberg *et al.*, 2007; Moss *et al.*, 2010) and to a suite of regional and local-scale disturbances including destructive fishing and overfishing, poor coastal and urban development and pollution (Knowlton & Jackson, 2008).

The management challenges associated with coral reef vulnerability include at least two key facets: (i) reducing pressures and exposures to stress, and (ii) support of the system's resilience to these threats. Coral reef managers are increasingly shifting their focus from strictly stress abatement to including a broader support of ecosystem resilience – i.e. supporting ecosystem processes that lower sensitivity, promote recovery and enhance adaptive capacity (e.g. Marshall & Shuttenberg, 2006; GBRMPA, 2009; McClanahan *et al.*, 2012). This shift has been reinforced by an increase in adaptive management efforts and the implementation of systems approaches to management and conservation (e.g. Chapin *et al.*, 2010; McCook *et al.*, 2010). Resilience provides an important framework for these more integrated and dynamic approaches and helps managers deal with the combined and often synergistic impacts of global and local stressors (Tompkins & Adger, 2004).

Climate change and ocean acidification scenarios for this century (Cao *et al.*, 2007; Moss *et al.*, 2010) are expected to challenge the natural resilience of tropical coral reefs (Anthony *et al.*, 2011). This is in part driven by increased coral bleaching risk (van Hooidonk & Huber, 2009; van Hooidonk *et al.*, 2013), increased storm intensity (Knutson *et al.*, 2010; Emanuel, 2013), increased reef fragility to storms (Madin *et al.*, 2008) and reduced coral growth (Reynaud *et al.*, 2003) and recovery rates (Hoegh-Guldberg *et al.*, 2007; Albright & Langdon, 2011). From a reef management and policy perspective, this means that climate change and ocean acidification will, firstly, increase the need for efforts to abate regional- and local-scale stressors (i.e. those open to on-the-ground management intervention) on coral reefs, increase the vulnerability of reef-dependent people and, thirdly, increase the need to enhance ecosystem resilience (Kennedy *et al.*, 2013).

Adaptive resilience-based management (ARBM) was developed from studies of the dynamics of linked social and ecological systems (Anderies *et al.*, 2006) and has influenced systems thinking of managers across terrestrial, freshwater and marine systems (Chapin *et al.*, 2009; Rist *et al.*, 2013). Despite ARBM being a recommended approach for coral reefs (Hughes *et al.*, 2010; Graham *et al.*, 2013) and readily incorporated into management documents (e.g. GBRMPA, 2009), there are few examples of practical implementation of resilience principles in the adaptive management and decision-making on coral reefs (Maynard *et al.*, 2010; Weeks & Jupiter, 2013).

The key objective of this paper is to present a framework that can help reef managers and conservation practitioners identify viable intervention options and make effective decisions to reduce coral reef vulnerability under complex environmental and social scenarios based on a complex systems understanding. We argue that practical implementation of ARBM could be enhanced through an approach that more formally integrates key principles of ecosystem vulnerability, ecological resilience, disturbance regimes, management options and structured decision-making. We then present mechanisms by which resilience principles can be made operational (sensu Sarkar & Margules, 2002) to support the adaptive management of coral reefs and dependent societies under regional and global environmental change.

The concepts of resilience and vulnerability in the context of managing social-ecological systems

Supporting ecosystem resilience provides opportunities to enhance the system's ability to cope with extrinsic pressures (including those beyond the direct influence of coral reef managers), and to reorganize and/or recover between disturbances, thereby reducing the vulnerability of the ecosystem and dependent societies. We use the ecological resilience definition to describe ecosystem resilience, broadly defined as the capacity of a system to absorb disturbances and reorganize, while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks

Correspondence: Kenneth R.N. Anthony, tel. +61 417 857 682, fax +61 747 534 528, e-mail: k.anthony@aims.gov.au

(Holling, 1973; Gunderson, 2000; Nyström *et al*., 2008). Within coral reef ecosystems, ecological resilience is the result of biological and ecological processes facilitating recruitment, regrowth, repair and reassembly. These processes occur along multiple dimensions including levels of organization, trophic structure (Bellwood *et al*., 2004), time (Anthony *et al*., 2011) and space (Nyström & Folke, 2001). Resistance, which is the capacity to withstand disturbances such as storm damage, and recovery from such disturbances, are both components of ecological resilience (Nyström *et al*., 2008).

Resilience has also been a formative concept in understanding dynamics and trajectories of social systems. Similar to ecological resilience, social resilience describes the capacity of societies and individuals to cope and adapt to change, and it often depends on the existence of institutions that learn and store knowledge, and which are creative and flexible in approaching problems (Gunderson & Holling, 2002). Importantly, and based on resilience theory, social and ecological systems are often intrinsically coupled and constantly face change together. Consequently, managing resilience of the linked 'socio-ecological' system is a way to integrate and manage the interactions and feedbacks between people and nature (Berkes & Folke, 1998; Chapin *et al*., 2010; Folke *et al*., 2010).

Ecosystem vulnerability is the risk that average state of the system falls to an unacceptable level (Mumby *et al*., 2014). Broadly, vulnerability is defined as the product of three key system properties: (i) exposure to stressors, pressures or disturbances, (ii) sensitivity (or lack of resistance) to such exposure and (iii) the capacity to adapt to and/or recover from disturbances (Füssel & Klein, 2006; Marshall *et al*., 2013). If low ecosystem vulnerability is the fundamental management objective, then it can be achieved via actions to (i) reduce exposure, (ii) support resilience (resistance and recovery/adaptive capacity) of the linked socio-ecological system, or (iii) both.

As climate change and ocean acidification unfold, increasing the exposure of marine ecosystems to a suite of global stressors, the vulnerability of coral reefs is expected to increase via eroded resilience (Anthony *et al*., 2011; Mumby *et al*., 2014) and enhanced disturbance regimes (Hoegh-Guldberg *et al*., 2007). Thus, viable management options and effective actions to reduce reef vulnerability to a variety of stressors will require considerations of a growing set of innovative management alternatives that can both tackle stressors and enhance ecosystem resilience locally or regionally (Game *et al*., 2014). Importantly, however, there are limits to an ecosystem's natural resilience (Thrush *et al*., 2009), and managers need to take those limits into account. In the following we introduce and review resilience models and drivers of resilience processes to first provide a system's context for adaptive coral reef management under environmental change.

Resilience models – stability landscapes

Stability landscapes (Scheffer *et al*., 2001; Scheffer & Carpenter, 2003) provide a useful conceptual representation of ecosystem resilience for coral reefs (Hughes *et al*., 2010) and how different stressors affect ecosystem behaviour. In essence, stability landscapes are three-dimensional representations of how a system (indicated by a ball) gravitates towards system equilibria (bottom of valleys) following disturbances (pulse-type stressors, see below) within a space described by ecosystem state (x-axis) and environmental conditions (press-type stress regimes, y-axis, Fig. 1). In this representation, resilience is proportional to valley depth in the state dimension (Scheffer *et al*., 2012) and the height of hills forming barriers to the system transitioning into another gravitational basin (e.g. from corals to macroalgae; Bellwood *et al*., 2004) following a pulse-type disturbance. Simulations and analytical models of coral reef dynamics based on empirical data demonstrate that the characteristics of stability landscapes are shaped by ecosystem processes, and by their interactions and feedbacks between stressors and processes (Mumby *et al*., 2007; Anthony *et al*., 2011; Scheffer *et al*., 2012). Importantly, because ecosystem dynamics and processes are associated with substantial uncertainty, the location of gravitational basins, equilibria and thresholds on stability landscapes must be viewed as probabilistic and used to provide guidelines only.

Reefs with different tendencies to form alternate stable states (Mumby *et al*., 2012; Roff & Mumby, 2012) display different stability landscapes (Scheffer *et al*., 2001). Coral reef systems displaying alternate stable states between coral and macroalgae have only been demonstrated unequivocally for Caribbean systems; Indo-Pacific systems tend to display single equilibrial states (Roff & Mumby, 2012; but see also Cheal *et al*., 2013). For representation, we base our examples of ARBM on two contrasting types of stability landscapes: one with a pronounced tendency to form alternate stable states (e.g. corals and macroalgae forming opposite but simultaneous basins of attraction), and one with only a single equilibrial state for a given set of environmental conditions (e.g. *either* corals *or* macroalgae forming a gravitational basin, Fig. 1). Thresholds (conditions representing increased probability of abrupt shifts between contrasting states) exist in both types (Scheffer & Carpenter, 2003), but have different risk implications (Fig. 1). First, systems displaying

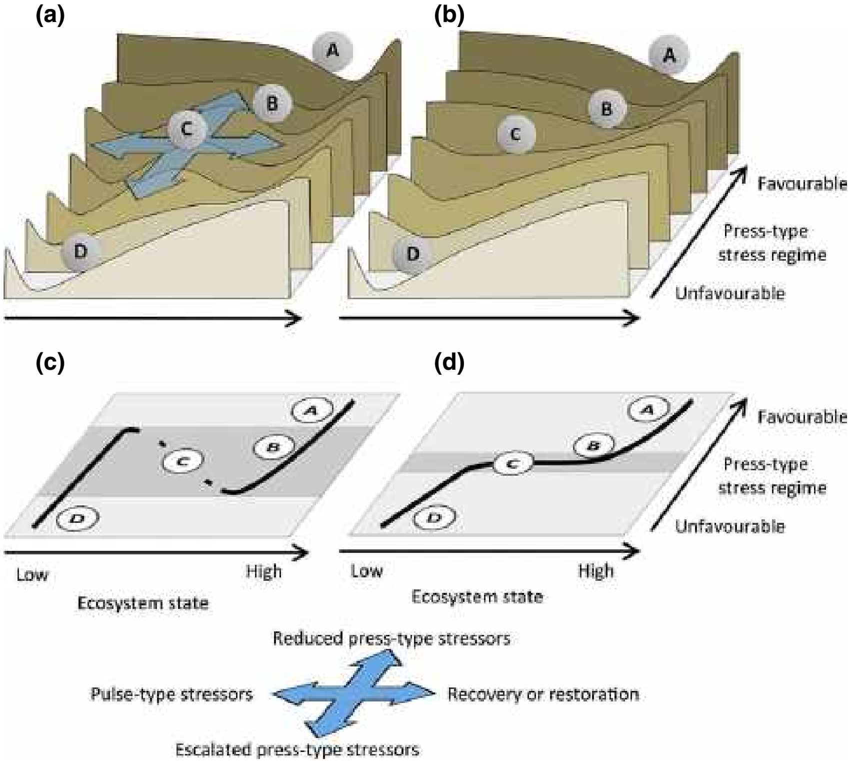

Fig. 1 Examples of ecosystem stability landscapes, based on the conceptual model by Scheffer *et al.* (2001), illustrating the change in system dynamics as a function of system state and environmental conditions (press-type stress regime). Panel (a) represents coral reef ecosystems that show bistable states (e.g. Caribbean reefs), and panel (b) represents reefs that show single equilibrial states (e.g. Indo-Pacific reefs, Roff & Mumby, 2012). The dynamics of the system (represented by the behaviour of a ball) are determined by four sets of forces: (i) pulse-type stressors, (ii) recovery processes and active restoration, (iii) press-type stressors leading to declining environmental conditions and (iv) improvement in press-type conditions. Resilience is largely characterized by the shape of the landscape slice under a given environmental condition (press-type stress regime). Note that scales on *y*-axes are not comparable between models.

alternate stable states have two environmental thresholds. One marks the transition between a coral-dominated regime and a coral-macroalgae bistable regime. This is indicated by the transition from condition A to B in Fig. 1a, crossing the upper edge of the shaded zone in Fig. 1c. The other marks the transition from the bistable regime into an algal-dominated one. This is shown as a transition from scenario C to D in Fig. 1a, and a move out of the shaded zone in Fig. 1c. This example is typical of Caribbean reef systems where the locations of dynamic thresholds along the press-type stress regime axis are functions of a suite of environmental pressures, most prominently water quality, algal growth rate and overfishing of herbivores (Mumby *et al.*, 2007; Roff & Mumby, 2012).

Expanded models demonstrate that the locations of these thresholds are strongly affected by ocean warming and acidification (Anthony *et al.*, 2011). Secondly, systems without a propensity to form alternate stable states display one, though dynamic, threshold, which marks an increased probability for shifts between coral- and macroalgal-dominated regimes. The crossing of this threshold is indicated in Fig. 1b and d as a transition from scenario B to C across the narrow shaded zone. Again, the location of this threshold is strongly driven by the combination of press-type stressors, including ocean warming and acidification (Anthony *et al.*, 2011). In a later section we show that the two types of stability landscapes have different implications for resilience-based management across environmental scenarios and geographical settings, but that a set of general rules apply to both.

Environmental and human drivers of resilience

Understanding which environmental or anthropogenic stressors impact resilience, and which do not, is a critical basis for ARBM (Table 1). A key functional categorization for understanding the implications of different stressors is that of pulse (acute) vs. press (chronic) (Scheffer *et al.*, 2001). In the general working model for resilience in Fig. 1, pulse-type stressors move the system state (the ball) from right to left (x-axis) over a short timeframe (acute disturbance events), while press-type stressors move the system downwards to less favourable conditions over longer timeframes. Depending on the system (i.e. the stability landscape and the location of thresholds), increased press-type stress can reduce resilience to pulse-type disturbances (e.g. a shift from scenario A to B or C in Fig. 1a and b), in part by making the system more susceptible to pulse-type stressors. In the context of ARBM, processes of reef recovery or active restoration are forces directly opposing pulse-type stressors (Fig. 1). Here, fast coral recovery, and potentially widespread restoration, can increase resilience by promoting gravitation towards equilibrium before the next pulse-type disturbance occurs. Conversely, reduced press-type stressors, for example through environmental management of water quality or overfishing, can enhance resilience by moving the system towards the safe side of the environmental threshold and into the coral-dominated regime where pulse-type disturbances are less likely to trigger a phase shift (e.g. from scenarios B to A).

Pulse-type stressors. On coral reefs, pulse-type stressors include tropical cyclones, coral bleaching events, destructive fishing, crown-of-thorns starfish (CoTS) outbreaks, and flood events (Table 1). These events may not impact directly on resilience processes, but they episodically send the system back to an earlier successional state (leftward system shift in Fig. 1). In systems with high resilience under favourable conditions (scenario A in Fig. 1), pulse events may not cause sustained reductions in ecosystem values if the system has time to recover or reorganize (rightward shifts) between events (Halford *et al*., 2004; Roff & Mumby, 2012). Pulse-type stress events that occur with high frequency or severity, however, increase the demand for fast recovery and reorganization, and hence the demand for high resilience (Anthony *et al*., 2011). The recent decline in coral cover on Australia's Great Barrier Reef (GBR) is an example of how increased frequency and severity of pulse-type stressors (a series of severe cyclones, repeated CoTS outbreaks and two extensive coral bleaching events) can overwhelm an ecosystem's resilience (De'ath *et al*., 2012; Table 1).

Under business-as-usual carbon emissions, coral bleaching events are predicted to increase in frequency and severity (van Hooidonk *et al*., 2013), and the intensity of tropical storms is likely to be amplified by warming seas in some ocean basins (Knutson *et al*., 2010; Mendelsohn *et al*., 2012). A warming climate thus promotes an increase in globally and regionally driven pulse-type stressors.

Press-type stressors. Press-type stressors, such as sustained pollution, sedimentation, overfishing and ocean acidification are key threats to reef resilience (Nyström *et al*., 2008). They influence species sensitivity, rate of coral reef recovery, growth and maintenance, and the interactions between desirable and undesirable system components (e.g. corals vs. fleshy macroalgae). The continuum from low to high press-type stress regimes represents environmental conditions in Fig. 1, ranging from unfavourable (e.g. sustained reductions in goods and services) to favourable (resilience processes intact and scope for goods and services). Specifically, on the stability landscapes in Fig. 1, press-type stressors act on the system in a direction perpendicular to pulse-type stressors.

Classic examples of press-type stressors with clear management levers reefs are overfishing of herbivorous fish leading to loss of control of macroalgae (Hughes, 1994), enhancement of macroalgal growth via nutrient enrichment (McCook *et al*., 2001) and changing sedimentation and turbidity regimes (Erftemeijer *et al*., 2012). Stressors that have mixed pulse-press characteristics are likely to both reduce resilience and intensify system perturbations (Table 1). For example, coral bleaching events triggered by ocean warming reduce coral abundance, growth and reproduction (Baird & Marshall, 2002; McClanahan *et al*., 2012) and increase susceptibility to diseases (Harvell *et al*., 2002). Similarly, sedimentation in coastal waters can occur as dredging events, major run-off events from rivers (e.g. as soil erosion), but also potentially through increased background turbidity regimes (Schaffelke *et al*., 2012). Once large amounts of sediment are deposited in shallow coastal waters, a shift to a persistent high-turbidity regime is likely as sediment banks are resuspended by waves and (tidal) currents (Larcombe *et al*., 1995).

A decision-support framework for ARBM

A key step in operationalizing resilience for management is to identify the 'levers' that link to the resilience and vulnerability of the ecosystem and the dependent social systems (Fig. 2). The framework presented here builds on adaptive management (Holling, 1978; Schreiber *et al*., 2004; Argent, 2009; Rist *et al*., 2013) in which environmental, ecological and social information is evaluated against management goals and objectives (Fig. 2A) and is used as a basis for management decisions (Fig. 2B). The framework consists of three broad elements: (i) a management system (Fig. 2A–G), (ii) environmental and anthropogenic drivers/activities leading to stress on the ecosystem, which can be influenced to varying degrees

Table 1 Key stressors on coral reefs, their pulse- vs. press-type characteristics and their role in adaptive resilience-based management (ARBM)

Stressor	Pulse/Press	Drivers or activities	Impact	Resilience processes affected	Potential management levers (see also Table 2)
Storms	Pulse (stochastic)	Natural cycles, climate change	Structural damage, floods and sediment-ation	Recovery and connectivity if damage is extensive	Preparedness and recovery planning locally; compensatory measures
Destruct-ive fishing	Pulse	e.g. bomb fishing, poison fishing	Structural damage, mortality of flora and fauna	Recovery, reproduction, recruitment and connectivity if damage is extensive	Increase incentives for nondestructive harvest of resource through education, regulation and enforcement
Crown-of-thorns starfish (CoTS)	Pulse	Nutrient enrichment, natural cycles	Coral mortality	Recovery, recruitment and connectivity if mortality is extensive	Improved management of catchment, protection of CoTS predators, tactical CoTS control
Thermal anomalies	Pulse, with press-type after-effects	Climate change, natural cycles	Coral bleaching, diseases and mortality	Reduced growth and reproduction, and potentially connectivity if impact is extensive	Identify sites that may have lower vulnerability; protect from local stressors; manage for enhanced recovery
Sedimenta-tion/ turbidity	Mixed depending on source	Mixed: land use and river catchment practices, flooding, resuspension, coastal construction	Sediment stress and light limitation, enhancement of algal growth	High turbidity from re-suspension can cause long-term suppression of coral recovery and provide competitive advantage to other benthic groups such as algae and sponges	Improved management of catchment land use through education, regulation, incentives and penalties. Restore land vegetation. Control coastal development activities.
Nutrient enrichment	Press, but pulse if linked to flood events	Mixed: land use and river catchment practices, flooding	Enhanced algal growth, increased turbidity	Increases susceptibility of corals to thermal bleaching. Provides competitive advantage to algae, which can suppress coral recovery.	Improved management of sewage and intensive agriculture activities through education, regulation, incentives and penalties
Pollution (herbicides, pesticides and heavy metals)	Press, but pulse if linked to flood events or marine incidents	Land-based (urban and agriculture) and from shipping	Toxicity, affects metamorphosis and larval survival.	Reduced coral growth and reproduction. Suppresses reef supply-side ecology.	Improved management of urban, agricultural and shipping activities through education, regulation, incentives and penalties
Ocean acidification	Press	Direct CO_2 effect, point and nonpoint sources of low pH runoff	Reduced coral growth and strength, enhanced algal growth	Coral growth rates, skeletal strength and recruitment reduced.	Identify sites that could have lower vulnerability and target for protection from local stressors, control land-based sources of pollutants that decrease pH (e.g. nitrogen/sulfur oxides)
Decline in herbivores	Press	Human use	Reduced algal mortality, algal overgrowth of corals	Potentially drive phase shift to macroalgae, exacerbated by nutrients, warming and acidification	Improved fisheries management through education, regulation, incentives and penalties.

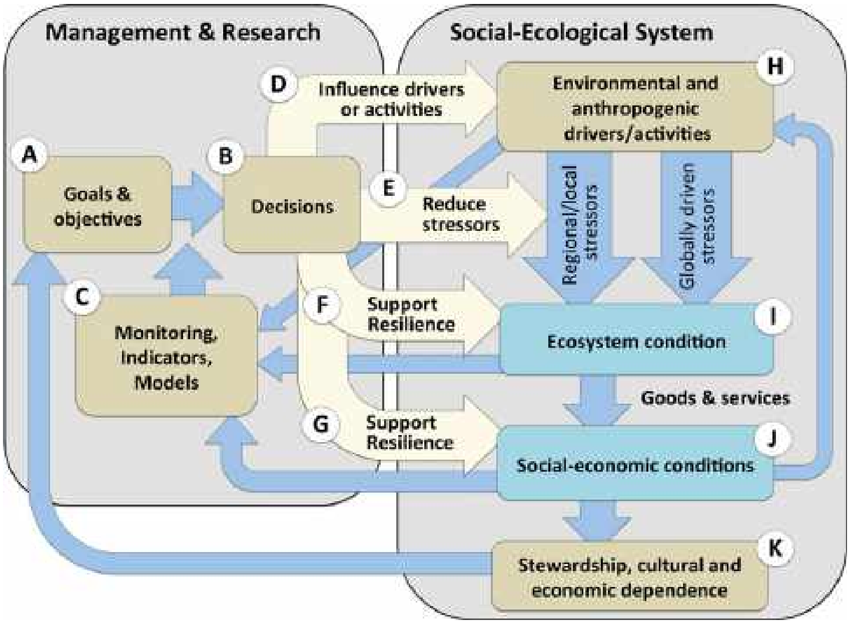

Fig. 2 System diagram outlining the functional linkages within the operational adaptive resilience-based management (ARBM) framework, consisting of a management and research component (left box, A–G) and the stressors/activities/drivers and conditions of the social-ecological systems (right box, H–K). The system is dynamic as information flowing from the ecological and social systems is used to update objectives and specific decisions to intervene and manage drivers, activities or stressors influencing resilience processes.

by management levers (Fig. 2H), and (iii) the linked ecological and social systems (Fig. 2I–K). Environmental, ecological and social conditions and impacts all feed back to the management system. As ecological and social systems change in response to stress, the management system records the changes via ecological monitoring, indicators or models (Fig. 2C), and via social indicators (Fig. 2J). Four avenues for action are possible: (i) managing drivers or activities leading to stress (Fig. 2D); (ii) managing stressors directly (E); (iii) supporting ecosystem resilience (F); and (iv) supporting social resilience (G). The degree to which effort and resources should be allocated among these four avenues depends on the environmental, ecological and socio-economic benefits derived from those actions.

Setting objectives for successful ARBM. Effective management and decision-making require clear goals and fundamental objectives (Gregory *et al.*, 2012), and establishing objectives is the first step of the ARBM framework (Possingham *et al.*, 2001) (Fig. 2A). The origin of objectives is illustrated by the link between objectives and the social drivers, which are themselves linked to the social- economic benefits derived from the ecological system (Fig. 2J–K). To set meaningful objectives, managers need to define what system states are desirable and should be aspired to, and what system states are undesirable and should be avoided (recognizing that conflicts may exist as to what is desirable to whom) and what management intervention is most needed. Objectives and data on system state are hence strongly linked and directly inform decision-making (Fig. 2A–C). For coral reefs, high abundance and biodiversity of corals and fish are characteristic desirable states associated with rich goods and services, whereas shifts to macroalgal dominance and a depauperate fish community represent undesirable states (McClanahan *et al.*, 2002; GBRMPA, 2009; Hughes *et al.*, 2010).

Data supporting resilience models and ARBM decision-making. Monitoring of environmental variables and the state and behaviour of the system, and analyses of data and model projections against conservation objectives, all form part of the decision-making process (Nichols & Williams, 2006). Here, the decision framework and linked ecosystem models need to account for the dynamics of the ecosystem and model uncertainty (Carpenter *et al.*, 2005; Mumby *et al.*, 2014), and to evaluate how the system is likely to be affected by future conditions (Anthony *et al.*, 2011). Static measures of desirable states on coral reefs, such as high coral cover and fish abundance and diversity, can be poor indicators of resilience (Mumby *et al.*, 2014). High coral cover can be the legacy of past favourable conditions and can fail to alert the decision-maker to declines in resilience, for example reduced recruitment potential or reduced herbivory

(Bellwood *et al.*, 2004). Such reefs can be prone to a phase shift that might prove difficult to reverse (Nyström *et al.*, 2012).

Some state variables can provide information about a range of ecosystem values that underpin resilience. Such variables, termed resilience indicators, are used to substitute simple resilience models (McClanahan *et al.*, 2012). Examples of resilience indicators on coral reefs include structural complexity (which supports a rich fauna of fish and invertebrates, Jones *et al.*, 2004), coral disease prevalence (McClanahan *et al.*, 2012), substrate quality for coral recruitment, including abundance of crustose coralline algae that facilitate coral settlement (Harrington *et al.*, 2004), the distribution of important functional groups, such as herbivores (Bellwood *et al.*, 2004) and their demographic structure (Nyström *et al.*, 2008). Other indicators with close links to resilience processes are competitive strengths between corals and macroalgae (Barott *et al.*, 2012) and the abundance and diversity of juvenile corals (Mumby & Steneck, 2008). Also, microbial pathogens are showing increasing potential as early warning systems for stress to coral reef communities (McDole *et al.*, 2012).

Structured decision-making in ARBM. The decision-making process governs how actions are best identified and implemented to meet objectives based on existing environmental, ecological and social conditions. We integrate the resilience concept with a simple, well-tested system of structured decision-making that has been widely adopted in environmental and conservation planning (Possingham *et al.*, 2001; Gregory *et al.*, 2012). The decision-making system includes a series of elements condensed into two key groups: (i) data or models of system states and responses to stressors of concern, and (ii) management options or alternatives, and their social, economic and realistic feasibility and consequences. While our framework is applicable in a wide range of settings, managers need to incorporate their specific geographic and socioeconomic conditions, spatial and temporal scales and the system's present status and trajectory. Importantly, managers will need to assess the short and long-term conservation benefits of each option identified through application of the ARBM framework against the financial costs, social impacts and political implications.

We integrate decision-making processes into the ARBM framework by requiring that management actions always attempt to satisfy the fundamental objectives, for example to minimize vulnerability. In the following section, we apply the ARBM framework to coral reef examples in different environmental and socio-economic settings.

Applying ARBM under local and regional pressures

States and environmental settings for coral reefs span the full range depicted in Fig. 1. How the ARBM framework is applied to support management decisions under different regional and global environmental scenarios depends in part on the socio-economic setting. To illustrate this, we convert Fig. 1 to a two-dimensional representation of coral reef stability landscapes (Fig. 3). Specifically, we use the location of thresholds and shape of system equilibria as guidance only. Again, we acknowledge uncertainty and therefore only work with general rules rather than assuming detailed understanding of ecosystem dynamics, variation around equilibria, and the resilience within gravitational basins. Here we first examine how ARBM can be applied to local and regional-scale scenarios assuming mild ocean warming and acidification (Fig. 3a and b) and subsequently address how progressed ocean warming and acidification change the actions required to maintain system resilience (Fig. 3c and d).

Reefs in the wider Caribbean straddle scenarios A to D in Fig. 3a. In general they are characterized by low species diversity and abundance of key groups such as branching hard corals (Burman *et al.*, 2012), placing them at the lower end of the resilience spectrum, potentially due to low functional redundancy compared to Indo-Pacific reefs (Roff & Mumby, 2012). The propensity of Caribbean reefs to form alternate stable states has implications for ARBM. In particular, slow erosion of resilience via press-type stress (typically overfishing of herbivorous fish and nutrient enrichment, Mumby *et al.*, 2006, 2007) make these systems susceptible to a phase shift triggered by a single pulse disturbance. This is illustrated by a shift from scenario B to C in Fig. 3a. Here, critical management actions can be two-pronged. First, efforts to reduce herbivore over-fishing and nutrient run-off (upward green arrow) can shift the system out of the bistable state regime (C in shaded area in Fig. 3a) and into the single equilibrial state regime (B). Second, enhanced connectivity through networks of protected areas (Almany *et al.*, 2009), local coral restoration (Rinkevich, 2005) and potentially algal removal can potentially push the system (green rightward arrow in scenario C) across the unstable equilibrium (dashed line) from algal to coral domains (Fig. 3a). Restoration efforts and other direct control efforts are likely to be effective only at small spatial scales where a particular reef represents substantial goods and services, and in socio-economic settings characterized by a strong sense of stewardship and political responsibility, for example reefs in Florida (Moberg & Ronnback, 2003). However, once the system is degraded to scenario D, i.e. into the single equilibrial basin dominated by macroalgae, no

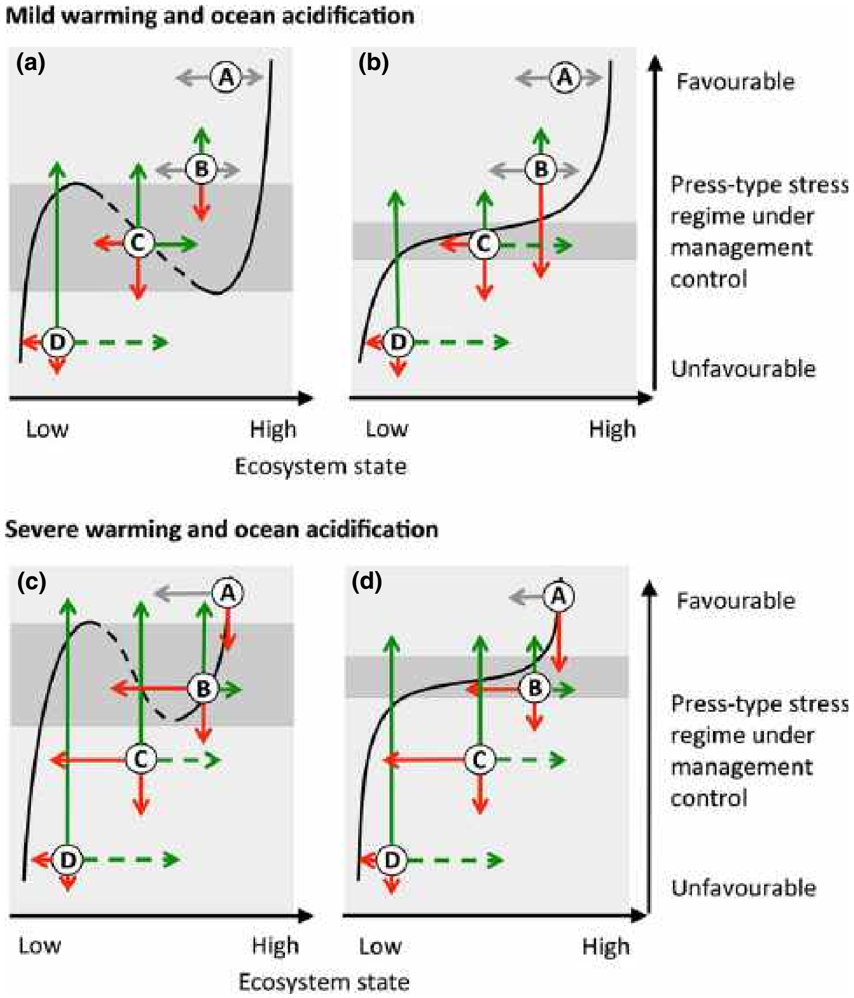

Fig. 3 Two-dimensional conceptual representation of system behaviour for the four environmental scenarios and resilience categories (a–d) in Fig. 1, and management actions needed to improve system condition and resilience under mild and severe climate change and ocean acidification. Solid lines represent stable equilibria (basins of attraction) and the dashed line the unstable equilibrium (threshold). Grey arrows indicate perturbations or environmental changes that do not represent immediate risks. Red arrows are perturbations that can potentially lead to an unwanted phase shift or reinforce an already low (or degraded) ecosystem state, and green arrows are resilience-based management actions (see also text). The lengths of arrows indicate the severity of disturbances (press or pulse), propensity for recovery or efficacy of efforts needed to move the system to the safe side of a threshold. The grey areas represent the conditions where a pulse-type disturbance may trigger a phase shift. The figure is modified from Figs 1 and 2 in Scheffer *et al.* (2001). Thresholds for regime shifts under ocean warming and acidification are guided by model simulations using GBR corals (Anthony *et al.*, 2011).

level of restoration or enhanced connectivity can restore coral resilience (green dashed arrow). The most effective ARBM options for scenario D are management actions that reduce press-type disturbances (upward green arrow in Fig. 3a, actions D and E in Fig. 2). If these measures fail to improve reef condition, adaptation programs that enhance the resilience of reef-dependent communities and explore alternative livelihoods for reef-dependent industries may become the only viable ARBM strategies (action G in Fig. 2).

Reef in the Indo-Pacific are generally assumed to display single equilibrial states (Roff & Mumby, 2012). Managing for resilience in these systems needs to be particularly concerned with the environmental set of conditions that represent a threshold for a regime shifts between coral and algal dominance (Fig. 3b). The shape and location of state equilibria, and hence the width and steepness of the threshold, vary strongly as a function of the nature and strengths of feedbacks in the system (Mumby & Steneck, 2008; Nyström *et al.*, 2008). In general, the prioritization of resilience-based management options for reefs that display single equilibrial states should not differ from those that show alternate stable states if the key ARBM objective is to keep the system in the coral-dominated single-state regime using the precautionary principle (scenario A in Fig. 3a and b).

Importantly, reef systems do not occupy specific locations in the stability landscapes, but are likely to have representatives across the landscapes. For example, the condition of Australia's Great Barrier Reef (GBR) ranges between scenario A and D, depending on geography. Water quality (turbidity, sedimentation, nutrients and other pollutants) in inshore regions of the central and southern GBR has declined in pace with intensified agricultural activities in river basins (catchments) draining into GBR waters (Brodie *et al.*, 2012). In the context of Fig. 3, water quality degradation contributes to the lowering of the suitability of environmental conditions (Fabricius, 2011), i.e. moving the system into a regime with reduced resilience and hence increased likelihood of a shift to an undesirable state (e.g. red arrows from B and C in Fig. 3b). Although herbivorous fishes are not targeted commercially on the GBR, declining water quality inshore suppresses herbivore abundance (Cheal *et al.*, 2013), potentially lowering the threshold for a regime shift. Also, experimental and correlative evidence suggests that outbreaks of crown-of-thorns starfish (CoTS) are linked to inputs of nutrients into the northern/central GBR, promoting the survival and recruitment of CoTS larvae and increased predation of corals GBR-wide (Brodie *et al.*, 2005; Fabricius *et al.*, 2010). This is an example of a press-type stressor leading to consequential pulse-type disturbances. Other hypotheses include reduced top-down control of CoTS in fished areas of the GBR (Pratchett *et al.*, 2014). GBR reef managers have a variety of ARBM options and management levers available. First, primary long-term management levers are actions on drivers or activities (e.g. land-use and coastal development practices) that alleviate press-type stressors (D in Fig. 2). Second, direct control of CoTS can, if effective, reduce the severity of the starfish outbreak (E and F in Fig. 2). Thirdly, large-scale spatial planning, including a network of protected areas (Fernandes *et al.*, 2005), can help maintain key ecosystem goods and services on priority reefs (points F and I in Fig. 2). These actions all contribute to reducing press-type stressors (Table 1, green solid arrows in Fig. 3b). In addition, direct CoTS control on selected reefs by starfish culling (Kenchington & Kelleher, 1992; Pratchett *et al.*, 2014) can, if effective, actively push the system to a higher (coral) state, which in combination with improved water quality can potentially bring the system to, or keep it, on the safe side of the threshold (dashed arrow on C in Fig. 3b).

The GBR and Florida represent socio-economic settings where the links between ecosystem conditions and management decisions and actions are strong, where a sense of stewardship prevails, and where resources are available for monitoring and management actions (McCook *et al.*, 2010). In contrast, reefs in the Coral Triangle (CT) support different social systems, and exist in contrasting political and cultural environments that influence the setting of management goals and objectives. Coral reefs in the CT are some of the richest and most diverse in the world, but many are severely overfished and subject to pollution from urbanization (Burke *et al.*, 2012). Similar to the GBR and the Caribbean, reefs in the CT cover the full span of scenarios in Fig. 3a and b, but different local pressures apply and different ARBM solutions are relevant. In areas with low human populations where traditional marine tenure is strong, reef resilience across broad spatial scales are high because of a relatively low level of local threats and a strong sense of stewardship and ownership of marine resources. Conversely, in heavily populated areas, herbivore overfishing, destructive fishing practices and pollution are important causes of resilience loss on coral reefs, and are priority management levers (Table 2E). In the context of the ARBM framework, two key impediments to ARBM management actions in heavily populated areas are: (i) intense pressures on the ecosystem from a growing coastal population (Fig. 2H), and (ii) a relatively weak sense of stewardship and political responsibility (Fig. 2K). Several approaches to ARBM are needed in the CT. Firstly, education and capacity-building of local communities and regional government bodies are critical (Fig. 2K, Table 2D and G), especially demonstrating how improved reef ecosystem condition can benefit the social-economic system. In addition, economic development and social-political transformations that reduce the external drivers on these factors is essential (Cinner *et al.*, 2009).

ARBM challenges under global environmental change

Ocean warming and ocean acidification are among the most significant long-term threats to coral reefs (Hoegh-Guldberg *et al.*, 2007). While global threat reduction is outside the control of managers, local and regional actions can enhance resilience and adaptive capacity locally. The challenge for ARBM, however, is that ocean warming and acidification influence the stability landscape of coral reef ecosystems (Fig. 3c and d) by directly impacting on processes that underpin resilience. These include reduced coral growth rates (Reynaud *et al.*, 2003; De'ath *et al.*, 2009), enhanced competitive strength of algae over corals (Diaz-Pulido *et al.*, 2011), disease risk (Ritchie, 2006) , reduced net reef accretion (Silverman *et al.*, 2009) and susceptibility to breakage by storms (Madin *et al.*, 2008). Further,

Table 2 Priority levers for adaptive resilience-based management (ARBM) across three geographical and socio-economic examples. Letters D to G refer to intervention points in Fig. 2

	Management levers			
Example	D: Influence drivers and/or activities	E: Reduce stressors	F: Support ecosystem resilience	G: Support social-economic resilience
Great Barrier Reef	Influence national emissions policies through education and awareness-raising around climate change and linkages between land use and run-off	Improve land-use management to reduce pollution in receiving waters; maintained fisheries management	Networks of no-take areas (spatial planning for connectivity and population viability of key species); control CoTS at local scales	Work with fishers and tourism operators to help build resilience in their industries
Coral Triangle	Education of local communities and regional government bodies	Reduce fishing of herbivores; stop destructive fishing practices; reduce pollution	Networks of no-take areas (spatial planning for connectivity and population viability)	Capacity-building of local communities and regional government bodies, support alternative livelihoods
Florida Reef System	Education and awareness-raising around climate change and linkages between land use and land run-off	Reduce nutrient and sediment loads; reduce fishing pressure; manage pressures from recreational use	Coral and reef habitat restoration in combination with networks of no-take areas	Work with local communities and the tourism industry to develop adaptation strategies including livelihood transitioning

nutrient enrichment reduces resistance to thermal stress in corals, which exacerbates bleaching risk (Wooldridge & Done, 2009; Cunning & Baker, 2012). The result is a lowered threshold for local-scale press-type stressors such as pollution and reduced herbivory (Anthony *et al.*, 2011). This is shown in Fig. 3c and d as an upward shift in the environmental threshold. As a consequence, manageable press-type stress conditions that are relatively favourable today may be unfavourable under future ocean warming and acidification. This consequence is illustrated by scenario B in Fig. 3. Under mild warming and acidification, reef systems in scenario B are in the coral-dominated regime for both models (Fig. 3a and b). Without changes in local stressors or management regimes, these reefs will be captured by the shifting environmental threshold as warming and acidification progress (Fig. 3c and d). Similarly, reefs in the bistable regime (Fig. 3a) or near the environmental threshold (Fig. 3b) under mild warming and acidification, are likely to be shifted into the algal-dominated regime under severe warming and acidification. The implications are that ocean warming and acidification will make it increasingly harder for management actions to maintain reefs in a coral-dominated state (illustrated by upward green arrows in Fig. 3c and d). Further, if ocean warming leads to stronger storms (e.g. Knutson *et al.*, 2010) and/or more frequent and severe coral bleaching events (e.g. van Hooidonk & Huber, 2009) the future management challenge will also need to overcome the stronger episodic reductions in reefs state (red leftward arrows in Fig. 3c and d).

One avenue for dealing with the growing challenge of globally driven stressors in an ARBM context is through a spatial understanding of both pulse- and press-type stress exposures, and consequent spatial resilience and options for management planning (McLeod *et al.*, 2012) (Table 1). Here, improved fisheries management and the design of marine protected area networks (supporting ecosystem resilience, Fig. 1f, Table 2F), building on the principles of habitat representation, connectivity and risk spreading (McLeod *et al.*, 2009; Grantham *et al.*, 2013) can improve the sustainability of coral reefs under local-scale human pressures as well as under climate change. Importantly, however, because the zone of influence for local-scale stressors as well as for their management are a fraction of the global zone of influence of climate change and ocean acidification, managers are likely to be forced to increasingly consider prioritization of reef areas with high intrinsic resilience and/or less disturbance-prone reef areas with high connectivity (Game *et al.*, 2008).

Lastly, while global-scale stressors per se can only be addressed at scale through global carbon emissions policies, managers can play an important role in influencing the development of national and global emissions policies by minimizing emissions of management operations and encouraging others to do so through education and by raising awareness (Table 2D).

Discussion

The operational adaptive resilience-based management (ARBM) framework presented here provides a structured approach for incorporating resilience concepts into conservation and natural resource management of coral reefs. Traditionally, biodiversity conservation has been characterized by efforts to reduce a system's exposure to pressures (e.g. Brooks *et al.*, 2006). While this is still valid, the ARBM approach provides a lens that explores a broader set of strategic options to sustain resilience in a changing environment and across socioeconomic settings.

The ARBM framework, building on adaptive management (Argent, 2009) integrated with resilience principles (Folke *et al.*, 2010), bridges the gap between resilience theory and conservation practice by integrating the adaptive management cycle with resilience models (Figs 1 and 2). Although widely applicable, the ARBM framework is not designed to provide a recipe for specific management actions. Instead, it is a structure that guides adaptation of management goals and helps identify management strategies that can better accommodate external system drivers and inte-rnal system dynamics under global environmental change.

Climate change and other accumulating global pressures have caused a re-evaluation of the conceptual model that underpins management decisions on coral reefs. In particular, the pervasive and largely inexorable effects of climate change and ocean acidification challenge the expectation that ameliorating local threats will result in preservation of the system in a desirable state. As indicated by the green arrows in Fig. 3, climate change and ocean acidification (lower panels) will effectively raise the bar for management efforts as resilience becomes eroded (increased press-type stress) and thresholds for regime shifts are shifted. Importantly, however, if resilience becomes eroded by global pressures, most regional and local-scale management actions can only counteract pressures in a fraction of the zone of influence of ocean warming and acidification. Therefore, there are limits to the extent ARBM can maintain reef resilience under climate change and ocean acidification despite navigating a strategic path on the stability landscape in Fig. 3. Also, with limited resources for investment into coral reef management, spatial prioritization (Game *et al.*, 2008) and trade-offs of ecosystem goods and services as desirable states are likely to become increasingly relevant under environmental change.

Conclusions

There is now a robust base of scientific knowledge about the determinants of system resilience of coral reefs (Nyström *et al.*, 2008; Anthony *et al.*, 2011; McClanahan *et al.*, 2012). We apply two alternative stability landscapes for coral reefs to capture generic models across Caribbean and Indo-Pacific reefs, and to provide underpinnings for adaptive resilience-based management across environmental and socio-economic settings. We demonstrate that management of press-type stressors with regional or local-scale levers are the most effective way to enhance resilience, and that driving the system to the safe side of thresholds for regime shifts (whether using the bistable or single equilibrial state model) should be the key objective for ARBM. Where possible, direct action on pulse-type disturbances in addition to remedial action on press-type stressors can be an optimal approach to restoring resilience. Water quality management and direct CoTS control on the GBR, and herbivore fisheries management and reduced nutrient pollution on Caribbean and Indo-Pacific reefs are key examples. Restoration is effective only under environmental conditions within a bistable regime or within a coral-dominated single equilibrial state regime.

In summary, the ARBM framework provides reef conservationists and resource managers with a tool to integrate resilience into decision-making and help prioritize system components for management focus, i.e. management levers. It also enables managers to identify knowledge gaps that are limiting their ability to implement the most effective strategies for reducing system vulnerability. An important application of this framework is the identification of options for increasing overall system resilience by supporting the resilience of industries or communities that depend on ecosystem goods and services – i.e. by facilitating the inclusion of social resilience management into the arsenal of strategies available to coral reef managers. Through application, testing and further development, we believe that this framework will support smarter management actions that in turn will support the resilience of social-ecological systems in a rapidly changing world.

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millennial[5]. To understand the findings of Bordbar and colleagues that initial conditions had regionally differing effects on projections, we need to consider that the Atlantic and the Pacific exert distinct influences on internal variability. For oceans, long-term internal variability involves deep ocean processes, and the DSL is an integrated quantity throughout the entire ocean depth, including the deep layers. The North Atlantic is deep but relatively narrow, whereas the Pacific and tropical oceans are wide but can be considered as relatively shallow due to ocean stratification, which limits vertical mixing. This may explain why initial conditions exert more influence over DSL projections for the North Atlantic than the Pacific (Fig. 1a).

In addition to the single model approach using the Kiel Climate Model[3], Bordbar and colleagues[1] employed the multi-model ensemble approach by looking at similar projections from the CMIP5 models[6]. Their model-to-model comparison of the DSL signal and spread confirms that the Kiel Climate Model is representative of the latest-generation coupled climate models. With the CMIP5 ensemble and additional CO_2 emission scenarios such as RCP4.5 and RCP8.5, model uncertainty can be quantified, as well as the scenario uncertainty[7]. It turns out that all three uncertainty sources are important in centennial DSL projections (Fig. 1b).

This systematic analysis of DSL projections provides a comprehensive understanding of the associated uncertainty and suggests that oceanic initial conditions need to be taken into account for optimal DSL projections. This would require close collaboration between climate-modelling, data-assimilation and ocean-observation communities, particularly in light of the sparse observational data available for the deep ocean. In addition, we need to further and better assess the abilities of different models to reproduce centennial and longer-scale natural variability, as revealed by proxy records and long-term reanalysis data[5]. Filling in such gaps would allow seamless transitions from near-term predictions to long-term projections, and would provide more accurate climate and sea-level information to governments and societies. ❐

Jianjun Yin is in the Department of Geosciences, University of Arizona, Tucson, Arizona 85721, USA.
e-mail: yin@e-mail.arizona.edu

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MARINE BIOLOGY

The coral disease triangle

The underlying causes of biodiversity loss can be numerous and difficult to identify. Now evidence suggests that disease outbreaks triggered by warming oceans are a primary cause of the disappearance of Caribbean coral reefs.

John F. Bruno

Is a warmer world a sicker world? Disease is widely recognized as a primary cause of biodiversity loss and ecosystem degradation in aquatic and terrestrial ecosystems. Rapid, regional population declines in trees, amphibians, mammals and even sea-stars have all been linked to disease outbreaks. One explanation is global warming[1]. Higher than normal temperatures are thought to increase the occurrence and severity of disease outbreaks through several mechanisms, including increased pathogen virulence and weakened host immune systems owing to physiological stresses. Writing in *Nature Climate Change*, Randall and van Woesik[2] report that seemingly subtle increases in ocean temperature have completely altered the seascape of Caribbean reefs by triggering disease outbreaks in crucial, habitat-forming coral species.

Caribbean reefs are primarily built by two types of coral: massive, long-lived colonies of *Orbicella* species (formerly known as *Montastraea*) and fast-growing *Acropora* species, which form branching colonies (Fig. 1). Historically, these two taxa dominated Caribbean reefs, but populations of species from both genera have largely collapsed across the region. Their loss means flatter reefs that no longer provide hiding places for other organisms (including fishes that people eat), do not buffer coastal communities from storms, and cannot grow vertically in response to sea-level rise.

The proximate cause of the *Acropora* decline is white-band disease[3] — a tissue-degrading condition caused by an unknown pathogenic bacterium[4]. Outbreaks of this disease in the Caribbean appeared quite suddenly in the late 1970s and early 1980s, leading reef scientists to suspect that the causative pathogen was introduced to the region, perhaps via the Panama Canal or in ballast water carried by cargo ships. Until now, however, attempts to understand this disease focused almost entirely on the pathogen and largely failed to consider how changing environmental conditions might have facilitated this problem. To investigate these possible influences, Randall and van Woesik combined data from diver-conducted surveys for white-band disease from 473 Caribbean reefs with satellite records of ocean surface temperature. They found that higher temperatures are strongly related to the occurrence of disease — findings that directly link ocean warming with the transformation of an ecosystem at an enormous spatial scale.

Climate change ecologists evaluate how different aspects of temperature are changing to measure global warming. For example, are winters or summer nights less cool? Is the summertime peak a little higher each decade? Are heat waves getting longer or more intense? These different metrics have different potential consequences for people and wildlife. Moreover, for a given

Figure 1 | Colonies of *Orbicella* (left) and *Acropora* (right) corals in the Caribbean. Images courtesy of: left, © Vilainecrevette/Alamy; right, Christian Ziegler/Getty.

species, one metric might be benign while another is deadly. Ecologists rarely know which to investigate beforehand. Randall and van Woesik[2] assessed several 'thermal stress' metrics, including increases in winter minimums, summer maximums and 30-year warming trends, and found that these metrics successfully predicted the observed outbreaks. They also found strong evidence for temperature thresholds that, when exceeded, were likely to trigger disease. For example, colonies of *A. cervicornis* were more likely to be infected if winter ocean temperature was not cooler than 27.5 °C. For *A. palmata*, the winter threshold was 28.5 °C. White-band disease in *A. cervicornis* was also more common when temperature exceeded 33 °C and in *A. palmata* when the long term warming trend was greater than 0.015 °C per year. Increasing winter water temperatures have also been found to be correlated with increased severity of yellow band disease in *Orbicella* corals[1], possibly because cooler winter temperatures impair the pathogen or generally enable corals to recover from summer temperature stress and build up energy reserves.

Defining the relationship between ocean warming and coral disease can be difficult. Numerous aspects of ocean warming and potential response lags need to be considered, as do other factors that can influence where and when outbreaks occur, such as coral abundance, nutrient concentration and water depth[5,6]. If these factors are not accounted for, the fingerprint of temperature can be faint, potentially leading to a false-negative result. The concept that several factors are necessary — but alone are not sufficient — for an outbreak to occur, is called the 'disease triangle'. This idea, which stems from epidemiology, is that the host, the pathogen and the environment all play a part, and all three components need to be considered to understand and manage a disease. In many cases, the environment is itself a complex unit, comprising multiple triggers and other players, such as predators that can transmit the pathogen or create wounds that enable infections[7].

Although ocean warming had not been suspected to be the underlying cause of the observed decline of *Acropora* throughout much of its range — until now — one policy response had already recognized the importance of the environment to the decline of this species. *A. palmata* and *A. cervicornis* have been listed as threatened under the US Endangered Species Act, and the forward-thinking Draft Recovery Plan for these corals[8], released in 2014, recommends that we "curb ocean warming and acidification impacts to health, reproduction, and growth, and possibly curb disease threats, by reducing atmospheric greenhouse gas concentrations." However, the temperature-mitigation criterion (preventing temperature from exceeding 30 °C during spawning periods) was set to limit future or additional stress from bleaching and impaired reproduction, and Randall and van Woesik's findings[2] suggest that this season-specific limit will not prevent further disease outbreaks.

Although we might not be able to directly treat diseased corals or eradicate their pathogens, we can mitigate environmental conditions, such as thermal stress, that enable outbreaks. Randall and van Woesik's clear indication of the correlation between ocean warming and disease outbreaks in corals is further evidence that we need to get serious about our collective response to climate change. A coral-reef recovery plan that responds to their findings would require emissions reductions that would eventually return atmospheric concentrations of CO_2 to below 350 parts per million — the level considered to be the safe limit for coral reef survival[9] and roughly the concentration that had been reached when the white band disease outbreaks began.

John F. Bruno is in the Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA.
e-mail: jbruno@unc.edu

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Thermal Stress and Coral Cover as Drivers of Coral Disease Outbreaks

John F. Bruno[1*], **Elizabeth R. Selig**[2], **Kenneth S. Casey**[3], **Cathie A. Page**[4], **Bette L. Willis**[4], **C. Drew Harvell**[5], **Hugh Sweatman**[6], **Amy M. Melendy**[7]

1 Department of Marine Sciences, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States of America, **2** Curriculum in Ecology and Department of Marine Sciences, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States of America, **3** National Oceanographic Data Center, National Oceanic and Atmospheric Administration, Silver Spring, Maryland, United States of America, **4** Australian Research Council Centre of Excellence in Coral Reef Studies, School of Marine and Tropical Biology, James Cook University, Townsville, Queensland, Australia, **5** Section of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, United States of America, **6** Australian Institute of Marine Science, Townsville, Queensland, Australia, **7** Department of Epidemiology, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States of America

Very little is known about how environmental changes such as increasing temperature affect disease dynamics in the ocean, especially at large spatial scales. We asked whether the frequency of warm temperature anomalies is positively related to the frequency of coral disease across 1,500 km of Australia's Great Barrier Reef. We used a new high-resolution satellite dataset of ocean temperature and 6 y of coral disease and coral cover data from annual surveys of 48 reefs to answer this question. We found a highly significant relationship between the frequencies of warm temperature anomalies and of white syndrome, an emergent disease, or potentially, a group of diseases, of Pacific reef-building corals. The effect of temperature was highly dependent on coral cover because white syndrome outbreaks followed warm years, but only on high (>50%) cover reefs, suggesting an important role of host density as a threshold for outbreaks. Our results indicate that the frequency of temperature anomalies, which is predicted to increase in most tropical oceans, can increase the susceptibility of corals to disease, leading to outbreaks where corals are abundant.

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Introduction

Climatic and oceanographic conditions can modify a wide variety of ecological processes. For example, ocean temperature can control species ranges, the strength of species interactions, the dispersal and survival of marine larvae, and the rates of metabolism and speciation [1–6]. Additionally, anomalously high temperature and other environmental stresses can influence the severity and dynamics of infectious diseases by increasing host susceptibility and pathogen virulence [7,8]. For example, the severity of human epidemics including cholera [9–11] and tick-borne encephalitis [12] are both related to temperature and, possibly, to recent climate change [13]. Temperature and climate change have also been implicated in plant and animal disease outbreaks in both terrestrial and aquatic habitats [7,14–17], and could influence coral disease severity [18–20], potentially accelerating the global loss of coral reefs.

Corals are the foundation species of tropical coral reef ecosystems. They directly facilitate thousands of associated species by generating the physically complex reef structure [21,22]. Reductions in coral abundance can cause rapid loss of reef biodiversity [23]. The hypothesized link between anomalously high temperatures and coral disease outbreaks is supported by small-scale field studies indicating that prevalence and the rate of within-colony spread of several coral diseases are higher during the summer [24–30]. Such seasonal changes in disease severity could be driven in part by higher summertime temperature, but could also be caused by a variety of other abiotic factors that vary seasonally within sites. Additionally, such investigations do not directly address the role of temperature anomalies in driving the conspicuous variability of coral disease severity among years and locations [30–32] that has long intrigued coral reef ecologists. Missing are large-scale, longitudinal investigations that combine long-term monitoring of multiple populations with accurate, fine-grained measurements of local temperature anomalies. Longitudinal studies (i.e., the repeated sampling of individuals or populations) help control for potential confounding factors and inherent temporal variability [33]. Such powerful epidemiological approaches are rarely applied to marine epidemics (but see [34,35]), which has limited our understanding of potential links between temperature and disease outbreaks in the ocean, especially at large spatial scales.

Here we describe a regional-scale test of the hypothesis that ocean temperature can influence disease frequency. We analyzed the relationship between the frequency of white syndrome in scleractinian corals and of warm temperature anomalies across the Great Barrier Reef (GBR). Forty-eight reefs were monitored for 6 y (1998–2004), and reef-specific

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Abbreviations: GBR, Great Barrier Reef; OISST, Optimum Interpolation Sea Surface Temperature; SST, sea surface temperature; WSSTA, weekly sea surface temperature anomaly

* To whom correspondence should be addressed. E-mail: jbruno@unc.edu

Author Summary

Coral reefs have been decimated over the last several decades. The global decline of reef-building corals is of particular concern. Infectious diseases are thought to be key to this mass coral mortality, and many reef ecologists suspect that anomalously high ocean temperatures contribute to the increased incidence and severity of disease outbreaks. This hypothesis is supported by local observations—for example, that some coral diseases become more prevalent in the summertime—but it has never been tested at large spatial scales or over relatively long periods. We tested the temperature–disease hypothesis by combining 6 years of survey data from reefs across 1,500 kilometers of Australia's Great Barrier Reef with a new ocean temperature database derived from satellite measurements. Our results indicate that major outbreaks of the coral disease white syndrome only occurred on reefs with high coral cover after especially warm years. The disease was usually absent on cooler, low-cover reefs. Our results suggest that climate change could be increasing the severity of disease in the ocean, leading to a decline in the health of marine ecosystems and the loss of the resources and services humans derive from them.

weekly sea surface temperature anomalies (WSSTAs; the frequency of deviations ≥ 1 °C) were derived from a satellite sea surface temperature (SST) database. White syndrome is an emerging disease of Pacific reef-building corals, reported in 17 species from families including Acroporidae, Pocilloporidae, and Faviidae, which comprise the majority of dominant species on the GBR [30]. Severe white syndrome outbreaks can affect coral composition and cover [30]. Little is known about the etiology of white syndrome, although it is presumably infectious and the characteristics are similar to Caribbean white diseases such as white band and white plague [36]. Like the Caribbean white diseases, white syndrome could comprise a group of distinct diseases with similar signs [30]. White syndrome can cause either partial or whole colony mortality and is characterized by a white band of tissue or recently exposed skeleton that moves across the colony as the disease progresses [30,37].

Results

White syndrome has been present on the GBR since at least the beginning of systematic disease monitoring in 1998, but its frequency increased 20-fold in 2002 [30]. This rise came after a year in which the region experienced its second warmest summer in the 20-y satellite record, with 58% of reefs having weekly anomalies of 1 °C or higher. However, even during the peak of the outbreak, there was considerable variation in disease frequency among reefs (0 to 343 cases per 1,500 m^2) (Figure 1B). WSSTA also varied substantially among reefs, especially during the warm summers of 1998/1999 and 2001/2002 when some reefs were anomalously warm for 30 wk of the year, but the weekly temperatures on many others never deviated from the long-term local averages (i.e., WSSTA $= 0$).

Reefs with relatively high coral cover and WSSTA had the greatest white syndrome frequency (Table 1). From the negative binomial regression model, the parameter estimates for the three covariates (WSSTA, coral cover, and the interaction between the two) were positive (i.e., they predicted an increase in frequency) and highly significant (all $p < 0.000$; Table 2). The interaction term (WSSTA × coral cover) explained a statistically significant amount of the increase in frequency of disease among all the covariates in the model ($\chi^2 = 17.49$, $df = 1$, $p < 0.0000$). The deviance statistic for the negative binomial model was 1.0201, suggesting a very good fit to the data. Disease frequency predicted for nine WSSTA–coral cover combinations (based on the tenth, 50th, and 90th observed quintiles of these covariates) is presented in Table 3. The observed and predicted values indicate that disease frequency only increases substantially with the combination of extreme levels of both covariates. The model is a fairly conservative predictor of this relationship because the observed number of cases with high WSSTA and high coral cover (Table 1) was actually higher than predicted by the model.

Discussion

Influence of Warm Temperature Anomalies

The frequency of warm temperature anomalies was positively related to white syndrome frequency across the GBR. The disease surveys documented considerable variation in white syndrome frequency (0 to 343 cases per 1,500 m^2) among years and reefs. Our results suggest that this variance was caused in part by the number of warm temperature anomalies during the year preceding the disease surveys. A positive effect of high temperature on the severity of coral disease outbreaks might be caused by physiological stress impairing host immunity [8,38,39]. WSSTA, our metric of thermal stress, is based on the frequency of warm anomalies of 1 °C or higher because short-term temperature increases of this degree can cause measurable physiological stress in a coral host [40–46]. WSSTA summarized temperature anomalies throughout the year, including winter anomalies that might also affect the susceptibility of corals to disease [46]. Increased densities of symbiotic dinoflagellate algae (zooxanthellae) at the beginning of winter and the subsequent accumulation of coral-tissue biomass throughout cooler months are thought to influence coral responses to future stresses [47]. These processes are compromised by longer warm periods during the summer or warmer than usual winter temperatures [45]. In fact, winter warming could have the dual effect of predisposing hosts to disease and facilitating more rapid pathogen growth [7]. Summertime anomalies could also increase pathogen virulence by initiating virulence factors [48] or increasing the growth of pathogens [39] for which the normal summertime temperature is below the thermal optima.

Influence of Coral Cover

Our results also indicate that thermal stress is necessary, but not sufficient, for white syndrome outbreaks to occur. Coral cover must also be high; generally 50% or higher (Table 1). White syndrome was uncommon during the 12 mo after the summer of 1998/1999 when WSSTAs were more frequent and occurred at more sites than during 2002/2003. But in 1998/1999, total coral cover was less than 50% at the 20 reefs with the highest WSSTA (Figure 2A), and there was a weak negative relationship between WSSTA and cover ($p = 0.09$, linear regression analysis; Figure 2A). In contrast, in 2002/2003, there was a positive association between WSSTA and coral cover ($p = 0.05$, Figure 2B). This was possible because

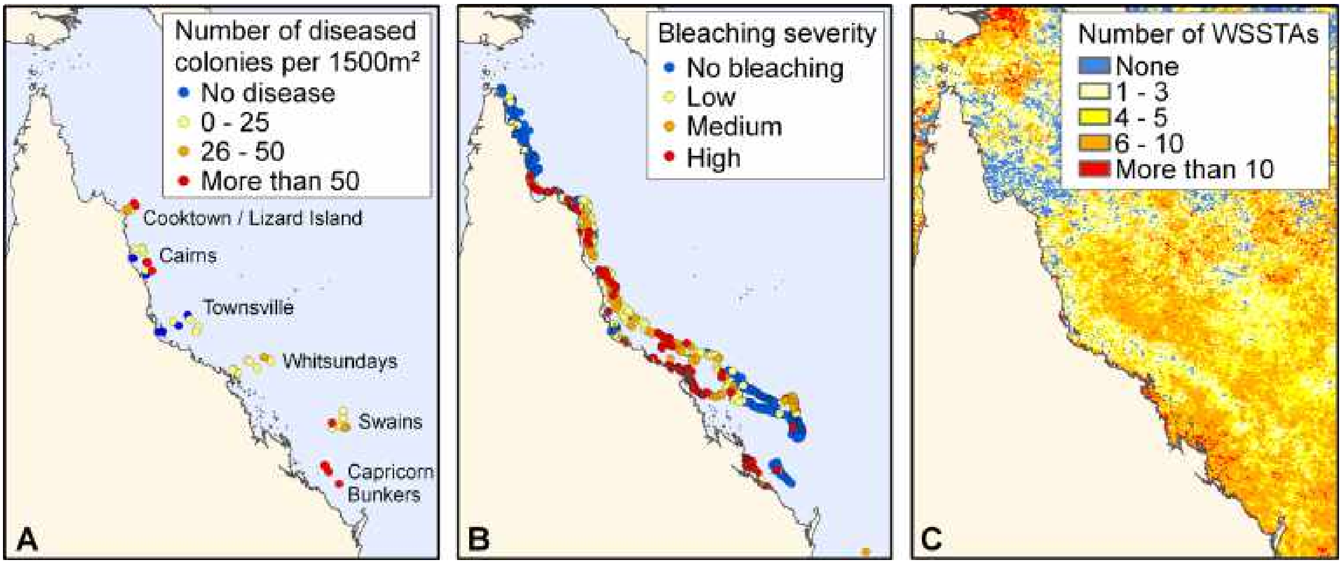

Figure 1. Study Sites and Disease Conditions during the Peak of White Syndrome Frequency in 2002

(A) Frequency of white syndrome cases from March 2002 to March 2003; (B) bleaching intensity for scleractinian coral in March 2002 (modified from Berkelmans et al., 2004 [73]); and (C) WSSTAs in 2002.
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there was no reef-specific correlation of WSSTA between 1998/1999 and 2002/2003 ($p = 0.90$, Figure 2C).

Total coral cover is a reasonable estimation of host abundance in this system because the susceptible species are the competitively dominant space holders [30,49]. A positive relationship between host density and disease prevalence has been clearly demonstrated in many host-pathogen systems [35,50–52], and is considered a hallmark of the infectious process [53]. High host density can have several effects on disease dynamics. For example, it is most often associated with greater rates of horizontal transmission [54–56], leading to localized increases in prevalence. High coral cover reduces the distance between neighboring coral colonies [57] and thus between infected and healthy hosts, increasing the potential for horizontal disease transmission between corals in close proximity. In addition, host density can be positively related to the density of disease vectors [58,59], although no specific vector(s) have been identified for white syndrome.

Independent of host density, total coral cover itself, including the abundance of nonsusceptible individuals and species, might also be causally linked with increased white syndrome frequency. A wide variety of biological properties of coral reefs are related to coral cover. For example, the abundance and composition of fishes and invertebrates that could act as disease vectors are tightly linked with total coral cover and reef heterogeneity [21,23]. Competitive interactions among corals increase nearly exponentially with total coral cover and, on the GBR, are relatively rare when cover is below 50% [57]. Corals compete directly by damaging the tissue of neighboring colonies with tentacles and digestive filaments [60]. These encounters usually cause lesions and local tissue necrosis [60] that could facilitate pathogen transmission and colony infection. Additionally, uninfected hosts likely experience physiological stress and a reduction in fitness on high-cover reefs from such direct competitive encounters [61] as well as from indirect competition such as shading [60], which could also reduce disease resistance.

Regardless of the relative importance of these and other potential mechanisms for increased host susceptibility or disease transmission where coral cover is high, there is a cover threshold of approximately 50% (Table 1) for white syndrome outbreaks and, frequently, even for the occurrence of this disease on a reef. No white syndrome cases were recorded on 45% of the reefs with cover less than 50% ($n =$ 235). In contrast, 88% of reefs with cover greater than 50%

Table 1. Observed Number of White Syndrome Cases

WSSTA	Coral Cover (%)		
	0–24	25–49	50–75
0 WSSTAs	0.9 ± 0.3 (24)	0.9 ± 0.3 (18)	10.4 ± 4.8 (7)
<5 WSSTAs	3.6 ± 1.2 (53)	9.8 ± 3.2 (40)	23.3 ± 5.7 (21)
≥5 WSSTAs	4.7 ± 2.1 (49)	4.5 ± 1.0 (50)	80.1 ± 27.3 (20)

Values are the mean number of white syndrome cases/1,500 m^2 ± 1 SE as a function of WSSTA and coral cover. Values in parentheses are the number of sampled reefs in each category.
doi:10.1371/journal.pbio.0050124.t001

Table 2. Coefficient Estimates

Parameter	Estimate	Standard Error	*p*-Value (Wald)
Intercept	1.776	0.232	< 0.000
WSSTA	0.875	0.023	< 0.000
Coral cover	1.034	0.005	< 0.000
Coral cover × WSSTA	1.003	0.001	< 0.000

Results of the negative binomial regression population-averaged model. Model-based standard errors (SE) are also shown.
doi:10.1371/journal.pbio.0050124.t002

Table 3. Predicted Number of White Syndrome Cases

WSSTA	Coral Cover (%)		
	9.2	25.8	56.6
0	5.1	6.2	10.7
3	4.9	6.1	11.0
18	4.9	8.2	28.7

Values are the predicted number of white syndrome cases/1,500 m^2 based on negative binomial regression model as a function of WSSTA and coral cover. Low, medium, and high values of each covariate represent the tenth, 50th, and 90th quintiles of the data.
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had at least one infected colony ($n = 47$). Such thresholds for pathogen colonization or persistence based on host density or other factors are theoretically predicted and typical of the dynamics of many wildlife diseases [8,35].

The technique used to measure the intensity of community-wide white syndrome outbreaks (i.e., counting the number of infected colonies) could lead to a spurious relationship between coral cover and disease frequency, since more colonies could be sampled at higher-cover reefs. This potential artifact was accounted for by including coral cover as a covariate in the statistical model. Additionally, our results indicate that this potential sampling effect did not occur, or at least was undetectable. For example, disease frequency is very low and essentially constant across reefs with coral cover ranging from 0% to 50% (Table 1). Furthermore, the significant WSSTA × coral cover interaction term indicates that the coral cover effect was nonadditive. Finally, on the GBR and other Indo-Pacific reefs, coral cover and colony density generally are not positively related [62]. During the early stages of reef recovery after a major disturbance when nearly all colonies are small and coral cover is very low [62], colony density and cover can be positively related [57,63]. However, when coral cover is high, reefs are usually dominated by large colonies [62], and density and cover are typically negatively related [57]. On the GBR, this frequently observed parabolic relationship between coral cover and colony density is caused by the domination of high-cover reefs by large tabular colonies that exclude smaller non-tabulate species [49]. This was the case in our study on the highest cover reefs in the Cooktown/Lizard Island and Capricorn Bunkers sectors (Figure 1A) where most of the white syndrome outbreaks occurred (C. Page, personal communication). Therefore, our sampling design could in fact *underestimate* disease severity on very high-cover reefs, diminishing the measured importance of coral cover.

Ocean Temperature and the Impacts of Disease

Diseases can cause dramatic changes in host populations and can have lasting effects on the structure and functioning of marine ecosystems by reducing the abundance of keystone consumers and habitat-forming foundation species [19,53,64,65]. For example, a pandemic wasting disease of eelgrass populations in the 1930s caused widespread losses along the Atlantic coasts of Canada, the United States, and Europe [66]. In some affected areas, the disease was estimated to have reduced stands to less than 1% of their normal abundance [67]. Oyster diseases in the Chesapeake Bay, where the pathogen *Perkinsus marinus* has caused annual mortality ranging from 24% to 57%, contributed to the commercial collapse of the regional oyster industry and to the regional loss of oyster reef habitat [68]. Similarly, an unidentified disease decimated populations of the keystone herbivore *Diadema antillarum* in the 1980s throughout the Caribbean [69,70]. During the same time period, white band disease dramatically reduced the abundance of the two most abundant Caribbean corals, *Acropora palmata* and *A. cervicornis,* causing changes in reef structure unprecedented in the last 3,000 y [71,72].

The impacts of marine epidemics could increase if warm temperature anomalies become more frequent or extreme [13,18,19] as predicted by several climate change models [41]. Additionally, temperature could have locally additive or even synergistic impacts if the prevalence of disease or multiple diseases and non-infectious bleaching is increased by warm temperature anomalies [29,38]. For example, bleached corals could be more susceptible to infection [38]. The peak of the white syndrome outbreak occurred after the very warm austral summer of 2001/2002, concomitant with the most severe bleaching episode—in terms of number of reefs affected and intensity of bleaching—ever recorded on the GBR [73]. On some reefs, bleaching and outbreaks of atramentous necrosis, another GBR coral disease, occurred nearly simultaneously [29]. But surprisingly, across the GBR, there was little spatial concordance between bleaching and white syndrome severity in 2001/2002. The most intensive bleaching during 2001/2002 was concentrated in the central latitudes [73] where white syndrome frequency was generally

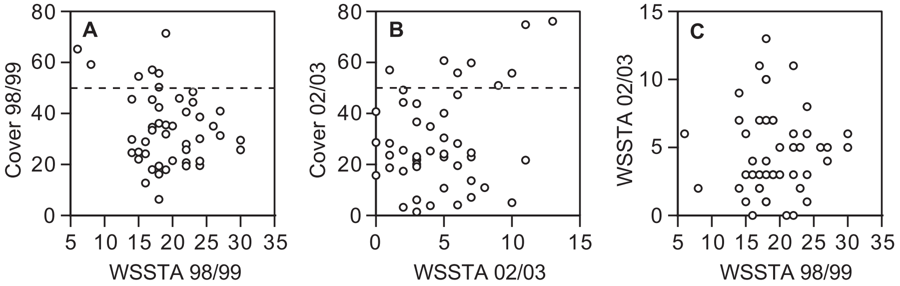

Figure 2. Relationship between Coral Cover and Thermal Stress

(A and B) Relationships between thermal stress (number of WSSTAs) and total scleractinian coral cover during the two warmest summers of the study. Dashed line represents the empirical cover threshold of 50% that is generally required for high white syndrome frequency.
(C) Relationship of thermal stress between the summers of 1998/1999 and 2002/2003 at 48 reefs on the GBR.
doi:10.1371/journal.pbio.0050124.g002

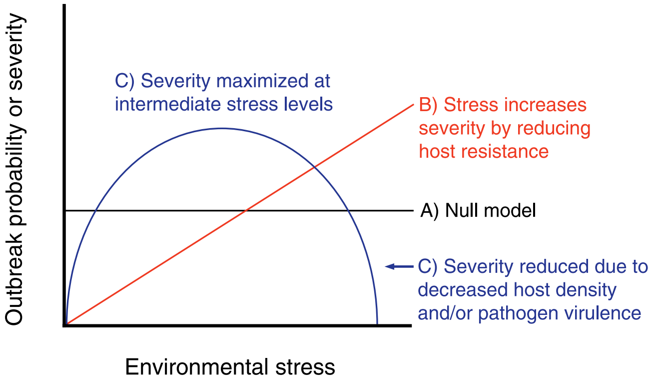

Figure 3. Predicted Effects of Environmental Stress on Disease Severity

Conceptual model of potential effects of environmental stress (magnitude or frequency) on the probability or severity (e.g., prevalence or impacts on host populations) of disease outbreaks. The model includes three possible scenarios: (A) the null model of no effect, (B) a positive, linear effect of stress such as when host density is unrelated to incidence and when the pathogen is not negatively affected by the stress, and (C) a parabolic stress effect.

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very low (Figure 1). In contrast, there was little or no bleaching on reefs in the southern GBR, including the Capricorn Bunkers sector, where white syndrome outbreaks were most severe (Figure 1). The causes of this negative correlation are unclear, but could include variable host susceptibility, local species composition, thermal history, and prior disturbances. Regardless of potential causes, the segregation of these two impacts of anomalously high temperatures might limit local coral loss, but could lead to additive net declines in coral cover across the region.

Alternatively, rising ocean temperature or an increase in summertime anomalies could inhibit marine epidemics. Environmental stress is often assumed to increase disease severity, but stresses that directly reduce host density can have the opposite effect [8] (Figure 3). The role of coral cover in mediating the influence of temperature on disease frequency suggests that temperature could have an important inhibitory effect on white syndrome via bleaching-induced coral mortality. High temperatures only 1–2 °C above the normal summer maximum can cause bleaching and mass coral mortality [41,42], leading to a reduction in host density and total coral cover. Therefore, anomalously high water temperature could, in contrast to our results, reduce the prevalence of coral diseases with host density or coral cover thresholds. However, host density is not always related to the spread of disease, such as when the disease is not infectious, if local secondary transmission is rare, and when pathogens originate outside the local host population or in other host species [8]. In such cases, the relationship between stress and disease severity is generally predicted to be positive [8] (Figure 3).

Environmental stress can also reduce the intensity or probability of outbreaks by negatively affecting pathogen fitness or virulence [8]. It is possible that coral pathogens are negatively affected by anomalously high water temperature. In fact, laboratory studies have found that beyond thermal optima, coral pathogens can have reduced photosynthetic [74] and growth rates [39]. Direct, negative effects of environmental stresses on either hosts or pathogens could cause a parabolic relationship between the magnitude or frequency of environmental stresses and disease incidence, with outbreaks occurring mainly at intermediate stress levels (Figure 3). Thus, future increases in thermal anomalies or other forms of environmental stress could decrease the probability and severity of marine epidemics.

Paradoxically, management activities that increase host abundance could facilitate epidemics. Indeed, most of the major coral reef epidemics over the last 20 y have been of high-density hosts. Caribbean examples include acroporid white band disease outbreaks [71], the *D. antillarum* epidemic [69,70], and sea fan aspergillosis [75]. Once the density of these hosts was sufficiently diminished, prevalence often decreased [34], and host populations began to recover [76,77].

Conclusions

Warm temperature anomalies and coral cover are clearly important drivers of white syndrome on the GBR. No previous study has demonstrated a link between ocean temperature and coral disease dynamics, especially at regional spatial scales. Our results are supported by basic epidemiological principles, and could apply to other coral disease systems and to disease ecology in general. However, coral disease dynamics are likely to be affected by a variety of biotic and abiotic factors, the relative importance of which will vary among regions, scales, and species [32]. In some locations, coral disease outbreaks are apparently decoupled from temperature, and several other factors are also known or suspected to influence the dynamics of coral and other marine diseases [19]. For example, the severity of at least three coral diseases is linked with nutrient concentrations [25,32,75], whereas the frequency of others, like white syndrome, is greatest on remote reefs in highly oligotrophic waters [30].

Coral reefs around the world have been dramatically transformed over the last several decades as coral cover decreased and reefs became dominated by macroalgae [71,78–80]. These changes affect entire coral reef ecosystems, resulting in declines in biodiversity, fisheries yield, and other ecosystem services [81]. Our results indicate warm temperature anomalies can drive outbreaks of coral disease under conditions of high coral cover. The general increase in coral disease prevalence and the emergence of several new coral diseases over the last two decades [20,82,83] could also have been caused in part by thermal anomalies. Deciphering these and other effects of increasing temperature on disease dynamics in the ocean presents an urgent challenge to marine scientists.

Materials and Methods

Disease and coral cover surveys. Surveys of white syndrome frequency and total coral cover (i.e., the percentage of the bottom covered by living scleractinian corals) were performed by the Australian Institute of Marine Science Long-term Monitoring Program. The 48 surveyed reefs are grouped within six latitudinal sectors that span nearly 1,500 km of the GBR from 14° S to 24° S (Figure 1A). Surveys were performed annually between 1998 and 2004 using SCUBA along a depth contour of 6 to 9 m on the northeast flank of each reef. The frequency of white syndrome cases on each reef (number/1,500 m^2) was measured by counting the number of infected colonies within 15 permanent 50-m × 2-m belt transects [30,84]. The percentage of the substrate covered with living, hard (scleractinian) coral tissue was quantified on 15 permanent 50-m transects, within a 25-cm-wide belt along the transect using a video camera [85]. A point sampling technique was then used to estimate live coral cover from the videos in the laboratory [85].

Satellite temperature database and thermal stress metric. We derived weekly sea surface temperature values for each reef from a newly developed 4-km Advanced Very High Resolution Radiometer Pathfinder temperature anomaly dataset (Version 5.0) developed by the National Oceanic and Atmospheric Association and the University of Miami's Rosenstiel School of Marine and Atmospheric Science. This dataset covers the longest time period (1985–2004) at the highest resolution of any consistently processed, global satellite temperature dataset. We used nighttime, weekly-averaged values with a quality level of four or better [86]. Some plausible values were given low-quality levels by the Pathfinder algorithm, which eliminates any observation with an SST more than 2 °C different than a relatively coarse resolution SST field based on the Version 2 Reynolds Optimum Interpolation Sea Surface Temperature (OISST) value, a long-term, in situ–based dataset [86,87]. Therefore, we included observations if the SST was greater than the OISST, but less than the OISST + 5 °C. Gaps in the record caused by persistent cloudiness were filled using simple temporal interpolation to provide a complete weekly time series at each reef spanning 1985–2004.

We generated a 19-y, weekly SST climatology (i.e., a long-term record) for the 4×4-km grid cell that encompassed each reef. A 5-wk running mean was then used to smooth each gap-free climatology to minimize any unusual fluctuations caused by periods of limited data availability. Although thermal stress metrics have been created to predict bleaching events from satellite SST data [73,88,89], little is known about the thresholds relevant to coral disease. In general, increases of 0.5–1.5 °C for several weeks can induce coral bleaching [42]. We assumed that temperatures that may lead to bleaching and physiological stress in corals [42,45] could also potentially increase susceptibility to disease [7].

In a pilot study, we created 16 different metrics of thermal stress. After initial screening, Akaike Information Criteria (AIC) identified WSSTA as the metric that best explained the relationship between temperature and disease (three of the other metrics and the selection procedure are described in [37]). WSSTA quantified the frequency of high-temperature anomalies experienced by coral hosts and by the potential white syndrome pathogen(s), during the 52 wk prior to the annual disease surveys. WSSTAs represent the number of annual deviations of 1 °C or higher from a mean climatology calculated from records between 1985 and 2004 for that calendar week at that reef. Thus, the metric is both week specific and location specific, and considers deviations from local climatological averages, i.e., typical SST throughout the year, including wintertime high-temperature anomalies that could also influence coral fitness and susceptibility to infection [46]. Because recent field and laboratory studies indicate that corals on the GBR are significantly adapted to local thermal conditions [43,90], we based WSSTA on the local SST climatology created independently for each of the 48 reefs. Furthermore, our long-term, fine-grained measurements of SST and SST anomalies match the scale of the biological surveys, eliminating the usual mismatch between climate and health data that has plagued similar studies of human and wildlife disease dynamics [91].

Statistical analysis. We used negative binomial regression to model the relationship between thermal stress and coral cover and the frequency of white syndrome cases (i.e., the number/1,500 m^2). Negative binomial regression was ideal for this analysis because the dependent variable was continuous and overdispersed (i.e., the variance exceeds the mean). The covariates in the model included WSSTA, coral cover, and the interaction term, which represents the multiplicative relationship between coral cover and temperature. Because there is a biologically plausible mechanism by which an interaction between coral cover and temperature could affect the overall outcome (i.e., the influence of thermal stress could be coral cover dependent), it was important to include this interaction as a covariate. A host density threshold is a common signature of infectious disease outbreaks of humans and other marine taxa such as viral diseases of seals [50,52,53]. Total coral cover or the abundance of susceptible species could both influence disease frequency and the effect of temperature on frequency. Coral cover was also included in the model to account for the potential positive relationship between cover and disease frequency based solely on the fact that the number of surveyed colonies may have increased with coral cover.

Because the individual sampling units (reefs) were nested within larger groupings (sectors), this factor was included as a stratification variable to control for the main effect of variance within and between sectors. We used the general estimating equations (GEE) (i.e., population averaged) to estimate parameters of the negative binomial model, which accounted for the repeated measurement of the individual sampling unit (reefs, each sampled once a year for six consecutive years). An autocorrelative structure was initially included; however, the parameter was sufficiently close to zero (0.01 ± 0.05 standard error [SE]) to consider the autocorrelative effects negligible, and thus was not included in the final model. We also calculated a deviance statistic (i.e., deviance/degrees of freedom) to assess the goodness of fit of the model. If the model and the designated distribution are correct, this value should be approximately 1.0.

Many longitudinal datasets with continuous dependent variables are modeled using Poisson regression [33]. However, the variance structure of the related regression model, the negative binomial, includes a random dispersion term and is thus more flexible and appropriate in assessing the relationship between the covariates and an overdispersed dependent variable [92,93]. We did run a Poisson regression model, and the deviance statistic was 24.4203, indicating a poor fit to the data. Zero inflation, that is, the possibility of the existence of a population of hosts for which the outcome cannot happen (e.g., reefs with no susceptible individuals), was also of potential concern. To address this issue, we fit zero-inflated negative binomial and Poisson regression models. There was no difference in parameter estimates from the standard models; thus, the simplest negative binomial model was used in the final analysis. All regression analyses were conducted using Intercooled Stata 9.1 (Stata Corporation, http://www.stata.com).

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Reef-coral refugia in a rapidly changing ocean

CHRIS CACCIAPAGLIA and ROBERT VAN WOESIK

Department of Biological Sciences, Florida Institute of Technology, 150 West University Blvd, Melbourne, FL 32901, USA

Abstract

This study sought to identify climate-change thermal-stress refugia for reef corals in the Indian and Pacific Oceans. A species distribution modeling approach was used to identify refugia for 12 coral species that differed considerably in their local response to thermal stress. We hypothesized that the local response of coral species to thermal stress might be similarly reflected as a regional response to climate change. We assessed the contemporary geographic range of each species and determined their temperature and irradiance preferences using a *k*-fold algorithm to randomly select training and evaluation sites. That information was applied to downscaled outputs of global climate models to predict where each species is likely to exist by the year 2100. Our model was run with and without a 1 °C capacity to adapt to the rising ocean temperature. The results show a positive exponential relationship between the current area of habitat that coral species occupy and the predicted area of habitat that they will occupy by 2100. There was considerable decoupling between scales of response, however, and with further ocean warming some 'winners' at local scales will likely become 'losers' at regional scales. We predicted that nine of the 12 species examined will lose 24–50% of their current habitat. Most reductions are predicted to occur between the latitudes 5–15°, in both hemispheres. Yet when we modeled a 1 °C capacity to adapt, two ubiquitous species, *Acropora hyacinthus* and *Acropora digitifera*, were predicted to retain much of their current habitat. By contrast, the thermally tolerant *Porites lobata* is expected to increase its current distribution by 14%, particularly southward along the east and west coasts of Australia. Five areas were identified as Indian Ocean refugia, and seven areas were identified as Pacific Ocean refugia for reef corals under climate change. All 12 of these reef-coral refugia deserve high-conservation status.

Keywords: climate, corals, persistence, refugia, temperature

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Introduction

Coral reefs support the world's most diverse marine assemblages, and they provide goods and services for adjacent human populations (Costanza *et al*., 1997; Costanza *et al*., 2014). However, rapid climate change is increasing the frequency and intensity of temperature anomalies and is consequently causing coral mortality and changes to the species composition of many coral reefs worldwide (Loya *et al*., 2001; Hughes *et al*., 2003; Hoegh-Guldberg *et al*., 2007). Indeed, the Intergovernmental Panel on Climate Change (IPCC, 2013) has shown that the average ocean surface temperature has increased by 0.11 °C (±0.09 to 0.13 °C) per decade over the last 60 years. This rate of change is highly likely to increase under a 'business as usual' climate-change scenario, identified as Representative Concentration Pathway (RCP) 8.5 (Fig. 1).

The average sea surface temperature (SST) is predicted to increase 3.1 °C by 2100, under a RCP 8.5 climate-change scenario, if radiative forcing continues to rise, without stabilization and mitigation. Such a rapid rate of ocean warming has been unprecedented in the past several hundred millennia (Hoegh-Guldberg *et al*., 2007), and some authors suggest that corals on modern coral reefs are at the highest risk of extinction since the Cretaceous–Tertiary mass extinction event, approximately 65 million years ago (Veron, 1995, 2008; Wood, 1999). Hoegh-Guldberg *et al*. (2007) even suggested that because corals are already living near their thermal maximum, further increases in temperatures will most likely lead to local, regional, and even global extinction of many coral species.

Thermal stress

The global models that examine climate-change effects on reef corals rightly express concern that ocean warming will have serious consequences. Yet most global models suggest that few reef corals will survive beyond the 2 °C temperature rise predicted for the tropical oceans within the next hundred years (Frieler *et al*., 2012). Such predictions, however, disagree with field studies of climate-change impacts on coral reefs that show persistence in some regions (Thompson & van Woesik, 2009; McClanahan *et al*., 2011; Pandolfi *et al*., 2011) and persistence in some habitats (van Woesik *et al*., 2012a). The disagreement between the global

Correspondence: Robert van Woesik, tel. + 1 321 674 7475, fax: + 1 321 674 7238, e-mail: rvw@fit.edu

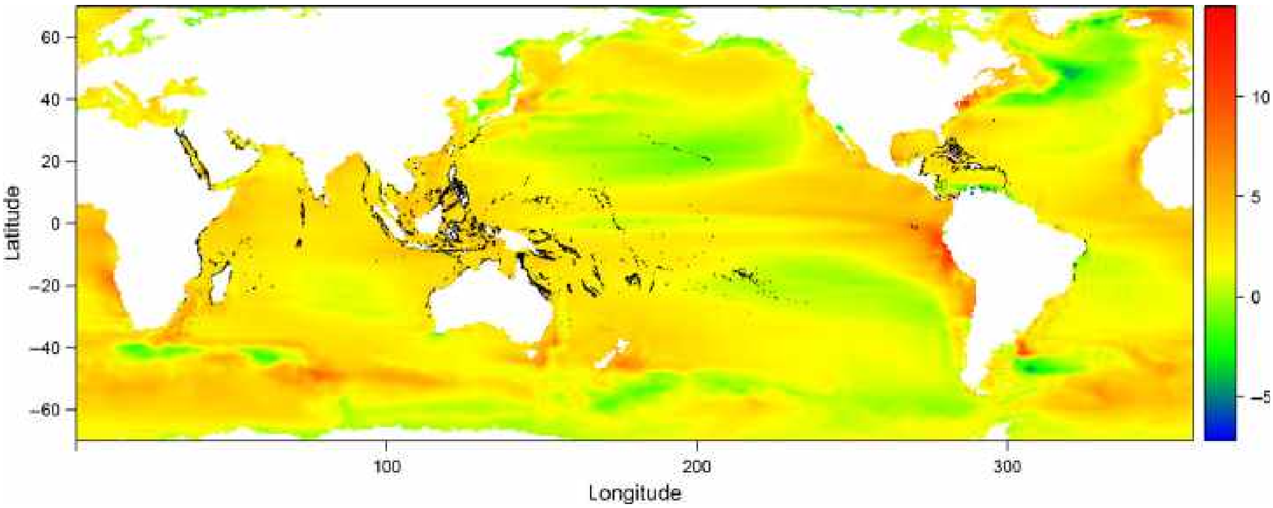

Fig. 1 Predicted change in mean sea surface temperature (°C) between 2012 and 2100 under a Representative Concentration Pathway 8.5 'business as usual' climate-change scenario. The black dots are where modern coral reefs are located. Sea surface temperature data were gathered from Bio-Ocean Rasters for Analysis of Climate and Environment (ORACLE, http://www.oracle.ugent.be/). Current raster data from Bio-ORACLE were derived from Aqua-Moderate Resolution Imaging Spectroradiometer (MODIS) satellite for the years 2002–2009 (Tyberghein *et al.*, 2012), which are in grids of 5 arc min (*c.* 9.2 km). Sea surface temperature data predicted for 2100 (using an A2 scenario, >800 ppm CO_2) were downloaded from http://www.oracle.ugent.be/download.html; these data stemmed from the World Climate Research Programme Coupled Model Intercomparison Project (WCRP CMIP3) multi-model database (http://esg.llnl.gov:8080/index.jsp).

models and contemporary field studies is likely a consequence of the global models treating the tropical oceans as homogenous, and the large 'pixel' size of the global models (ranging from ~2500 to 49 000 km^2), which therefore ignore refugia on coral reefs that are generally found at a local scale of 10–100 km^2 (van Woesik *et al.*, 2012a).

Thermal stresses have been spatially variable in the oceans in the past and are likely to be spatially variable in the future (Thompson & van Woesik, 2009). For example, reef corals in Kenya have been subjected to frequent and extreme thermal-stress events, particularly in 1998, which caused extensive coral bleaching and mortality (McClanahan *et al.*, 2007). By contrast, corals on reefs south of Kenya, in Mozambique and Madagascar, have been subjected to fewer and less extreme thermal anomalies than Kenya (Maina *et al.*, 2008) and have consequently shown less extensive coral bleaching and mortality (McClanahan *et al.*, 2011). Similarly the eastern and central tropical Pacific Ocean, including the Marshall Islands, have experienced frequent (3–5 years) anomalously high temperatures over the last few decades, whereas in Micronesia (Pohnpei, Kosrae, Chuuk, and Yap), west of the Marshall Islands, the anomalously high temperatures have been less frequent (~50 years) (Thompson & van Woesik, 2009). Still, the western Pacific Ocean has been warming faster than elsewhere (England *et al.*, 2014), and extensive bleaching has been recorded in the coral triangle (Guest *et al.*, 2012), which includes the Philippines and Indonesia, supporting the world's most diverse reefs. Such spatial and temporal variability prompts the critical question: Where are the climate-change refugia? Indeed, one of the most immediate challenges we face with a rapidly changing climate is to predict where coral species are most likely to survive, and then protect those refugia from regional and local impacts.

Refugia

Refugia have been defined as areas that will support reef-coral populations, and to which reef corals can retreat to, persist in, and subsequently expand from, under changing environmental conditions (Ashcroft, 2010; Keppel *et al.*, 2012). Refugia can be identified by either: (1) examining biogeographic patterns using paleo-proxies (Mosblech *et al.*, 2011) or genetic markers (Avise, 2000), or (2) investigating the processes that are likely to create refugia. The first approach has been useful to examine refugia through glacial and interglacial events (Colinvaux *et al.*, 1997), whereas the latter approach is potentially more useful for identifying contemporary and future refugia, which are a consequence of unprecedented rates of environmental change that are caused by the emissions of greenhouse gases (Keppel *et al.*, 2012).

Refugia can be defined as either macrorefugia or microrefugia (Mosblech *et al.*, 2011). Macrorefugia are commensurate with the regional scales of global climate models, whereas microrefugia usually exist at local scales (van Woesik *et al.*, 2012a). Macrorefugia are viewed as large areas where the current climatic conditions are maintained by the year 2100 and hence will allow organisms to persist without the necessity to rapidly adapt. Microrefugia are similar to macrorefugia, in that they allow organisms to persist under climate change, although they are small pockets, with benign environmental conditions, located in regions that are not necessarily environmentally conducive to species persistence. Although macrorefugia are easier to detect than microrefugia, because microrefugia are limited by the grain size of the environmental and species-presence data, both are of conservation interest (Ashcroft, 2010).

We used a species distribution modeling approach to identify macrorefugia in the Pacific and Indian Oceans. First we assessed the contemporary geographic range of a given species, and the climatic envelope within that range. That information was then combined with downscaled information from global climate models to predict where each species is likely to exist in the future. This study had two main objectives: (1) construct a framework to quantify the range shifts of corals species by the year 2100, using downscaled global climate models under the 'business as usual scenario'; and (2) quantify regions where coral species are most likely to be retained, lost, and gained by the year 2100. Within our model predictions we also included a capacity for species to adapt to thermal stress, which we set at 1 °C change by the year 2100, or a rate of 0.05 °C increase in thermal tolerance per generation for *Acropora* species (van Woesik & Jordán-Garza, 2011). We hypothesized that the response of the coral species to thermal stress at local scales, of 10–100 km^2, would be similar to the response of coral species to climate-change related thermal stress at regional scales, of 1000–10 000 km^2.

Materials and methods

Environmental parameters

Sea surface temperature data were gathered from Bio-Ocean Rasters for Analysis of Climate and Environment (ORACLE) (http://www.oracle.ugent.be/). Current raster data from Bio-ORACLE were derived from the Aqua-Moderate Resolution Imaging Spectroradiometer (MODIS) satellite for the years 2002–2009 (Tyberghein *et al.*, 2012), which were adjusted spatially using bilinear interpolation to grids of 5 arc min (*c.* 9.2 km). The range of SST values (°C), between the latitudes 37°N–37°S, was calculated as the maximum minus the minimum temperature for the 8-year time span at each grid cell. The short, 8-year time frame was used to match the time frame of the photosynthetically available radiation (PAR). PAR (E m^{-2} day^{-1}) data were derived from the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month) from 1998 to 2007. Individual monthly raster files were stacked in a geographic information system QGIS (www.qgis.org) and then imported into R (R Core Team, 2014), where all values greater than zero were used to determine the range for the 10 years (in the R package 'raster', Hijmans *et al.*, 2014). The grid size of PAR was in 5 arc min (*c.* 9.2 km). A shapefile of depth (m) was made using NOAAs bathymetric database in R with the getNOAA.bathy function in the 'marmap' package. This shapefile was used to mask out all depths >20 m, at least for the present analysis, to get a sense of shallow-reef response.

Coral distributions

We examined the global distribution of reefs using ReefBase (www.reefbase.org). Shapefiles of reefs were downloaded to QGIS and used as the base layer. We examined the distribution of 12 coral species that were found in the Indian and Pacific Oceans using Veron (2000), IUCN's Red List http://www.iucnredlist.org/technical-documents/spatial-data, and Wallace (1999). The 12 coral species were selected based on their long-term response to a major thermal stress in Okinawa, Japan (Loya *et al.*, 2001; van Woesik *et al.*, 2011). Long-term 'winners' (van Woesik *et al.*, 2011) on the reefs of Okinawa were: (1) *Acropora digitifera*, (2) *Acropora hyacinthus*, (3) *Goniastrea aspera*, and (4) *Porites lobata* (Fig. 2). Coral species that did not appear to change in abundance were: (5) *Cyphastrea chalcidicum*, (6) *Favia speciosa*, (7) *Favites halicora*, and (8) *Leptastrea pruinosa*. Long-term 'losers' on the reefs of Okinawa were: (9) *Porites horizontalata*, (10) *Montipora aequituberculata*, (11) *Seriatopora hystrix*, and (12) *Stylophora pistillata* (Table 1). We hypothesized that the response of the 12 coral species to thermal stress on the local reefs of Okinawa might be similarly reflected as a regional response to climate change.

The distributions of all 12 coral species were recorded as either present or absent within the ecoregions defined by Veron *et al.* (2009). Presence points were randomly selected from the reefs within 'ecoregions' (*sensu* Veron *et al.*, 2009) that allegedly supported each coral species. Absence points were selected from ecoregions from which we were 95% certain the coral species of interest was absent (see Supporting Information document). These certainties were determined using a probability of detection algorithm at depths ≤20 m. Constraining the depth of the species absence points allowed specific determination of the environmental parameters that were most likely affecting each particular species. We extracted both the range of SST and the range of photosynthetically available radiation from the raster files to characterize the environmental 'climate' where the species were present, and where the species were absent (N = 3000 points, at grid cells of 9.2 km). The environmental data points were weighted by the number of 'ecoregions' in which each species was either present or absent.

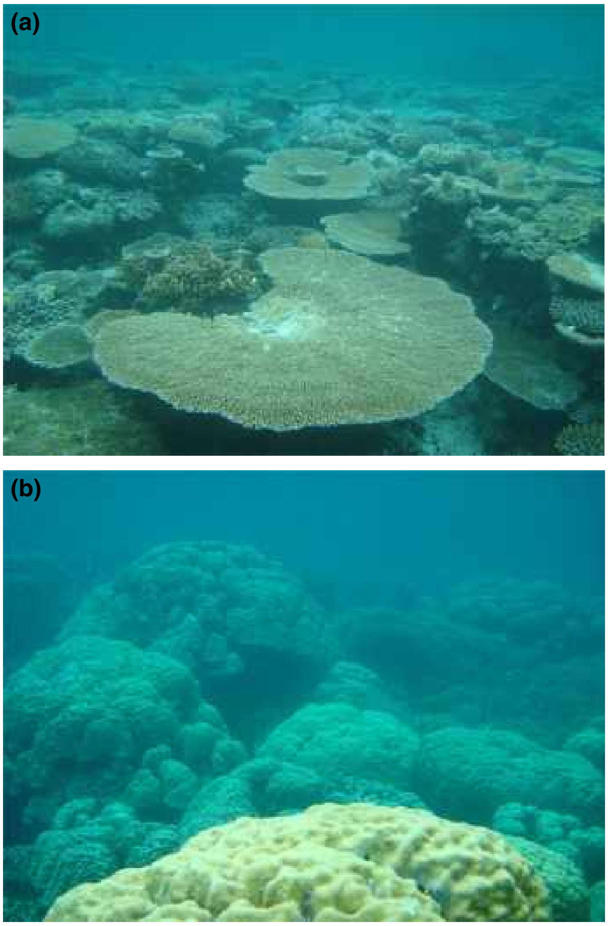

Fig. 2 (a) *Acropora hyacinthus*, which is the table-like structure in the foreground and (b) massive *Porites lobata* colonies on the reefs of Palau.

Species distribution model

We used a logistic regression model to predict the coral species using the logit-link function and a binomial error distribution, as follows:

$$y_i = \log(P_i/1 - P_i) = b_o + b_1 x_i + b_2 z_i + b_3 x_i . z_i + e_i, \qquad (1)$$

where y_i was the observed binary response (presence or absence) at site i, P was the probability of presence, and $(1 - P)$ was the probability of absence, x_i and z_i were the explanatory environmental variables at site i, and e was the binomial error term. We used a k-fold algorithm (in the R package 'dismo', Hijmans *et al*., 2013) to randomly select training and evaluation sites, which created a vector that assigned each row in the data matrix to a group between 1 and k. Both presence and absence data were partitioned and used for training (80%) and testing (20%). The k-fold algorithm was repeated 100 times, and the model run that recorded the highest area under the receiver operating characteristic curve (AUC) was subsequently used for further analyses. To increase sensitivity (i.e., the true positive fraction) and specificity (i.e., the true negative fraction), we used a threshold where the sum of the sensitivity and specificity was highest. Values above the threshold were transformed to presence values (1), and values below the threshold were transformed to absence values (0). We then used the AUC to describe the relationship between the correctly predicted presences (sensitivity), and the incorrectly predicted absences (1−specificity). AUC values close to 1 suggested that the sites that were predicted to have high suitability were also sites where the species of interest was present. Similarly, sites that were predicted to have low suitability were also sites where the species of interest was absent. An AUC of 0.5 suggested that the predictions were no better than random.

Constraints and masks

Geographic masks were designed to eliminate false negatives, without lowering the credibility of the model. Four masks were applied to the model outputs. First, a mask was applied to constrain dispersal, limiting the potential range of dispersion to no more than a conservative 10 km per year beyond the contemporary range of each coral species (Miller & Munday, 2003; Shanks *et al*., 2003). The dispersal mask coupled the logistic model with contemporary spawning (van Woesik, 2010) and genetic studies (Ayre & Hughes, 2000), which show evidence of high local retention of larvae. The dispersal mask also realistically restricted potential dispersal capacity under ocean warming (O'Connor *et al*., 2007; Figueiredo *et al*., 2014). To implement the dispersal mask, all longitudes outside of 5°N or 5°S (*c*. 550 km) of the sampled presence points were masked from the model. Second, to focus on shallow-reef systems, all coral reefs >20 m were masked out. Third, because freshwater causes coral mortality, the 12 largest subtropical and tropical river outflow areas were masked out depending on the size of their drainage basins (see Supporting Information for details). Fourth, localities that experienced temperatures <18 °C, for any time of the year, were masked out of all model runs because reef corals are unlikely to survive temperatures below 18 °C for more than 3 months (Veron, 1995), and reef accretion is unlikely below these temperatures (Kleypas *et al*., 1999).

Predictions

After training the model and verifying the outputs with AUC scores, the models were run using future SSTs, while keeping photosynthetically available radiation constant. The mask constraining the corals to a minimum temperature of 18 °C was modified in accordance with the 'business as usual' RCP 8.5 climate-change scenario. The SST data that are predicted to occur by 2100 data was downloaded from http://www.oracle.ugent.be/download.html; these data stemmed from the World Climate Research Programme Coupled Model Intercomparison Project (WCRP CMIP3) multi-model database (http://esg.llnl.gov:8080/index.jsp) for A2 (>800 ppm until 2100) and were calculated using predicted values from 2087 to 2096. The data were adjusted spatially using bilinear interpolation to grids of 5 arc min (*c*. 9.2 km), which was the same grid size as the present SST data.

Table 1 Contemporary estimates of relative-habitat occupancy of 12 coral species in the Pacific and Indian Oceans and changes in relative-habitat occupancy by 2100

Species	Coral morphology	AUC	Current habitat km^2	Lost habitat km^2	Future habitat km^2	New habitat km^2	Sea surface temperature (SST) range $(P(>\lvert z\rvert))$	Photosynthetically available radiation (PAR) range $(P(>\lvert z\rvert))$	SST:PAR interaction $(P(>\lvert z\rvert))$	Percentage habitat change
Porites lobata	Massive	0.98	5 148 364 ± 76 503	29 135 ± 5194	5 868 671 ± 66 752	747 486 ± 30 178	0.157	0.888	0.072	+14% ± 0.7%
Stylophora pistillata	Branching	0.80	4 754 730 ± 159 862	392 493 ± 55 460	4 783 592 ± 157 966	331 273 ± 33 537	<0.001*	0.004*	<0.001*	+0.6 ± 0.8%
Montipora aequituberculata	Foliose	0.81	4 831 538 ± 64 630	372 734 ± 21 363	4 839 462 ± 66 560	316,671 ± 24 267	0.016*	0.015*	0.001*	+0.2 ± 0.6%
Goniastrea aspera	Massive	0.93	4 536 698 ± 107 342	1 506 761 ± 109 669	3 467 030 ± 222 193	383 517 ± 14 288	0.190	<0.001*	0.014*	−24 ± 3.1%
Favia speciosa	Massive	0.77	3 794 371 ± 281 193	1 429 924 ± 170 181	2 870 067 ± 397 393	416 221 ± 56 388	0.644	0.020*	0.285	−25.9 ± 6%
Favites halicora	Massive	0.92	4 367 782 ± 105 582	1 607 213 ± 89 007	3 181 840 ± 198 013	360 343 ± 14 175	0.004*	0.029*	0.853	−27.6 ± 2.8%
Acropora hyacinthus	Tabulate	0.98	4 418 005 ± 83 431	1 633 415 ± 76 707	3 186 888 ± 165 470	342 701 ± 12 198	0.672	<0.001*	0.003*	−28.1 ± 2.3%
Cyphastrea chalcidicum	Encrusting	0.95	4 366 384 ± 106 755	1 639 216 ± 104 426	3 151 371 ± 214 418	365 462 ± 16 010	0.001*	0.030*	0.852	−28.3 ± 3%
Acropora digitifera	Branching	0.96	4 295 530 ± 110 146	1 709 384 ± 84 191	3 000 173 ± 196 458	343 369 ± 13 594	0.576	<0.001*	0.007*	−30.6 ± 2.8%
Seriatopora hystrix	Branching	0.97	4 190 195 ± 118 109	1 704 489 ± 72 177	2 876 779 ± 180 792	306 614 ± 12 810	0.095	<0.001*	0.045*	−31.7 ± 2.4%
Leptastrea pruinosa	Encrusting	0.93	4 090 089 ± 123 979	1 743 593 ± 79 780	2 754 947 ± 196 699	323 801 ± 12 357	0.039*	0.038*	0.173	−33.1 ± 2.6%
Porites horizontalata	Branching	0.96	2 805 764 ± 27 586	1 794 596 ± 14 343	1 403 780 ± 36 485	295 357 ± 4871	<0.001*	0.484	<0.001*	−50 ± 0.8%

The coarse-grained (9.2 km) grid tended to over-estimate occupied reef area, and therefore the estimates of habitat occupancy are merely relative estimates that are useful for comparative purposes and should not be used as estimates of absolute changes in coral-reef area. This table depicts: (1) area under the receiver operating characteristic curve (AUC) scores, (2) change in relative-habitat occupancy between current and future models, and (3) significance of environmental conditions for the model runs. The 'Current habitat' indicates the relative area of habitat (using the 9.2 km coarse grid) in which the coral species will be found in 2014. 'Future habitat' is the predicted habitat occupancy in the year 2100. 'Lost habitat' is the relative area of habitat that is predicted to be lost by 2100. 'New habitat' is where the species currently does not occur, but will likely occur and occupy habitat in the year 2100. SST and PAR range ($P(>|z|)$) indicates significance (*) of the environmental parameters in the model. Percentage habitat change is either positive (+) or negative (−), which is the difference between the present species habitat occupancy, and the habitat occupancy predicted by the model by 2100. All ± signs are 95% confidence intervals.

We were particularly interested in comparing the contemporary estimates of habitat occupancy of each of the 12 coral species with the predicted estimates of habitat occupancy by the year 2100. The coarse-grained (9.2 km) grid tended to over-estimate occupied reef area, and therefore the estimates of habitat occupancy are merely relative estimates that are most useful for comparing current and future occupancy, and should not be used as estimates of absolute reef area. The highest AUC value from each of the 100 *k*-fold outputs was chosen to run each model. This procedure was repeated 25 times for each species to quantify the uncertainties as confidence intervals for each distribution, and for predicted changes in distributions through time. An adaptation scenario was also incorporated into the future model by reducing the predicted 2100 thermal range by 1 °C, which was an approximately 0.012 °C range increase per year, or, for an *Acropora*, amounted to approximately 0.05 °C range increase per generation (van Woesik & Jordán-Garza, 2011).

Results

Changes in species distributions

The logistic regression model showed that the range of photosynthetically available radiation (PAR) was a significant predictor of the distribution ($P < 0.05$) of ~80% of the selected 12 coral species, whereas SST was a significant predictor of only ~50% of the 12 coral species in this study (Table 1). The interaction between SST and PAR was a significant predictor of 60% of the corals (Table 1). The model showed that the ubiquitous, reef-crest dwelling tabulate coral *A. hyacinthus* (Fig. 2) is predicted to lose 28% (±2.3%) of its current habitat by 2100 (Fig. 3a, Table 1). Most of the loss is predicted to occur in the Philippines, Indonesia, Papua New Guinea, the northern Great Barrier Reef, and along the southern Japanese archipelago (Fig. 3a). Yet with a 1 °C potential to adapt, which is approximately 0.05 °C per generation, *A. hyacinthus* is expected to only lose 5.6% (±1.8%) of its current reef habitat (Fig. 3b). Similarly for the dominant Indo-Pacific coral *A. digitifera*, the model predicted that the species will lose 31% (±2.8%) of its reef habitat by 2100 (Table 1), but with a 1 °C potential to adapt, *A. digitifera* will only lose 5.9% (±1.6%) of its current habitat.

Our results also suggest that *P. lobata* will gain approximately 14% (±0.7%) new habitat (Table 1) and is expected to extend its global distribution by 2100 (Fig. 4), particularly into southeastern and southwestern Australia, and southern Japan. *Stylophora pistillata*

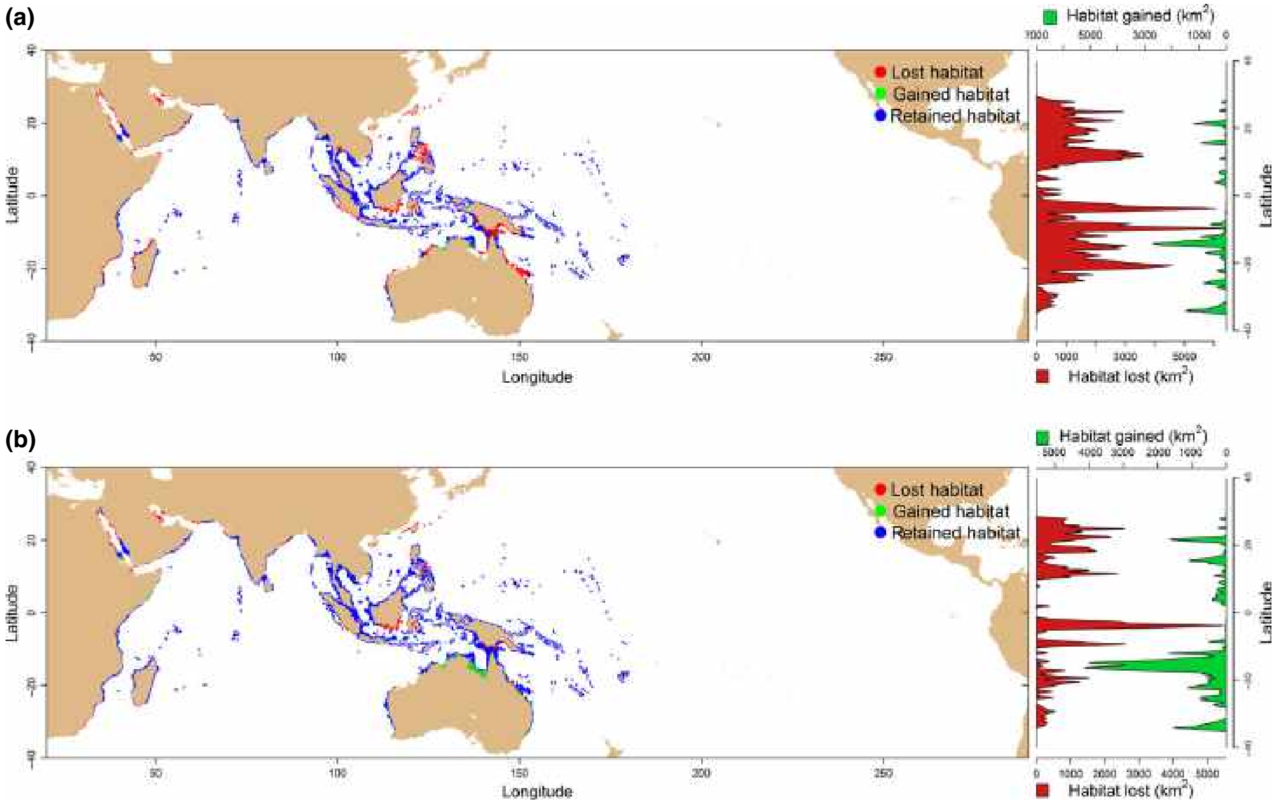

Fig. 3 *Acropora hyacinthus*. (a) Predicted lost (red), gained (green), and retained (blue) habitat under a 'business as usual' Representative Concentration Pathway (RCP) 8.5 climate-change scenario in 2100; (b) Predictions for the habitat changes by 2100 with a 1 °C adaptation under a 'business as usual' RCP 8.5 climate-change scenario.

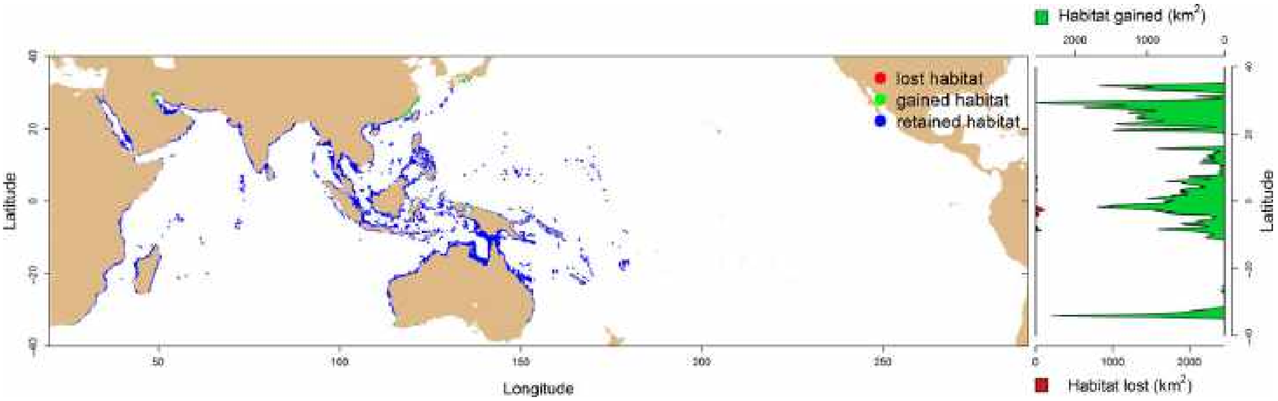

Fig. 4 *Porites lobata*. Predicted lost (red), gained (green), and retained (blue) habitat under a 'business as usual' Representative Concentration Pathway 8.5 climate-change scenario in 2100.

and *M. aequituberculata* are predicted to maintain their occupied habitat by 2100 (Table 1). *Goniastrea aspera* is predicted to lose about 24% (±3%) of its current habitat by 2100. *Favia speciosa and F. halicora* are predicted to lose around one-fourth of their current habitat, whereas *C. chalcidicum*, *S. hystrix*, and *L. pruinosa* are all predicted to lose between to 28% and 33% of their current habitats by 2100 (Table 1). The most extreme loss is predicted for the branching *P. horizontalata* with 50% loss of habitat by 2100 (Table 1). There was a significant ($P < 0.001$) positive exponential relationship between the current area of habitat that coral species occupy, and the predicted area of habitat that will be occupied by 2100 (Fig. 5).

Refugia

This study identified areas where current climatic conditions are likely to be maintained by the year 2100. Five areas were identified as climate-change refugia for reef corals in the Indian Ocean: (1) southwestern Madagascar, (2) the Maldives, (3) the Chagos Archipelago, (4) Western Australia, and (5) the Seychelles. Seven areas were identified as climate-change refugia for reef corals in the Pacific Ocean: (6) northern Indonesia, (7) Micronesia, (8) the northern Marshall Islands, (9) the southern Great Barrier Reef, (10) the Solomon Islands, (11) Vanuatu, and (12) French Polynesia (Fig. 6). Taken together, the predicted change in the spatial distribution of the 12 coral species showed considerable fragmentation, and a particularly high loss of coral species richness between the latitudes 5–15° in both hemispheres (see Fig. 6; for a detailed, global perspective, of the predicted changes by 2100 see the Google Earth Refugia.kmz file in the Supporting Information).

Discussion

Latitudinal shifts

Over the next 85 years, thermally sensitive coral species, such as *A. hyacinthus*, will most likely lose up to

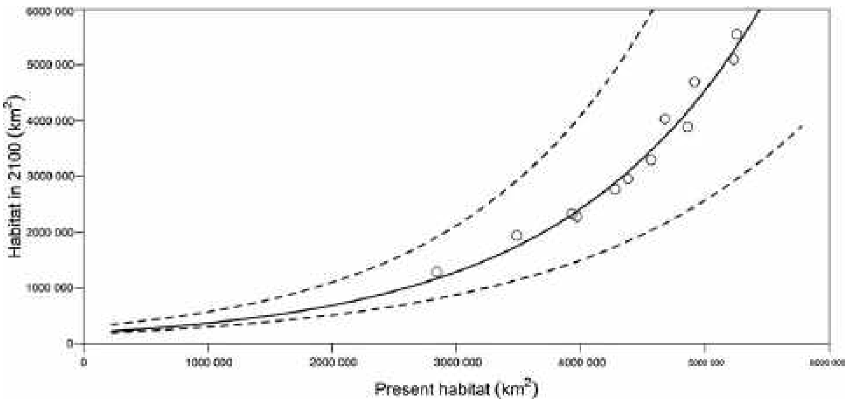

Fig. 5 The relationship between the current estimated habitat occupancy of coral species and the habitat occupancy that is predicted by 2100. The open circles are the present data plotted against data calculated by the species distribution models. The continuous line reflects the relationship: Habitat occupancy (km^2) in 2100 = *exp* [12.18 + 0.00000063. present-habitat occupancy (km^2)], and the dashed lines are the 95% confidence intervals. The relationship was significant ($P < 0.001$).

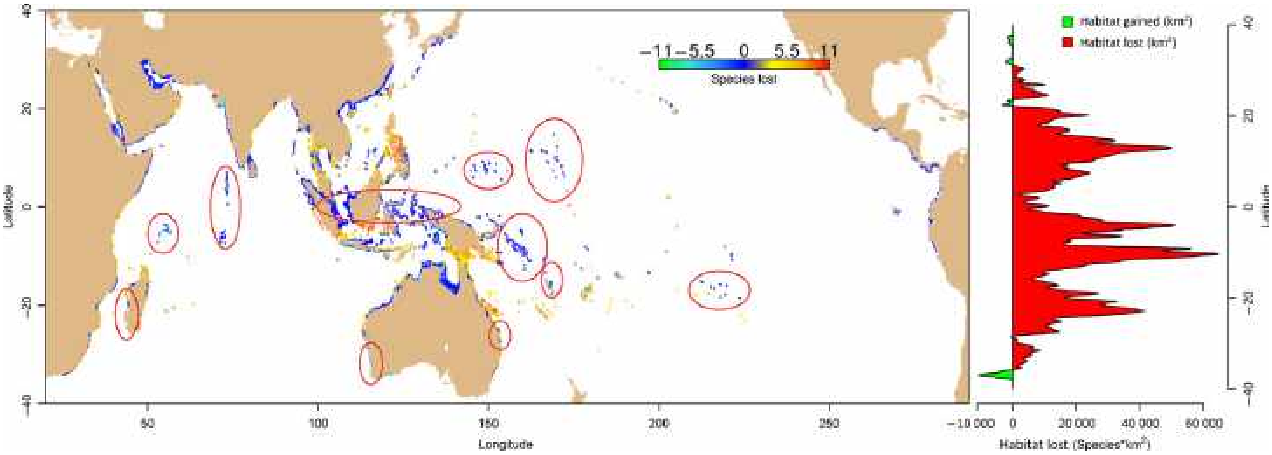

Fig. 6 Spatial distribution of the 12 coral species examined in the present study in the coral triangle in 2014 compared with the predicted spatial diversity of the 12 coral species examined in 2100 under a 'business as usual' Representative Concentration Pathway (RCP) 8.5 climate-change scenario. The red circles highlight the predicted macrorefugia.

26–30% of their current habitat because of higher SSTs. Most reductions in habitat are predicted to occur between the latitudes 5–15°, in both hemispheres, particularly in the Philippines, southern Indonesia, and Papua New Guinea. Other habitat reductions will most likely occur along the northern Great Barrier Reef, the Red Sea, and along the reefs of eastern Africa. By contrast, the global increases in minimum sea surface temperature at high latitudes are predicted to expand the latitudinal extent of several coral species to places that were previously considered too cold for coral growth.

The results in the present study largely agree with other studies on range expansion 'out-of-the-tropics', including the study by Baird *et al.* (2012) that showed the southern expansion of four *Acropora* species along the east coast of Australia. This southern expansion will likely continue until corals become light limited at high latitudes. The most unexpected result of the present study was the lack of northward expansion of several species along the western Pacific Ocean, particularly along the Japanese islands by 2100. The results of our model contrast with the recent study by Yamano *et al.* (2011) that showed northern range expansion of *A. hyacinthus* over the last two decades along the main islands of Japan. The differences in the modeled results and the results by Yamano *et al.* (2011) maybe a consequence of the difference in the time frames of the studies. While Yamano showed arange expansion from 1988 to 2010, the global climate models show extreme temperature ranges around the Japanese islands by 2100 (Fig. 1), which may preclude temperature sensitive *A. hyacinthus* and *A. digitifera* from the northern Japanese islands (Fig. 3a). The modeled results suggest that the recent northern expansion of reef corals along the Japanese islands may be, therefore, short-lived. Indeed, Veron (1992) showed considerable turnover in species composition on the northernmost reefs of Japan over the last 6000 years. Alternatively, the modeled results in the present study may miss the fine-grained microrefugia where *Acropora* species might persist in the northern Japanese islands in 2100.

More disturbing, perhaps, is the prediction that some Indo-Pacific *Acropora* species, at least the *Acropora* species that were analyzed in the present study, will not be able to live in parts of the tropics. Particularly striking is the predicted change in the spatial distribution of coral species richness, and the projected heterogeneous nature of that richness between the latitudes 5–15°, in both hemispheres (Fig. 6). If, however, thermally sensitive corals, such as *A. hyacinthus*, are able to adapt to a 1 °C increase in temperature, over the next 85 years, the predictive model shows limited habitat loss. Yet, whether these species can adapt to rapid climate change is still an open question.

Species traits

The vulnerability of a coral species to increasing thermal stress is a combination of the duration and intensity of thermal exposure, and the inherent sensitivity of the species (Moritz & Agudo, 2013). Some coral species are invariably resistant to thermal stress, whereas other coral species are sensitive to thermal stress and are being lost from regional-reef systems (Loya *et al.*, 2001). Still other coral species are physiologically sensitive to thermal stress in the short term, yet their ubiquitous distribution and high fecundity allows rapid recovery, and hence persistence over the long term. We hypothesized that the response of coral species to thermal stress at local scales, using isolated field studies, might be similarly reflected as a response to climate change at regional scales. We showed, instead, considerable decoupling between scales of response, and that some 'winners' at local scales are likely to be 'losers' at regional scales. For example, 10 years after a thermal stress event on Okinawa the long-term 'winners' were *A. digitifera*, *A. hyacinthus*, *G. aspera*, and *P. lobata* (van Woesik *et al.*, 2011). The present study showed that *P. lobata* is likely to be one of the few long-term 'winners' under further ocean warming.

At a time of much warmer oceans than today (~10 °C warmer on average), during the Eocene (56–34 million years before present) (Zachos *et al.*, 2001), coral reefs supported mainly encrusting and massive coral colonies and supported few multiple-branched coral colonies (Coates & Jackson, 1985; Budd *et al.*, 2011). Recent studies have also shown that branching coral morphologies are more susceptible to thermal stresses than massive and encrusting colonies (Loya *et al.*, 2001; McClanahan *et al.*, 2004). The results in Table 1, however, do not conform to the conventional paradigm that all encrusting and massive colonies should survive in preference to branching corals, at least by 2100. For example, the present study predicted that the branching coral *S. pistillata* will maintain its distribution, whereas some massive faviids are predicted to lose up to 28% of their current habitat (Table 1). The shift away from the conventional coral-morphology paradigm in the present study may be a consequence of numerous factors, including inherent differences in life-history traits other than morphology, and potentially a latent effect of analyzing widely distributed species.

Adaptation and persistence

Recent genetic studies have shown that the widely distributed corals in the genus *Pocillopora*, in the Indian and Pacific Oceans, have geographically restricted haplotypes, which suggests local adaptation, and minimal gene flow between some clades across oceanic regions (Forsman *et al.*, 2013). In the present study, we characterized the environmental conditions in which the present-day species were located, which we assumed reflected their environmental tolerance (i.e., their fundamental niche). These environmental conditions were then used to estimate the potential distribution of the coral species under climate change. The most obvious, overarching trend in our study was the significant ($P < 0.001$) positive exponential relationship between the current area of habitat occupancy and the predicted area of habitat occupancy by 2100 (Fig. 5). The results suggest that widely distributed coral species will lose relatively less area than geographically restricted species. Yet, local adaptation is not captured by species distribution models, because the models assume that a widely distributed species can also tolerate the entire range of the environmental conditions in which it is found. Although a broad geographic distribution does not necessarily render the entire population tolerant to a wide array of global temperature changes, and does not guarantee immunity to regional extinction (van Woesik *et al.*, 2012b), geographic ubiquity does suggest that portions of a widely distributed coral species might have an inherent capacity to adapt to climate change.

Recent studies have shown that the most vulnerable species to climate-change forcing are environmentally sensitive, stenotopic coral species (Burman *et al.*, 2012). For example, the loss of stenotopic corals from many reefs has left the eurytopic, generalist species as the dominant corals on most contemporary Floridian reefs. The transition in dominance from stenotopic to eurytopic coral species, mirrors similar transitions elsewhere in the Caribbean, both in recent decades and in the geologic past (Edinger & Risk, 1994). However, in a recent study, van Woesik *et al.* (2012b) showed that vulnerability to changing climates in the past was largely attributed to species traits and was not simply a function of geographic distribution in the Caribbean.

Generalist coral species clearly have inherent traits that allow for range expansion. Is the issue then simply that only generalists will tract with climate-change temperatures? Rare species, by definition, have restricted geographic ranges and are generally considered 'vulnerable' because of their small population size. Although it is well known that populations with low genetic diversity have low adaptive potential (Futuyma, 2009), it is unclear how rare, endemic species can survive at all (Birkeland *et al.*, 2013). Yet they do survive! Some rare species are even able to survive through climate extremes, often in microrefugia (10–100 km^2), while some widespread species perish (Mosblech *et al.*, 2011; van Woesik *et al.*, 2012b). For example, in a recent study in Palau, corals on nearshore reefs bleached less and suffered lower mortality than corals on patch reefs and outer reefs, even though the temperatures nearshore were higher than elsewhere. A higher than average vertical attenuation of light, caused by naturally high suspended particulate matter, appeared to buffer the local nearshore corals from thermal stress. Such microrefugia are often lost using the predictions from coarse-grain global climate models (Donner *et al.*, 2005; van Hooidonk *et al.*, 2013), and such microrefugia were not 'captured' in the present study.

Deep-reef refugia

Mesophotic reefs, between 30 and 150 m, are also considered to be important refugia for shallow reefs (Riegl & Piller, 2003). Although we did not consider deep, mesophotic reefs as refugia in the present study, there are several caveats when assuming that mesophotic reefs will act as shallow-reef refugia. For example, there was a recent discovery of large stands of *S. hystrix* at 35–45 m (Sinniger *et al.*, 2012) near the Okinawan study site (Loya *et al.*, 2001), mentioned above. Although these corals are extensive on the mesophotic reefs, *S. hystrix* was not recorded on the shallow reefs for over 10 years (van Woesik *et al.*, 2011). Similarly, van Oppen *et al.* (2011) showed clear genetic differences between shallow and deep *S. hystrix* populations on the Great Barrier Reef, but showed homogenous, genetic populations across the shallow and mesophotic reefs in Western Australia. Therefore, the existence of adjacent mesophotic reefs does not directly infer larval connectivity with shallow reefs (see also Serrano *et al.*, 2014). Considerable work needs to be done to firstly map mesophotic reefs adjacent to shallow coral reefs, secondly to determine the extent of genetic connectivity between the mesophotic reefs and the adjacent shallow reef-coral populations, and thirdly to identify microrefugia.

In conclusion, the present study identified 12 climate-change macrorefugia, which we define as areas that will support reef-coral populations, and to which reef corals can retreat to, persist in, and subsequently expand from, under a 'business as usual' climate-change scenario, identified as RCP 8.5, that is expected by 2100. In the Indian Ocean, reef-coral climate-change refugia were identified in southwestern Madagascar, the Maldives, the Chagos Archipelago, Western Australia, and the Seychelles. In the Pacific Ocean, climate-change refugia were identified in northern Indonesia, Micronesia, the northern Marshall Islands, the southern Great Barrier Reef, the Solomon Islands, Vanuatu, and French Polynesia. All 12 reef-coral refugia need protection from local and regional disturbances and land-use change, and they clearly deserve the highest conservation status because they may be the only locations where modern coral reefs can survive climate change.

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Supporting Information

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

Data S1. Cacciapaglia and van Woesik.
Data S2. GoogleEarth kmz file of Figure 6.

Before the Secretary of Commerce

Petition for Protective Regulations Under Section 4(d) of the Endangered Species Act for the Conservation of Threatened Corals

Pillar coral, Dendrogyra cylindrus. *Photo credit: NOAA Fisheries*

Center for Biological Diversity

20 February 2020

Notice of Petition

Wilbur Ross, Secretary of Commerce
U.S. Department of Commerce
1401 Constitution Ave. NW
Washington, D.C. 20230
Email: WLRoss@doc.gov, TheSec@doc.gov

Dr. Neil Jacobs, Acting Under Secretary of Commerce for Oceans and Atmosphere
U.S. Department of Commerce
1401 Constitution Ave. NW
Washington, D.C. 20230
Email: neil.jacobs@noaa.gov

Chris Oliver, Assistant Administrator
NOAA Fisheries
1315 East-West Highway
Silver Spring, MD 20910
Email: chris.w.oliver@noaa.gov

Petitioner:

Kristin Carden, Ph.D./J.D.
Oceans Program Scientist, *on behalf of the*
Center for Biological Diversity
1212 Broadway #800
Oakland, CA 94612
Phone: 510.844.7100 x327
Email: kcarden@biologicaldiversity.org

Sarah Uh

Sarah Uhlemann
Senior Attorney & International Program Director, *on behalf of the*
Center for Biological Diversity
2400 NW 80th Street, #146
Seattle, WA 98117
Phone: (206) 324-2344
Email: suhlemann@biologicaldiversity.org

Pursuant to Section 4(d) of the Endangered Species Act (ESA, Act), 16 U.S.C. § 1533(d), 50 C.F.R. § 424.10, and Section 553 of the Administrative Procedure Act, 5 U.S.C. § 553(e), the Center for Biological Diversity (Center) hereby petitions the Secretary of Commerce, acting through the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NMFS), to promulgate a rule under Section 4(d) of the ESA to provide for the conservation of the 20 threatened coral species listed under the ESA on 10 September 2014. (*See* 79 Fed. Reg. 53852 (Sept. 10, 2014).)

Specifically, the Center urges NMFS to extend all prohibitions of ESA Section 9 (with limited exceptions to promote science and restoration as provided in ESA Section 10) to and promulgate additional protective regulations needed for survival and recovery of the listed corals. Upon receipt and review of this petition, the Center requests that NMFS make specific findings as to whether, for the 20 listed coral species: (1) protective regulations are necessary and advisable, and (2) the specific regulations proposed herein are necessary and advisable. We petition NMFS to issue regulations addressing the following: extension of ESA Section 9 prohibitions; trade; disease; habitat degradation; fishing; water pollution; and greenhouse gas emissions (specifically as they affect ocean warming and acidification).

The Center is a non-profit, public interest environmental organization dedicated to the protection of native species and their habitats through science, policy, and environmental law. The Center has more than 1.7 million members and online activists throughout the United States and internationally. The Center and its members are concerned with the conservation of endangered species and the effective implementation of the ESA.

Respectfully submitted this 20th day of February, 2020.

Table of Contents

I. Introduction

A. Regulatory History

On 10 September 2014, NMFS published a final rule listing 20 coral species as threatened under the Endangered Species Act, including five Caribbean coral species (*Dendrogyra cylindrus*, *Orbicella annularis*, *Orbicella faveolata*, *Orbicella franksi*, and *Mycetophyllia ferox*) and fifteen Indo-Pacific coral species (*Acropora globiceps*, *Acropora jacquelineae*, *Acropora lokani*, *Acropora pharaonis*, *Acropora retusa*, *Acropora rudis*, *Acropora speciosa*, *Acropora tenella*, *Anacropora spinosa*, *Euphyllia paradivisa*, *Isopora crateriformis*, *Montipora australiensis*, *Pavona diffluens*, *Porites napopora*, and *Seriatopora aculeata*). (79 Fed. Reg. 53852 (Sept. 10, 2014).) NMFS determined that the most important threats contributing to extinction risk for these species are ocean warming, disease (as related to climate change), and ocean acidification. (*See id.*) NMFS stated that "these impacts are currently occurring, and are expected to worsen, posing increasingly severe effects on the species considered in this final rule." (*Id.*)

On 13 January 2015 the agency solicited public comment on its notice of proposed rulemaking for protective regulations for these coral species under section 4(d) of the ESA. (80 Fed. Reg. 1616 (Jan. 13, 2015).) NMFS has yet to take further action on the promulgation of these regulations. The threats facing these species continue unabated, and a 4(d) rule is needed more urgently than ever.

To ensure the 20 listed corals species are protected from climate change, trade, and the myriad local threats imperiling their survival and recovery, the Center submits this petition requesting that NMFS promulgate for their protection a 4(d) rule under the ESA. The Center requests that this rule extend all ESA Section 9 prohibitions (including prohibitions on import, export, take, and all commercial activities, with limited exceptions for scientific and restoration activities that benefit the corals' survival and recovery) and provide additional protective regulations that address, *inter alia*, the threat posed to the corals by greenhouse gas pollution.

B. Threats Facing Coral Reef Ecosystems in General

i. Climate Change

As NMFS determined in its final listing rule, climate change underlies three primary existential threats facing these 20 coral species: ocean warming, disease, and ocean acidification. Ocean warming and acidification caused by greenhouse gas pollution are wreaking havoc on reef ecosystems worldwide. The world's oceans have absorbed more than 90 percent of the excess heat caused by climate change, resulting in average sea surface warming of 0.7°C (1.3°F) per century since 1900. (USGCRP 2017). Global average sea surface temperature is projected to rise by 2.7°C (4.9°F) by the end of the century under a higher emissions scenario. (USGCRP 2017). In addition, climate change contributes to marine heat waves—periods of extreme warm surface temperatures—which have become longer-lasting and more frequent in recent decades. The number of heat wave days doubled between 1982 and 2016 and is projected to increase 23 times under 2°C warming. (Frolicher *et al.* 2018). At present, 87 percent of marine heat waves are attributable to human-induced warming. (*Id.*)

Scientific research definitively links anthropogenic ocean warming to the catastrophic, mass coral bleaching events that have been documented since 1980 and are increasing in frequency alongside increasing atmospheric CO_2 concentrations. (Hoegh-Guldberg *et al.* 2007; Donner *et al.* 2009; Eakin *et al.* 2010; NMFS 2015; Hughes *et al.* 2017; Hughes *et al.* 2018b; Manzello *et al.* 2018; Cheng *et al.* 2019; Leggatt *et al.* 2019). These bleaching events occur when the thermal stress of rising ocean temperatures disrupts the relationship between corals and their algal symbionts.[1] (Hughes *et al.* 2017). When the corals expel these symbionts, they lose their color and suffer nutritional stress and physiological damage. (*Id.*) Prolonged bleaching often results in high levels of coral mortality. (*Id.*) Severe bleaching has increased five-fold in the past several decades and now occurs every six years on average, which is too frequent to allow corals to fully recover between bleaching events. (Hughes *et al.* 2018b; *see also* Neal *et al.* 2017 (noting that in the Caribbean, many important reef-building corals have not recovered from repeated bleaching events).) Most reefs worldwide will suffer annual bleaching scenarios by 2050, and such events may occur sooner—perhaps in the next decade—in the Florida Keys. (van Hooidonk *et al.* 2013; Hughes *et al.* 2018b; Manzello *et al.* 2018).

The global coral bleaching event that lasted from 2014 to 2017 was the longest, most widespread, and likely most destructive on record, affecting more reefs than any previous mass bleaching event and causing bleaching at previously sheltered reef sites. (Heron *et al.* 2017; Eakin *et al.* 2018; Raymundo *et al.* 2019). A 2017 scientific review concluded that "unless rapid advances to the goals of the Paris Climate Change Agreement occur over the next decade," coral reefs will likely "degrade rapidly over the next 20 years, presenting fundamental challenges for the 500 million people who derive food, income, coastal protection, and a range of other services from" these ecosystems. (Hoegh-Guldberg *et al.* 2017).

More frequent, strong El Niño events also trigger coral bleaching. Unfortunately, high sea surface temperatures are no longer restricted to El Niño years; in fact, "tropical sea surface temperatures are warmer now during current *La Niña* conditions that they were during El Niño events three decades ago." (Hughes *et al.* 2018b) (emphasis added). Additionally problematic to long-term health and persistence of corals are the permanently elevated sea surface temperatures associated with climate change. (*Id.*) Scientists have found that sea surface temperatures only 1-2°C above ambient can induce bleaching in corals; global sea surface temperatures have already increased 1°C since pre-industrial times. (Heron *et al.* 2017). Scientists predict that ocean warming in the tropics will make life for corals physiologically impossible in the next 20-50 years. (Price *et al.* 2019).

Exacerbating the harms from rising temperatures is ocean acidification. The global ocean has absorbed more than a quarter of the CO_2 emitted to the atmosphere by human activities, which has increased its surface acidity by more than 30 percent.[2] This increase has occurred at a rate likely faster than anything experienced in the past 300 million years. (USGCRP 2017; Hönisch *et al.* 2012). Ocean acidity could increase 150 percent by the end of the century if CO_2 emissions continue unabated. (Orr *et al.* 2005; Feely *et al.* 2009). By reducing the availability of key

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[1] *See also* Manzello *et al.* (2018) (discussing the relationship between symbiont and coral bleaching resistance).

[2] Simpson *et al.* (2009) correlate a Caribbean open-ocean aragonite saturation state of 4.0, which is needed to protect corals from degradation from ocean acidification, with an atmospheric CO_2 level of 340 to 360 ppm—far below current levels.

chemicals (namely, aragonite and calcite), ocean acidification negatively affects a wide range of calcifying marine creatures like corals by hindering their ability to build skeletons and by disrupting metabolism and critical biological functions. (Fabry *et al.* 2008; Kroeker *et al.* 2013). The adverse effects of ocean acidification already are reducing calcification rates in coral reefs worldwide, leading to reef bioerosion and dissolution.[3] (Albright *et al.* 2016; Heron *et al.* 2017; Eyre *et al.* 2018). Acidification coupled with elevated temperatures also reduces coral larval survival and settlement. (Pitts 2018).

Climate change also exacerbates coral disease, leading to widespread declines of threatened and endangered species. (Randall & van Woesik 2017). For example, white-band disease led to precipitous declines (on the order of 92-97%) of once-abundant Caribbean elkhorn and staghorn corals. Research indicates that these disease outbreaks were driven by heat stress from rising ocean temperatures. (71 Fed. Reg. 26,852, 26,872 (May 9, 2006); Randall & van Woesik 2015; van Woesik & Randall 2017). Pillar corals (*Dendrogyra cylindrus*), which have suffered catastrophic declines in Florida in recent years, succumbed to black band disease that first emerged following bleaching events in 2014 and 2015 spurred by abnormally high water temperatures. (Lewis *et al.* 2017).

In sum, climate change threatens corals through elevated temperatures, which lead to bleaching events and the spread of coral disease, as well as through ocean acidification, which reduces larval survival and impedes reef formation and maintenance.

ii. Coral Collection and Trade

Trade poses a threat to many coral species. The large and complex global aquarium industry trades an estimated 50 million coral reef animals each year, including corals and marine ornamental fish. (Rhyne 2012). While trade in coral as souvenirs and curio predominated for decades, in the 1980s, the trade shifted to live coral for aquarium trade. (Wood, Malsch & Miller 2012).

The United States is the world's major importer of corals, importing approximately 70 percent of all live corals and 90 percent of all Scleractinia (stony coral) species documented in trade. (Rhyne 2012; Bruckner 2001). The number of corals imported into the United States has varied over the years, with over 600,000 live coral pieces imported in 2006 (Rhyne 2012). Some reports suggest U.S. imports of live corals declined after 2006 due to the economic downturn and an increase in aquaculture-produced specimens; other reports, however, suggest a sharp increase in total coral imports into the U.S. after 2006 and an increase in live coral imports internationally between 2000 and 2009 (Craig *et al.* 2012, Rhyne 2012, Wood, Malsch & Miller 2012).

Our review of 2014 data from the U.S. Fish and Wildlife Service Law Enforcement Management Information System (LEMIS) supports the latter reports and demonstrates that imports of live coral into the United States have increased since 2006. The LEMIS database revealed over 691,000 live coral pieces/specimens imported into the United States in 2014. The vast majority of shipments were live coral (around 52,000 total shipments). In addition to these reported

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[3] Eyre *et al.* (2018) predict that "reef sediments globally will transition from net precipitation to net dissolution when seawater Ω_{ar} reaches 2.92 ± 0.16 (expected circa 2050 CE)."

numbers, undocumented coral specimens trade in a black market. An estimated 20 percent of the overall coral trade is illegal (Thornhill 2012).

While coral aquaculture helps mitigate wild coral removal to some degree, the industry is not yet of sufficient size to completely relieve pressure on wild stocks. Further, the percent of traded corals that come from aquaculture versus wild stocks remains unclear. One report posits that, as of 2010, aquaculture (primarily from Indonesia) contributed approximately 20 percent of total live traded coral (Wood, Malsch & Miller 2012). Another report that looked at 2011 data found only 2 percent of coral imports were captive-bred, with 98 percent of traded coral sourced from the wild. (Craig *et al.* 2012). Our review of 2014 LEMIS data showed that ~75 percent of imported coral shipments were marked as either "captive" or "farmed."[4] These wildly different estimates of the percent of aquaculture-based corals in trade mean that we cannot say, with any certainty, that aquaculture has relieved collection pressure on wild stocks. Such pressure likely remains significant and poses a serious threat to coral reef ecosystems.

The deleterious effects of coral extraction to supply the aquarium and curio trades are well-documented. (Bruckner 2001; Bruckner 2002; Craig *et al.* 2012; Thornhill 2012; Wood, Malsch & Miller 2012; Dee 2014). Coral collection can cause significant impacts including habitat damage, decreased survival, and exotic species introduction; overharvest can, in some cases, lead to localized extinction (79 Fed. Reg. at 53,901; Bruckner 2002; Rhyne 2012; Thornhill 2012; U.S. Coral Reef Task Force 2000). Further, many harvested corals ultimately are discarded—a deplorable waste. (79 Fed. Reg. at 53,901). Due to their slow growth rates and irregular recruitment, stony corals are particularly vulnerable to overexploitation by extraction. (Bruckner 2002). As described by one expert, coral extraction can be "considered consumption of a non-renewable resource" because it can take centuries or longer to replace harvested specimens. (Bruckner 2001).

Numerous countries recognize the threat that extraction poses to coral reefs and have proposed or adopted legislation prohibiting harvest and trade in corals, including the Philippines, Mozambique, Vietnam, Vanuatu, and the Marshall Islands. (Bruckner 2001; Wood, Malsch & Miller 2012). Indeed, extraction of corals is highly restricted here in the United States (*e.g.*, collection is illegal in Hawaii), yet the United States itself has not restricted coral imports beyond compliance with the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)[5] which, as described below, offers only minimal protections to ESA-listed corals. (Bruckner 2001; Dee 2014). This remains problematic given the United States' outsize role in the international coral trade. In 2000, the International Working Group of the U.S. Coral Reef Task Force[6] produced a report discussing the United States' role in that trade. (U.S. Coral Reef Task Force 2000). It recognized the U.S. as the primary consumer of live coral for the aquarium trade and outlined the serious implications of overharvest, including "loss of

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[4] "Farmed" corals are those born in captivity with parents that mated in wild; they do not qualify legally as "captive-bred" under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

[5] CITES is an international agreement that seeks to ensure that international trade in specimens of animals and plants does not threaten their survival.

[6] In recognition of the importance of coral reefs and coral reef preservation, President Clinton in 1998 ordered the formation of the U.S. Coral Reef Task Force, which continues to meet today. (Executive Order 13,089 (June 11, 1998)). The Task Force was directed to "develop, recommend, and … secure implementation of measures necessary to reduce and mitigate coral reef ecosystem degradation," including from "over-fishing, over-use, and collection of coral reef species." (*Id.*)

diversity[,] . . . severe localized extirpations . . . [and] phase shifts within the coral reef ecosystem resulting in the decrease in survival or extinction of coral species." (*Id.*) It also noted "serious concerns that the international trade in live and raw coral, live rock, and coral products is not sustainable" despite CITES regulation.

Accordingly, the Report recommended that new measures be adopted to regulate U.S. trade in coral reef species. While the Report did "not recommend a complete restriction on all trade in marine aquarium organisms," it did recommend that the United States: (1) "prohibit domestic harvest and the import or export of coral reef species and products listed under [CITES] that are not sustainably managed," and (2) "prohibit the import or export of any coral reef species unless accompanied by certification that the products were not taken through the use of destructive fishing practices." (*Id.*) The United States has not taken action on these recommendations, and trade remains a threat to wild coral species including those listed on 10 September 2014.

C. Threats Facing the 20 Listed Coral Species

The threats just described, including climate change and trade, put the survival and recovery of the 20 listed coral species at risk. Local stressors including habitat degradation, fishing, and water pollution exacerbate these threats and complicate coral conservation. Both Caribbean and Indo-Pacific species continue to suffer from exposure to these collective threats, as described in more detail below.

The loss of the live coral cover over the past few decades in the Caribbean has been dramatic, averaging 60-80% since the 1980s. (Jackson *et al.* 2014; Rippe *et al.* 2017; Chan *et al.* 2019). In some places, such as off the Florida Reef Tract, offshore coral reef cover is ≤ 5% since the late 1990s and declining. (Manzello *et al.* 2015). Macroalgae invasion, bleaching, dredging, disease, and climate change all contribute to these corals' decline, and new threats continue to emerge. (Randall & van Woesik 2017).

Ongoing research confirms the dire circumstances facing the listed Caribbean corals. Critical framework species including the *Orbicella* complex have experienced sharp declines, with concomitant reductions in structural habitat complexity, diversity, and reef-dependent species abundance. (Edmunds 2015; Manzello *et al.* 2015; Rippe *et al.* 2017; Walker 2018). Three listed star corals in the Caribbean—boulder star coral (*Orbicella franksi*), mountainous star coral (*O. faveolata*), and lobed star coral (*O. annularis*)—have experienced long-term declines in reproduction following bleaching events caused by high water temperatures, which scientists warned "may be catastrophic for the long-term [population] maintenance." (Levitan *et al.* 2014).

Kabay reports "devastating losses of live tissue … following the bleaching and disease events impacting the Florida Reef Tract in 2014, 2015, and 2016," and concludes that "the southeastern Florida population of pillar coral [*Dendrogyra cylindrus*] is at serious risk of local extinction."[7] This pillar coral's limited sexual reproduction, asynchronous spawning, low juvenile survival rates, low recruitment, and propensity to fragmentation, bleaching, and disease (including white plague and stony coral tissue loss disease) make it particularly vulnerable. (Bernal-Sotelo, Acosta & Cortés 2019; Meyer *et al.* 2019). Chan *et al.* (2019) cite "[p]rojections indicat[ing] a

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[7] *See also* Walker 2018 (discussing multi-year outbreak of coral disease in Florida's reef).

high likelihood that *D. cylindrus* will become extinct in the Northern Greater Caribbean within a few decades."[8]

The listed Indo-Pacific coral species likewise face threats from both local and global stressors. The 1997-98 El Niño event caused large-scale coral bleaching and mortality, with long-term effects on reef structure, composition, and recovery. (DeVantier & Turak 2017). A global bleaching event in 2016-17 compounded these effects. (*Id.*) DeVantier and Turak's (2017) comprehensive survey of Indo-West Pacific coral reef species richness and abundance highlights the plight of some of the listed species. *Acropora rudis*, for example, was found at only four of 3,075 sites surveyed. (*Id.*)

Climate change is devastating all the listed corals, and a growing body of scientific research highlights the imperative of reducing the fossil fuel emissions driving ocean warming. Scientists have urged "immediate global action to curb future warming … to secure a future for coral reefs." (Hughes *et al.* 2017). Indeed, "drastic reductions in CO2 emissions are essential—the only real solution—to giving coral reefs … a chance to survive climate change." (Heron *et al.* 2017).

As discussed above, one of the primary threats to the listed coral species posed by climate change is elevated ocean temperature. Elevated temperatures have been shown to cause "complete larval mortality and inhibited … settlement of *O. faveolata*." (Pitts 2018). Elevated temperatures coupled with acidification also have been shown to reduce larval survival and settlement of *O. faveolata* by half as compared to a control treatment. (*Id.*) Scientists have linked climate-driven increases in sea surface temperature to outbreaks of white-band disease in *Acropora palmata* and *A. cervicornis*; this disease drove catastrophic region-wide declines of these once-dominant reef building corals. (*Id.*) Chan *et al.* (2019) report that a recent thermal stress event triggered a severe disease outbreak and precipitous population decline in *D. cylindrus* in Florida. These scientists forecast that an increasing frequency of warm water events, coupled with associated disease outbreaks, will lead to the local extinction of *D. cylindrus* in the Florida Keys in modern times. (*Id.*) Such extinctions will have ecosystem-wide ramifications, destabilizing communities and degrading ecosystem function. (Edmunds 2015; Chan *et al.* 2019).

The significant trade in stony corals likewise poses a threat to the 20 listed coral species, particularly the Indo-Pacific species. Stony coral species represent over half (56%) of corals in trade, with *Acropora* and *Euphyllia* comprising the top two genera imported "live." (Craig *et al.* 2012, Rhyne 2012). While all stony corals are listed under CITES, data documenting the species and volume of stony corals in trade remains limited. (CITES 1985). Further, a loophole exists in CITES that allows substantial trade in these species despite their "protection" under this treaty. Specifically, Parties to CITES have agreed to allow nations to trade in stony corals while documenting only a coral's genus. (CITES Res. Conf. 12.3.) Accordingly, it is difficult to ascertain which *species* of coral are traded and at what volume. There thus exists a substantial risk that rare species will be overexploited despite CITES protection. (Rhyne 2012).

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[8] *See* Bernal-Sotelo, Acosta & Cortés 2019 (noting that *D. cylindrus* reefs in Old Providence "are no longer in good condition; mortality even exceeds the expected values for highly degraded areas").

While this CITES loophole means we lack a comprehensive dataset that would illuminate global trade in the 20 listed coral species, the U.S. LEMIS database confirms that many of the ESA-listed coral species remain in trade. A review of 2014 LEMIS data documents that, of the 20 ESA-listed coral species, eight were imported into the United States that year: *Acropora jacquelineae*, *A. lokani*, *A. pharaonis*, *A. retusa*, *A. rudis*, *A. speciosa*, *A. tenella*, and *Euphyllia paradivisa*. (*See* Table 1 and Appendix A).

Species	**No. of Specimens Imported in 2014**
Acropora jacquelineae	229
Acropora lokani	159
Acropora pharaonis	34
Acropora retusa	26
Acropora rudis	26
Acropora speciosa	90
Acropora tenella	30
Euphyllia paradivisa	3587
Total	**4181**

Table 1. Listed coral species imported into the United States in 2014. Numbers obtained from the LEMIS database.

However—and highlighting the problem posed by the CITES loophole described above—only 10 percent of the coral shipments appearing in the LEMIS database in 2014 documented the species' name. Approximately 28,000 imported coral specimens were labeled only with their genus name: *Acropora*, *Euphyllia*, *Montipora*, *Pavona*, *Porites*, or *Seriatopora*. An additional 380,000 individual specimens were labeled only as the order Scleractinia. (*See* Appendix A.) It thus remains possible that all of the Indo-Pacific threatened corals and some of the Caribbean corals were imported that year, without being identified to the species-level.[9]

The discussion of trade in this petition calls into question NMFS's conclusion in the final listing rule that the risk from the aquarium trade for the 20 listed coral species is "low." (79 Fed. Reg. at 53,901.) While the other threats to corals discussed in this petition are considerable, the overall fragility of coral reef ecosystems requires that threats from extraction and trade be addressed. (Bruckner 2000). As NMFS itself recognized in its final 4(d) rule for elkhorn and staghorn corals, even if trade is a "lesser stressor" (as compared to, *e.g.,* climate change) it is more easily amenable to management and such management can "contribute to the conservation of . . .

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[9] NMFS extended ESA Section 9's prohibitions on trade, import, and export to threatened staghorn coral (*Acropora palmata*) and elkhorn coral (*Acropora cervicornis*) even though the agency could not document any U.S. import or extraction from U.S. waters of those species. (73 Fed. Reg. at 64,270.) It is possible, however, that the species were traded but only documented by the genus or order name.

[coral] species by slowing the rate of decline and reducing the synergistic effects of multiple stressors on the species." (*See* 73 Fed. Reg. 64,264, 64,265 (Oct. 29, 2008).) Regulation of trade in the 20 listed coral species is thus necessary and advisable.

II. Section 9 Protections for the Listed Corals: Basis, Rationale, and Proposed Content

A. Section 4(d) of the Endangered Species Act Requires Regulations that Ensure the Survival and Recovery of Listed Species, Including Section 9 Protections

The Endangered Species Act seeks to "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, [and] to provide a program for the conservation of such endangered species and threatened species." (16 U.S.C. § 1531(b).) Congress intended threatened and endangered species to be afforded the highest of priorities through the Act. (*See Tenn. Valley Auth. v. Hill*, 437 U.S. 153, 153 (1978).) NMFS has a duty under the ESA to use its authorities to conserve the 20 threatened coral species listed as threatened on 10 September 2014. (16 U.S.C. § 1536(a)(1).)

The ESA provides many tools to conserve imperiled species. For example, section 7 prevents agencies from taking actions that jeopardize listed species; section 4 requires the development and implementation of recovery plans; and section 9 prohibits anyone from taking endangered species. More specifically, section 9 prohibits:

> (A) import [of] any such species into, or export [of] any such species from the United States;
> (B) take [of] any such species within the United States or the territorial sea of the United States;
> (C) take [of] any such species upon the high seas;
> (D) possess[ion], sell[ing], deliver[ing], carry[ing], transport[ing], or ship[ping], by any means whatsoever, any such species taken in violation of subparagraphs (B) and (C);
> (E) deliver[ing], receiv[ing], carry[ing], transport[ing], or ship[ping] in interstate or foreign commerce, by any means whatsoever and in the course of commercial activity, any such species;
> (F) sell[ing] or offer[ing] for sale in interstate or foreign commerce any such species; or
> (G) violat[ing] any regulation pertaining to such species or to any threatened species of fish or wildlife listed pursuant to section 1533 of this title and promulgated by the Secretary pursuant to authority provided by this chapter.

(16 U.S.C. § 1538 (a)(1).)

While the prohibitions of Section 9 do not apply automatically to threatened species, ESA § 4(d) grants NMFS the authority to extend these protections to threatened species. (16 U.S.C. § 1538 (a)(1); *Sweet Home Chapter of Communities for a Great Oregon v. Babbitt*, 1 F.3d 1, 7-8 (D.C. Cir. 1993) ("The second sentence [of § 1533(d)] gives the FWS discretion to apply any or all of the § 1538(a)(1) prohibitions to threatened species without obligating it to support such actions with findings of necessity.”).) Section 4(d) also provides that “the Secretary *shall* issue such regulations as he deems necessary and advisable to provide for the conservation[10] of [threatened] species.” (16 U.S.C. § 1533 (4)(d) (emphasis added).) This latter duty is mandatory per the plain language of the statute. (*See Forest Guardians v. Babbitt*, 174 F.3d 1178, 1187 (10th Cir. 1998) (“when a statute uses the word ‘shall,’ Congress has imposed a mandatory duty upon the subject of the command”); *Sweet Home*, 1 F.3d at 7-8 (“the first sentence of § 1533(d) contains the ‘necessary and advisable’ language and mandates formal individualized findings. This sentence requires the FWS to issue whatever other regulations are ‘necessary and advisable,’ including regulations that impose protective measures beyond those contained in § 1538(a)(1).”).)

In *Defenders of Wildlife v. Andrus*, the court construed the relationship between section 4(d) and the Act’s requirement to recover species, stating:

> It is clear from the face of the statute that the Fish and Wildlife Service, as part of Interior, must do far more than merely avoid the elimination of a protected species. It must bring these species back from the brink so they may be removed from the protected class, and it must use all methods necessary to do so. The Service cannot limit its focus to what it considers the most important management tool available to it to accomplish this end. … [T]he agency has an affirmative duty to increase the population of protected species.

(428 F. Supp. 167, 170 (D.D.C. 1977).) Consequently, NMFS must provide for the survival and recovery of the 20 threatened coral species through the issuance of a 4(d) rule that both extends Section 9’s prohibitions and includes additional protective regulations necessary and advisable for the listed corals’ conservation.

i. Section 9 Protections Are Necessary and Advisable for the Listed Corals’ Conservation

NMFS can decline to extend Section 9’s prohibitions only if doing so will serve to conserve the species. (*Sierra Club v. Clark*, 755 F.2d 608, 612-13 (8th Cir. 1985) (Service’s discretion to issue regulations under section 4(d) “is limited by the requirement that the regulations he is to issue must provide for the *conservation* of threatened species” (emphasis in original)); *State of Louisiana, ex rel. Guste v. Verity*, 853 F.2d 322, 332-33 (5th Cir. 1988) (conservation is a “mandatory duty”).)

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[10] Under the ESA, “conservation” of threatened and endangered species means “to use and the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this chapter are no longer necessary. Such methods and procedures include, but are not limited to, all activities associated with scientific resources management such as research, census, law enforcement, habitat acquisition and maintenance, propagation, live trapping, and transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, may include regulated taking.” (16 U.S.C. § 1532(3).)

Here, the 20 listed coral species require the protections of section 9 for their conservation and recovery, as evidenced by ample support in the final listing rule, status report, management report, scientific literature, and this petition. (Brainard *et al.* 2012; NMFS 2012; 79 Fed. Reg. 53,852). Section 9's prohibitions will redress key local threats to the corals including fishing and sedimentation (*see* Cunning *et al.* 2019) and collection and trade (*see* 79 Fed. Reg. at 53,886). Section 9 prohibitions also will help protect corals from black market trade.[11]

ii. Existing Regulatory Mechanisms Are Inadequate to Protect the Listed Corals from Threats Covered by Section 9

Section 9 prohibitions further are warranted because existing regulatory mechanisms are inadequate to fully protect the 20 listed coral species. The patchwork of foreign and domestic federal, state, and local programs (*e.g.,* fisheries, coastal, and watershed laws and regulations) provides only piecemeal protection to the listed coral species. (*See* 79 Fed. Reg. at 53,903.) For example, in its decision to list these corals as threatened, NMFS concluded that "local threats have impacted and continue to impact corals across their ranges … [and] that, collectively, the existing regulations are not currently preventing or controlling local threats across the entire range[s]" of the listed species. (*Id.* at 53,906.) In fact, NMFS stated that it could not establish the "current status and effectiveness of local regulation of impacts from local threats for any [of the 20 listed Caribbean or Indo-Pacific] species in any given location." (*Id.* at 53,865.)

International agreements likewise fail to adequately protect the listed corals. While stony corals are listed on Appendix II of CITES, that treaty does not address domestic trade, take, or other threats. Moreover, as described above and recapped here, CITES provides only weak and poorly implemented protections for stony corals and loopholes allow unregulated and likely unsustainable trade. For example, for Appendix II species, CITES only requires exporting nations to issue permits; it neglects to require import permits for listed species. Thus, the United States does not review whether imported stony corals were taken legally or in a manner "not detrimental" to the species' survival. Instead, the U.S. relies on the typically unverified assurances of exporting nations. Serious questions have been raised about the veracity of non-detriment findings issued by exporting nations, particularly Indonesia, the source of approximately 80 percent of corals imported into the United States. (U.S. Coral Reef Task Force 2000; Wood, Malsch & Miller 2012).

In addition, due to identification challenges, the U.S. Fish and Wildlife Service (the U.S. agency lead for CITES negotiation and implementation) and many CITES Parties have exempted stony coral sand (stony corals < 2mm) and coral fragments (stony corals 2-30 mm) from CITES permit requirements, finding such specimens are not "readily recognizable" species. (50 C.F.R. § 23.92(c)(4); CITES Resolution Conf. 11.10.) Thus, the identity of many species in trade remains unknown and unquantifiable.

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[11] While listing these 20 corals under the ESA was crucial for their survival and recovery, listing is known to promote the creation of black markets in protected species. (*See, e.g.,* 73 Fed. Reg. at 64,270 (extending section 9 prohibitions to elkhorn and staghorn corals in part because of the risk of a black market after listing the species as threatened; also citing sturgeon eggs and elephant ivory as examples of this phenomenon).)

Finally, and perhaps most importantly, CITES Resolution Conf. 12.3 allows exporting nations of certain CITES-listed corals (including *Mycetophyllia* spp., *Acropora* spp., *Anacropora* spp., *Euphilia* spp. (dead), *Montipora* spp., *Pavona* spp., *Porites* spp., and *Seriatopora* spp.) to record the species in trade at the genus level on their export permits; the exact species traded need not be identified. As described above, without naming a specimen to the species level, it is impossible to track how much trade is conducted in any individual species and precludes a nation's ability to find that trade is not "detrimental to the survival of th[e] species" as required under CITES Art. IV. This loophole effectively eliminates CITES protection for many of the species discussed in this petition. This loophole also presents numerous challenges in documenting and evaluating trends in trade. (79 Fed. Reg. at 53,865.)

Other international treaties similarly fail to offer needed protections to the listed coral species. In December 2014, Parties to the Specially Protected Areas and Wildlife (SPAW) Protocol included on Annex II four coral species, including two of the ESA-listed species: *Orbicella (Montastraea) annularis* and *Orbicella (Montastraea) faveolata*). The SPAW Protocol prohibits "the taking, possession or killing [of] … or commercial trade" in Annex II-listed fauna. (SPAW Protocol 1990.) The United States entered a reservation as to these four coral species in order to conduct an interagency review. (*See* 80 Fed. Reg. 42,088 (July 16, 2015).) Until the reservation is lifted (which we have urged NMFS to do in the past, *see* Center comments dated Sept. 14, 2015, and herein again request), SPAW cannot afford its protections to the listed coral species.

In sum, existing regulatory mechanisms fail to provide the 20 listed coral species with sufficient protection from existential threats including trade. NMFS can and should apply all the protections of section 9 to the 20 threatened coral species because, absent these protections, the corals will remain vulnerable to extinction.

B. Proposed Section 9 Prohibitions for the Listed Corals

Given that existing regulatory mechanisms fail to provide adequate protection to the 20 listed coral species, we petition NMFS to promulgate a 4(d) rule extending to these species all Section 9 prohibitions (with limited exceptions for scientific research and restoration activities that benefit the corals).

Since these corals face a similar suite of threats, the 4(d) rule could be modeled off of the 4(d) rule for elkhorn and staghorn corals. (*See* 50 C.F.R. § 223.208.) As a starting point, NMFS should make it a violation to evade enforcement, destroy gear or wildlife, or make false statements about activities prohibited with respect to listed corals. Similar to subsection (c) and Table 1 of 50 C.F.R. § 223.208, NMFS can include in its 4(d) rule exceptions to Section 9 prohibitions for agencies engaged in Caribbean and Indo-Pacific coral conservation through scientific research and restoration activities. In considering which agencies to except for research and restoration, NMFS must ensure that the agencies' permit programs are adequately restrictive and effective to ensure conservation benefits for the listed corals (absent the additional requirements of obtaining a separate incidental take permit under section 10 of the Act). NMFS also should prohibit issuance of incidental take statements to federal agencies undergoing section 7 consultation on any of the listed coral species unless the action agency has in place a section 7(a)(1) program for coral conservation. (16 U.S.C. § 1536.) Suggested 4(d) rule language is provided in sections (b) and (c) of Appendix B to this petition.

Just like elkhorn and staghorn corals, the 20 listed coral species face numerous local and global threats that individually and collectively have significant, negative effects on the species throughout their ranges. Such threats include, but are not limited to, climate change; collection and other direct take activities; anchoring, groundings, and gear abrasion; habitat damage; and pollution and contamination. The prohibitions of section 9 will help protect these corals from direct and indirect take, in turn preserving populations of corals and their symbionts, slowing rates of decline, reducing synergistic effects of multiple stressors, and assisting with recovery. (*See, e.g.*, 73 Fed. Reg. at 64,271.)

III. Additional Protections Are Necessary and Advisable for the Listed Corals' Survival and Recovery

A. The 4(d) Rule Should Reflect and Integrate the Best Available Science to Effectively Mitigate Key Threats to the Listed Coral Species

NOAA's Final Recovery Plan for Elkhorn and Staghorn Corals explains in detail the need for coral protections and effective management actions to facilitate coral persistence and recovery. (NMFS 2015). That Plan notes that the extant "patchwork of laws, regulations, policies, and management actions has been largely ineffective in assuring the survival" of elkhorn and staghorn corals. It states that the corals' recovery will require "uniform policies and regulations across their entire geographic ranges," a reduction in atmospheric CO_2 concentrations, and comprehensive regulations to reduce regional threats (*e.g.*, improved design and enforcement of fishing regulations, marine protected area designation, wastewater treatment, and land use plans protective of coral reefs). (*Id.*)

Recent research supports and builds upon these recommendations. This new science on corals, which covers a broad range of topics including ocean warming, ocean acidification, bleaching, overfishing, coastal pollution (both nutrient and heavy metal),[12] coastal development, and coral collection, supports the propriety of extending section 9 and adding other needed protections to promote the survival and recovery of the 20 threatened coral species. Some of the science provides NMFS with broad-scale recommendations to consider in the development of a 4(d) rule. For example, Anthony *et al.* (2015) recommend local- and regional-scale management of "press-type" stressors (*e.g,*. pollution, sedimentation, overfishing, ocean warming, ocean acidification) as the most effective way to enhance coral resilience. (*See also* Chan *et al.* 2019 (noting as important causes of coral reef decline: climate change, disease, pollution and nutrient runoff, and the loss of important herbivores); Cunning *et al.* 2019 (discussing harms from and importance of managing local stressors like dredging); Rogers *et al.* 2015 (suggesting management strategies grounded in reef condition and biophysical characteristics[13]). Other research is region- or species-specific. For example:

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[12] *See* Morgan *et al.* (2017) for a discussion of copper impacts on *O. franksi*.

[13] For example, Rogers *et al.* (2015) recommend reserves as an effective management tool for reefs with high structural complexity. For reefs where complexity has been lost, the study recommends a broader set of management

i. Caribbean Corals

A comprehensive IUCN report on the status and trends of Caribbean coral reefs during the past four decades recommends the implementation of strong regulations and adaptive legislation to systematically reduce key threats to corals. (Jackson *et al.* 2014). Control of myriad stressors is paramount for coral survival and recovery; as Bernal-Sotelo, Acosta & Cortés (2019) state, "[t]he cumulative effect of multiple stressors is the key factor affecting coral survival around the world." As the sum total of disturbances to which corals are exposed increases, so too does isolation and risk of local extinction. (DeVantier & Turak 2017).

Recommended local and regional management measures for Caribbean corals include stopping overfishing, restoring herbivorous fish (including parrotfish) populations, imposing strict regulations on coastal development and pollution, and establishing large and effectively enforced marine protected areas. (*See generally* Jackson *et al.* 2014; *see also* Anthony *et al.* 2015 (recommending herbivorous fishery management and nutrient pollution reduction for Caribbean coral restoration); Adam *et al.* 2015 (recommending the institution of comprehensive regional management actions to reduce direct sources of coral mortality including sedimentation, pollution, and nutrient loading, as well as the restoration of ecological processes, such as herbivory, to enable coral persistence and recovery); Bernal-Sotelo, Acosta & Cortés 2019 (advising mitigation of local stressors to protect local reef complexes, including water quality, regulation of land- and water-based activities (including anchoring), and development of recovery plans for coral species); Cunning *et al.* 2019 (discussing harms from dredging); Otaño-Cruz *et al.* 2019 (discussing harms of sedimentation)).

ii. Indo-Pacific Corals

In the Indo-Pacific region, management measures to increase herbivorous fish populations and decrease nutrient loading appear important for increasing coral resilience to climate change-related threats. (Anthony *et al.* 2015; Graham *et al.* 2015). Graham *et al.* (2015) investigated conditions under which reefs were able to recover from a major climate-induced coral bleaching event; this event caused unprecedented region-wide mortality of Indo-Pacific corals amounting to more than 90% loss of live coral cover. The study found a much higher probability of recovery for structurally complex reefs located in deeper water where nutrient loads were low and density of juvenile corals and herbivorous fishes was relatively high. (*Id.*)

B. Proposed Content of Additional Protective Regulations: Local Stressors

Per the mandate of 16 U.S.C. § 1533(d), NMFS must promulgate necessary and advisable protective regulations beyond those found in section 9 to ensure the conservation of the 20 listed coral species. We petition NMFS to issue regulations addressing other existential local threats including, but not limited to, trade, disease, habitat degradation, fishing, and water pollution.

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actions such as the provision of artificial complexity, coral restoration, fish aggregation devices, and herbivore management.

C. Proposed Content of Additional Protective Regulations: Climate Change

A 4(d) rule also is crucial for protecting corals against their greatest emerging threat: climate change. As ocean temperatures rise and ocean chemistry changes, life for coral species becomes increasingly difficult. According to the most recent IPCC report, "The impacts of warming, coupled with ocean acidification, are expected to undermine the ability of tropical coral reefs to provide habitat for thousands of species, which together provide a range of ecosystem services (*e.g*., food, livelihoods, coastal protection, cultural services) that are important for millions of people." (Hoegh-Guldberg *et al.* 2018). Even with only 1.5°C of global warming, scientists predict that the majority (70-90%) of tropical coral reefs will be lost.[14] (*Id.*) At 2°C, 99% of these corals will disappear.[15] (*Id.*)

The Endangered Species Act offers NMFS the authority and mandate to address climate change-related threats to imperiled species. The harms to corals from anthropogenic climate change and ocean acidification are imminent and well-documented, and there exists a clear causal link between greenhouse gas emissions and these harms. Conservation of these 20 coral species will require significant and immediate reductions in greenhouse gas emissions and NMFS should use the full suite provisions offered by the Endangered Species Act to address this critical threat. Greenhouse gas regulations should mandate emissions reductions consistent with limiting global warming to 1.5°C above pre-industrial levels, in line with the Paris Agreement and the science presented by the Intergovernmental Panel on Climate Change (IPCC) in its 2018 *Special Report on Global Warming of 1.5°C.* Such a limit will require that global carbon pollution be cut nearly in half by 2030 and reach net zero by 2050. From the standpoint of global equity and capacity to lead, the United States should phase out its carbon emissions significantly faster than those global benchmarks.

It is undisputed that immediate and rapid greenhouse gas reductions are essential to stopping the trend toward coral extinction and ensuring the listed species' recovery. The final listing rule identifies ocean warming, ocean acidification, and disease (which has been linked to warming temperatures, *see* Randall & van Woesik 2015) as primary contributors to extinction risk for the 20 listed coral species. (79 Fed. Reg. at 53,890-53,896.) Similarly, NOAA's Final Recovery Plan for Elkhorn and Staghorn Corals identifies ocean warming and disease as the most serious threats to these corals, followed by ocean acidification. (*See* NMFS 2015.) The agency states that increasing ocean temperatures and acidification resulting from present and projected global atmospheric CO_2 levels will impede elkhorn and staghorn recovery. To address these threats, the Recovery Plan establishes specific recovery criteria for ocean temperature and aragonite saturation state conditions that must be met to recover elkhorn and staghorn corals, including:

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[14] In the Caribbean, Frieler *et al.* (2012) show that limiting warming to ~1ºC above pre-industrial levels is needed to protect Caribbean coral reefs from degradation. A 1ºC target is consistent with an emissions trajectory that peaks in the next few years at 400 ppm, declines sharply thereafter (~6% decline per year), and returns atmospheric CO_2 to below 350 ppm in the early 2100s. (Hansen *et al.* 2013).

[15] *See also* Lane *et al.* (2013) (projecting that an emissions scenario resulting in a CO_2 concentration of 427 ppm in 2100 would be insufficient to protect corals and would likely result in coral cover in South Florida and Puerto Rico dropping below 5% by 2050, and below 1% by 2100).

- A reduction of sea surface temperatures across the listed species' geographic ranges to Degree Heating Weeks less than 4;
- Mean monthly sea surface temperatures below 30°C during coral spawning periods; and
- Restoration of open ocean aragonite saturation to a state greater than 4.0.

Id.; *see also* NOAA Satellites & Bleaching, Hughes *et al.* 2018a (discussing impacts of degree heating weeks > 4 on Great Barrier Reef corals)). Achieving these conditions will require stringent emissions reductions that return atmospheric CO_2 to below 350 ppm. (*see* NMFS 2015).

A robust body of scientific research clearly supports the notion that protecting the listed corals from extinction and ensuring their recovery requires that the U.S. adopt greenhouse gas mitigation regulations significantly stronger than those currently in force or proposed. Existing national and international regulatory mechanisms to abate greenhouse gas pollution are insufficient to address the threats posed to corals by climate change. NMFS notes this inadequacy alongside its finding that greenhouse gas emissions "pose[] an extinction risk threat to all corals vulnerable to climate-related threats." (79 Fed. Reg. at 53,906.) The agency concludes that "none of the major global initiatives appear to be ambitious enough … to minimize impacts to coral reefs and prevent what are predicted to be severe consequences for corals worldwide." (*Id.* at 53,903.) Scientific research indicates that the current global emissions pathway, which is exceeding the Representative Concentration Pathway (RCP) 8.5 pathway, will lead to mass coral extinction. The U.S. must adopt an emissions pathway more stringent than RCP 2.6 to protect and recover listed corals.[16] NMFS may use the requested 4(d) rule to help achieve this goal.

IV. Conclusion

As demonstrated in this petition, the promulgation of a 4(d) Rule that extends the protections of ESA Section 9 and embodies additional protective regulations addressing both local and global stressors including climate change is both necessary and advisable for the conservation and recovery of the 20 coral species listed as threatened on 10 September 2014. We look forward to seeing NMFS reinitiate and complete the process of 4(d) Rule promulgation in the coming months.

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[16] On the global scale, van Hooidonk *et al.* (2013) present global projections for ocean warming and acidification impacts on coral reefs from IPCC AR5 climate models using RCPs. Even the lowest emissions pathway considered (RCP 2.6), 88% of reef locations experience severe bleaching events annually by the end of the century. In an RCP 2.6 Pathway, CO_2 concentrations peak at ~430ppm around 2050 and then decline to ~400 ppm by the end of the century.

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Appendix A:
LEMIS Data

Appendix B:
Proposed Regulatory Language

Corals.

(a) *Affirmative Actions*

(1) The Secretary shall withdraw the United States' reservation as to the four coral species (*Acropora cervicornis, Acropora palmata, Orbicella (Montastraea) annularis, Orbicella (Montastraea) faveolata*) added to the Specially Protected Areas and Wildlife (SPAW) Protocol in December 2014 (*see* 80 Fed. Reg. 42,088 (July 16, 2015)) and ban all commercial trade in these species.

(b) *Prohibitions.*

(1) The prohibitions of section 9(a)(1) of the ESA (16 U.S.C. 1538(a)(1)) relating to endangered species apply to the five Caribbean coral species (*Dendrogyra cylindrus, Orbicella annularis, Orbicella faveolata, Orbicella franksi,* and *Mycetophyllia ferox*) and fifteen Indo-Pacific coral species (*Acropora globiceps, Acropora jacquelineae, Acropora lokani, Acropora pharaonis, Acropora retusa, Acropora rudis, Acropora speciosa, Acropora tenella, Anacropora spinosa, Euphyllia paradivisa, Isopora crateriformis, Montipora australiensis, Pavona diffluens, Porites napopora,* and *Seriatopora aculeata*) listed as threatened in 50 C.F.R. § 223.102(e), except as provided in part (c) below.

(2) It is unlawful for any person subject to the jurisdiction of the United States to do any of the following:

(i) Fail to comply immediately, in the manner specified at § 600.730 (b) through (d) of this title, with instructions and signals specified therein issued by an authorized officer, including instructions and signals to haul back a net for inspection;

(ii) Refuse to allow an authorized officer to board a vessel, or to enter an area where fish or wildlife may be found, for the purpose of conducting a boarding, search, inspection, seizure, investigation, or arrest in connection with enforcement of this section;

(iii) Destroy, stave, damage, or dispose of in any manner, fish or wildlife, gear, cargo, or any other matter after a communication or signal from an authorized officer, or upon the approach of such an officer or of an enforcement vessel or aircraft, before the officer has an opportunity to inspect same, or in contravention of directions from the officer;

(iv) Assault, resist, oppose, impede, intimidate, threaten, obstruct, delay, prevent, or interfere with an authorized officer in the conduct of any boarding, search, inspection, seizure, investigation, or arrest in connection with enforcement of this section;

(v) Interfere with, delay, or prevent by any means, the apprehension of another person, knowing that such person committed an act prohibited by this section;

(vi) Resist a lawful arrest for an act prohibited by this section;

(vii) Make a false statement, oral or written, to an authorized officer or to the agency concerning applicability of the exceptions enumerated in paragraph (c) of this section relating to the five listed Caribbean coral species and fifteen listed Indo-Pacific coral species;

(viii) Make a false statement, oral or written, to an authorized officer or to the agency concerning applicability of the exceptions enumerated in paragraph (c) of this section relating to the five listed Caribbean coral species and fifteen listed Indo-Pacific coral species;

(ix) Make a false statement, oral or written, to an authorized officer or to the agency concerning the fishing for, catching, taking, harvesting, landing, purchasing, selling, or transferring fish or wildlife, or concerning any other matter subject to investigation under this section by such officer, or required to be submitted under this part 223;

(x) Attempt to do, solicit another to do, or cause to be done, any of the foregoing.

(3) Any federal agency triggering consultation under section 7 of the ESA, 16 U.S.C. § 1536, for any of the 20 listed coral species shall not receive an incidental take statement the affected coral species unless that agency has in place a section 7(a)(1) coral conservation program.

(c) *Affirmative defense.* In connection with any action alleging a violation of this section, any person claiming the benefit of any exception, exemption, or permit under this section has the burden of proving that the exception, exemption, or permit is applicable, was granted, and was valid and in force at the time of the alleged violation, and that the person fully complied with the exception, exemption, or permit.

(d) *Exceptions.* Exceptions to the prohibitions of section 9(a)(1) of the ESA (16 U.S.C. 1538(a)(1)) applied in paragraph (b) of this section relating to the five listed Caribbean coral species and fifteen listed Indo-Pacific coral species are described in the following paragraphs (1) through (5):

(1) Permitted scientific research and enhancement. Any export or take of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species resulting from conducting scientific research or enhancement directed at those coral species is excepted from the prohibitions in ESA sections 9(a)(1)(A), (B) and (C) provided a valid research or enhancement permit has been obtained from one of the following Federal or state agencies: NOAA National Ocean Service National Marine Sanctuary Program, National Park Service, U.S. Fish and Wildlife Service, **[OR OTHER RELEVANT GOVERNMENT AGENCY]**. The exportation or take must be in compliance with the applicable terms and conditions of the applicable research or enhancement permit, and the permit must be in the possession of the permittee while conducting the activity. Export of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species from the United States to conduct excepted research or enhancement activities requires a CITES export permit from the U.S. Fish and Wildlife Service in addition to the research permit for collection. Import of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species into the United States to conduct excepted research or enhancement activities must be in compliance with the provisions of section 9(c) of the ESA.

(2) Restoration activities. Any agent or employee of governmental agencies listed in **[TABLE X]** may take the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species without a permit, when acting in the course of conducting a restoration activity directed at those species taken which is authorized by an existing authority (see [**TABLE X]** to this section). Take of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species during such restoration activity is excepted from the prohibitions in ESA sections 9(a)(1)(B) and (C). An excepted restoration activity is defined as the methods and processes used to provide aid to injured individuals of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species.

(3) Section 10 scientific and enhancement permits. The Assistant Administrator may issue permits authorizing activities that would otherwise be prohibited under **[CFR SECTION]** for scientific purposes or to enhance the propagation or survival of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species, in accordance with and subject to the conditions of part 222, subpart C-General Permit Procedures.

(4) Section 10 incidental take permits. The Assistant Administrator may issue permits authorizing activities that would otherwise be prohibited under **[CFR SECTION]** in accordance with section 10(a)(1)(B) of the ESA (16 U.S.C. 1539(a)(1)(B)), and in accordance with, and subject to the conditions of part 222 of this chapter. Such permits may be issued for the incidental taking of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species.

(5) Section 7 Interagency consultation. Any incidental taking that is in compliance with the terms and conditions specified in a written statement provided under

section 7(b)(4)(C) of the ESA (16 U.S.C. 1536(b)(4)(C)) shall not be considered a prohibited taking of the five listed Caribbean coral species or fifteen listed Indo-Pacific coral species pursuant to paragraph (o)(2) of section 7 of the ESA (16 U.S.C. 1536(o)(2)), subject to the constraints imposed by **[THIS CFR SECTION (b)(3)].**

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Fallen Pillars: The Past, Present, and Future Population Dynamics of a Rare, Specialist Coral–Algal Symbiosis

Andrea N. Chan[1]*, Cynthia L. Lewis[2,3], Karen L. Neely[4,5] and Iliana B. Baums[1]

[1] Department of Biology, Pennsylvania State University, University Park, PA, United States, [2] Department of Biology, Florida International University, Miami, FL, United States, [3] Florida Keys Marine Lab, Long Key, FL, United States, [4] Department of Marine and Environmental Sciences, Nova Southeastern University, Fort Lauderdale, FL, United States, [5] Florida Fish and Wildlife Conservation Commission, Marathon, FL, United States

With ongoing changes in climate, rare and ecologically specialized species are at increased risk of extinction. In sessile foundation fauna that reproduce asexually via fragmentation of existing colonies, the number of colonies does not reflect the number of genets and thus can obscure genotypic diversity. Colonies that are the product of fragmentation are not visually distinguishable from colonies that stem from sexual recruits. For this reason, molecular markers are necessary to assess genotypic variation and population structure in clonal organisms such as reef-building corals and their endosymbiotic dinoflagellates. For the rare Caribbean pillar coral, *Dendrogyra cylindrus*, and its endosymbiotic dinoflagellate, *Breviolum dendrogyrum*, we use *de novo* microsatellite markers to infer past demographic changes, describe modern population structure, and quantify the frequency of asexual reproduction. Our analyses show that *D. cylindrus* comprises three distinct populations across the Greater Caribbean whereas the symbiont could be differentiated into four populations, indicating barriers to gene flow differ between host and symbiont. In Florida, host and symbiont populations reproduced mainly asexually, yielding lower genotypic diversity than predicted from census size. When multiple coral ramets were present, they often associated with the same clonal strain of *B. dendrogyrum*, pointing to the high fidelity of this relationship. Models of past demographic events revealed no evidence for historical changes in population sizes, consistent with the paleontological record of *D. cylindrus* indicating it has been rare for hundreds of thousands of years. The most recent global thermal stress event likely triggered a severe disease outbreak among *D. cylindrus* in Florida, resulting in a severe population decline. Projections indicate a high likelihood that this species will become extinct in the Northern Greater Caribbean within a few decades. The ecosystem consequences of losing rare coral species and their symbionts with increasingly frequent extreme warming events are not known but require urgent study.

Keywords: *Dendrogyra cylindrus*, climate change, population genetics, Symbiodiniaceae, rare species, clonal structure

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Rui Rosa,
Universidade de Lisboa, Portugal

Reviewed by:
Nancy Knowlton,
Smithsonian Institution, United States
Celia Schunter,
The University of Hong Kong,
Hong Kong
Daniel J. Thornhill,
National Science Foundation (NSF),
United States

***Correspondence:**
Andrea N. Chan
andrea.n.chan13@gmail.com

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INTRODUCTION

Ecologically rare species are predicted to be more vulnerable to environmental change and extinction risk with shifts in climate (Caughley, 1994; McKinney, 1997; Davies et al., 2004). Species are rare because they may inhabit narrow geographic ranges (Solórzano et al., 2016), occupy few specific habitats (Deák et al., 2018), and/or exhibit low abundance in nature (Rabinowitz, 1981). There are obvious consequences to having low population densities, including difficulties finding a mate (Stephens and Sutherland, 1999) and vulnerability to genetic drift (Ellstrand and Elam, 1993). Populations of rare species may become fragmented more easily due to the increased local extinction of small populations (Matthies et al., 2004; Blanquer and Uriz, 2010). The persistence of rare species is challenged when they are obligate partners of specific symbionts. For example, the endangered terrestrial orchid *Caladenia huegelii* associates with a specific mycorrhizal fungus throughout its range (Swarts et al., 2010). This specificity between partners has caused *C. huegelii* to be rare due to the limited suitable environmental conditions of the mycorrhiza. Consequentially, the strict niche characteristics of one partner in a symbiosis may drive the scarcity of the other. Further, intra-specific diversity in both partners and fidelity of genotype–genotype associations can play a role in how the symbiosis responds to changing conditions (Baums et al., 2014b; Parkinson and Baums, 2014; Parkinson et al., 2015). However, there are many rare species that are adapted to low population densities (de Lange and Norton, 2004; Flather and Sieg, 2007; Blanquer and Uriz, 2010), and these species persist for long periods of evolutionary time.

Rarity is sometimes obscured by the life history of the species, specifically in reference to the prevalence of asexual reproduction. Sessile organisms often reproduce by asexual fragmentation and while some are hermaphroditic, these may be self-incompatible (Scobie and Wilcock, 2009; Gitzendanner et al., 2012; Baums et al., 2013). As a consequence, large clonal stands of a rare species may exist that are unable to reproduce via sexual reproduction. Clonal populations of the rare dwarf shrub *Linnaea borealis* had low reproductive success due to a lack of nearby conspecifics, leading to increased geitonogamy (Scobie and Wilcock, 2009). Likewise, the aquatic plant *Decodon verticillatus* had reduced sexual reproduction in clonal populations at the northern range limit (Dorken and Eckert, 2001).

However, extensive clonal reproduction can also be beneficial, especially for rare species, by maintaining population sizes despite a lack of sexual recruitment. In other words, clonal propagation can provide a "storage effect" by increasing the persistence of individual genotypes when the influx of sexual recruits is low or absent due to unfavorable environmental conditions (Warner and Chesson, 1985; Boulay et al., 2014; Dubé et al., 2017). This storage effect is most pronounced when adults are long-lived, reproductive output is high, and population densities are low – such as in some mass-spawning corals – and thus may play an important role in maintaining intraspecies genetic diversity (Baums et al., 2006, 2014a; Boulay et al., 2014).

Census sizes of many Caribbean reef-building corals have declined dramatically over the past few decades. Yet, in recent coral surveys throughout the Caribbean, some species were consistently more abundant (e.g., *Orbicella faveolata*), while others were rare, such as the pillar coral *Dendrogyra cylindrus* (Edmunds et al., 1990; Ward et al., 2006; Steiner and Kerr, 2008; Miller et al., 2013). *Dendrogyra cylindrus* (Ehrenburg, 1834) is a conspicuous Caribbean coral in the family Meandrinidae. It is the only species in the genus, and it occurs between 1 and 25 m depths (Goreau and Wells, 1967). This species was originally characterized as a gonochoric broadcast spawner (Szmant, 1986), however, recent spawning observations in the Florida Keys have revealed that *D. cylindrus* can be hermaphroditic (Neely et al., 2018). *D. cylindrus* has been classified as vulnerable on the International Union for Conservation of Nature (IUCN) Redlist (Aronson et al., 2008), and was listed as threatened under the United States Endangered Species Act (NMFS, 2014). The fossil record supports the relative rarity of *D. cylindrus* through time, although there is localized evidence that pillar corals were more prevalent on Pleistocene reefs (Hunter and Jones, 1996). Corals in the genus *Dendrogyra* only appear 29 times in the Paleobiology Database, whereas there are 278 *Acropora palmata* fossils, 111 *Orbicella faveolata* fossils, and 160 *Meandrina* (a sister genus to *Dendrogyra*) fossils[1] (accessed February 18, 2018). Despite the growing concern over the persistence of this rare coral, no studies have described genotypic diversity, population connectivity, or past changes in population size in *D. cylindrus*.

Dendrogyra cylindrus forms an obligate symbiosis with another rare species, *Breviolum* (formerly *Symbiodinium* Clade B) *dendrogyrum* (LaJeunesse et al., 2018; Lewis et al., 2018). In recent surveys of Caribbean corals, *B. dendrogyrum* (formerly ITS2 type B1k) was only found to associate with *D. cylindrus*, indicating that it has a narrow habitat range (Finney et al., 2010). Assessing levels of within-species diversity is imperative to understanding the maintenance of and threats to the *D. cylindrus*-*B. dendrogyrum* mutualism. If co-dispersal between partners is occurring, then the population structure of both symbiotic species will be congruent (Werth and Scheidegger, 2012) and facilitate local adaptation (Baums et al., 2014b). In this study, we used *de novo* and existing microsatellite markers for host and symbiont to assess the null hypotheses of no population structure and no asexual reproduction in either species. We further hypothesized that coral colonies harbor *B. dendrogyrum* throughout the range of the host. Finally, we used a maximum-likelihood demographic model to assess the null hypothesis of no past changes in population size in *D. cylindrus*.

MATERIALS AND METHODS

Sample Collection

Samples of *D. cylindrus* were collected from 51 sites along the Florida Reef Tract ($n = 217$), three sites in Curaçao ($n = 24$), six sites in the U.S. Virgin Islands ($n = 40$), three sites in Belize ($n = 10$), and four sites in the Turks and Caicos Islands ($n = 17$) (**Figure 1**). Regions were visited in different years, but all samples were collected between 2013 and 2017. Because of the rarity of *D. cylindrus,* we targeted sites with known occurrences of the coral instead of attempting a random sampling scheme. Sampling

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[1] paleobiodb.org

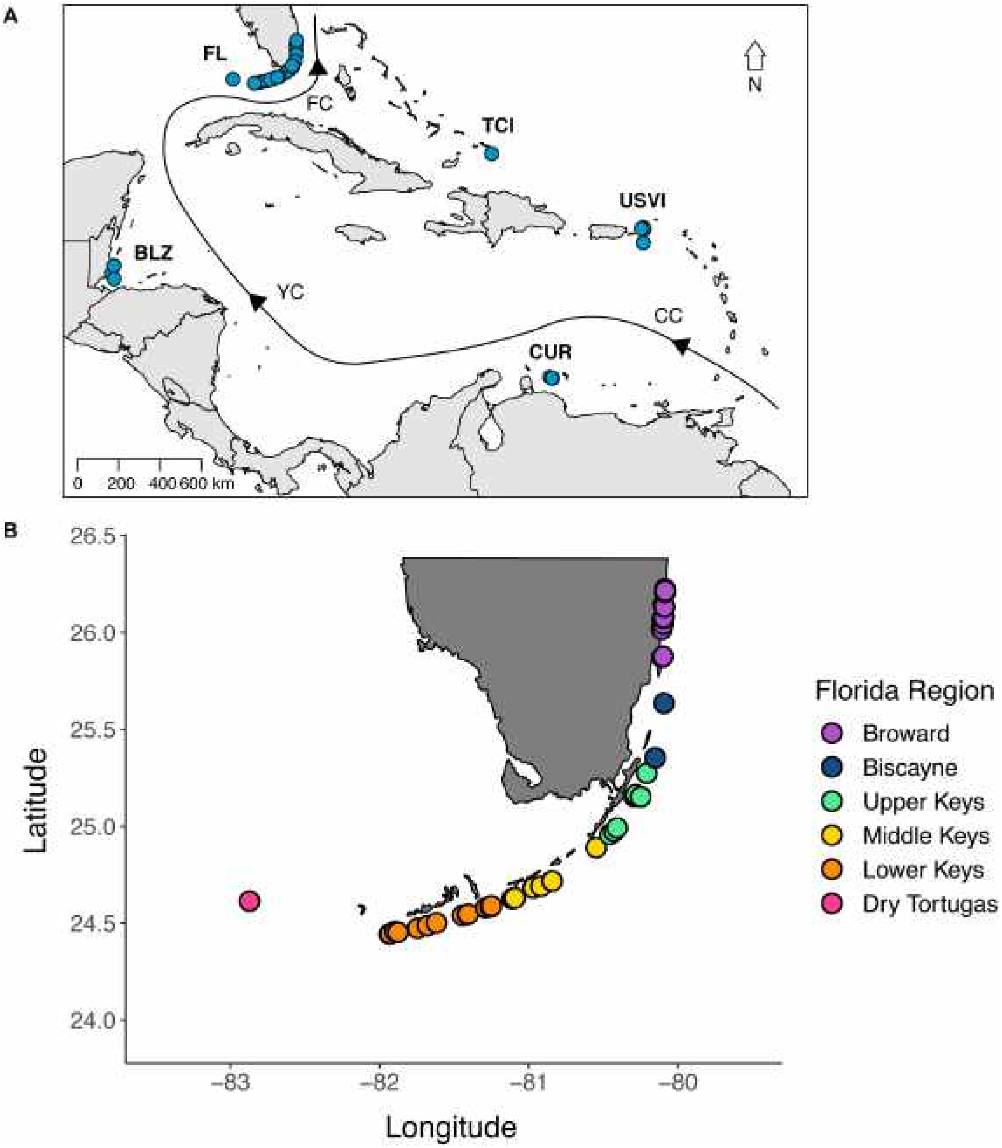

FIGURE 1 | (A) A map of the sites where tissue samples of *Dendrogyra cylindrus* were collected. Samples were collected from 51 sites along the Florida Reef Tract (FL), three sites in Curaçao (CUR), six sites in the U.S. Virgin Islands (USVI), three sites in Belize (BLZ), and four sites in the Turks and Caicos Islands (TCI). The black line with arrows indicates the direction of ocean currents. CC, Caribbean Current; YC, Yucatan Current; FC, Florida Current. See text for sample sizes. **(B)** A map of the Florida collection sites, colored by region. More samples were collected from Florida to enable the description of clonal structure and to delineate the relationship between genetic and geographic distance.

intensity was higher in Florida, but not exhaustive due to the threatened status of this species. At Florida sites containing many colonies, samples were collected from colonies throughout the site. When sites contained only a few colonies, all were sampled. Also, within-colony sampling (top, middle, and base) was done in Florida to determine if symbiont genotypes were represented consistently within a colony. *D. cylindrus* samples from all other regions were not collected in a spatially explicit way, rather, colonies were sampled haphazardly. Sampling was accomplished using a combination of clipping small pieces of tissue and conducting a biopsy of two or three polyps using the syringe technique (Kemp et al., 2008). All samples were preserved in 95% non-denatured ethanol. Global positioning system (GPS) coordinates were collected for the Florida colonies so that genetic and clonal diversity estimates could be related to geographic distance among colonies.

Microsatellite Design and Amplification

DNA was extracted from one sample from Florida using the illustra Nucleon PhytoPure Genomic DNA Extraction kit (GE Healthcare) and used as the starting material for generating molecular markers. Because this sample was from an adult colony, DNA from the coral host and dinoflagellate symbiont was sequenced on the Roche GS 454 FLX+ utilizing the Titanium Sequencing Kit (Roche, one half plate). Raw data is available from Penn State's ScholarSphere[2]. See Supplementary Materials for detail in primer design. After testing primers for successful amplification, host specificity, and variability, 11 markers were retained (**Supplementary Table 1**). These markers were combined into four multiplex reactions (labeled A through D, **Supplementary Table 1**) using the Multiplex Manager software[3]. Only markers labeled with different colored fluorescent dyes (Applied Biosystems) were combined. Multiplex reactions consisted of 1 μl of template DNA, 1.01x Reaction Buffer (New England Biolabs), 2.53 mM MgCl (New England Biolabs), 0.005 mg BSA (New England Biolabs), 0.202 mM dNTPs (Bioline), 0.051 μM of forward and reverse primer (Applied Biosystems), 0.75 U Taq polymerase (New England Biolabs), and nuclease-free water in a total reaction volume of 9.9 μl. Thermocycler parameters included an initial denaturation at 94°C for 5 min, 30 cycles of denaturing at 94°C for 20 s, annealing at 55°C (or 54°C) for 20 s, and extension at 72°C for 30 s, and a final extension at 72°C for 30 min. All PCR products were visualized using an ABI3730 (Applied Biosystems) automated DNA sequencer with an internal size standard (Gene Scan 500-Liz, Applied Biosystems) for accurate sizing. Electropherograms were analyzed using GeneMapper Software 5.0 (Applied Biosystems).

Existing Symbiodiniaceae B1 primers (Santos and Coffroth, 2003; Pettay and LaJeunesse, 2007; Andras et al., 2009) were tested on *D. cylindrus* samples from Florida and Curaçao, of which eight were variable and amplified the target product a majority of the time (**Supplementary Table 2**). These were combined into multiplex reactions (**Supplementary Tables 2, 3**). Thermocycler parameters (e.g., annealing temperatures) varied by multiplex (**Supplementary Table 3**). However, after conducting preliminary analyses using this set of markers, it became clear that additional markers would be necessary to increase our power of identifying clonal strains. See the supplement for details on *de novo* primer design and amplification conditions. The combined set of 15 microsatellite markers (**Supplementary Table 2**) was used to assess clonal and population structure of the algal symbiont.

Analysis of Population and Clonal Structure

Matching multilocus genotypes were identified using the Data Subset option in GenAlEx v. 6.5 (Peakall and Smouse, 2006). Samples with exact allele size matches at all microsatellite loci were considered to be asexually produced clones. The Multilocus Matches option (GenAlEx) was used to identify possible misidentified alleles, which were checked and corrected if necessary. Linkage disequilibrium tests were conducted using Genepop on the web 4.0 (Rousset, 2008) Option 2.1. Tests for Hardy–Weinberg equilibrium were conducted in GenAlEx v. 6.5 (Peakall and Smouse, 2006) and confirmed using exact tests in Genepop on the web Option 1.1 (**Supplementary Table 5**). The probability of identity (PI) describes the power of the microsatellite markers to distinguish closely related colonies (such as siblings) from colonies that are identical because they are the result of asexual reproduction (fragmentation). For the diploid *D. cylindrus*, PI was calculated in GenAlEx v. 6.5. The PI for the haploid symbiont was calculated as the sum of each allele's frequency squared in each population and multiplied across loci, in accordance with previous studies (Baums et al., 2014b).

Genotypic diversity indices for the coral host and symbiont, which included genotypic richness, diversity, and evenness, were calculated as in Baums et al. (2006) using the entire data set of multilocus genotypes (including clones) with complete allele calls at 10 microsatellite markers (excluding marker D48). Briefly, genotypic richness (N_g/N) was calculated by dividing the number of unique multilocus genotypes (N_g) by the total number of samples genotyped (N) and varies from near 0 (highly clonal) to 1 (no clones). Genotypic diversity (G_o/G_e) is the ratio of observed to expected genotypic diversity, and varies from 0 (mostly asexual population) to 1 (mostly sexual population). Expected genotypic diversity (G_e) for a solely sexually reproducing population was assumed to be equal to the sample size N. The final metric – genotypic evenness (G_o/N_g) – provides information about the longevity of different genotypes, and is the observed genotypic diversity (G_o) divided by the number of unique multilocus genotypes (N_g). Genotypic evenness ranges from near 0 (population dominated by few genets with many ramets) to 1 (population contains multiple genets with equal ramets). However, in sites with only one genet, genotypic evenness is no longer an informative metric since it automatically yields a value of one.

Unique multilocus genotypes (without clonal replicates) were clustered using the program STRUCTURE v. 2.3.4 to estimate the number of different populations of host and symbiont in the dataset (Pritchard et al., 2000). After initial testing, the admixture model with no location prior was used with correlated allele frequencies. The prior number of populations (K) was set from 1 to 6 with five replicate runs per K, a burnin of 100,000 and 1,000,000 Markov Chain Monte Carlo repetitions after the burnin using the package 'PARALLELSTRUCTURE' (Besnier and Glover, 2013) in R v. 3.4 (R Development Core Team, 2017). The optimal value for K was identified using the ΔK method (Evanno et al., 2005) implemented in the online program Structure Harvester (Earl, 2012). CLUMPAK was used to identify the consensus of inferred clusters for the different replicates of each K-value and to visualize the results (Kopelman et al., 2015). Additional estimators of the number of optimal populations (posterior probability, MedMeaK, MaxMeaK, MedMedK, and MaxMedK) were applied (Pritchard et al., 2009; Puechmaille, 2016). Because uneven sampling has been shown to underestimate the true K (Puechmaille, 2016), larger populations were randomly subsampled to create more even sample sizes across the five regions (see Results). The K value chosen by the most estimators was identified as the optimal number of populations. Global F_{ST}, or the proportion of genetic variation between subpopulations (Wright, 1951), was calculated using GENODIVE

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[2] https://scholarsphere.psu.edu/concern/parent/31z40kt37x/file_sets/x6969z327w

[3] www.multiplexmanager.com

(Meirmans and Van Tienderen, 2004) and the dataset with clonal replicates removed. The F_{ST} value adjusted for the maximum amount of within-population diversity (F'_{ST}) was also obtained from GENODIVE. Pairwise F_{ST} values between each of the five regions were calculated using GENALEX v. 6.5. The congruence of population structure and clonal reproduction in *D. cylindrus* and *B. dendrogyrum,* as well as the extent of clonal propagation, were compared. In cases where the symbiont population clusters identified by STRUCTURE did not correspond to geography, the symbiont species identity was confirmed by sequencing the Si15 microsatellite flanker region (Finney et al., 2010; Lewis et al., 2018).

Analysis of molecular variance (AMOVA) was employed to test the null hypotheses of an absence of population structure for the host and symbiont (Excoffier et al., 1992). Samples were grouped by region (identified using STRUCTURE and the optimal *K* value) and location (Belize, Florida, Turks and Caicos Islands, USVI, and Curaçao). The AMOVA option in GENALEX v. 6.5 was used to partition genetic variation from a distance matrix between regions and locations, using 9,999 permutations and assuming an Infinite Allele Model.

Global positioning system coordinates for all Florida colonies were used to create a geographic distance matrix, which was compared to the genetic distance matrix for *D. cylindrus*. Mantel tests of isolation by distance and spatial autocorrelation analyses were conducted in GENALEX v. 6.5.

Because of the small number of samples, a finding of no population structure could be due to a lack of power. Thus, simulations were conducted in POWSIM v. 4.1 to assess the power of the microsatellite data set to detect low levels of population differentiation. POWSIM estimates the lowest level of differentiation (F_{ST}) that can be detected in a simulated population with a minimum of 90% accuracy (Ryman and Palm, 2006). Significance was determined using Fisher's exact test.

Population Demographic Modeling

The modeling software MIGRAINE v. 0.5.2[4] was used to test for past changes in population size in the Florida *D. cylindrus* population. Samples from other locations were not grouped with Florida because population structure within a dataset yields inaccurate demographic parameter inference (Leblois et al., 2014). Additional unique multilocus genotypes were included for this analysis to increase the power of detecting historical population size changes ($n = 95$ total). The null model assuming a constant population size (OnePop) was run to estimate pGSM, which was close to 0.3. This parameter describes the geometric distribution of mutation step size under a generalized stepwise mutation model (GSM), which is most appropriate for microsatellite markers (Leblois et al., 2014). When we ran the model assuming one past change in population size (OnePopVarSize), we fixed pGSM at 0.3 and inferred the current ($2N\mu$) and ancestral ($2N_{anc}\mu$) population sizes, as well as the duration of the contraction or expansion event ($Dg/2N$) and the ratio of current to ancestral population size (N_{ratio}). We assumed a mutation rate (μ) of 5×10^{-4} per locus per generation, a value typical for microsatellite loci (Estoup and Angers, 1998). In addition, we also ran the OnePopFounderFlush model, which assumes two past changes in population size and infers a founder population size ($2N_{founder}\mu$) and two additional population size ratios ($N_{cur}N_{founder\ ratio}$ and $N_{founder}N_{anc\ ratio}$). Significant population size changes were detected using 95% confidence interval estimates of the population size ratios. If the value 1 (indicating the current and ancestral population sizes were identical) was outside of the 95% confidence interval, then the size change was significant. MIGRAINE uses sequential importance sampling algorithms (De Iorio and Griffiths, 2004a,b) to estimate parameters of past demographic changes from population genetic data. We used 2,000 points, 2,000 trees, and four iterations per run for the models with population size changes. The null model was run using 2,000 points, 100 trees, and three iterations. Two independent runs were conducted per model by changing the estimation seed. Additional model settings are included in the supplement (**Supplementary Table 4**).

Through the course of this study, we witnessed a severe decline in Florida *D. cylindrus* (Neely et al., unpublished data). During the summers of 2014 and 2015, water temperatures rose above 30.5°C in the Florida Keys[5], triggering a multi-year thermal stress event (Manzello, 2015; Lewis et al., 2017). After some coral colonies bleached in 2014, many contracted a tissue loss disease (Precht et al., 2016). This thermal stress-related disease outbreak led to a massive loss of Florida pillar corals. Some areas experienced higher disease prevalence than others (Neely et al., unpublished data). In Broward County (**Figure 1B**), 86% of the known colonies were lost in 2 years (Kabay, 2016). Severe hyperthermal events such as this one are expected to occur annually by 2042 on average under Representative Concentration Pathway (RCP) 8.5 (van Hooidonk et al., 2017), although there is projected heterogeneity along the Florida Reef Tract (van Hooidonk et al., 2015).

Prior to the most recent event, extensive coral bleaching from hyperthermal stress in the Caribbean occurred in 1997–1998, 2005, and 2010 (Eakin et al., 2010; Heron et al., 2016). If we assume that thermal stress events such as the 2014–2015 event in Florida occur twice per decade up until the estimated timing of annual severe bleaching (2042), we can estimate how many years are left before local extinction of *D. cylindrus* for each of three representative percent decline scenarios (80%, 50%, and 20%).

If we extrapolate our data on the number of coral genotypes and symbiont strains in our sample of 161 *D. cylindrus* colonies to the estimated total Florida population of 610 colonies (Lunz et al., 2016), we would expect to find 212 coral genotypes and 110 symbiont strains. Using our data on the *D. cylindrus* genotype frequencies and *B. dendrogyrum* strain frequencies, we simulated the decline of Florida *D. cylindrus* with future thermal stress-related disease events. We generated 610 *D. cylindrus* colonies using the statistical software R and assigned each colony a coral genotype and symbiont strain based off of the frequency distribution we observed in our sample of 161 colonies. For simplicity, we only assigned one

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[4] https://kimura.univ-montp2.fr/~rousset/Migraine.htm

[5] http://coralreefwatch.noaa.gov

strain per colony whereas in reality some colonies host more than one strain.

Because we do not know the actual rate of decline from the most recent thermal stress event and associated disease losses for all of Florida, we simulated a range of scenarios where 80%, 50%, and 20% of colonies survive each hyperthermal event. This model assumes that there is no sexual reproduction (a valid assumption for *D. cylindrus*, see section "Discussion"), no establishment of new clonal fragments, and no successful restoration. We also assume that each high temperature event is equally damaging, resulting in the same percent loss of colonies as the previous event. After running 100 simulations for each of the three rates of decline, we identified the number of thermal stress events that would cause local extinction of *D. cylindrus* in Florida. *D. cylindrus* was considered to be locally extinct once the average number of colonies (across the 100 simulations) remaining after a stress event was below one.

RESULTS

Genetic Diversity of *de novo Dendrogyra cylindrus* Microsatellite Markers

The microsatellite markers developed for *Dendrogyra cylindrus* ranged in allelic diversity from 6 to 15 and in effective allelic diversity from 2.047 to 6.849 (**Table 1**). Observed heterozygosity levels ranged from 0.399 to 0.954, expected heterozygosity within subpopulations (e.g., Florida, USVI) ranged from 0.533 to 0.888, and total heterozygosity ranged from 0.686 to 0.895 (**Table 1**). The total heterozygosity adjusted for sampling a limited number of populations ranged from 0.724 to 0.897 (**Table 1**). The heterozygosity values for all markers were relatively high (closer to the maximum value of 1), indicating high genetic variability for our samples (**Table 1**). Variability among inbreeding measures for the 11 markers were between −0.19 and 0.361, with most values close to zero (**Table 1**). The markers differed in their genetic variability, with D15 showing the lowest differentiation across all four measures (**Table 1**). D716 and D48 showed the most variability. Markers were tested for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium, if applicable (see **Supplementary Text**).

Clonal Structure and Spatial Analyses Along the Florida Reef Tract

Clonal structure analyses for the coral host revealed that the sampled colonies of *D. cylindrus* along the Florida Reef Tract were highly clonal when multiple colonies were present at a site. After genotyping 161 colonies from 51 different sites, we only found 56 unique multilocus genotypes. The Florida population of the coral host also had low values for genotypic richness, diversity, and evenness (**Figure 2**). The majority of sites contained only one colony. High genotypic diversity at a site usually occurred only when there were few colonies to sample at that site (**Figure 3A**). The sites where *D. cylindrus* was locally abundant (at least 10 colonies) have genotypic diversity values very close to zero. This indicates that within each site, the Florida coral colonies were predominantly the product of asexual reproduction. Genotypic evenness values calculated for sites with at least five genotyped samples revealed that most sites had values equal to 1 (**Figure 3B**). Most of these sites yielded an evenness of 1 because all sampled ramets belonged to the same genet. The host probability of identity values for all sampling regions were less than 1.0×10^{-10}, indicating a low probability of misidentifying closely related individuals (full siblings) as clonemates. The probability of identity values for the symbiont were all reasonably low (Waits et al., 2001), with the exception

TABLE 1 | Summary statistics per locus for 11 *de novo* microsatellite markers for *Dendrogyra cylindrus*.

Locus	N_a	N_{eff}	H_o	H_s	H_t	H'_t	G_{is}	†G_{st}	‡G'_{st} (Nei)	§ G'_{st} (Hed)	*D_{est}
D15	15	6.849	0.891	0.888	0.895	0.897	−0.004	0.008	0.010	0.091	0.083
D345	13	3.704	0.772	0.759	0.815	0.829	−0.017	0.069	0.085	0.339	0.290
D745	10	3.375	0.749	0.731	0.789	0.803	−0.025	0.073	0.090	0.322	0.268
D119	7	2.977	0.611	0.694	0.749	0.763	0.119	0.074	0.091	0.284	0.227
D430	9	3.421	0.721	0.736	0.761	0.767	0.021	0.032	0.040	0.145	0.116
D48	9	2.454	0.399	0.625	0.787	0.828	0.361	0.206	0.245	0.636	0.541
D520	13	5.861	0.865	0.862	0.882	0.887	−0.004	0.022	0.028	0.197	0.178
D559	6	3.036	0.732	0.696	0.758	0.773	−0.052	0.082	0.100	0.316	0.255
D397	11	3.865	0.690	0.774	0.795	0.800	0.109	0.027	0.033	0.140	0.117
D634	11	4.486	0.954	0.802	0.815	0.818	−0.190	0.016	0.020	0.098	0.083
D716	6	2.047	0.506	0.533	0.686	0.724	0.051	0.223	0.264	0.541	0.409
Overall	10.00	3.825	0.717	0.736	0.794	0.808	0.026	0.072	0.089	0.325	0.273
SE	0.894	0.432	0.050	0.030	0.018	0.016	0.038	0.021	0.026	0.064	0.052

*†G_{st} is a measure of genetic differentiation among populations that is generalized for markers with multiple alleles, and is analogous to F_{ST}. ‡The adjustment to this statistic formulated by Nei corrects for sampling a small number of populations (Nei, 1987). § Hedrick's G'_{st} is standardized relative to the maximum level of differentiation based on the heterozygosity within subpopulations (Hedrick, 2005). *Contrastingly, Jost's measure of population differentiation is independent of the within subpopulation diversity (Jost, 2008). N_a, number of alleles; N_{eff}, effective number of alleles; H_o, observed heterozygosity; H_s, heterozygosity within populations; H_t, total heterozygosity; H'_t, corrected total heterozygosity; G_{is}, inbreeding coefficient; G_{st}, fixation index; G'_{st}(Nei), Nei, corrected fixation index; G'_{st}(Hed), Hedrick, standardized fixation index; D_{est}, Jost's D differentiation. Standard errors were calculated by jackknifing over loci. All metrics were calculated using Genodive (Meirmans and Van Tienderen, 2004).*

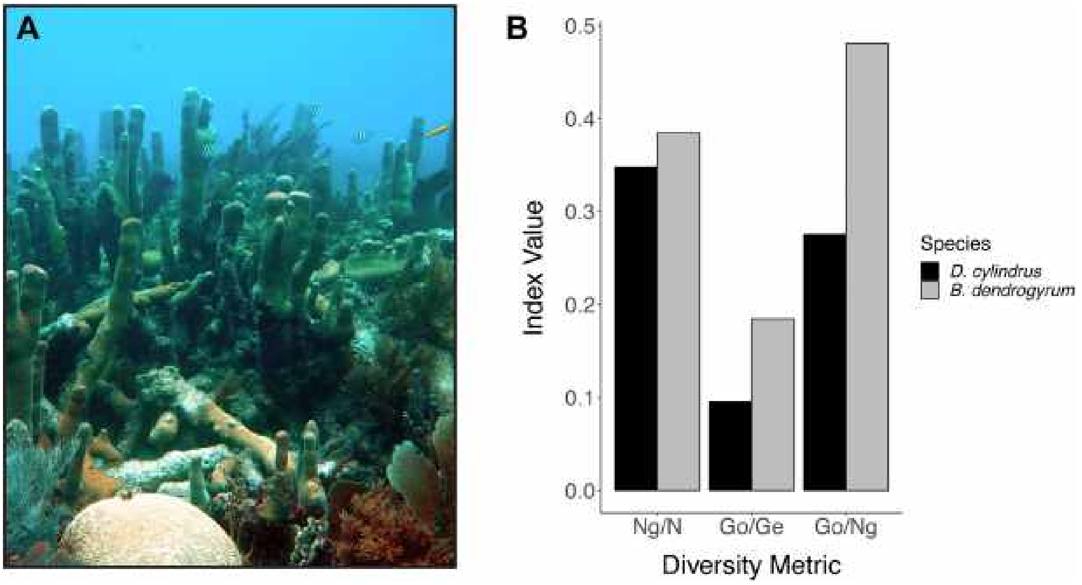

FIGURE 2 | (A) Photo of multiple colonies of *Dendrogyra cylindrus*, including a recently fragmented colony with new pillar growth in the foreground (photo credit: Iliana Baums). **(B)** Summary of the clonal structure of *Dendrogyra cylindrus* and its dominant algal symbiont *Breviolum dendrogyrum* in Florida. Genotypic richness (N_g/N), diversity (G_o/G_e), and evenness (G_o/N_g) are plotted on the *x*-axis and the value of the diversity index is plotted on the *y*-axis. N_g, number of genotypes; N, number of colonies sampled; G_o, observed genotypic diversity; G_e, expected genotypic diversity.

of the Turks and Caicos Islands region (Curaçao: 0.0036, USVI: 0.015, Florida: 1.5×10^{-5}, Belize: 0.003, Turks and Caicos: 0.092). Because sampling was biased toward increasing the number of unique genotypes in all regions except Florida, clonal structure could not be described elsewhere.

Breviolum dendrogyrum is likely haploid, and thus all samples with more than one allele were considered to be multiple infections. There was no spatial pattern in samples with single versus multiple infections along the Florida Reef Tract (**Supplementary Figure 1**). However, we could not assign a strain identity in samples with multiple alleles per locus or use these samples in population genetic analyses. After removing samples with multiple infections ($n = 98$) and samples that failed in one or more of the 15 microsatellite markers ($n = 97$), we obtained a subset of samples ($n = 111$) with complete multi-locus genotypes. Only 30 unique genotypes were found in Florida, with most strains confined to single reefs. The values for genotypic richness standardized to sample size (*Ng/N*), genotypic diversity (*Go/Ge*), and genotypic evenness (*Go/Ng*) were all higher in the algal symbiont compared to the host (**Figure 2B**). The richness values were the most similar, indicating that we found a similar number of unique genotypes of host and symbiont relative to the number of samples we genotyped for each species. The values for genotypic diversity were low in both host and symbiont (albeit, slightly higher in the symbiont), demonstrating that both species reproduced mostly asexually within a site. As was true for the coral host, due to the rarity of *D. cylindrus* and the frequency of multiple infections, few symbiont strains were genotyped per site. When examining genotypic diversity by site (**Figure 3A**), the sites with larger sample sizes had the lowest diversities. This again points to the dominance of asexual reproduction within a site. Genotypic evenness was higher in the symbiont relative to the host (**Figure 2**), meaning that the host population was dominated by relatively few highly replicated coral genotypes. Fewer samples with the same strain of *B. dendrogyrum* were identified compared to the host, partially because a strain genotype could not be called for many samples due to multiple infections and failures in one or more microsatellite markers.

For the coral host, all of the ramets belonging to the same genet were contained within a single collection site. This indicated that the dispersal abilities of asexual fragments of *D. cylindrus* were limited, with only one genet extending beyond 80 m (**Figure 4**). A single coral genet dominated most of our sites, however, three sites had two genets and one site contained three different genets (**Supplementary Figure 2A**).

A test of isolation by distance including only genets of *D. cylindrus* along the Florida Reef Tract revealed no significant correlation between genetic and geographic distance ($r^2 = 0.0001$). Spatial autocorrelation analysis using the complete dataset of *D. cylindrus* genotypes (including clones) in Florida ($n = 180$) revealed significant positive spatial autocorrelation up to distances of 60 m (**Supplementary Figure 3A**). However, when clones were removed, there was no significant spatial autocorrelation (**Supplementary Figure 3B**). These results indicate that the cause of the correlation between genetic distance and geographic distance over small distance classes is a result of asexual reproduction, likely via fragmentation, in *D. cylindrus*.

The genotype of the algal symbiont often corresponded with the genotype of the coral host when multiple colonies were present at a site, meaning that all of the ramets belonging to the same host genet were often symbiotic with the same clonal

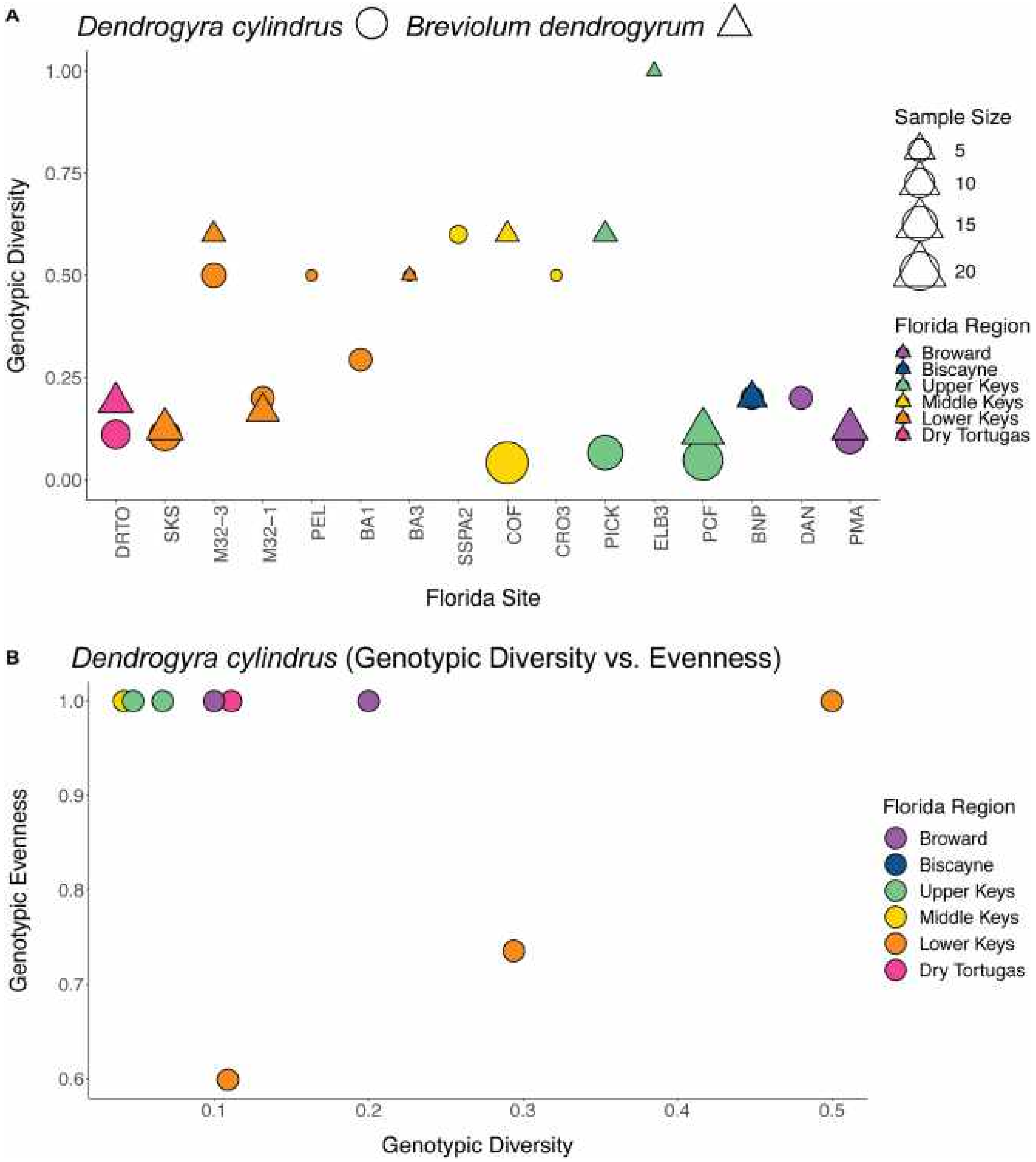

FIGURE 3 | Plots of genotypic diversity by Florida site for the coral host (circles) and symbiont (triangles) **(A)**, and a plot of genotypic diversity vs. evenness for the coral host **(B)**. Only sites with multiple genotyped colonies were included, with symbols scaled to sample sizes in **(A)**. For panel **(B)**, only sites with at least five samples genotyped were included. Sites are colored by region as in **Figure 1**.

strain of *B. dendrogyrum* (**Figure 5**). There were exceptions to this observation. For example, in the Pillar Coral Forest site in the Upper Keys, all of the colonies sampled were ramets of the same coral host genet. However, while 10 ramets associated with identical *B. dendrogyrum* strains, two ramets associated with distinct strains of *B. dendrogyrum* (**Figure 5C** and **Supplementary Figure 2**). The reverse was also observed, with the same symbiont strain found associated with different coral genets, although there was only one example of this pattern found within a site (**Figure 5B**). More often, the same symbiont strain was found in different coral genets at different sites, with dispersal distances ranging from tens of meters to a maximum of 3.44 km (**Figure 4**). However, no symbiont strains were shared between Florida regions (**Figure 1B**). We also sampled the same coral colony in different locations (e.g., top, middle, and base) to assess symbiont diversity. Of the five colonies that were sampled

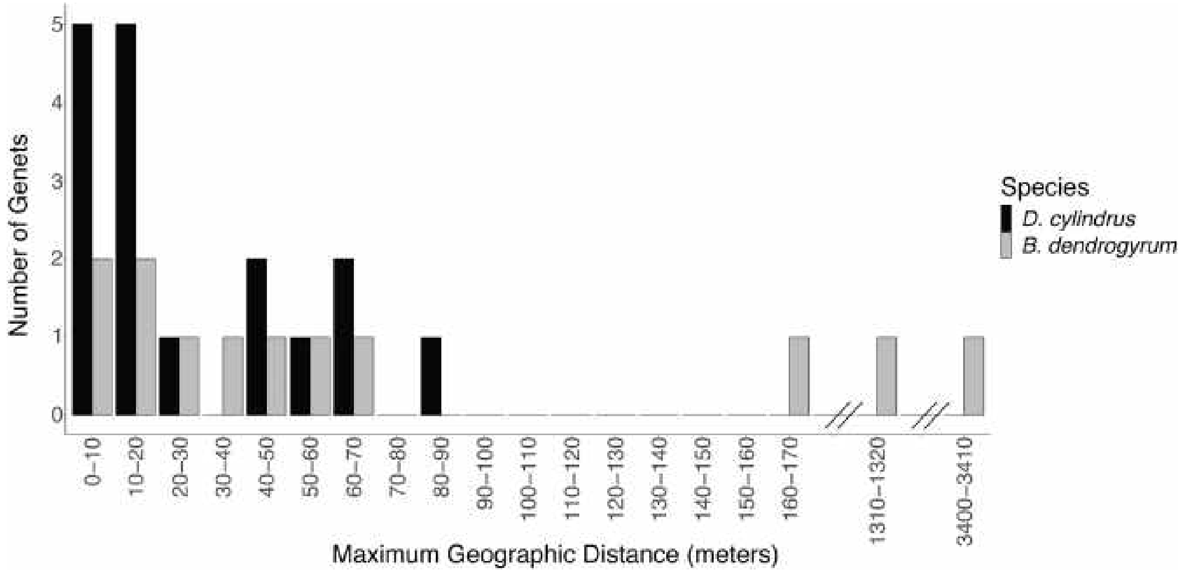

FIGURE 4 | The maximum geographic distance between ramets of the same genet of *Dendrogyra cylindrus* (black bars) and *Breviolum dendrogyrum* (gray bars). While no coral genets were shared between sites, symbiont strains were occasionally shared between sites. Note the discontinuous *x*-axis.

in this way and successfully genotyped, only one contained two different symbiont strains.

Population Structure Analyses

Strong genetic differentiation between populations was found, with a significant global F_{ST} value of 0.110 and an F'_{ST} value of 0.414. Bayesian clustering using the entire dataset of unique multilocus genotypes for the coral host revealed the presence of two to four clusters in the dataset. The different estimators for the optimum number of populations yielded different results. For example, the ΔK method (Evanno et al., 2005) yielded a K of 2 and the MaxMeaK with a spurious cluster threshold of 0.5 (a less conservative measurement) yielded a K of 4. In the STRUCTURE plot for $K = 2$, all of the Florida, Belize, and Turks and Caicos samples have a high probability of membership to the first cluster and all of the Curaçao and U.S. Virgin Islands samples have a high probability of membership to the second cluster (**Figure 6A**). When the same dataset was run in STRUCTURE setting $K = 3$ as the *a priori* number of populations in the dataset, an additional cluster corresponding to the individuals from Curaçao separates from the U.S. Virgin Islands (**Figure 6B**). The samples from the Turks and Caicos Islands also appear to be admixed. However, our dataset contained locations that were sampled unevenly. Thus, we randomly selected unique multilocus genotypes to a maximum size of 20 to remove the bias associated with uneven sampling (Puechmaille, 2016). When Bayesian clustering analysis was completed for this subsampled dataset, all of the K estimators yielded an optimal cluster number of three. The only exception was the ΔK method, which still indicated that there were two populations.

An AMOVA corroborated these results, with the largest pairwise F_{ST} value between Florida and Curaçao ($F_{ST} = 0.184$, p-value < 0.001, **Table 2**). The U.S. Virgin Islands and Curaçao were significantly differentiated, although less strongly ($F_{ST} = 0.045$, p-value < 0.001). The Turks and Caicos Islands were equally differentiated from Florida and the U.S. Virgin Islands ($F_{ST} = 0.046$, p-value < 0.001), further supporting that this is likely an area of admixture (**Table 2**).

We did not find significant population structure within Florida for the coral host. POWSIM v. 4.1 with 1000 simulation runs using the allele frequencies from our host marker set was used to test whether this result was due to a lack of power. Fisher's exact test revealed a high statistical power ($1-\beta = 0.97$) of detecting an F_{ST} value of 0.0195, and a low type I error rate ($\alpha = 0.0410$). Thus, our sample size of 50 individuals from Florida was adequate to detect low levels of population structure along the Florida Reef Tract (FRT) if present.

Population structure analyses were also conducted for *B. dendrogyrum*. Only 58 unique multilocus genotypes were found, after removing samples with multiple infections. Cluster analysis using STRUCTURE and a consideration of multiple estimators for the optimum number of populations revealed that the likely number of populations in the dataset is between 2 and 4 (**Figure 7**). However, there were locations in this dataset that were sampled more intensely than others, and consequentially we subsampled the locations with the largest sample size to a maximum value of 19. Because we found population structure for *B. dendrogyrum* within Florida, we subsampled by the six regions (**Figure 1**). Most of the K estimators indicated that there were likely four populations in the dataset. When the threshold for spurious clusters was set to a strict 0.8, some of the K estimators yielded a K of 2. The ΔK method alone indicated that the optimal number of populations was three. An AMOVA for the haploid *B. dendrogyrum* revealed that the highest amount of between-group variation was between sample locations ($\phi_{PT} = 0.513$, p-value $= 0.001$).

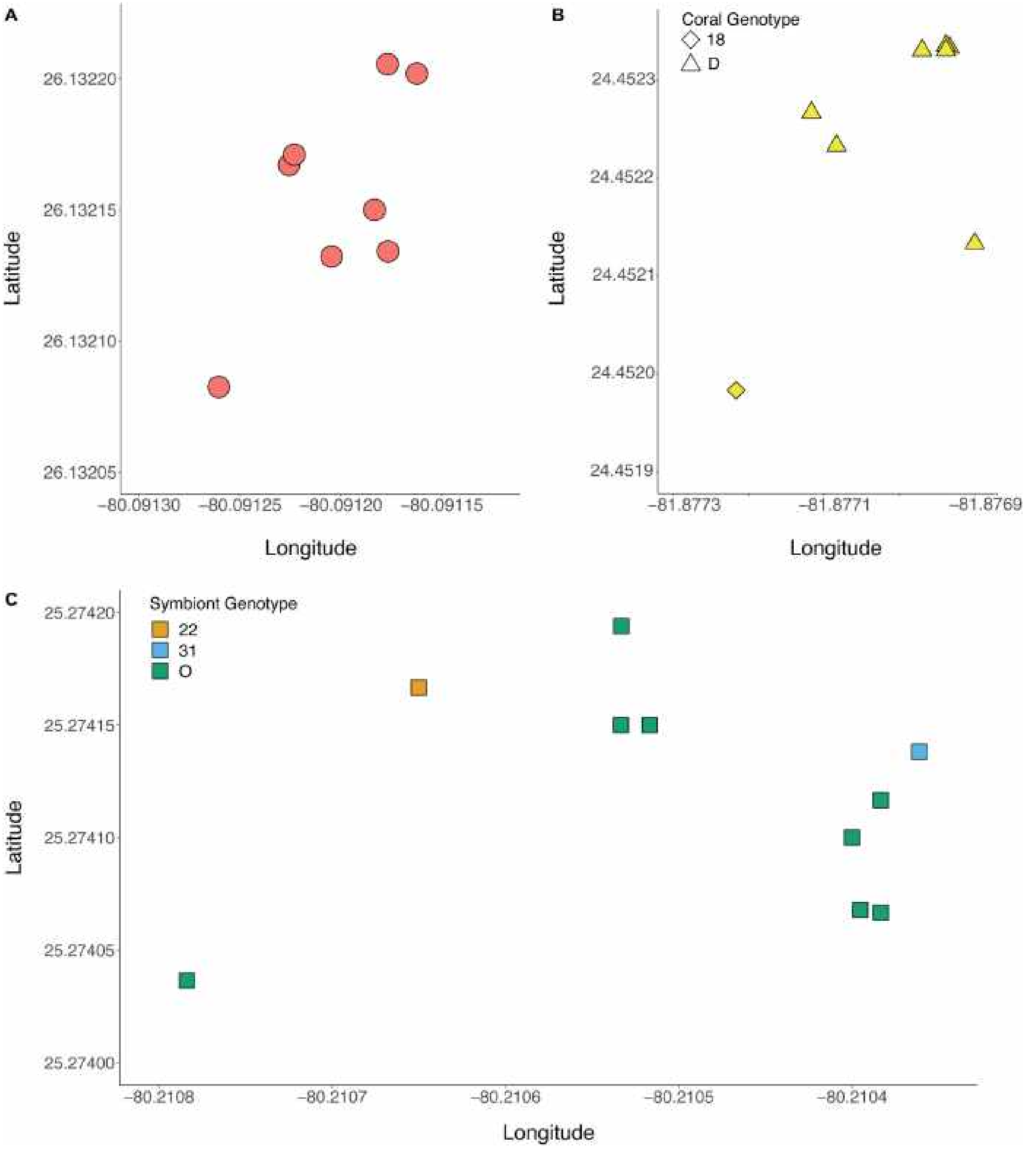

FIGURE 5 | Representative plots showing the spatial arrangement of genotyped colonies of *D. cylindrus* and associated strains of *B. dendrogyrum*. Within a site, most ramets of a coral genet associated with the same symbiont strain. **(A)** Pacific Mako Anchorage, a site in Broward County, **(B)** Sand Key Spa, a site in the Lower Keys, **(C)** Pillar Coral Forest, a site in the Upper Keys. The symbol shape corresponds to the coral genotype, and the color corresponds to the symbiont genotype.

These results indicate that the population structure of the algal symbiont did not match the population structure of the host. Notably, there was population structure within the FRT for the symbiont that was not found in the host. Some samples from Florida clustered more strongly with samples from Belize and the Turks and Caicos Islands than other Florida samples. Because this pattern of population assignment did not correspond with geography, four samples from the unique Florida cluster and three samples from Florida that clustered with the rest of the Caribbean were sequenced using microsatellite flanker sequences (Si15) to confirm that they all belonged to the same species. Comparing the Si15 sequences to representative sequences from

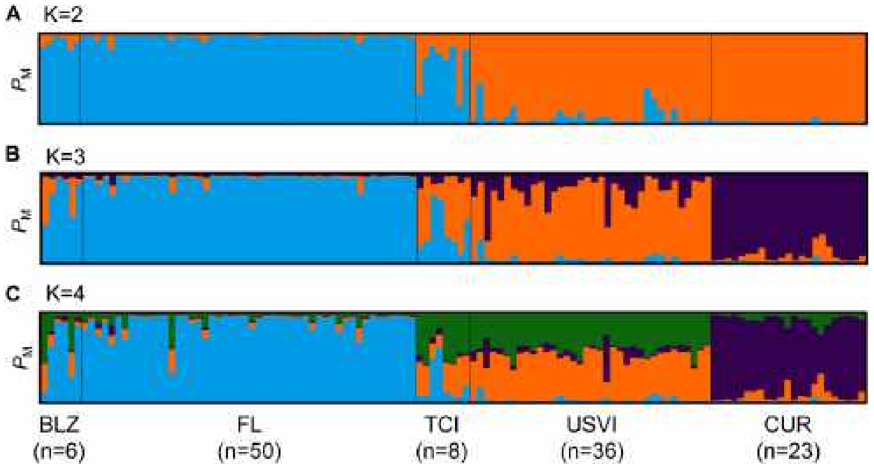

FIGURE 6 | Population structure results for *Dendrogyra cylindrus*. Each vertical bar represents a unique multilocus genotype. Probability of membership to a cluster is plotted on the *y*-axis. **(A)** STRUCTURE results for *D. cylindrus* revealed two separate clusters (*K* = 2, indicated by color). **(B)** STRUCTURE results for *D. cylindrus* when *K* = 3. **(C)** STRUCTURE results for *D. cylindrus* when *K* = 4. Individuals are grouped by sample location; abbreviations are the same as in **Figure 1**.

Symbiodinium Clade B (Finney et al., 2010) revealed that samples from the two clusters within Florida are indeed the same species (*B. dendrogyrum*).

Historical and Future Changes in Pillar Coral Population Sizes

Demographic modeling results revealed no evidence for past changes in pillar coral population size (**Figure 8**). In both the one continuous population size change (OnePopVarSize) and the two population size changes (OnePopFounderFlush) models, the upper limit of the 95% confidence intervals for the ancestral population size ($2N_{anc}\mu$, both models) and the founder population size ($2N_{founder}\mu$, OnePopFounderFlush model only) were undefined. The undefined upper limit meant that many possible population sizes for the ancestral and founder population were equally likely, including population sizes that were both larger and smaller than the 95% confidence interval for the current population size ($2N\mu$). This was further evidenced by the broad profile likelihood ratios for the ancestral and founder population sizes (**Figure 8**), and the population size ratios that included the value 1, indicating no significant change. To decide which of the three models best described our data, we used the Akaike Information Criterion (AIC) calculated based on the log likelihood and the number of parameters in each model (Anderson, 2007). The AIC values for the OnePop (798.94), OnePopVarSize (799.56), and OnePopFounderFlush (800.6) models were very close to one another. Because lower AIC values indicate better model fit, we conclude that the OnePop model with no past change in population size is the best model. However, the differences in AIC between models were very small, and thus it is possible that all three models do not accurately describe reality. Still, the results from the models assuming past demographic events failed to detect significant changes in population size, supporting our conclusion of no past changes in *D. cylindrus* populations.

The three projected rates of decline yielded a range of times to extinction for *D. cylindrus*. In the most conservative simulated scenario where 80% of colonies survived each hyperthermal event, it took 31 stress events for extirpation of *D. cylindrus* from the FRT. With 50% and 20% survival, it took 11 and 6 stress events, respectively, for local extinction to occur (**Supplementary Figure 4**). Because some coral colonies are ramets of the same genet, and these coral ramets often contain clonal strains of *B. dendrogyrum*, coral colonies are lost at a faster rate than coral genotypes and symbiont strains (**Supplementary Figure 4**). We then translated our results into years using our estimated frequencies of future hyperthermal stress events. If the rate of survival per thermal stress event throughout the Florida Reef Tract is 80% of colonies, all Florida pillar corals would be lost by 2066. Assuming 50% or 20% survival, we would expect *D. cylindrus* to become extinct in Florida in 2046 and 2039, respectively.

TABLE 2 | Pairwise F_{ST} values between *Dendrogyra cylindrus* samples from five Caribbean regions (below diagonal).

Curacao	USVI	Turks and Caicos	Florida	Belize	
0.000	0.000	0.000	0.000	0.000	**Curacao**
0.045	0.000	0.000	0.000	0.000	**USVI**
0.114	0.046	0.000	0.000	0.021	**Turks and Caicos**
0.184	0.126	0.046	0.000	0.166	**Florida**
0.157	0.104	0.037	0.010	0.000	**Belize**

The probability based on 9,999 permutations is shown above the diagonal. USVI, U.S. Virgin Islands.

DISCUSSION

The pillar coral, *Dendrogyra cylindrus,* and its obligate algal symbiont *Breviolum dendrogyrum* reproduce mostly via asexual processes within a site, with strains of the algae dispersing over

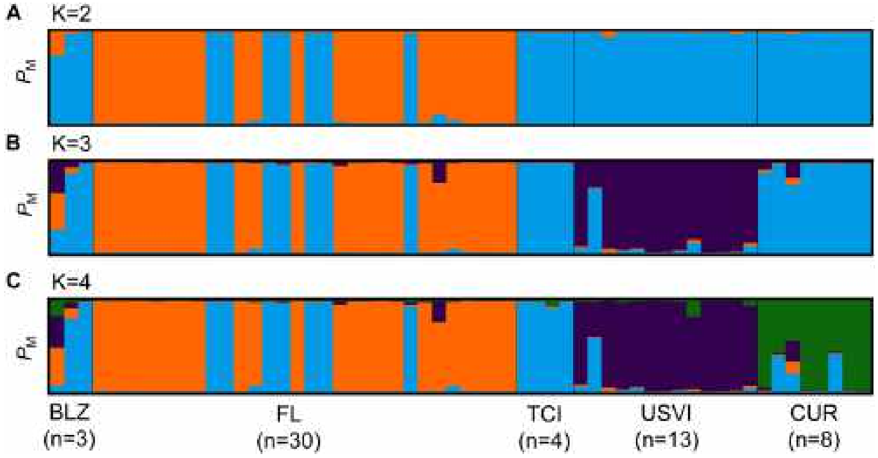

FIGURE 7 | Population structure results for *Breviolum dendrogyrum*. Each vertical bar represents a unique multilocus genotype. Probability of membership to a cluster is plotted on the *y*-axis. **(A)** STRUCTURE results for *B. dendrogyrum* when $K = 2$. **(B)** STRUCTURE results when *K* was set to 3. **(C)** STRUCTURE results when *K* was set to 4. Individuals are grouped by sample location; abbreviations are the same as in **Figure 1**.

much larger distances than host fragments (**Figure 4**). Barriers to gene flow were also not congruent between the partners but showed similarities with other coral–algal symbioses in the Caribbean (Baums et al., 2014b). As is often the case for corals (Baums, 2008), while asexual reproduction was prevalent, no signs of inbreeding were detected in the coral host and allelic diversity was greater than or comparable to other Caribbean reef-building coral species (Baums et al., 2005a; Baums et al., 2010; Rippe et al., 2017). Demographic modeling based on molecular data agreed with the geological record that *D. cylindrus* was historically not a dominant species on Caribbean reefs and yet was able to survive as the sole remaining species in the genus. The forecasted increasing frequency of extreme warm water events in combination with associated disease outbreaks, and the observed absence of sexual recruitment in this species, project a high likelihood that *D. cylindrus* will become locally extinct in the Florida Keys in modern times (see below). The consequences of the loss of rare coral species and their symbionts are unknown but evidence from other ecosystems indicates that losing rare species can destabilize communities and degrade ecosystem function (Theodose et al., 1996; Lyons and Schwartz, 2001; Mouillot et al., 2014).

Clonal Structure and Diversity

Clonal diversity indices for *D. cylindrus* and *B. dendrogyrum* in Florida were more typical of an asexual population (closer to 0) than a sexual one (closer to 1, **Figure 2**). Florida sites that contained multiple colonies of *D. cylindrus* were highly clonal, showed positive spatial autocorrelation, and had low genotypic diversity, indicating that the primary mode of reproduction over this scale is asexual fragmentation (**Figures 2**, **3** and **Supplementary Figure 3**). The prevalence of asexual reproduction in the elkhorn coral, *Acropora palmata,* was attributed to increased physical retention of fragments in certain habitats and low rates of sexual recruitment (Baums et al., 2006). Similar forces, as well as fragmentation from hurricanes, are likely responsible for high asexual reproduction in Florida *D. cylindrus*. This study was limited to assessing clonal structure in Florida alone, and thus future work should measure genotypic richness, diversity, and evenness in other locations.

Low genotypic diversity as a result of clonal reproduction is often identified in foundation species (Baums et al., 2006; Dubé et al., 2017; Gélin et al., 2017; Miller et al., 2018). Clonal reproduction can maintain high population densities in the absence of sexual reproduction (i.e., a storage effect) by increasing the number of established adults (Warner and Chesson, 1985). In benthic surveys of nine inshore to offshore sites in Key Largo, Florida, no juvenile colonies of *D. cylindrus* were discovered (Miller et al., 2010), indicating successful sexual recruitment of juvenile pillar corals is non-existent or very low. In addition, the Florida population of *D. cylindrus* is at the northern edge of this species' range. Previous work on clonal plants and corals has pointed to the prominence of asexual reproduction at the edge of species' geographical ranges, enabling marginal populations to persist despite low sexual recruitment (Silvertown, 2008; Boulay et al., 2014). Thus, recent reproduction in the Florida *D. cylindrus* population may be entirely asexual due to the lack of sexual recruits from neighboring populations and from within Florida.

The absence of successful sexual reproduction in *D. cylindrus* raises concerns about the longevity of this species, particularly in Florida. Because most sites tended to be occupied by a single coral genotype (**Figure 5** and **Supplementary Figure 2A**), it is possible that Florida *D. cylindrus* are already experiencing an Allee effect, wherein the density of compatible colonies is too low for successful sexual reproduction and population growth (Courchamp et al., 1999). Recent work describing instances of hermaphroditism in *D. cylindrus* are promising (Neely et al., 2018), and could increase local larval production if *D. cylindrus* is self-compatible. Despite the prevalence of asexual reproduction and the small census size, heterozygosity levels remain high, indicating that *D. cylindrus* is not inbred. Future studies of controlled crosses between different *D. cylindrus* genets and

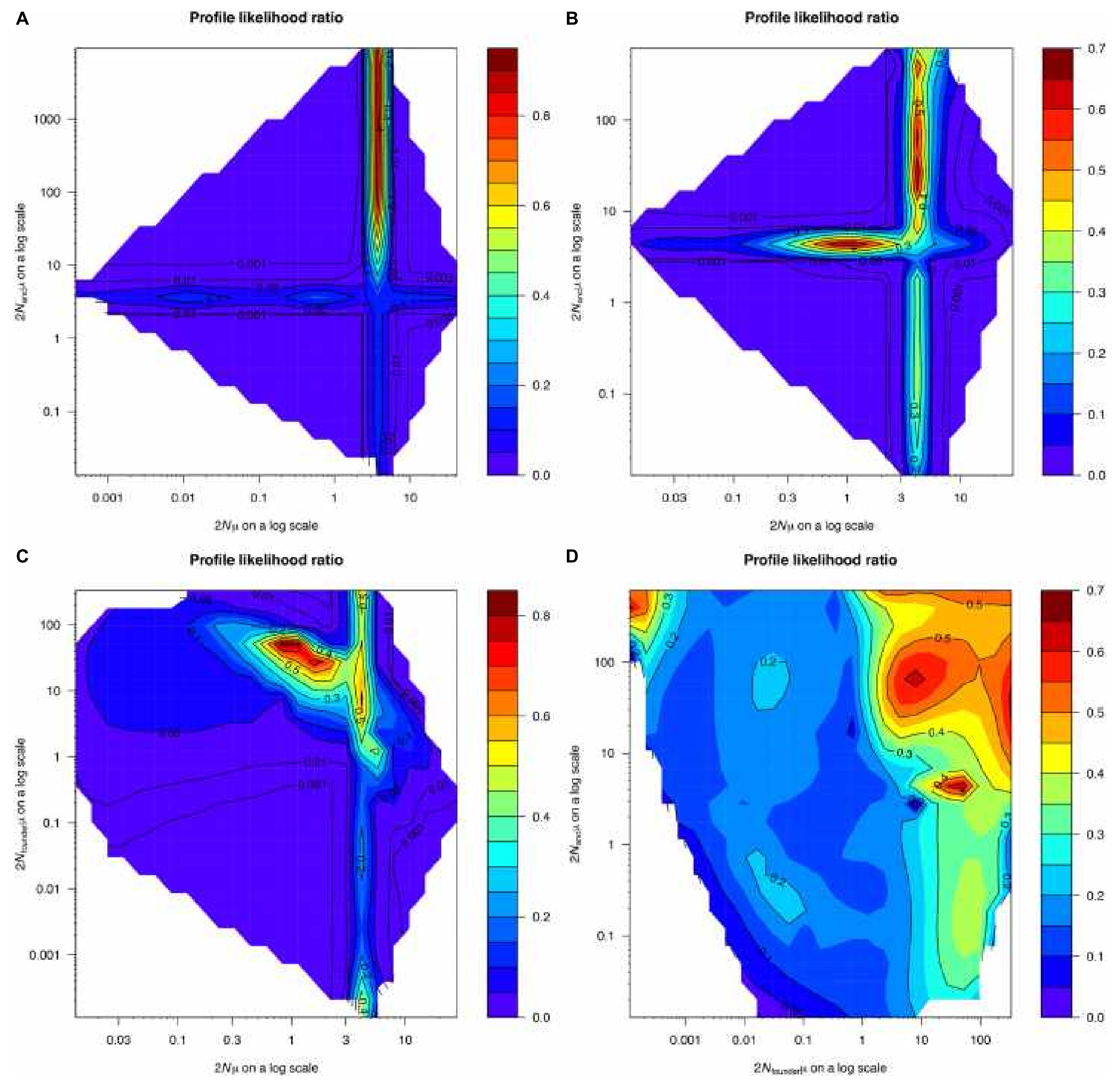

FIGURE 8 | Profile likelihood ratio of the current population size of *Dendrogyra cylindrus* (*x*-axis) and the ancestral population size of *D. cylindrus* (*y*-axis) from the OnePopVarSize model implemented using the software MIGRAINE **(A)**. Profile likelihood ratio plots for the OnePopFounderFlush model are shown for the current and ancestral populations **(B)**, for the current and founder populations **(C)**, and for the founder and ancestral populations **(D)**.

opposite sex ramets of the same genet are necessary to discern compatibility in this species (Baums et al., 2013).

The Florida population of *B. dendrogyrum* is also clonal, with the same symbiont strain often found in all of the ramets of a coral genet (**Figure 5**). Despite the physical damage and transportation of fragments to lower light micro-environments when pillars fragment and fall over, the association between a particular coral genotype and specific symbiont strain appears to be mostly stable. High fidelity between individual genotypes of symbiotic partners has been found previously in the Caribbean elkhorn coral (*Acropora palmata*) and its algal symbiont (*Symbiodinium 'fitti'*) (Baums et al., 2014b). In this system, different combinations of host genotypes with a symbiont strain were shown to possess distinct physiological responses to heat stress (Parkinson et al., 2015) but this is not always the case (Parkinson et al., 2018). It is unknown if different combinations of *D. cylindrus* genotypes and *B. dendrogyrum* strains could result in functional variation of the holobiont.

While coral genets were restricted to one site each, four pairs of sites did share symbiont strains. The symbiont is able to disperse asexually over larger distances than its coral host, although successful long-distance dispersal appears to be rare (**Figure 4**). A typical fragment dispersal distance for *D. cylindrus* is less than 60 m, as evidenced by the spatial autocorrelation analysis (see below and **Supplementary Figure 3**), although one genet extended over 80 m (**Figure 4**). Similarly, the asexual dispersal ability of *Symbiodinium fitti* was found to be significantly higher than its coral host, *A. palmata* (Baums et al., 2014b). However, the farthest asexual dispersal distance for *B. dendrogyrum* (3,440 m) was higher than what was found for *S. fitti* (greater than 2,000 m). While Symbiodiniaceae cells are constantly being expelled from the coral host, little is known about the persistence of their free-living stage (Thornhill et al., 2017). Despite similar morphologies, different species of Symbiodiniaceae may differ greatly in their abilities to disperse and infect new host corals.

While the storage effect provided by asexually produced colonies can be beneficial in the absence of environmental change, populations of foundation species with low genotypic diversity are more susceptible to disturbances. Increasing genotypic diversity in plots of the seagrass, *Zostera marina*, yielded higher resistance to disturbance by grazing geese (Hughes and Stachowicz, 2004). High intraspecies variation in crop plants increases plant fitness and agricultural yields, and decreases susceptibility to insect pests (Tooker and Frank, 2012). In addition, high genotypic diversity confers a greater ability for populations to recover from warm temperature stress events (Reusch et al., 2005), which are expected to become more frequent with climate change (Stocker et al., 2013).

Barriers to Gene Flow

Population structure results for *D. cylindrus* indicate that there are at least two genetic breaks in the Caribbean, resulting in three populations (K of 3 chosen by most K estimators). The first population includes samples from Florida, Belize, and the Turks and Caicos Islands, the second population includes samples from the U.S. Virgin Islands, and the third population comprises samples from Curaçao (**Figure 6**). Cluster analysis results and pairwise F_{ST} analyses revealed that there is little to no gene flow between Florida and either Curaçao or the USVI. A genetic break in this area has been well characterized in other corals (Vollmer and Palumbi, 2006; Baums et al., 2010; Foster et al., 2012; Andras et al., 2013; Rippe et al., 2017).

Dendrogyra cylindrus lacks population structure along the Florida Reef Tract, which was also found in both *A. cervicornis* and *A. palmata* using microsatellite markers (Baums et al., 2005b, 2010). POWSIM simulations revealed our set of microsatellite markers had sufficient power to detect an F_{ST} value as low as 0.0195. In contrast to the microsatellite results, an analysis of Florida *A. cervicornis* using SNPs found significant population structure within the Florida Reef Tract (Willing et al., 2012), and thus it is possible that higher resolution markers may resolve weaker population differentiation in *D. cylindrus*.

The genetic break between *D. cylindrus* in the USVI and Curaçao was weaker than the break between Florida and these two locations but again consistent with a similar genetic break in *A. palmata* (Devlin-Durante and Baums, 2017). It is possible that the Caribbean Current is restricting coral larval exchange between these two islands (**Figure 1A**). This current was shown to affect dispersal in other planktonic marine species (Díaz-Ferguson et al., 2010; Jossart et al., 2017), however, population genetic data for other coral species does not show a break in this area (Andras et al., 2013; Rippe et al., 2017).

After correcting for uneven sampling effort, the results for *B. dendrogyrum* population structure revealed four populations in the Caribbean (**Figure 7**). *B. dendrogyrum* strains in both Curaçao and the U.S. Virgin Islands separate as two populations distinct from the rest of the Caribbean. These genetic breaks are in concordance with the breaks observed in the host coral, *D. cylindrus*. However, there is population structure within the FRT for the algal symbiont, with some Florida individuals clustering with Belize and the Turks and Caicos Islands. A similar incongruence between the population structure of host and symbiont was found in *G. ventalina* (Andras et al., 2011, 2013) and *A. palmata* (Baums et al., 2005b, 2014b). A recent review explained the observed lower connectivity in horizontally transmitted algal symbionts relative to their coral hosts as potentially resulting from restricted dispersal as well as from resident symbionts outcompeting migrants (Thornhill et al., 2017). The inconsistency in population structure between host and symbiont supports that *D. cylindrus* obtains its symbionts horizontally (from the surrounding environment) and implies that gene flow occurs over different spatial scales in the partners (Baums et al., 2014b). Because such a small sample of symbiont strains was included from both Belize and the Turks and Caicos Islands, it is possible that the cluster containing these samples and some Florida samples is an artifact of STRUCTURE. Underrepresented populations can be incorrectly merged together by STRUCTURE (Puechmaille, 2016), although subsampling our larger populations and using additional K estimators reduced the uneven sampling bias.

Demographic Modeling of Pillar Coral Populations

Demographic modeling results using MIGRAINE revealed no evidence for past changes in population size in Florida *D. cylindrus*. This is consistent with previous descriptions of *D. cylindrus* as a naturally rare species (NOAA, 2014), and with the rarity of *D. cylindrus* in the fossil record (see section "Introduction"). Abundance can be high in localized areas, however, due to asexual fragmentation. This suggests that historically, *D. cylindrus* did not experience a range-wide decline since its first appearance in the fossil record during the late Pliocene/early Pleistocene (Budd, 2000).

The results from our forward projection model demonstrate that the increased frequencies of hyperthermal stress events will likely lead to extirpation of *D. cylindrus* in Florida in the near future. While these are simple projections of potential species decline that do not take into account the heterogeneity of abiotic and biotic factors along the Florida Reef Tract, they are still useful for demonstrating the severity of the current situation for pillar corals. Detailed demographic information about the actual loss of Florida *D. cylindrus* colonies, genotypes, and *B. dendrogyrum* strains will be crucial for successful species rehabilitation. If no active management strategies such as nursery rearing and propagation are enacted to enhance sexual reproduction and increase genotypic diversity (National Academies of Sciences Engineering and Medicine, 2018), we can expect pillar corals to disappear from Florida within just a few decades. Global change will continue to alter the composition of reefs if greenhouse gas emissions are not curbed.

The Consequences of Rare Species Loss

What are the consequences of losing rare species? Experimental removal of rare species was shown to reduce ecosystem resistance to invasion by an exotic grass (Lyons and Schwartz, 2001). It is possible that less common species significantly contribute to the proper maintenance of ecosystem function. Rare plant species were shown to more significantly impact nutrient cycling and retention in an alpine meadow compared to more abundant species (Theodose et al., 1996). In a comprehensive study of species occurrence datasets from coral reefs, alpine meadows, and tropical forests, rare species were repeatedly shown to predominantly support vulnerable functions (Mouillot et al., 2013). These vulnerable functions were defined as ecosystem roles with low redundancy, in that uncommon species with distinct trait combinations bolstered these particular functions. Despite the high diversity in these ecosystems, abundant species did not insure against the services lost by removing rare species (Mouillot et al., 2014). Therefore, maintaining these uncommon species is essential to overall community functional diversity.

When two rare species are combined in an obligate symbiosis, then the loss of one species would yield coextinction of the other (Koh et al., 2004). It is possible that *D. cylindrus* sexual recruits can survive by associating with *B. meandrinium* in the absence of *B. dendrogyrum* but the latter has never been found in another coral host species (Lewis et al., 2018). It is unknown whether there are free-living strains of *B. dendrogyrum*. Determining the degree to which the association is obligate for the host-specialist symbiont is beyond the scope of this study. Likewise, the functional roles of this rare coral–algal symbiosis are unknown, although the tall pillar morphology of this species may promote fish aggregating behavior (Shantz et al., 2015). Without knowing the ecological function of rare marine symbioses such as the one between *D. cylindrus* and *B. dendrogyrum*, it is prudent to assume important ecosystem contributions when forming conservation strategies (Lyons et al., 2005).

Continued unprecedented global change will cause further loss of biodiversity. Because species that are both rare and specialized are especially at risk of disappearing (Davies et al., 2004), studies of the ecology and evolution of these species are particularly timely and important. Recent work on *D. cylindrus* (Neely et al., unpublished data), including this study, has highlighted a lack of recent successful sexual recruitment. The ability of coral species to survive climate change hinges upon ongoing sexual reproduction, enabling selection for more resilient genotypes (Matz et al., 2018). Adaptation is thus extremely unlikely in *D. cylindrus*, necessitating continued *ex situ* efforts to understand spawning, larval development, and larval settlement in this unique Caribbean coral species (Marhaver et al., 2015). Additionally, more drastic measures, such as assisted gene flow, could become necessary (National Academies of Sciences Engineering and Medicine, 2018).

Coral reefs are currently experiencing global decline due to the loss of important herbivores, pollution and nutrient runoff, disease, and climate change (Bruno et al., 2007; Hoegh-Guldberg et al., 2007; Jackson et al., 2014). Since the 1980s, coral cover on Caribbean reefs has already declined by an average of 80% (Gardner et al., 2003). Losing rare species and their corresponding functions may further reduce reef resilience and thus exacerbate coral reef decline beyond what has been predicted (Hoegh-Guldberg et al., 2017; Hughes et al., 2017).

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of Convention on International Trade in Endangered Species of Wild Fauna and Flora Resolution Conf. 11.10 (Rev. CoP15). Coral samples were collected under Florida Keys National Marine Sanctuary permits FKNMS-2013-085-A1, FKNMS-2014-004-A1, FKNMS-2016-062, CITES AN001.12US784243/g, and Indigenous Species Research, Retention, and Export permit DFW16005T.

AUTHOR CONTRIBUTIONS

AC performed all molecular work and data analysis, and wrote the manuscript. CL and KN collected samples and edited the manuscript. IB directed the study, obtained funding, provided laboratory space, collected samples, and wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00218/full#supplementary-material

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CLIMATE CHANGE

How fast are the oceans warming?

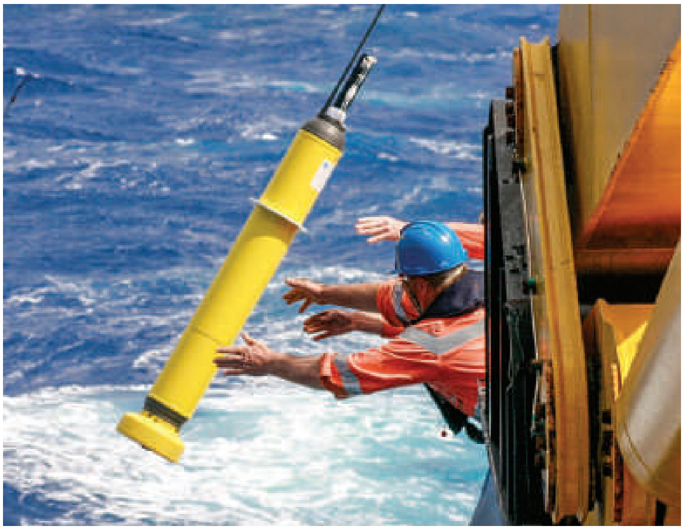
Observational records of ocean heat content show that ocean warming is accelerating

By **Lijing Cheng**[1]**, John Abraham**[2]**,**
Zeke Hausfather[3]**, Kevin E. Trenberth**[4]

Climate change from human activities mainly results from the energy imbalance in Earth's climate system caused by rising concentrations of heat-trapping gases. About 93% of the energy imbalance accumulates in the ocean as increased ocean heat content (OHC). The ocean record of this imbalance is much less affected by internal variability and is thus better suited for detecting and attributing human influences (*1*) than more commonly used surface temperature records. Recent observation-based estimates show rapid warming of Earth's oceans over the past few decades (see the figure) (*1*, *2*). This warming has contributed to increases in rainfall intensity, rising sea levels, the destruction of coral reefs, declining ocean oxygen levels, and declines in ice sheets; glaciers; and ice caps in the polar regions (*3*, *4*). Recent estimates of observed warming resemble those seen in models, indicating that models reliably project changes in OHC.

The Intergovernmental Panel on Climate Change's Fifth Assessment Report (AR5), published in 2013 (*4*), featured five different time series of historical global OHC for the upper 700 m of the ocean. These time series are based on different choices for data processing (see the supplementary materials). Interpretation of the results is complicated by the fact that there are large differences among the series. Furthermore, the OHC changes that they showed were smaller than those projected by most climate models in the Coupled Model Intercomparison Project 5 (CMIP5) (*5*) over the period from 1971 to 2010 (see the figure).

Since then, the research community has made substantial progress in improving long-term OHC records and has identified several sources of uncertainty in prior measurements and analyses (*2*, *6*–*8*). In AR5, all OHC time series were corrected for biases in expendable bathythermograph (XBT) data that had not been accounted for in the previous report (AR4). But these correction methods relied on very different assumptions of the error sources and led to substantial differences among correction schemes. Since AR5, the main factors influencing the errors have been identified (*2*), helping to better account for systematic errors in XBT data and their analysis.



Scientists deploy an Argo float. For over a decade, more than 3000 floats have provided near-global data coverage for the upper 2000 m of the ocean.

PHOTO: ALICIA NAVIDAD/CSIRO

Several studies have attempted to improve the methods used to account for spatial and temporal gaps in ocean temperature measurements. Many traditional gap-filling strategies introduced a conservative bias toward low-magnitude changes (*9*). To reduce this bias, Domingues *et al.* (*10*) used satellite altimeter observations to complement the sparseness of in situ ocean observations and update their global OHC time series since 1970 for the upper 700 m. Cheng *et al.* (*2*) proposed a new gap-filling method that used multimodel simulations to provide an improved prior estimate and error covariance. This method allowed propagation of information from data-rich regions to the data gaps (data are available for the upper 2000 m since 1940). Ishii *et al.* (*6*) completed a major revision of their estimate in 2017 to account for the previous underestimation and also extended the analysis down to 2000 m and back to 1955. Resplandy *et al.* (*11*) used ocean warming outgassing of O_2 and CO_2, which can be isolated from the direct effects of anthropogenic emissions and CO_2 sinks, to independently estimate changes in OHC over time after 1991.

These recent observation-based OHC estimates show highly consistent changes since the late 1950s (see the figure). The warming is larger over the 1971–2010 period than reported in AR5. The OHC trend for the upper 2000 m in AR5 ranged from 0.24 to 0.36 W m^{-2} during this period (*4*). The three more contemporary estimates that cover the same time period suggest a warming rate of 0.36 ± 0.05 (*6*), 0.37 ± 0.04 (*10*), and 0.39 ± 0.09 (*2*) W m^{-2}. [Note that the analysis in Domingues *et al.* (*10*) is combined with that in Levitus *et al.* (*12*) for 700 to 2000 m to produce a 0 to 2000 m time series.] All four recent studies (*2*, *6*, *10*, *11*) show that the rate of ocean warming for the upper 2000 m has accelerated in the decades after 1991 from 0.55 to 0.68 W m^{-2} (calculations provided in the supplementary materials).

Multiple lines of evidence from four independent groups thus now suggest a stronger observed OHC warming. Although climate model results (see the supplementary materials) have been criticized during debates about a “hiatus” or “slowdown” of global mean surface temperature, it is increasingly clear that the pause in surface warming was at least in part due to the redistribution of heat within the climate system from Earth surface into the ocean interiors (*13*). The recent OHC warming estimates (*2*, *6*, *10*, *11*) are quite similar to the average of CMIP5 models, both for the late 1950s until present and during the 1971–2010 period highlighted in AR5 (see the figure). The ensemble average of the models has a linear ocean warming trend of 0.39 ± 0.07 W m^{-2} for the upper 2000 m

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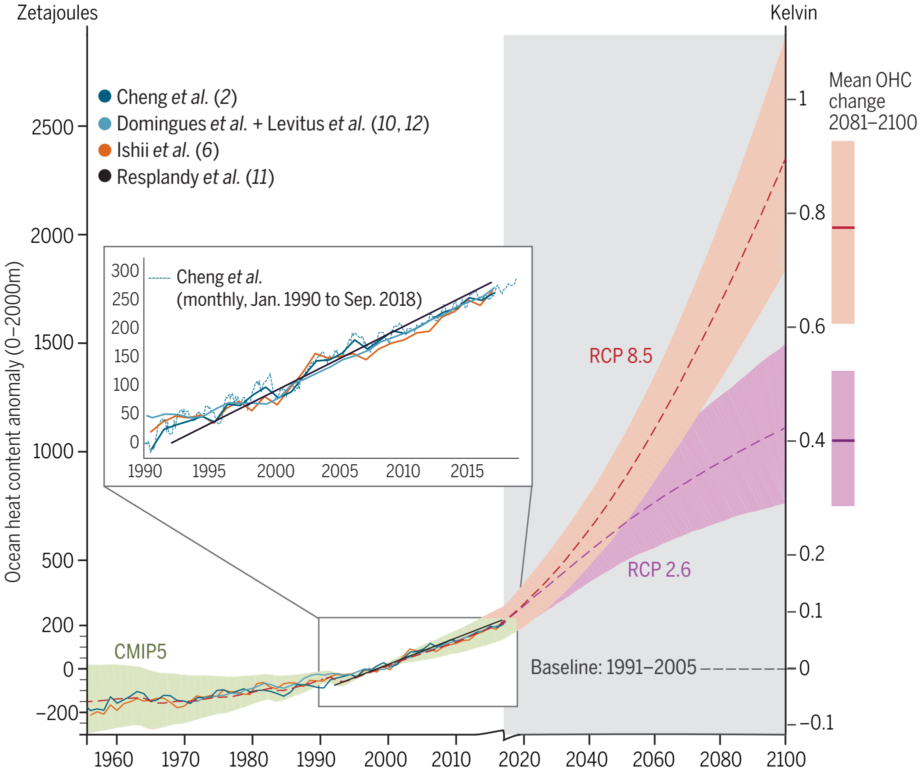
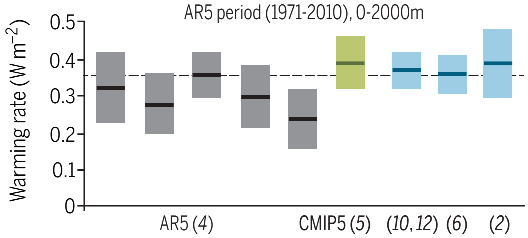
[1] International Center for Climate and Environment Sciences, Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing 100029, China. [2] School of Engineering, University of St. Thomas, 2115 Summit Avenue, St. Paul, MN, USA. [3] Energy and Resources Group, University of California, Berkeley, 310 Barrows Hall, Berkeley, CA 94720, USA. [4] National Center for Atmospheric Research, Post Office Box 3000, Boulder, CO 80307, USA. Email: chenglij@mail.iap.ac.cn

Past and future ocean heat content changes

Annual observational OHC changes are consistent with each other and consistent with the ensemble means of the CMIP5 models for historical simulations pre-2005 and projections from 2005–2017, giving confidence in future projections to 2100 (RCP2.6 and RCP8.5) (see the supplementary materials). The mean projected OHC changes and their 90% confidence intervals between 2081 and 2100 are shown in bars at the right. The inset depicts the detailed OHC changes after January 1990, using the monthly OHC changes updated to September 2018 [Cheng *et al*. (*2*)], along with the other annual observed values superposed.





Updated OHC estimates compared with AR5. The three most recent observation-based OHC analyses give ocean warming rates (depths from 0 to 2000 m) for 1971–2010 that are closer to model results than those reported in AR5. This increases confidence in the model projections (see supplementary materials for more detail). The error bars are 90% confidence intervals.

from 1971–2010 compared with recent observations ranging from 0.36 to 0.39 W m^{-2} (see the figure).

The relatively short period after the deployment of the Argo network (see the photo) in the early 2000s has resulted in superior observational coverage and reduced uncertainties compared to earlier times. Over this period (2005–2017) for the top 2000 m, the linear warming rate for the ensemble mean of the CMIP5 models is 0.68 ± 0.02 W m^{-2}, whereas observations give rates of 0.54 ± 0.02 (*2*), 0.64 ± 0.02 (*10*), and 0.68 ± 0.60 (*11*) W m^{-2}. These new estimates suggest that models as a whole are reliably projecting OHC changes.

However, some uncertainties remain, particularly for deep and coastal ocean regions and in the period before the deployment of the Argo network. It is important to establish a deep ocean observation system to monitor changes below 2000 m (*14*). It is also essential to improve the historical record, for example, by recovering undigitized OHC observations.

Simulations of future climate use a set of scenarios or plausible radiative forcing pathways based on assumptions about demographic and socioeconomic development and technological changes (*5*). Two scenarios shown in the figure project a substantial warming in the 21st century. For the Representative Concentration Pathways (RCP) 2.6 scenario, the models project an ocean warming (0 to 2000 m) of 1037 zettajoules (ZJ) (~0.40 K) at the end of the 21st century (mean of 2081–2100 relative to 1991–2005); this pathway is close to the Paris Agreement goal of limiting global warming to well below 2°C. For the RCP8.5 scenario, a business-as-usual scenario with high greenhouse gas emissions, the models project a warming of 2020 ZJ (~0.78 K). This level of warming would have major impacts on ocean ecosystems and sea level rise through thermal expansion; 0.78 K warming at 2100 is roughly equal to a sea level rise of 30 cm. This is in addition to increased sea level rise caused by land ice melt.

The fairly steady rise in OHC shows that the planet is clearly warming. The prospects for much higher OHC, sea level, and sea-surface temperatures should be of concerngiven the abundant evidence of effects on storms, hurricanes, and the hydrological cycle, including extreme precipitation events (*3*, *15*). There is a clear need to continue to improve the ocean observation and analysis system to provide better estimates of OHC, because it will enable more refined regional projections of the future. In addition, the need to slow or stop the rates of climate change and prepare for the expected impacts is increasingly evident. ■

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SUPPLEMENTARY MATERIALS

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Extensive coral mortality and critical habitat loss following dredging and their association with remotely-sensed sediment plumes

Ross Cunning[a,b,*], Rachel N. Silverstein[c,*], Brian B. Barnes[d], Andrew C. Baker[a]

[a] Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
[b] Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, 1200 South Lake Shore Drive, Chicago, IL 60605, USA
[c] Miami Waterkeeper, 2103 Coral Way, 2nd Floor, Miami, FL 33145, USA
[d] College of Marine Science, University of South Florida, 140 7th Avenue South, MSL119, St. Petersburg, FL 33701, USA

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ABSTRACT

Dredging poses a potential threat to coral reefs, yet quantifying impacts is often difficult due to the large spatial footprint of potential effects and co-occurrence of other disturbances. Here we analyzed in situ monitoring data and remotely-sensed sediment plumes to assess impacts of the 2013–2015 Port of Miami dredging on corals and reef habitat. To control for contemporaneous bleaching and disease, we analyzed the spatial distribution of impacts in relation to the dredged channel. Areas closer to dredging experienced higher sediment trap accumulation, benthic sediment cover, coral burial, and coral mortality, and our spatial analyses indicate that > 560,000 corals were killed within 0.5 km, with impacts likely extending over 5–10 km. The occurrence of sediment plumes explained ~60% of spatial variability in measured impacts, suggesting that remotely-sensed plumes, when properly calibrated against in situ monitoring data, can reliably estimate the magnitude and extent of dredging impacts.

1. Introduction

An increase in port deepening and widening projects is occurring worldwide to accommodate Neo-Panamax cargo ships following expansion of the Panama canal in 2016 (Ashe, 2018; Good, 2016; Wyss et al., 2012). Several dredging projects in shallow-water ports adjacent to coral reef areas along the eastern seaboard of the United States and the Caribbean have recently been completed, or are planned in the near future (Braley and Doyle, 2017; Good, 2016; Whitefield, 2016). Because of the fragility of coral reef ecosystems and their widespread decline, a critical assessment of environmental impacts, accompanied by an evaluation of best practices for monitoring and reducing them, are key conservation goals in light of continued dredging activities.

Coastal dredging and construction are known to cause significant harm to coral reef ecosystems (Bak, 1978; Dodge and Rimas Vaisnys, 1977; Erftemeijer et al., 2012). Dredging can impact corals and coral habitat through a variety of cause-effect pathways reviewed by Jones et al. (2016), including directly via sedimentation (the deposition of particulate matter on the benthos), and indirectly via increased turbidity and shading from sediment plumes. Sedimentation can potentially impact almost every biological function of corals, from feeding through reproduction (reviewed by Erftemeijer et al., 2012; Fabricius, 2005; Jones et al., 2015; Rogers, 1990). Although some degree of sedimentation is common on coral reefs, and some species may persist in turbid environments through long-term adaptation, high sedimentation is typically detrimental to reef development because corals require a hard substrate on which to settle and grow, and because it is energetically costly to remove sediment from their surfaces, either through ciliary action, mucus production, and/or hydrostatic polyp inflation (Bessell-Browne et al., 2017a; Dodge and Rimas Vaisnys, 1977; Humanes et al., 2017; Riegl and Branch, 1995; Stafford-Smith and Ormond, 1992). Due to the high energetic requirements of self-cleaning and the inability of corals to successfully open their polyps (Riegl and Branch, 1995), corals with ongoing sedimentation impacts may reduce feeding (Abdel-Salam and Porter, 1988; Erftemeijer et al., 2012; Szmant-Froelich et al., 1981). Combined with low light levels (indirectly from increased turbidity or directly as a result of smothering), which inhibit the photophysiology of algal symbionts (Abdel-Salam and Porter, 1988; Philipp and Fabricius, 2003; Piniak, 2007; Telesnicki and Goldberg, 1995; Weber et al., 2006), this can lead to coral starvation (Erftemeijer et al., 2012; Flores et al., 2012; Junjie et al., 2014) and reduced calcification and growth (Edmunds and Davies, 1989; Flores

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* Corresponding authors.
E-mail addresses: ross.cunning@gmail.com (R. Cunning), rachel@miamiwaterkeeper.org (R.N. Silverstein).

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et al., 2012; Humanes et al., 2017; Lirman et al., 2003; Miller et al., 2016; Moeller et al., 2016).

Corals exposed to heavy, chronic, or repeated sedimentation can be overwhelmed and unable to successfully rid themselves of sediment (Bak, 1978; Bessell-Browne et al., 2017a; Flores et al., 2012; Marszalek, 1981). When this occurs, corals – particularly those with mounding morphologies – begin to accumulate rejected sediment in “berms”, or piles of sediment around the colony perimeter (Miller et al., 2016), making sediment removal even more difficult as the berm increases in height. With enough sedimentation, energetically costly sediment removal mechanisms become exhausted, and corals can become partially or completely buried, resulting in mortality (Lirman et al., 2003; Marszalek, 1981; Miller et al., 2016; Nugues and Roberts, 2003; Riegl, 1995). Mortality commonly occurs first under sediment berms that pile up at colony bases, producing a condition of partial mortality around the base in a “halo” pattern (Marszalek, 1981; Miller et al., 2016).

Sedimentation has also been shown to inhibit coral sexual reproduction in a number of ways (Jones et al., 2015), including by impairing spawning success (Ricardo et al., 2016), fertilization (Ricardo et al., 2015), settlement (Babcock et al., 2002; Ricardo et al., 2017), and recruitment (Moeller et al., 2016). Sediment may also directly remove available recruitment space by covering hard surfaces required for larval settlement (Babcock and Davies, 1991; Ricardo et al., 2017). Recruitment may still be reduced even if sediment is subsequently removed, likely due to the negative impacts of sediment on crustose coralline algae, a key settlement cue (Ricardo et al., 2017). For recently-settled coral recruits, sedimentation tolerance may be at least an order of magnitude lower than for adult corals (Fabricius, 2005), and even relatively low sedimentation rates (16.6 $\mathrm{mg\,cm^{-2}\,d^{-1}}$) can result in mortality (Moeller et al., 2016). Even sediment that is not deposited on the seabed, but that is moving through the system, is likely to abrade and kill newly-settled coral recruits and other benthic organisms, in addition to blocking photosynthetically active radiation (Storlazzi et al., 2015).

Impacts from sedimentation specifically due to dredging activities can be even more harmful to corals and reef habitat compared to other types of sedimentation. Due to the rapid escalation in sediment load created by sudden commencement of dredging, the typical behavioral, acclimatory, and adaptive responses (for example, selection for particular coral species or morphologies) that normally operate at sites exposed to naturally high sedimentation (Lasker, 1980; Sofonia and Anthony, 2008) may not be able to operate effectively. Moreover, in contrast to other kinds of sedimentation events, such as hurricanes, that generate sediment over hours to days, dredging can generate high sediment conditions for months to years, exceeding the energetic reserves of corals that might otherwise be able to survive acute impacts caused by storms (Flores et al., 2012; Jones et al., 2015; Riegl and Branch, 1995).

The type of sediment released by dredging activities can also be different from naturally occurring sediment (Jones et al., 2016). Dredging sediment is often more fine-grained than natural coarse sediment, and these fine particles can cause higher turbidity (Fourney and Figueiredo, 2017), can take longer to settle out of the water column, can be distributed further (Duclos et al., 2013), and are more harmful to corals (Duckworth et al., 2017; Jones et al., 2015; Nugues and Roberts, 2003; Weber et al., 2006). When deposited on the benthos, this fine sediment may also have an adhesive, clay-like texture that is more resistant to bioturbation and dissipation (Jones et al., 2015), and is more likely to become anoxic (Piniak, 2007; Weber et al., 2006). Dredging can also release sediment from deeper strata than might be disturbed by natural events, generating additional sediment not already existing in the system and with distinct mineralogies compared to those found in reef environments (Saussaye et al., 2017; Swart, 2016). Releasing this sediment may result in acute acidification and/or eutrophication, and, particularly in areas such as shipping channels or ports (Nayar et al., 2007), may also release unwanted contaminants (Eggleton and Thomas, 2004; Jones, 2011; Su et al., 2002), sediment-borne pathogens (Hodgson, 1990; Voss and Richardson, 2006; Weber et al., 2012), or related immune impairment agents. Exposure to dredging plumes has been correlated with a doubling in the prevalence of white syndromes in corals on the Great Barrier Reef (Pollock et al., 2014), suggesting that dredging can either release potential pathogens and/or decrease coral health and compromise immunity.

The Port of Miami shipping channel bisects the Florida Reef Tract, and is immediately surrounded by areas designated under the U.S. Endangered Species Act (ESA) as critical habitat (defined as any area containing the physical and biological features essential to survival) for ESA-listed staghorn and elkhorn corals, of which hundreds of colonies (of *Acropora cervicornis*) were documented in 2013 within 150 m of the channel on the inner reef alone (McCarthy and Spring, 2014). Additional reef coral species listed as threatened under the ESA (including *Orbicella annularis*, *O. faveolata*, *O. franksi*, and *Mycetophyllia ferox*) have also been documented in the area (Dial Cordy and Associates, 2014a). These coral reefs and coral habitat are also designated as Essential Fish Habitat under the Magnuson Stevens Fishery Conservation and Management Act for species managed under the spiny lobster, snapper-grouper, and coral fishery management plans (NOAA Fisheries Service, 2017).

Dredging adjacent to the Florida reef tract took place to widen and deepen the Port of Miami shipping channel between November 20, 2013 and March 16, 2015 (~16 months). Dredged materials, consisting of chopped rock mixed with water, were pumped from the dredge to a spider barge which, in turn, pumped the material into scows (also known as hopper barges). The process of dewatering and overflow of sediment-laden water from the hopper barge deposits fine particles of dredged material into the water column (Jones et al., 2016), which, around the Port of Miami, created sediment plumes with an extent up to ~228 $\mathrm{km^2}$ (Barnes et al., 2015). Ultimately, an estimated 4.2 million $\mathrm{m^3}$ of material was dredged via pipeline, backhoe, and clamshell dredges, destined for a permitted offshore disposal location 2.4 km ESE of the project site at a depth of 120–240 m (Ocean Disposal Database, 2016).

Many dredging projects have historically suffered from data-poor monitoring efforts to determine impacts to coral reefs (Erftemeijer et al., 2012). However, in the case of the Port of Miami, surrounding coral resources were extensively monitored by an environmental consultancy, Dial Cordy and Associates (DCA), on behalf of Great Lakes Dredge and Dock Company, the dredging contractors for the U.S. Army Corps of Engineers (USACE), and on behalf of the Port of Miami (Miami-Dade County). Although this monitoring program concluded that the effects of dredging were minimal and attributed most observed coral mortality to a concomitant regional coral disease outbreak (Dial Cordy and Associates, 2017), state and federal agencies report that dredging impacts were widespread, severe, and long-lasting (Florida Department of Environmental Protection, 2014; Miller et al., 2016; National Marine Fisheries Service, 2016). These conflicting reports prompt the need for a comprehensive analysis of monitoring data to evaluate the contribution of dredging to observed reef impacts. Moreover, the extensive data collected in situ provides a unique opportunity to evaluate whether measured impacts on the benthos are correlated with satellite observations of sediment plumes. Although not a substitute for robust, in situ monitoring, demonstrating such a link would validate the use of remote sensing techniques to monitor and predict dredging and coastal construction impacts to benthic communities where data maybe lacking or unavailable, or where independent data sources are needed (Fisher et al., 2015).

Here, we apply rigorous, data-driven, statistical methods to DCA's in situ monitoring data to determine whether impacts to reef corals and habitat occurred as a result of dredging operations at the Port of Miami. Specifically, we investigate 1) whether dredging activities impacted the quality and quantity of corals and coral habitat, 2) whether dredging-related impacts can be distinguished from other regional disturbances that occurred contemporaneously, such as bleaching and disease, and

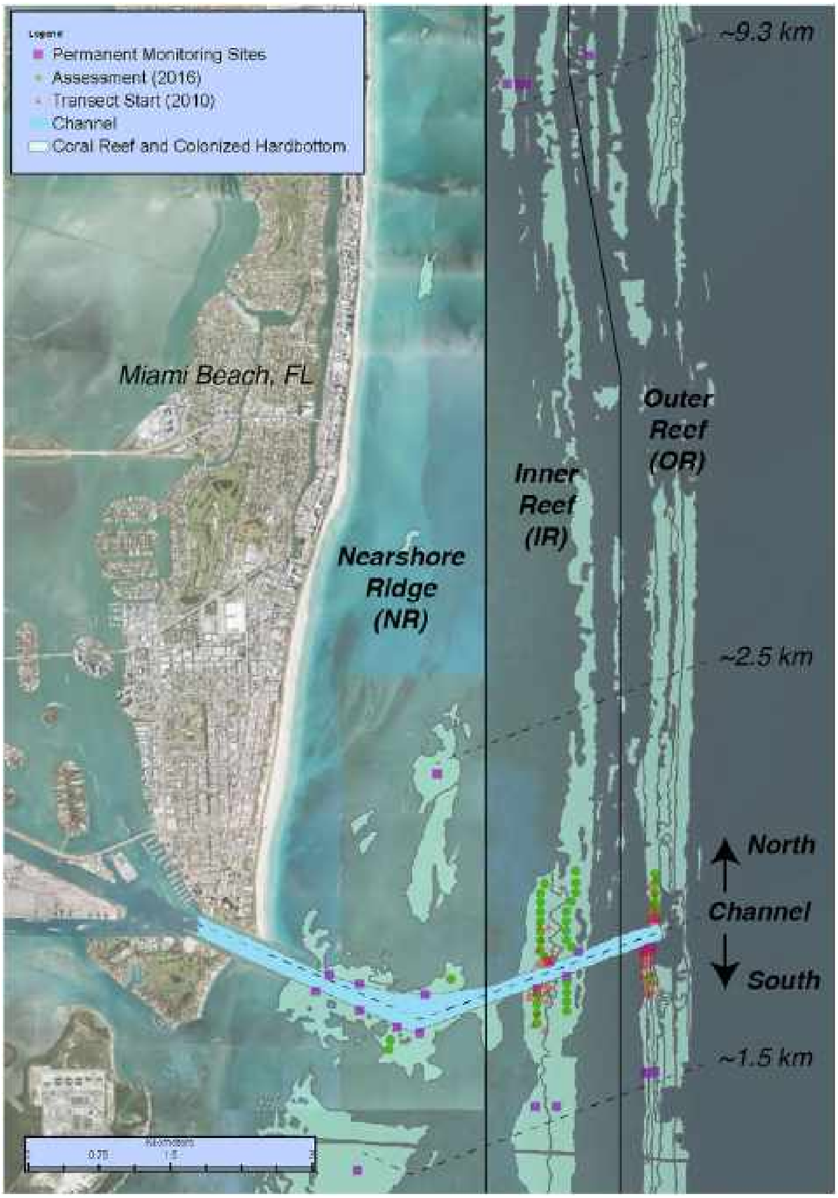

Fig. 1. Map of coral reef habitats and monitoring locations around the Port of Miami shipping channel. Permanent monitoring sites (n = 26) where data were collected throughout dredging are indicated by purple squares, while non-permanent transects used for coral density and/or sediment depth measurements at various distances from the channel are indicated by red triangles (2010; before dredging) and green circles (2016–2017; after dredging). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3) whether biological responses measured in situ can be predicted by remote sensing of dredging sediment plumes. Finally, we extrapolate from these data to estimate total coral losses and the full spatial extent of impacts from the Port of Miami dredging.

2. Methods

2.1. Study design and data provenance

The Port of Miami shipping channel, where dredging occurred, cuts across three tracts of coral reef and colonized hardbottom (Fig. 1), referred to (from west to east) as the nearshore ridge (NR), inner reef (IR), and outer reef (OR; terminology follows Walker (2009) and Miller et al. (2016), but note that USACE and DCA reports often refer to the inner reef as the middle reef). On each of these reefs, DCA monitored regions to the north (N) and south (S) of the channel (n = 6 regions). Within each region, monitoring was conducted in areas both adjacent to and away from the channel (n = 12 areas, Fig. 1). The monitoring areas away from the channel ranged from intermediate distances of ~1.3–2.4 km (NNR, SNR, SIR, SOR) to farther distances of 9.4 km away (NIR, NOR); monitoring areas immediately adjacent to the channel were located within 18–48 m (median = 23 m). Each monitoring area contained 1–3 replicate sites (n = 26 permanent monitoring sites; Dial Cordy and Associates, 2014a, 2014b). At each site, DCA (1) deployed sediment traps to measure sediment accumulation throughout dredging; (2) recorded video transects to analyze changes in benthic cover using Coral Point Count with extensions (CPCe; Kohler and Gill, 2006); and (3) tagged individual corals to monitor their condition over time (details below).

In addition to these data collected at permanent monitoring sites, data were also collected at a range of distances from the edge of the channel out to several hundred meters away (Fig. 1) at various timepoints before (Dial Cordy and Associates, 2012) and ~2 years after dredging (Dial Cordy and Associates, 2017). The metrics collected at these non-permanent sites included the density of corals (recorded both before and after dredging) and the depth of sediment (only recorded ~2 years after dredging). In addition to the DCA datasets, we also analyzed the presence of a sediment plume from dredging operations as detected by satellite imagery (details below).

All data (except remote sensing) were collected by DCA on behalf of Great Lakes Dredge and Dock, the USACE, or the Port of Miami, and were provided to the Florida Department of Environmental Protection (FDEP) for compliance with FDEP Permit No. 0305721-001-BI. We subsequently obtained these data by public records requests under the Florida Sunshine Laws. Data were supplied to FDEP in various spreadsheets which we integrated and standardized for downstream statistical analysis using R code (all data and analysis code is available on Github (http://github.com/jrcunning/pom-dredge) and archived at Zenodo (Cunning, 2019)). We did not independently verify DCA data entry from field notes, photographs, or videos, and we did not repeat intermediate data processing steps (e.g., CPCe analysis). We did, however, correct instances of data entry error (e.g., dates and species identifications) when such errors were apparent from context, and these modifications were also made using R code for transparency and reproducibility.

Our analyses focused on sediment trap accumulation, benthic sediment cover, and tagged coral condition throughout the dredging project, as well as correlations among these measured impacts and remotely-sensed sediment plumes. We also analyzed lasting impacts on the density of scleractinians and the depth of sediment in reef habitat approximately 2 years post-dredging. In the sections below, we describe for each analyzed dataset: 1) how DCA collected and processed samples and/or data (with reference to DCA reports for further detail); and 2) how we conducted downstream statistical analyses to quantify impacts to corals and reef habitat.

2.2. Sediment plume detection

Plumes of sediment in the water column (Fig. 2A) were detected using satellite imagery following the methods of (Barnes et al., 2015). Coordinates corresponding to the 26 permanent monitoring sites were mapped onto satellite imagery to determine presence or absence of a sediment plume on each day for which data were available (dependent on weather conditions and image quality). For each monitoring region, a binomial generalized additive model was used to model the frequency of sediment plume presence over time during dredging operations. To estimate the spatial extent of dredging impacts on the reef, the presence of sediment plumes during the dredging period was quantified for pixels along three north-south transects centered over the NR (longitude = 80.115°W), IR (80.0997°W), and OR (80.0894°W), positioned at 250 m intervals from 15 km south of the channel to 15 km north ($n = 396$ pixels).

2.3. Sediment trap accumulation

Sediment trap accumulation was measured by DCA using three sediment traps (1″ inner diameter PVC pipe with 500 mL collection bottle) deployed at each permanent monitoring site on a continuous basis between 2013-10-15 and 2015-07-20, for intervals that varied among sites and ranged from 10 to 89 days ($n = 1287$ sediment samples in total). Each sediment sample was separated into coarse and fine components using a U.S. Standard #230 sieve (the cut-point between very fine sand and coarse silt; Wentworth, 1922), dried at 150 °F for ≥24 h, and weighed to the nearest 0.01 g (Dial Cordy and Associates, 2015a, 2015b). Masses were divided by the duration of trap deployment to calculate sediment accumulation rates in g day^{-1}. We analyzed only 'fine' trapped sediment, as this is more likely derived from dredging than natural processes. Due to disparities between sediment trap accumulation and benthic sediment deposition (Storlazzi et al., 2011), these data should be interpreted as sediment inputs that are either depositing or moving through the system.

To analyze these data, we used a Poisson generalized additive model to estimate the fine sediment trap accumulation rate in each monitoring area as a smooth function of time (using the midpoint of each sampling interval), weighted by trap deployment duration. To calculate total trap accumulation at each of the 12 monitoring areas during the dredging project, we summed the fitted daily accumulation rates for all days between 2013-11-20 (beginning of dredging) and 2015-03-23 (one week after dredging was completed).

2.4. Benthic sediment cover

The proportion of the benthos occupied by sediment was monitored by DCA using video transects recorded along three 20 m transects at each monitoring site between 2013-11-07 and 2016-08-20 ($n = 1772$ video transects; dates recorded vary among sites since data were collected at a site only when dredge operations were within 750 m). Between 27 and 80 still frames (median = 40) were extracted from each video transect and analyzed using CPCe with 10 points overlaid on each frame. Points overlaying tape, wand, or shadow were excluded, resulting in a range of 1–10 points analyzed per frame (median = 8). Points were classified into a range of benthic categories, of which we focus on "sand", which was used to indicate presence of sediment (Dial Cordy and Associates, 2015b). Two sites (HBN1 and HBN2) were omitted because they are considered a different habitat type (referred to as scattered coral/rock in sand) and/or were influenced by a "sand wave" during baseline surveys, reducing the frequency of data collection (Dial Cordy and Associates, 2014b).

To analyze these data, we used a binomial generalized additive mixed model to estimate sediment cover as a smooth function of time, with site and transect as random factors. Models were fitted only to portions of the time series with < 20-week gaps between data points.

2.5. Tagged coral condition

DCA observers tagged and monitored individual coral colonies throughout the project, recording a variety of condition codes that reflected coral health and/or impacts of sedimentation (Dial Cordy and Associates, 2015b). The complete collated dataset contained $n = 23{,}537$ observations of 650 tagged corals at 26 permanent monitoring sites between 2013-10-14 and 2016-08-20 (dates vary among sites since data were collected from a site only when dredge operations were within 750 m). We analyzed coral sediment burial as the occurrence of either "PBUR" (partial burial) or "BUR" (complete burial) condition codes over time using a binomial generalized additive mixed model for each monitoring area, with site, transect, and species as random factors.

To quantify partial mortality due to sedimentation, we analyzed occurrence of the "PM" condition code (defined by DCA as partial mortality specifically due to sedimentation; Dial Cordy and Associates, 2015a) using a binomial generalized linear mixed model (GLMM) with site, transect, and species as random factors. A colony was counted as having experienced partial mortality due to sedimentation if it was recorded with the "PM" condition code at any time during dredging operations. The same analysis was conducted for total mortality (condition code = "DEAD"); however, since some corals may have died due to a concomitant disease outbreak, we additionally analyzed total mortality for the subset of tagged coral species not observed with disease during monitoring (*Acropora cervicornis*, *Agaricia agaricites*, *Agaricia lamarcki*, *Madracis decactis*, *Mycetophyllia* spp., *Porites astreoides*, *Porites porites*, *Siderastrea siderea*, *Stephanocoenia intersepta*), which lowered statistical power but allowed us to isolate potential dredging impacts from disease-related mortality. Further estimates of total mortality are derived from changes in coral density (Section 2.8).

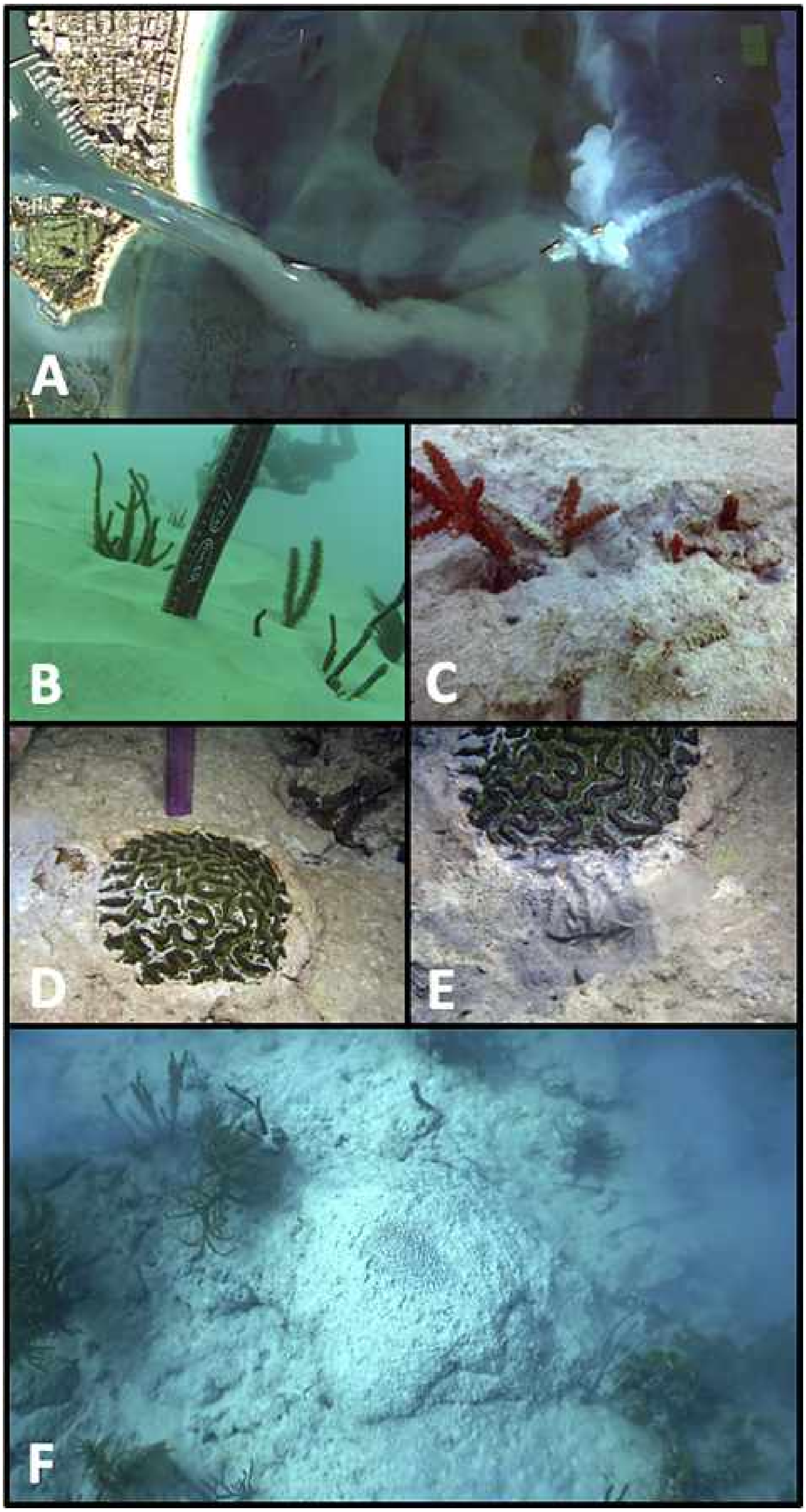

Fig. 2. Representative photographs of sediment plumes and benthic impacts. (A) Sediment plumes spread from dredging activity in the channel on 2013-12-30 (photo: Google Earth). (B) Sediment covers the benthos on the NIR reef < 250 m from the channel on 2015-01-30, with the tops of gorgonians protruding from ~7 cm of sediment (photo: R Silverstein). (C) A colony of *A. cervicornis* is partially buried in sediment 150 m from the channel on the NIR in September 2014 (photo: Coastal Systems International). (D) A *Colpophyllia natans* colony is partially buried with a berm of rejected sediment around its perimeter on 2014-07-22 (photo: (Florida Department of Environmental Protection, 2014)). (E) The same *C. natans* colony after sediment was removed from the base of the colony, revealing significant partial mortality. (F) Dead coral skeletons on the NIR reef < 150 m from the channel on 2015-06-23. Sediment was removed from the top of the large colony in the center to reveal skeletal structure. (Photo: R Silverstein).

2.6. Relationships among measurements

For each of the independent in situ measurements made at permanent monitoring areas (plume presence, fine sediment accumulation, benthic sediment cover, partial or complete coral burial, and partial coral mortality from sediment), we calculated aggregated metrics for each area and analyzed their pairwise correlations. Dredge plume presence was calculated as the proportion of days that a dredge plume was present (Fig. 3); sediment accumulation was calculated as the total accumulation of fine sediment in traps during the project (kg m^{-2}; Fig. 5); benthic sediment cover was calculated as the mean daily proportion of the benthos covered by sediment (Fig. 6); coral burial was calculated as the mean daily probability of coral burial (Fig. 7); coral mortality was calculated as the cumulative probability of partial

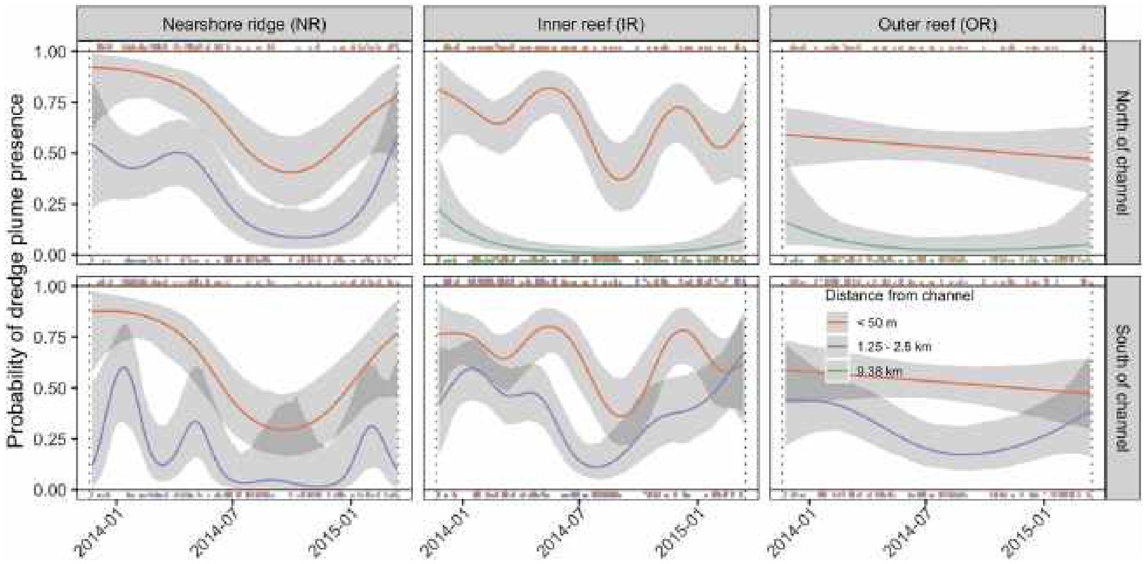

Fig. 3. Presence of a sediment plume as detected by satellite data throughout the dredging project. Smooth lines are GAM fits for each monitoring area (± 95% CI), colored according to distance from channel. Points in margins indicate the presence or absence of the dredge plume on a given date (data not available for all dates). Vertical dotted lines indicate the beginning (2013 − 11 − 20) and end (2015-03-16) of dredging operations.

mortality from sediment among tagged corals (Fig. 8). Metrics derived from time series (e.g., benthic sediment cover, coral burial) only include dates for which data were available from all monitoring areas. Pairwise linear regressions were performed for these aggregated metrics, and R^2 values calculated to determine the proportion of variability of the response explained by each predictor.

To estimate the magnitude of potential benthic impacts based on the sediment plume presence between 15 km south and 15 km north of the channel (Section 2.2), linear transformations using these regression models were made based on the proportion of days that a plume was detected at a given pixel.

2.7. Sediment depth

Sediment depth was measured by DCA ~2 years after dredging (between 2016-09-12 and 2017-05-30; Dial Cordy and Associates, 2017) at 1 m intervals along two perpendicular 50 m transects centered at increasing distances from the channel within the linear reef habitat (as defined by Walker, 2009). The distribution of sediment depth measurements was highly positively skewed, and therefore a quantile regression approach was taken. For each transect (containing $n = 51$ measurements), quantiles were computed to reflect the depth of sediment recorded in 1%, 10%, 25%, and 50% of measurements. These quantiles were then analyzed by linear regression with reef, direction, and log(distance from channel) as predictors.

2.8. Scleractinian abundance

To detect changes in scleractinian abundance, we analyzed the number of corals counted by DCA along belt transects at varying distances from the channel before dredging (in 2010 and 2013; Dial Cordy and Associates, 2014a, 2014b) and ~2 years after dredging (late 2016/early 2017; Dial Cordy and Associates, 2017). In 2010 and 2016–17, all corals ≥1 cm were recorded, while in 2013 only corals ≥3 cm were recorded. For some observations, diameter information was missing, so we assumed these corals were ≥3 cm. Across all of these timepoints, 11,166 scleractinians were counted along 482 transects, comprising 33 species, including ESA-listed *A. cervicornis*, *M. ferox*, *O. annularis*, *O. faveolata*, and *O. franksi*.

We analyzed the density of 'large' (defined as ≥3 cm) corals as a function of distance from channel in each monitoring area using a Poisson generalized linear mixed model, with timepoint (before or after dredging) as an additional fixed factor, and site, transect, and survey date as random factors. For the SIR, one data point was a highly influential outlier (Cook's distance = 1.34, while all other points < 0.12), and was removed from the analysis. The density of 'small' corals (< 3 cm) was analyzed in the same way. For each monitoring region, fitted values were used to test for differences in scleractinian density before vs. after dredging both adjacent to (20 m) and further away from (300 m) the channel.

Fitted values for declines in coral density (corals m^{-2}) at 1 m intervals moving away from the channel in each monitoring region (sufficient data available only for the IR and NOR) were multiplied by the total area of reef habitat at that distance within each region in order to estimate the total number of corals lost due to dredging activity. Area was calculated in ArcGIS as the aggregate sum of coral reef and colonized hardbottom habitat using mapping data from (Walker, 2009).

3. Results

3.1. Sediment plume detection

The frequency of sediment plume (e.g., Fig. 2A) detection by satellite was higher in the permanent monitoring areas closer to the channel (Fig. 3). In late 2013, after dredging commenced, plumes occurred with very high frequency (77–92% of days) near the channel on the NR and IR, and were also frequent on the OR (58% of days), as well as all monitoring areas within 1.25–2 km (33–50% of days; Fig. 3). In contrast, sediment plumes were detected on only 14–17% of days during the same time period 9.4 km away. In 2014 through the end of dredging in 2015, sediment plumes were almost never detected (3–4% of days) 9.4 km away, but still occurred with variable but high frequency at all intermediate distance monitoring areas (16–38% of days) and channelside areas (53–65% of days; Fig. 3).

3.2. Sediment trap accumulation rates

Fine sediment accumulation measured by sediment traps was highest at locations near the channel, and in particular, on the NR and IR (Fig. 4, 5). Fine sediment accumulation rates showed peaks in late 2013, spring 2014, and late 2014, and began to decline after dredging ended (Fig. 4). The highest rates of fine sediment accumulation were

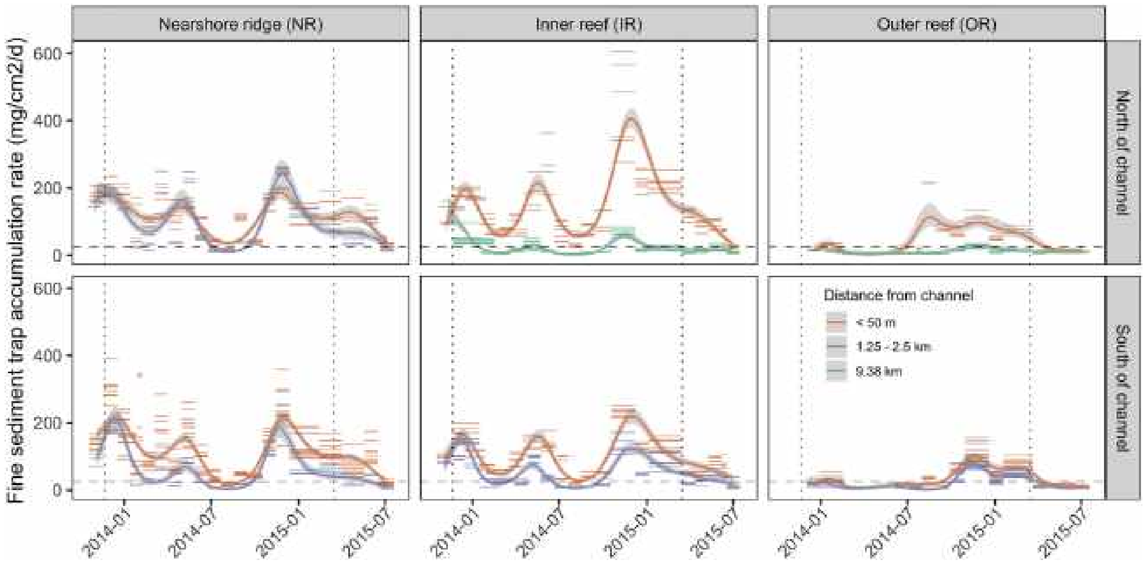

Fig. 4. Accumulation rates of fine sediment in sediment traps throughout the dredging project. Horizontal line segments indicate measured rates of fine sediment accumulation in each trap over each deployment period. Smooth lines are GAM fits for each monitoring area (± 95% CI), colored according to distance from channel. Vertical dotted lines indicate the beginning (2013-11-20) and end (2015-03-16) of dredging operations. The horizontal dashed line indicates a threshold of 25 mg cm^{-2} d^{-1}; sediment deposition rates exceeding this threshold over 30 days may cause severe stress leading to mortality (Nelson et al., 2016).

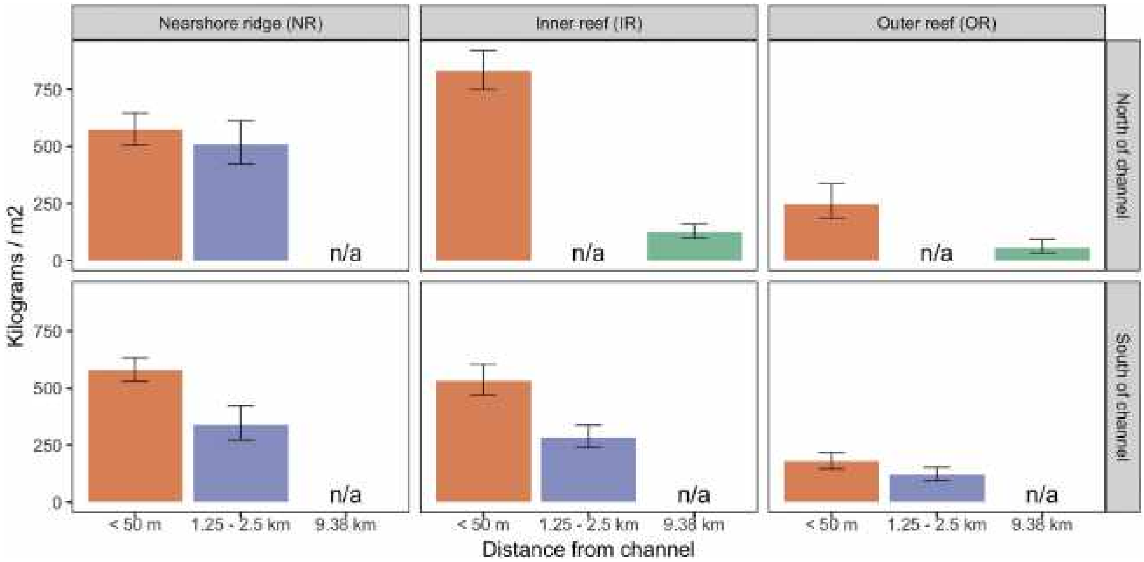

Fig. 5. Total amount of fine sediment accumulated in sediment traps in each monitoring area throughout dredging operations. Bars indicate the sum of fitted daily fine sediment accumulation rates between 2013-11-20 and 2015-03-16 (Fig. 4) for each monitoring area (± 95% CI). Bars are colored corresponding to distance from channel, and 'n/a' indicates areas that were not monitored.

recorded in late 2014 when the NIR channelside area received over 400 mg cm^{-2} d^{-1} on average, with one trap measuring 606 mg cm^{-2} d^{-1} over a 51-day period. During the same time period, traps 9.4 km away from the channel on the NIR measured 10 times less sediment (58.3 mg cm^{-2} d^{-1}). The total fine sediment accumulation over the entire dredging project (Fig. 5) was highest at the NIR channelside area (830 kg m^{-2}).

3.3. Benthic sediment cover

Sediment cover on the benthos (e.g., Fig. 2B) increased during dredging, with channelside areas naturally low in sediment cover (0–10%; IR and OR) becoming 50–90% covered in sediment for most of the duration of dredging (Figs. 6, S1). Intermediate-distance monitoring areas (1.25–2.5 km away) also experienced increases in sediment cover, peaking at 50–70% in late 2014. By contrast, areas located 9.4 km away were typically < 25% sediment, and never exceeded 50%. Mean daily percent sediment cover (± 1 s.d.) was 61.1 ± 16.0% near the channel, 35.8 ± 21.6% at intermediate distances, and 15.4 ± 8.5% at 9.4 km away. Sediment cover over time was temporally correlated with sediment trap accumulation rates for most areas (Fig. S2; median correlation coefficient = 0.51 with median lag time = 33 days), indicating that sediment deposition drove the observed increases in sediment cover.

3.4. Burial of corals

There was only one record of partial burial by sediment (out of 1211 observations of tagged corals, 0.08%) prior to the start of dredging. After dredging began, the probability of partial or complete coral burial

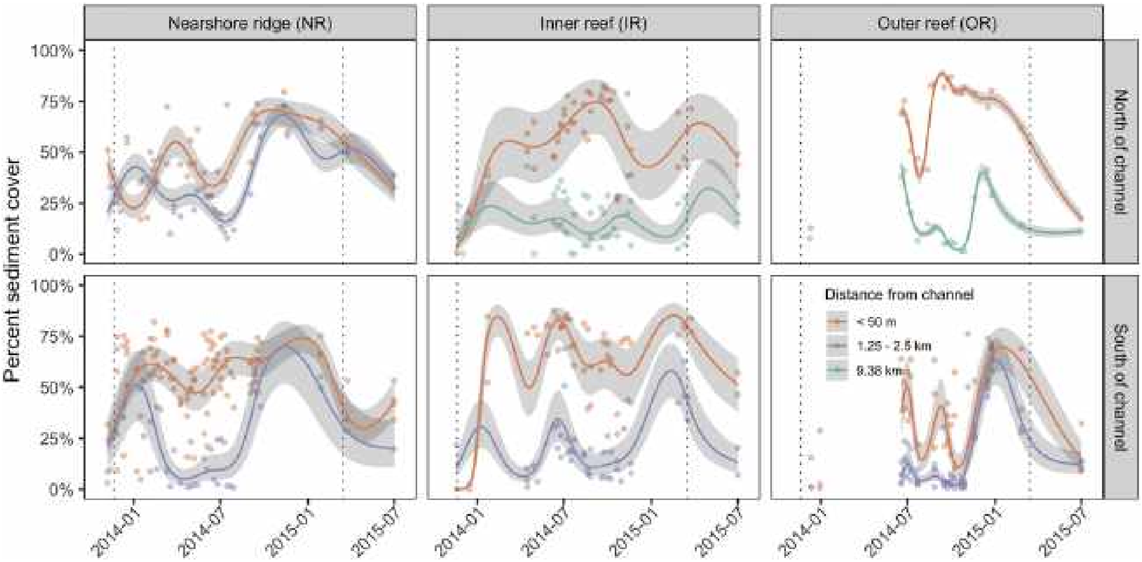

Fig. 6. Percent sediment cover at each monitoring area during dredging operations. Points indicate the mean percent sediment cover for each transect measured by CPCe analysis, and smooth lines show GAMM fits for each monitoring area (± 95% CI). Fitted lines are colored by distance from channel. Vertical dotted lines indicate the beginning (2013-11-20) and end (2015-03-16) of dredging operations.

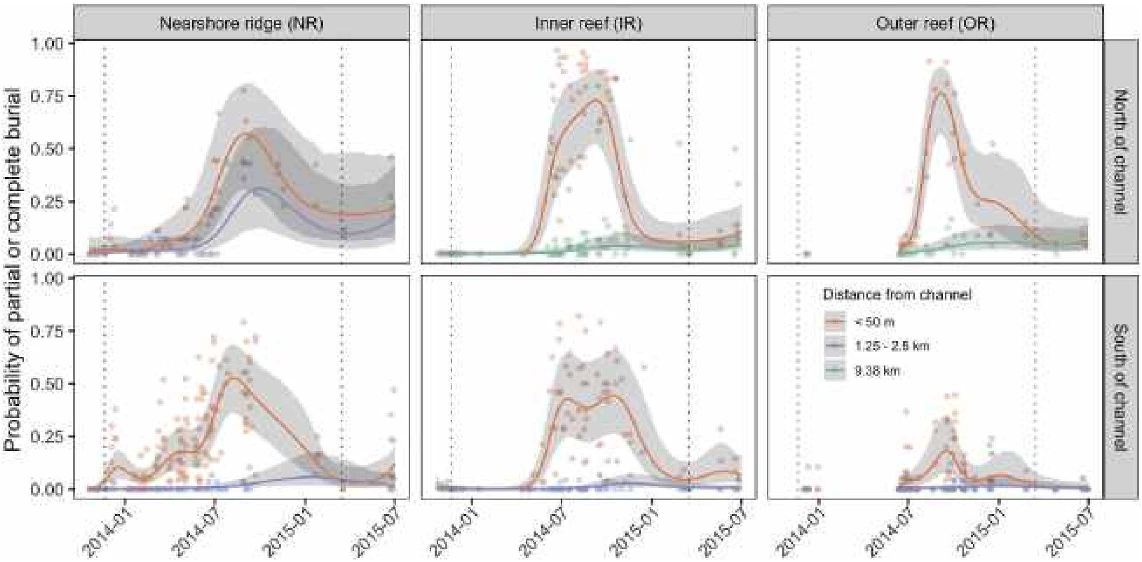

Fig. 7. Probability of partial or complete coral burial by sediment in each monitoring area during dredging operations. Points indicate the proportion of living tagged corals in each monitoring area observed on a given date as either partially or completely buried in sediment. Lines represent GAMM fits for each monitoring area (± 95% CI) colored by distance from channel. Vertical dotted lines indicate the beginning (2013-11-20) and end (2015-03-16) of dredging operations.

(e.g., Fig. 2C, D) rose sharply in areas, first on the NR in late 2013/early 2014, and then on the IR and OR in mid to late 2014 (Fig. 7). The probability of partial or complete burial reached 57–76% at all northern channelside areas by late August/early September 2014. At southern channelside areas, probabilities peaked at 44.5–52.7% on the NR and IR, but reached only 18.3% on the OR. At all intermediate and far distances, probabilities remained below 6%, with the exception of the NNR area (2.3 km away), which peaked at 31.2%.

3.5. Coral mortality

Partial mortality due to sedimentation (e.g., Fig. 2E) was frequently observed for tagged corals, especially in channelside areas, where the cumulative prevalence was 56.8–74.7% (except the SOR at 24.1%; Fig. 8). In addition to partial mortality due to sedimentation, tagged corals also experienced total mortality (e.g., Fig. 2F), although causes of total coral mortality were not necessarily known. To eliminate disease as a possible cause of death and isolate total mortality due to sedimentation, we analyzed data from only those coral species not observed with disease by DCA during the monitoring period. Among these non-disease-susceptible tagged corals, the probability of total mortality was 36% on the NIR adjacent to the channel, but only 7% at a distance of 9.4 km (Fig. S4). Other monitoring regions also showed trends of higher partial and total mortality in areas closer to the channel. Mortality of non-tagged corals is presented in Section 3.8.

3.6. Correlations among metrics in permanent monitoring areas

Measured impacts of dredging were highly correlated across the 12 monitoring areas (Fig. 9). Areas where sediment plumes were more frequently detected had higher rates of sediment trap accumulation, higher proportions of the benthos covered in sediment, higher

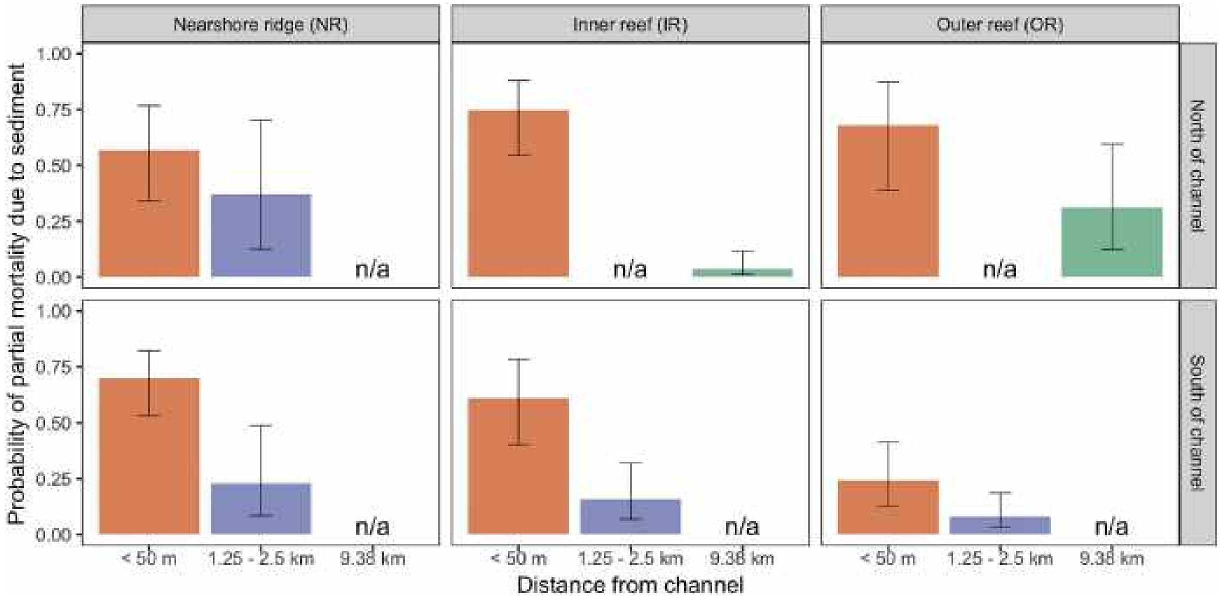

Fig. 8. Coral partial mortality due to sedimentation in each monitoring area throughout dredging operations. Bars indicate the predicted probability (± 95% CI) of tagged corals being observed with the condition code PM (partial mortality due to sedimentation) at any point through March 2015 (the final month of dredging operations). Bar colors correspond to distance from channel, and 'n/a' indicates areas that were not monitored.

probabilities of corals being partially or completely buried in sediment, and higher rates of coral partial mortality. Each of these metrics were highly positively correlated with each other (R^2 values between 0.51 and 0.90), and were statistically significant (all p-values < 0.01).

The frequency of sediment plume presence predicted an average of 62% of the spatial variability among all the other analyzed parameters, including sediment trap accumulation (52%), mean benthic sediment cover (73%), mean probability of coral burial (65%), and cumulative probability of partial mortality to corals (59%) across permanent monitoring sites. Using this predictive power, we estimated the likely magnitude and extent of these impacts based on the occurrence of sediment plumes in satellite imagery over each reef ranging from 15 km south to 15 km north of the channel (Fig. 10). The frequency of sediment plumes was ~55–70% near the channel, and decreased with distance from channel, with a skew toward higher frequency to the north. Based on these data, probable dredging-related impacts within 2–3 km include a ~4- to 9-fold increase in fine sediment input (an additional ~200–500 kg/m^2 depositing or moving through the system), a ~2- to 4-fold increase in benthic sediment (covering an additional 15–40% of the reef, on average, for 16 months), and a ~5- to 12-fold increase in coral partial mortality (affecting an additional ~20–55% of corals; Fig. 10). Sediment plumes further predict a doubling in partial mortality out to ~5 km south and ~9 km north of the channel, and some level of impact as far as ~10 km south and ~15 km north (the full range of plume detection).

3.7. Alteration of habitat 2 years post-dredging

Two years after dredging, significant portions of the benthos to the north of the channel were found to be covered in deep sediment (Fig. 11). One quarter of the NOR near the channel was covered by 10 cm or more of sediment, with pockets (~1% of the reef area) up to 30 cm deep. One quarter of the NIR was under 3 cm or more of sediment, with pockets over 10 cm deep. Based on sediment depth data for the NIR and NOR, the percent of area 20 m from the channel covered in at least 1 cm of sediment was 47% and 55%, respectively, while at 500 m, this decreased to 12% and 16%. While sediment depth data was not collected pre-dredging, three sites were surveyed for benthic sediment cover both before dredging and again two years later (Fig. S5): two channelside sites with very low sediment cover before dredging (0.2 and 1.2%) had significantly higher sediment cover two years post-dredging (19.4 and 34.0%; fold-changes of 14 and 156), while a third site located ~1 km away on the SIR had no change in sediment cover (21.8% to 21.5%).

3.8. Impacts to coral populations

Two years after dredging, the density of corals ≥3 cm at ~20 m from the channel was significantly reduced in all reef areas (Fig. 12); these reductions in coral density ranged from ~26–43% (SIR, SOR, NIR) up to 50–64% (NNR, SNR, NOR). Where sufficient data exist, declines in coral density lessened moving away from the channel, such that at 300 m away, changes in coral density were not statistically significant (except for a marginally significant ($p < 0.1$) decline of 43% on the NOR).

The density of small corals (1–2 cm diameter) near the channel was even more reduced two years after dredging (Fig. 13). On the NIR, SIR, and NOR, small corals declined by ~80% (NIR: 78.8%, $p < 0.01$; SIR: 80.1%, $p < 0.1$; NOR: 78.3%, but not significant). At 300 m away from the channel, small corals were still reduced by 72.3% on the NIR ($p < 0.1$), and, though not significant, were 67.3% lower on the SIR, and 62.8% lower on the NOR. The same analyses were also repeated with only coral species that were not observed with disease to isolate dredging-related impacts; these analyses produced very similar results (Figs. S6, S7). As additional evidence of the disproportionate loss of small corals in these areas, size-frequency distributions of the coral populations within 100 m of the channel showed a higher mean size of corals after dredging at NIR ($p < 0.0001$), SIR ($p < 0.0001$), and SOR ($p < 0.001$) relative to before dredging (Fig. S8).

By multiplying the declines in coral density by the total reef area in each region (where data exist, i.e., at three of six monitoring areas and only out to 500 m), we estimate that over half a million corals were killed during the dredging period (Table 1). In some cases, the distances in Table 1 are less (192 m on the SIR and 349 m on the NIR) because there was no estimated decline in density beyond that point (Fig. 11). The greatest losses (> 400,000 corals, ~71.5%) occurred in the small size class (< 3 cm) on the inner reef (Table 1).

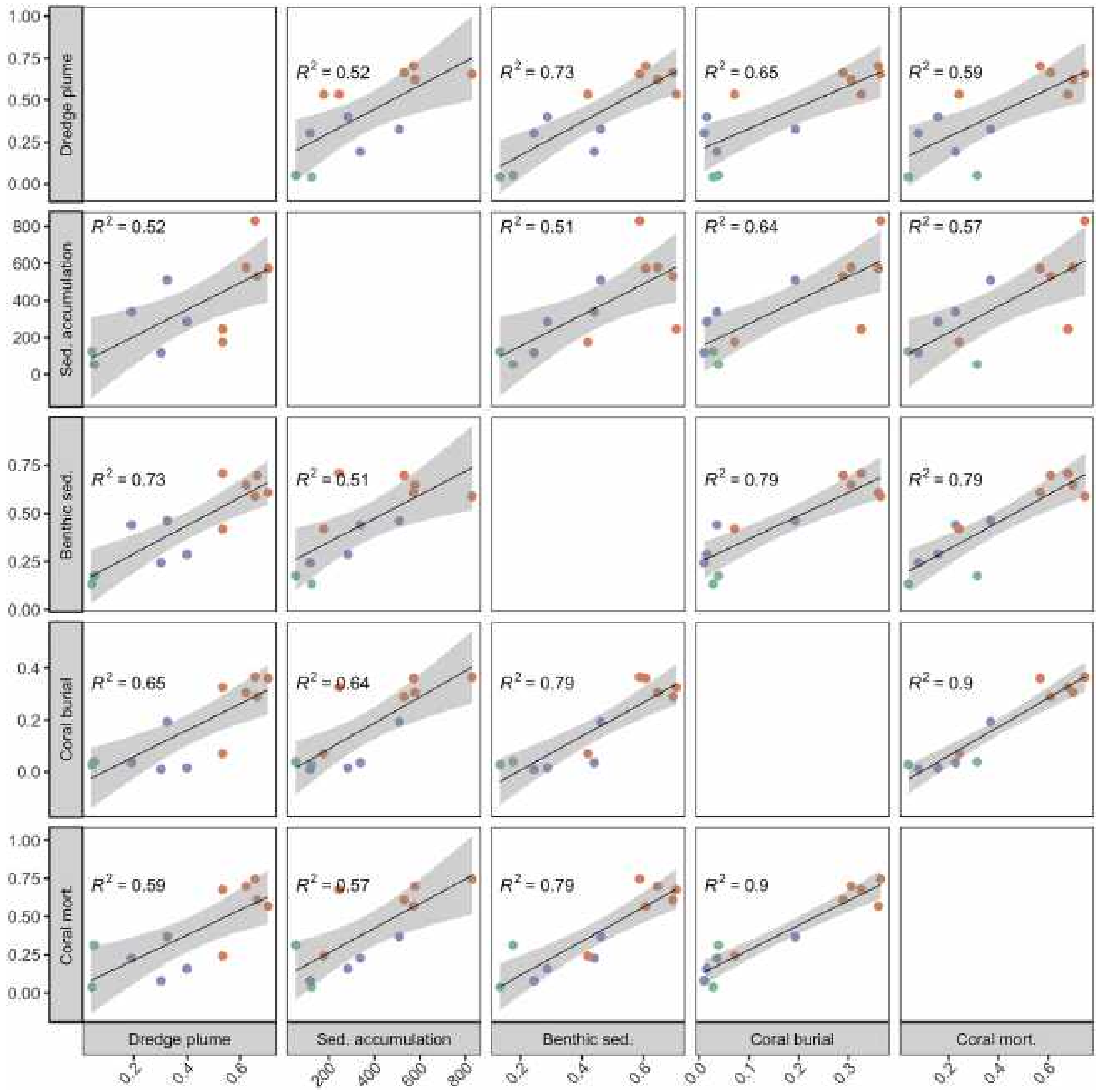

Fig. 9. Correlations among multiple metrics measured across monitoring areas. Points represent monitoring area ($n = 12$) colored by distance from channel (green ≤ 50 m; blue = 1.25–2.5 km; red = 9.38 km). Metrics are as follows: Dredge plume = proportion of days dredge plume present (Fig. 3); Sed. accumulation = total fine sediment trap accumulation during project (kg m^{-2}; Fig. 6); Benthic sed. = mean daily proportion benthic sediment cover during project (Fig. 5); Coral burial = mean daily probability of coral burial during project (Fig. 7); Coral mort. = probability of partial mortality due to sedimentation among tagged corals (Fig. 8). Metrics derives from time series (e.g., Benthic sed., Coral burial) only include dates for which data were available from all monitoring areas. Each panel displays a linear regression and the proportion of variation in the response explained by the predictor (R-squared). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Impacts from dredging at the Port of Miami

These analyses reveal significant impacts of dredging-related sedimentation on corals and the quality and quantity of coral habitat surrounding the Port of Miami shipping channel. Sediment plumes were detected with high frequency within several kilometers to the north and south of the channel (Figs. 3, 10), indicating that potential impacts from dredging were widespread and sustained over the 16-month project duration. Sediment trap data indicate that nearly ~830 kg of fine sediment per m^2 were input to reef habitats near the channel (Fig. 5), and that high sediment inputs occurred out to at least 2.5 km (Figs. 4, 5). Modeling work by Nelson et al. (2016) suggests that sedimentation rates > 25 mg cm^{-2} d^{-1} for 30 days (i.e., 7.5 kg m^{-2} over a single 30-day period) are likely to cause severe coral stress and mortality; over the 20 months of sediment trap monitoring, this threshold was exceeded, on average, 84.0% of the time at sites adjacent to the channel, 66.7% of the time at intermediate distance sites (1.25–2.5 km), and 15.2% of the time at the farthest sites (9.4 km; Fig. 4).

As some of this sediment deposited on the benthos, reef habitat initially low in sediment cover became 50–90% covered in sediment during dredging operations (Fig. 6). In addition to major impacts to existing benthic organisms (discussed below), the consequences of reef habitat being mostly buried for ~16 months likely include a significant reduction in larval recruitment. With at least two spawning and recruitment cycles (2014 and 2015) potentially affected by high sedimentation and suspended sediment, it is likely that area reefs experienced reduced fertilization, recruitment, and juvenile survivorship (e.g., Babcock et al., 2002; Fabricius, 2005; Moeller et al., 2016; Ricardo et al., 2015, 2016). Therefore, in addition to the effects documented here, dredging likely had detrimental, but as-yet-unquantified, effects on the ability of corals at these sites to undergo successful sexual reproduction. Indeed, elevated turbidity – even for a single month – has

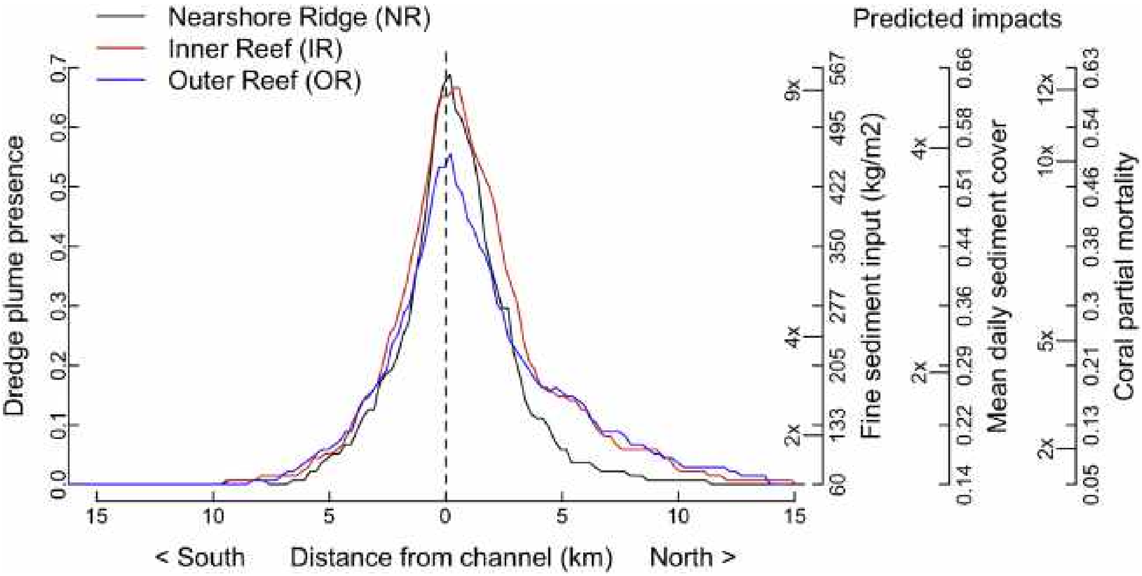

Fig. 10. Predicted magnitude and extent of dredging impacts based on dredge plume occurrence. Lines indicate the frequency of dredge plume presence throughout dredging operations based on satellite imagery along linear transects from 15 km north to 15 km south of the channel on the nearshore ridge, inner, and outer reefs. Axes on the right show predicted impacts based on linear transformations of dredge plume presence according to the models in Fig. 9. Additional ticks are added to transformed axes to indicate relative fold-changes ('2 × ', etc.) above baseline values in the absence of a plume. The baseline values at the bottom of the transformed axes correspond to the y-intercepts of the regressions in Fig. 9, i.e., the level of impact expected with a sediment plume is entirely absent.

been found to reduce coral recruitment from 80% to 10% (Fourney and Figueiredo, 2017). Surveys conducted on affected reefs near the Port of Miami dredging in 2014 found no coral recruits due to fine sediment covering the benthos (Florida Department of Environmental Protection, 2014).

As the benthos became covered in sediment, corals were also buried. By mid to late 2014, ~50–75% of tagged corals adjacent to the channel (except on the SOR) were partially or completely buried in sediment (Fig. 7). Consistent with these rates of burial, ~50–75% of tagged corals adjacent to the channel (except the SOR) also suffered partial mortality due to sedimentation (Fig. 8). In populations of colonial organisms, partial mortality (e.g., of large colonies) is as important as whole-colony mortality (e.g., of small colonies) in driving changes in total tissue biomass (Meesters et al., 1996), and in determining changes in population-level parameters like fecundity (Denley and Metaxas, 2016). Colonies are also less likely to recover from partial mortality in high sediment conditions (Meesters et al., 1992).

Whole-colony mortality was assessed in multiple ways: by direct observations of tagged corals, and by changes in total coral density before and after dredging. However, unlike the other metrics analyzed here, complete mortality has the potential to be confounded by regional bleaching and/or disease events that were occurring contemporaneously (Walton et al., 2018). Therefore, to distinguish dredging impacts from these regional disturbances, we analyzed (1) spatial patterns in proximity to dredging, (2) impacts to coral species not affected by disease, and (3) impacts to coral size classes with varying

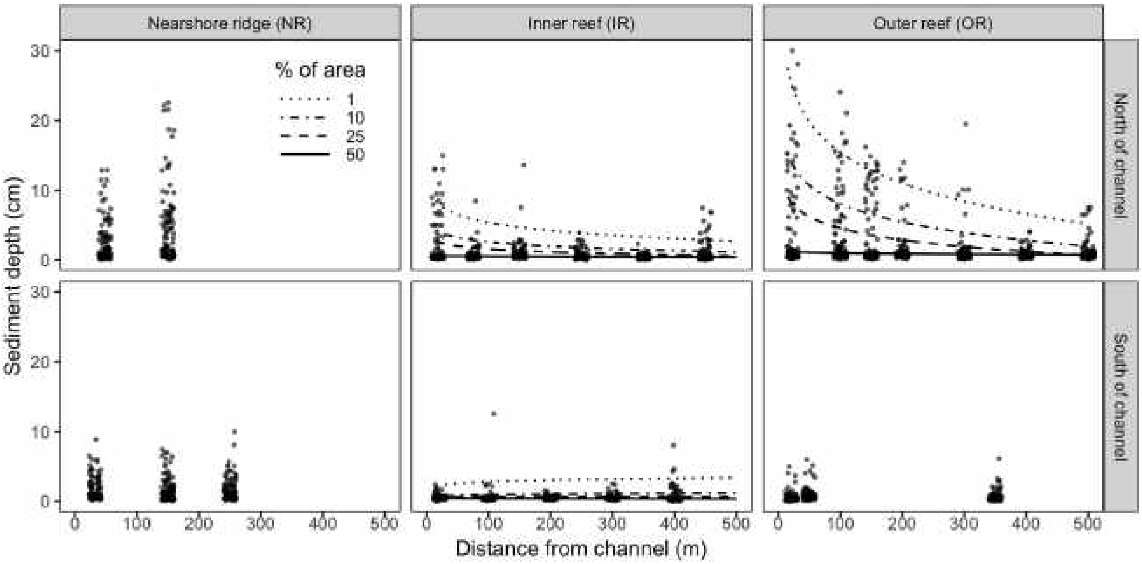

Fig. 11. Depth of sediment in relation to channel measured ~2 years after dredging operations. Dots represent individual sediment depth measurements along transects, jittered around the distance from the center of the transect to the channel in each monitoring region. Lines represent quantile regressions across transects as a function of log(distance from channel), indicating that at a given distance from the channel (on the x-axis), sediment with a particular minimum depth (on the y-axis) covered X% of the reef (where X is the quantile of the regression, e.g. 1%, 10%, etc.).

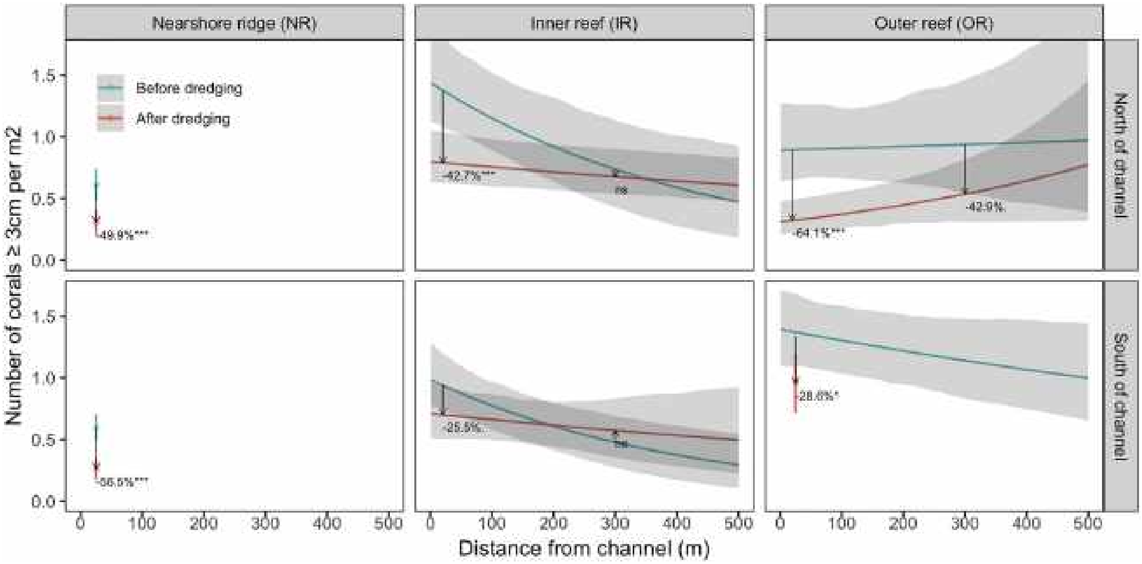

Fig. 12. Density of corals ≥ 3 cm within 500 m from the channel in each monitoring region before and after dredging operations. Data 'before' dredging were collected in 2009 and 2013, and data after dredging were collected in 2016–2017. GLMM fits are shown as lines for the regions and times in which data were collected at > 2 points beyond 50 m, and otherwise as points including only data from within 50 m of the channel. Shaded regions and error bars represent 95% CI's. Text annotations indicate the results of tests for differences between timepoints at 20 m and 300 m from the channel (*** = $p < 0.0001$; ** = $p < 0.001$; * = $p < 0.01$; . = $p < 0.1$; ns = not significantly different).

vulnerability to sediment burial. Among the tagged coral species not affected by disease during monitoring (Section 2.5), complete mortality was 5 × higher near the channel (36%) compared to 9 km away (7%) on the NIR (Fig. S4). Consistent with this high mortality near the channel, we also found 25–80% reductions in total coral density after dredging, and these declines lessened in severity moving away from the channel (Figs. 12, 13). This spatial pattern of coral loss suggests these impacts were caused directly by dredging or its interaction with other stressors (e.g., Bessell-Browne et al., 2017b), since bleaching or disease alone would not be expected to cause more severe mortality closer to the channel. Even coral species never observed with disease, when analyzed separately, showed the same decline in density and relationship with distance from the channel (Figs. S6, S7), providing additional evidence that dredging, not disease, was the driving factor. Furthermore, 1–2 cm corals, which could more easily be buried by sediment due to their small size, suffered disproportionate declines of up to 80% (which were also more severe closer to the channel), again implicating sediment burial as the cause. Finally, the observed declines in coral density around the Port of Miami far exceeded the regional estimate of 11.6% decline (2013–2016) as a result of bleaching and disease (Walton et al., 2018). This extensive coral mortality increased directly with proximity to the channel, affected even disease-resistant species, and disproportionately impacted small corals. Taken together, these findings cannot be explained by regional bleaching or disease, and instead indicate local disturbance in the channel as causing the majority of coral loss. While in theory, some other unidentified factor associated

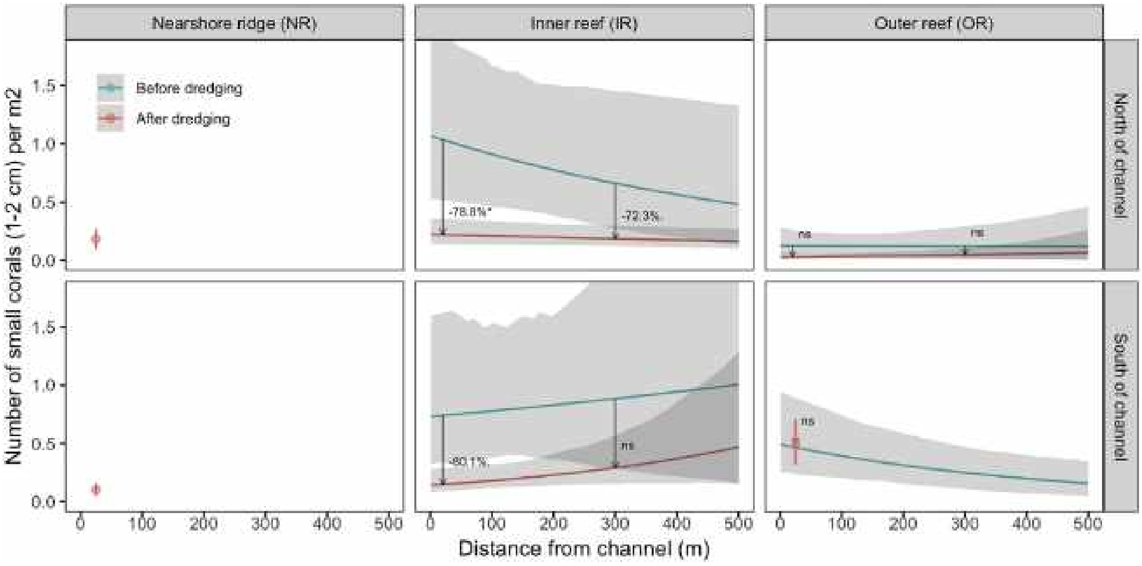

Fig. 13. Density of small corals (1–2 cm) within 500 m from the channel in each monitoring region before and after dredging operations. Data 'before' dredging were collected in 2010, and data after dredging were collected in 2016–2017. GLMM fits are shown as lines for the regions and times in which data were collected at > 2 points beyond 50 m. Shaded regions and error bars represent 95% CI's. Text annotations indicate the results of tests for differences between timepoints at 20 m and 300 m from the channel (*** = $p < 0.0001$; ** = $p < 0.001$; * = $p < 0.01$; . = $p < 0.1$; ns = not significantly different).

Table 1
Estimated coral loss two years after dredging within 500 m of the dredged channel. Losses were estimated by multiplying declines in density per m^2 (see Figs. 12, 13) by the reef area in each region at increasing distance from the channel out to a maximum distance of 500 m (the extent of data collection), or the distance at which density estimates before and after dredging intersected (whichever was lesser). Coral density data were only available for three of six reef regions. 'Out to (m)' and 'From area (km^2)' indicate the distance from channel, and total area, within which the estimate of coral loss took place.

Direction	Reef	Size class	Corals lost	Out to (m)	From area (km^2)
Northern	Inner	< 3 cm	203,249	500	0.86
Northern	Inner	≥ 3 cm	72,982	349	0.75
Southern	Inner	< 3 cm	197,917	500	1.51
Southern	Inner	≥ 3 cm	16,912	192	1.3
Northern	Outer	< 3 cm	11,082	500	1.87
Northern	Outer	≥ 3 cm	58,636	500	1.87
Total			**560,778**		

with the channel could have produced this channel effect, all lines of evidence point to dredging activity as the direct cause.

By multiplying the declines in coral density (where data exist) by the total area of coral habitat (Walker, 2009), these data indicate that at least half a million corals were lost within 500 m of the channel as a result of dredging activities (Table 1). Moreover, this may be a conservative estimate of total coral loss, because it only includes areas where sufficient data were collected (i.e., only three out of six reef regions, and only out to a distance of 500 m from the channel). Impacts likely occurred in the other three reef regions and at distances > 500 m, as our analyses below indicate. Consequently, the actual amount of coral lost as a result of dredging is likely to be much higher (millions of colonies).

In addition to these significant coral losses, surviving corals and portions of coral colonies likely also suffered sublethal impacts including growth reductions (confirmed empirically by Miller et al. (2016)), depletion of energy and lipid reserves, and decreased immunity associated with the physical challenges of sediment removal and stress from the eutrophication, acidification, and light attenuation caused by suspended sediment (Erftemeijer et al., 2012; Fourney and Figueiredo, 2017; Jones et al., 2015; Pollock et al., 2014; Riegl and Branch, 1995). Corals in the vicinity of the plume or that suffered direct sedimentation also may have been more susceptible to the regional disease outbreak (Pollock et al., 2014; Stoddart et al., 2019; Voss and Richardson, 2006), and this could be investigated directly in future research.

Our combined analysis of a number of independent physical and biological metrics reveals highly significant positive correlations between sediment plume presence, sediment trap accumulation, areal sediment cover, coral burial, and coral partial mortality. This indicates that, despite their independent nature, each of these metrics is a good predictor of the others across the spatial extent of monitoring (Fig. 9). Indeed, correlations between these metrics are not surprising, because they reflect a causal sequence of events linking dredging activity to coral mortality, in which dredge plumes spread from the site of origin, sediment is deposited on the benthos, and this sediment buries and kills corals. Nevertheless, explicitly quantifying these relationships is important because we show that 62% of the variability in sediment impacts to reef corals and habitat measured in situ can be explained by the occurrence of remotely-sensed sediment plumes. While this relationship will vary from project to project, it suggests that when calibrated against an appropriate set of in situ monitoring data (such as was done here), the footprint and magnitude of impact of dredging operations can be estimated based on satellite observations.

At the Port of Miami, we used the predictive power of these remotely-sensed sediment plumes to extrapolate potential impacts beyond the range of in situ data collection, greatly expanding our ability to assess impacts over spatial scales that are much larger than the original design of the monitoring program. Based on the occurrence of sediment plumes spanning ~25 km of the Florida Reef Tract to the north and south of the channel (Fig. 10), we can predict that dredging operations input hundreds of kilograms of fine sediment per m^2 and buried > 25% of the reef as far as 3 km away, doubled coral partial mortality from sediment 5–10 km away, and had potential impacts as far as 15 km from the dredged channel.

Dredging-related impacts were not only widespread, but also long-lasting, as indicated by sediment cover and depth measurements taken ~2 years after dredging. Although comparable sediment cover data prior to dredging exist for only three sites (making it difficult to quantify changes comprehensively), these data show that two years later, sediment cover was unchanged at one site 1.25 km away, but remained elevated ten- to a hundred-fold at two sites near the channel (Fig. S5). Sediment depth was also not measured prior to dredging, but the very low sediment cover measured on the inner reef (0–1%; Fig. S5) suggests that depths at these locations must have also been near zero. Two years after dredging, > 1 cm of sediment covered ~50% of the NIR and NOR near the channel, but only ~12–16% of the reef 500 m away (Fig. 10); this spatial pattern suggests that the deeper sediment near the channel resulted from dredging. These persistent sediment deposits are particularly detrimental as these areas are designated as critical habitat for threatened *Acropora* corals. Even a "thin veneer" of sediment may impair settlement in some corals (Ricardo et al., 2017), and standing sediment deeper than 1 cm is considered to render an area non-functional as recruitable coral habitat (National Marine Fisheries Service, 2016). In the *Acropora* Recovery Plan, habitat of suitable quality is defined as hard substrate free of sediment cover as required for larval recruitment, with recruitment failure identified as a key conservation challenge (National Marine Fisheries Service, 2015). Therefore, the impacts documented here represent a significant and long-lasting loss of living resources and critical habitat for these ESA-listed corals, as well as other reef species.

4.2. Recommendations for future dredging near coral reefs

These findings are particularly relevant in light of future dredging operations planned in the vicinity of coral reefs. Before the Port of Miami dredging project commenced, environmental assessments predicted "temporary", "localized", and "insignificant" sedimentation impacts to corals and coral habitat, stretching only as far as 150 m from the channel (Florida Department of Environmental Protection, 2012; National Marine Fisheries Service, 2011; U.S. Army Corps of Engineers, 2004). Impacts were not expected to exceed the permitted 7.07 acres of coral habitat impact (by direct removal of habitat for channel expansion; Florida Department of Environmental Protection, 2012). In contrast, we show sedimentation impacts were directly observed at least 2.5 km from the channel (Figs. 3–8), with predicted impacts (based on sediment plume occurrence) as far as 10–15 km away (Fig. 10). The impacts described here show that the project exceeded the pre-construction predictions in terms of: (1) geographic area, by one to two orders of magnitude; (2) severity, with hundreds of thousands to millions of corals either partially or totally killed, including those listed as threatened on the Endangered Species Act; and (3) permanence, lasting at least two years post-dredging. These impacts show that the measures put in place to ensure only temporary and insignificant impacts (Florida Department of Environmental Protection, 2012; National Marine Fisheries Service, 2011; U.S. Army Corps of Engineers, 2004) were insufficient to protect corals and coral habitat.

To avoid similar outcomes, future dredging projects should extend their predicted areas of impact and related monitoring and mitigation. For example, "intermediate" distance locations (1.25–2.5 km from the channel) were originally designed as "control" locations for near-channel sites (Florida Department of Environmental Protection, 2012), but were located within the area of dredging impact. A lack of sufficient pre-dredging monitoring data also hinders an even more comprehensive assessment of coral habitat impacts. While we did not directly analyze turbidity measurements, turbidity limits established at 29 NTUs above background (Florida Department of Environmental Protection, 2012) were only reported to have been exceeded on very few occasions, yet severe impacts to surrounding coral reefs still occurred. Based on these findings, we support Fourney and Figueiredo (2017) in recommending a reduction of US-EPA allowable turbidity from 29 NTU above background to < 7 NTU near coral reefs. We also echo other authors' recommendations of a moratorium on all sediment-releasing activities before, during, and after coral spawning periods, which also coincide with times of year when thermal stress is expected to occur (Bessell-Browne et al., 2017a; Miller et al., 2016; Moeller et al., 2016).

Coral reefs in Florida and elsewhere are under increasing threats from a range of global threats, particularly climate change, that are not easily within the scope of local management actions. Given these declines, additional attention must be paid to protecting the corals that remain and preventing avoidable impacts from human activities, such as dredging that, unlike climate change, can be managed at the local level.

5. Conclusions

This report describes a spatially explicit statistical approach to estimate impacts to coral health and reef resources as a result of dredging at the Port of Miami from 2013 to 2015. Multiple, independent datasets, ranging from remotely-sensed dredge plumes to benthic sediment cover to partial mortality of tagged corals, all show strong increases with proximity to the dredging site, and are also highly correlated with one another. Taken together, these approaches indicate that local dredging-related sedimentation, not regional disturbances such as disease or bleaching, was the cause of these observed impacts. The extensive data collected by DCA allowed us to establish, for the first time, direct, quantitative links between remotely-sensed sediment plumes and in situ benthic impacts, revealing potential effects of the Port of Miami dredging along a 25 km segment of the northern Florida Reef Tract (from 10 km south of the channel to 15 km north). These dredging activities resulted in a 10- to 100-fold increase in sediment cover on nearby reefs, and a likely loss of over a million corals from affected areas in the vicinity. The geographic scope, longevity, and severity of these impacts far exceeded pre-dredging predictions, indicating a pressing need to re-evaluate environmental thresholds, monitoring, mitigation, adaptive management, and enforcement to avoid similar harm to corals and coral habitat as a result of dredging activities in the future.

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Declaration of competing interest

Miami Waterkeeper was a co-plaintiff in an Endangered Species Act litigation regarding impacts to coral reefs resulting from the 2013–15 dredging activities at the Port of Miami. This litigation concluded in August 2018. At time of submission (December 2018) Miami Waterkeeper is a co-plaintiff in another environmental litigation regarding dredging at Port Everglades (Ft. Lauderdale, FL). Author R. Silverstein is currently the Executive Director and Waterkeeper of Miami Waterkeeper.

Appendix A. Supplementary information

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2019.05.027.

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Species Richness and Relative Abundance of Reef-Building Corals in the Indo-West Pacific

Lyndon DeVantier * and Emre Turak

Coral Reef Research, 10 Benalla Rd., Oak Valley, Townsville 4810, QLD, Australia; emreturak@wanadoo.fr
* Correspondence: Ldevantier@aol.com

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Abstract: Scleractinian corals, the main framework builders of coral reefs, are in serious global decline, although there remains significant uncertainty as to the consequences for individual species and particular regions. We assessed coral species richness and ranked relative abundance across 3075 depth-stratified survey sites, each < 0.5 ha in area, using a standardized rapid assessment method, in 31 Indo-West Pacific (IWP) coral ecoregions (ERs), from 1994 to 2016. The ecoregions cover a significant proportion of the ranges of most IWP reef coral species, including main centres of diversity, providing a baseline (albeit a shifted one) of species abundance over a large area of highly endangered reef systems, facilitating study of future change. In all, 672 species were recorded. The richest sites and ERs were all located in the Coral Triangle. Local (site) richness peaked at 224 species in Halmahera ER (IWP mean 71 species Standard Deviation 38 species). Nineteen species occurred in more than half of all sites, all but one occurring in more than 90% of ERs. Representing 13 genera, these widespread species exhibit a broad range of life histories, indicating that no particular strategy, or taxonomic affiliation, conferred particular ecological advantage. For most other species, occurrence and abundance varied markedly among different ERs, some having pronounced “centres of abundance”. Conversely, another 40 species, also with widely divergent life histories, were very rare, occurring in five or fewer sites, 14 species of which are ranked as “Vulnerable” or “Endangered” on the International Union for Conservation of Nature (IUCN) Red List. Others may also qualify in these Threatened categories under criteria of small geographic range and population fragmentation, the utility of which is briefly assessed.

Keywords: corals; species richness; relative abundance; Indo-West Pacific; IUCN Red List

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1. Introduction

Reef building corals, the zooxanthellate Scleractinia, collectively form a widespread and diverse taxonomic group across the tropical Indian, Pacific and Atlantic Oceans. More than 830 species are extant [1], at least 600 of which occur in the Indo-West Pacific (IWP) centre of diversity, the Coral Triangle (CT), with a second, less diverse centre present in the western Indian Ocean [2–4]. Diversity attenuates both latitudinally and longitudinally away from these centres. The Atlantic diversity centre in the Caribbean Sea has a unique fauna at species level, beyond the scope of this study.

Individual species range widely in their distributions, with a small number of endemics restricted to particular regions, often at the geographical extremities of reef development or coral growth. These regions include the Red Sea, Arabia and western Indian Ocean, Japan, southern Australia and eastern Pacific [3]. Other species are widespread across much of the Indo-Pacific. Within their distribution ranges, individual species vary widely in abundance in space and time, reflecting local, regional and meta-population dynamics. Since the 1980s, researchers have become increasingly concerned about the perceived declines in coral diversity and abundance [5,6], usually measured as reduction in coral cover.

Most such studies have focused on small geographic scales, usually a small part (10s–100s m^2) of a single reef [7–10], several larger scale, long-term monitoring programs (in e.g., Great Barrier Reef, Indonesia, Caribbean Sea) collectively forming part of the Global Coral Reef Monitoring Network [11] notwithstanding. Individually, such studies have provided useful insights about ecological processes and trends in coral and reef state at local and regional scale [12,13], and collectively have contributed to the emerging picture of the deteriorating state of coral reefs globally [14,15]. However, they are not ideal studies for evaluating conservation status of individual species, nor for identifying specific centres of diversity or abundance, necessary responses to increasing concern for the future viability of corals, as reefs continue to be polluted and overexploited, and oceans warm and acidify [16–18].

The initial International Union for Conservation of Nature (IUCN) Red List assessment [19] found that a lack of data on coral population sizes and trends required using loss of reef area as a proxy for population declines. This approach led to approximately one-third of the species assessed being listed in threatened categories, and inspired various assessments of extinction risk at regional or global scales [20–23]. The Red List assessment also highlighted the lack of accessible information on the richness and abundance of corals that exists at local to global geographic scales, despite our own and others' work over the past two decades in widespread IWP regions [2,3,10,23–36].

In this paper we provide robust estimates of the local and regional species richness and relative abundance of most species of reef-building coral in the IWP from 1994 to 2016. Using a standard sampling regime, we have compiled species lists and ranked relative abundance estimates from survey sites distributed at the Red Sea, Arabian Sea and Madagascar in the west to Micronesia and Fiji in the east (Figure 1, Table 1). Four large IWP regions received particular focus, with multiple surveys in Arabia, Eastern Australia, Micronesia and the Coral Triangle, the latter widely recognized as the centre of diversity both for corals [3,37], and for tropical marine biota more generally [38–40].

The more than two-decadal time span of this study encompassed a broad range of disturbances operating at local to regional to global scales. Most notable among these was the 1997–1998 El Niño event which caused mass coral bleaching and mortality across large areas of the IWP [17,41], with cascading effects on recovery and the subsequent composition of coral communities. Hence our results describe the richness and relative abundance of IWP reef-building corals during a period of significant change, although excluding the much more recent global bleaching event of 2016–2017.

In considering the implications of these impacts, we also examine how our abundance estimates relate to the results of the IUCN Red List assessment [19]. This was based on assessing population trends, specifically rates of population decline from loss of reef area through disturbance. Of particular interest, because of their potential vulnerability, are the rarer species, which we classify here as follows:

Diffusive—typically sparsely distributed across a broad geographic range;
Geo-suffusive—geographically limited (occurring in a relatively small geographic area, e.g., northern Red Sea);
Habitat-suffusive—habitat limited (confined to one or few habitats, e.g., reef flat, mesophotic zone).

It is important to note that these categories are not exclusive, and that some species may exhibit more than one form of rarity, illustrated later herein.

Table 1. Summary of broad locations surveyed in each ecoregion (ER) using the "Corals of the World" ER names, together with estimated ecoregional and site coral species richness.

ER Name, Number	Main Survey Locations (and Countries)	Survey Year(s)	No. of Sites	Species Richness: ER Total Number of Spp.; Site Mean (SD) and Range Across Sites
Red Sea north-central, ER 2	Mainland coast and islands from near Jeddah north to Jordan border (Saudi Arabia)	1997–1999	145	240; 60 (15) 22–98
Red Sea south, ER 3	Mainland coast and islands from near Saudi Arabian border south to Bab Al Mandeb (Yemen)	1994–1995	43	166; 34 (17) 3–67
Socotra Archipelago, ER 7	Socotra, Abd al Kuri, Samha and Darsa islands and islets (Yemen)	1997–1999	93	254; 44 (18) 8–94
Gulf of Aden, ER 140	Mainland coast and islands of Bir Ali and Balhaf area and Sikha Isl. (Yemen)	1998	13	98; 36 (8) 28–51
Lakshadweep, ER 20	Kadmat and Amini Islands, Arabian Sea (India)	2000	14	119; 36 (18) 0–66
Madagascar north, ER 15	Nosy Be area, from Nosy Iranja north to Nosy Hao (Madagascar)	2003	36	292; 90 (23) 33–125
Andaman Sea, ER 26	Phuket area, mainland coast and islands from near Palong and Koh Phi Phi north to Similan and Koh Surin (Thailand)	2005	54	290; 65 (18) 15–104
Vietnam south, ER 48	Nha Trang Bay, Nui Chua National Park, Con Dao islands (Vietnam)	2003–2005	97	381; 92 (21) 40–148
Sunda Shelf, ER 145	Patch reefs and coastal islands (Brunei Darussalam), Anambas island group (Indonesia)	2008–2009, 2012, 2014	103	467; 115 (29) 21–187
Hong Kong, ER 51	Hong Kong islands and mainland (China)	2001	240	78; 20 (12) 3–45
Philippines north, ER 45	Batangas Bay – Verde Passage, Luzon (Philippines)	2007	16	348; 127 (23) 80–156
Pohnpei and Kosrae, Micronesia, ER 65	Pohnpei island, Ant and Pakin Atolls (Federated States of Micronesia)	2005	71	320; 56 (15) 16–85
Yap Islands, Micronesia, ER 63	Ngulu and Ulithi Atolls, Yap (Federated States of Micronesia)	2007	54	204; 57 (12) 21–78
Palau, ER 61	North Reef, Velasco and Kayangel Atolls (Palau)	2009	51	333; 89 (22) 10–141
Sulu Sea, ER 43	Derawan, East Kalimantan, including Berau Delta area, from Panjang area south to Kakaban Isl., Melalungan and Muaras Atolls and Seliman Bay (Indonesia), El Nido area and north Palawan mainland and islands (Philippines)	2004, 2009	149	505; 123 (28) 43–183

Table 1. *Cont.*

ER Name, Number	Main Survey Locations (and Countries)	Survey Year(s)	No. of Sites	Species Richness: ER Total Number of Spp.; Site Mean (SD) and Range Across Sites
Lesser Sunda Islands and Savu Sea, ER 33	Bali and Nusa Penida, west Lombok, Komodo, West Timor and Roti (Indonesia), west and north coasts and Atauro Isl. (Timor Leste)	1995, 2006, 2008, 2011–2012, 2016	248	490; 75 (32) 2–164
Celebes Sea, ER 42	Bunaken islands and North Sulawesi coast, Bangka Isl., Lembeh Strait, and Sangihe-Talaud islands including Tahulandang, Siao, Sangihe, Karakelong and the Nanusa group (Indonesia)	2000, 2004–2005	160	475; 79 (29) 24–171
Banda Sea and Moluccas, ER 36	Banda islands including Banda Neira, Pulau Run, Ai and Hatta, and Wakatobi islands including Pulau Wangiwangi and Tomea, Koro Maha and Kaledupa Atolls (Indonesia)	2003–2004	86	416; 78 (15) 47–133
Halmahera, ER 41	Halmahera west, north and east coasts from Ternate to Buli Bay and Morotai (Indonesia)	1997, 2008	89	472; 102 (46) 30–224
Raja Ampat, Papua, ER 40	All main islands and offshore reefs, including Misool, Kofiau, Batanta, Gag, Wayag, Kawe and Waigeo Isl., Papua (Indonesia)	2002	94	478; 87 (26) 19–165
Papua south-west coast, ER 38	Fak Fak – Kaimana and Triton Bay coasts and islands, Papua (Indonesia)	2006	68	473; 117 (40) 28–205
Cenderawasih Bay, Papua, ER 39	Biak, Numfoor and Yapen islands and inner bay (Indonesia)	2006	66	475; 122 (32) 70–215
Bismarck Sea, New Guinea, ER 69	New Britain and New Ireland, including Kimbe and Stettin Bays, Manus Isl., Tigak area and New Hanover Isl. (Papua New Guinea)	2002, 2004, 2006	155	465; 95 (24) 41–150
Milne Bay, Papua New Guinea, ER 71	Mullins Harbour area, Goodenough and Collingwood Bays, d'Entrecasteaux and Amphlett Island groups, Fergusson and Normanby Isl. (Papua New Guinea)	2000, 2007	85	432; 89 (21) 43–150
Solomon Islands and Bougainville, ER 70	Main island groups including Florida, Isabel, Choiseul, Shortlands, New Georgia, Russell, Guadalcanal and Makira Isl. (Solomon Islands)	2005	114	442; 91 (20) 42–143
Great Barrier Reef far north and Torres Strait, ER 73	Princess Charlotte Bay, nearshore islands and reefs (Australia)	2001, 2011	32	329; 89 (23) 37–133
Great Barrier Reef north-central, ER 74	Lizard Island area south to Whitsunday Islands, including nearshore, mid- and outer continental shelf reefs (Australia)	1994–1997, 2001–2002, 2011	582	369; 46 (25) 0–129
Great Barrier Reef south-east, Pompey and Swain Reefs, ER 76	Pompey reefs (Australia)	2002	3	148; 92 (10) 83–102
Great Barrier Reef south, ER 77	Percy Islands south to Keppel Islands, including nearshore and mid continental shelf reefs (Australia)	1995, 2002	43	216; 40 (18) 6–84
Moreton Bay, east Australia, ER 78	Hervey Bay and Sunshine Coast (Australia)	2008-10	25	114; 36 (14) 16–59
Fiji, ER 101	Naitauba Isl., Taveuni Isl., Viti Levu Isl. (Fiji)	2010, 2012	46	344; 75 (28) 30–136

Figure 1. Map of the Indo-West Pacific showing the 31 coral ecoregions sampled. Ecoregion (ER) names are provided in Table 1. Map courtesy of "Corals of the World" [1].

2. Methods

A standard method of Rapid Ecological Assessment (REA, [26]) was employed from 1994 to 2016 at 3,075 individual reef sites, their specific coordinates being recorded using portable GPS. Sites were assigned to an ecoregional classification [3] (Figure 1, Table 1). The 31 ERs collectively represent approximately 45% of Indo-Pacific reef area, based on GIS mapping (Tom Bridge, personal communication, Townsville, Australia) and include the major population centres of most IWP corals [2,3]. Some restricted range endemics, such as those of the Hawaiian Islands, East Pacific, Japan and South-West Australia, were not surveyed.

While sampling frequency and intensity were not standardized within or among ERs, the survey method was constant and a series of methodological issues were considered and addressed (see Table 2). Sampling was opportunistic, in most instances based on the requirements of specific surveys for a variety of research and conservation projects conducted for government and non-government organizations. On some surveys we worked together, on others only one surveyor was present. With these constraints, individual survey sites in each ER were selected, as far as practicable, to provide the broadest range of reef habitat types exposed to different environmental conditions. Surveys covered all main reef types, including fringing, patch, platform and barrier reefs, atolls, and non-reefal coral communities.

Our goal at each site was to compile during a roving diver survey a taxonomic inventory of coral species, including a visual estimate of the relative abundance of each taxon, in an area of no greater than 5000 m^2 (typically approximately 50 m across-slope × 100 m along-slope). This area is much larger than the 200–300 m^2 usually recommended as sufficient for sampling local species richness [32]. We also made visual estimates of the size frequency distributions and levels of injury of the species present, and of overall coral cover, none of which is presented herein.

The majority of surveys were conducted on self-contained underwater breathing apparatus (SCUBA), other than where logistics did not permit (e.g., some sites on Roti in Lesser Sunda ER), when the compressor failed and snorkel was used. Survey swims were typically initiated towards the base of the reef slope (typically < 50 m maximum depth where reef topography and/or regulations allowed). Sites also included reef lagoons and back reef margins where accessible. The mesophotic zone below 40 m depth was not adequately sampled, because of restricted dive time, and neither was the inner reef flat intertidal zone in water shallower than 0.5 m depth.

Wherever the reef slope had sufficient depth and breadth, two adjacent sites were sampled, on the deeper and shallower slopes respectively. The division between neighbouring deep and shallow sites was based on the more-or-less abrupt depth-related shift in coral community structure. This typically occurs at around 8–10 m depth below reef crest, but the actual depth varied among sites in relation to local topographic and physico-chemical conditions, notably attenuation in illumination and wave energy. Adjacent deep and shallow sites did not overlap.

During each survey swim, the primary observer recorded an inventory of the reef-building corals present on water-proof datasheets, to species level wherever possible [2,25,42–55] (among other taxonomic references), but otherwise to genus and growth form (e.g., *Porites* sp. of massive growth-form, but see later in Methods). When present, the secondary observer acted as dive buddy, taking photographs and, where permitted, collecting specimens as necessary. Whenever practicable, these roles were interchanged to minimize fatigue, in accordance with safe diving practice. Time of survey at each site was not fixed, but rather was dependent on local species richness. Hence depauperate sites were surveyed more rapidly than speciose ones.

At the end of each survey swim, the compiled species inventory was reviewed, and each taxon was ranked in terms of its relative abundance in the local coral community, where rank 1 represented locally rare corals, rank 2 locally uncommon corals, rank 3 locally common corals, rank 4 locally abundant corals, and rank 5 locally dominant corals. The dominant rank also included, though only rarely, very large mono-specific coral stands that may have been formed by clones, in which it can prove difficult to determine numbers and extent of individual colonies.

These ordinal ranked categories approximate a log 4 scale and provide an estimate of the numbers of coral colonies (or individuals for solitary taxa) in each taxon, rather than its contribution to benthic cover. These ranks are similar to those long employed in vegetation analysis [56–58].

2.1. Coral Identification

It was not possible, visually, to identify all corals to species level in the field. Many species, particularly in the speciose genus *Acropora*, share close morphological similarities with others, and taxonomic disagreements regarding species boundaries continue to exist among specialists, an issue confounded by episodic hybridization [33]. We have listed species for which we have taxonomic or other identification concerns in Table S1.

Extensive use of underwater photography, initially using Nikonos cameras and subsequently digital equipment, aided confirmation of field identifications of taxonomically difficult species. Where additional information was necessary for identification, and with permission of relevant management authorities, small samples, usually < 20 cm on longest axis, were removed from living coral colonies in situ, leaving the majority of most sampled colonies in place. Living tissue was later removed from the specimens by bleaching with household bleach. The dried specimens were labelled, examined and identified, as far as possible to species level. Many of these specimens were identified during and immediately after the field surveys, and remain in museums or universities in their countries of origin. Other specimens provided significant taxonomic challenges, and were shipped, with appropriate Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) documentation, to the Australian Institute of Marine Science and/or Museum of Tropical Queensland, Australia, for detailed study. This has, to date, resulted in the publication of some 20 previously undescribed species [2,59,60].

Some broadly distributed species, and others that encompass a range of morphologies, can form species complexes of sibling and/or cryptic species. Some such species have recently been subdivided based on genetic and morphological analyses [53,55,61–63]. We have incorporated, where practicable, the recent revisions, as accepted in the Corals of the World website [1], ascribing new names to prior records based on our photographic records and/or samples.

Table 2. Methodological considerations and constraints, modified from Veron et al. [3].

Issue	Our Approach
Field survey method: estimating local and regional richness	All methods have their advantages and limitations. Ours is based on a long-established approach to rapid ecological assessment, pioneered by terrestrial botanists and adapted to coral reefs [24]. It does not deliver quantitative estimates of species' abundance, but does provide robust "semi-quantitative" estimates. It is more effective than traditional quantitative methods in estimating local and regional species richness, facilitating the active searching for species at each site, rather than being restricted to a defined quadrat area or transect line. At site level, the present method has regularly returned a two- to three-fold increase in coral species records in comparison with line transects conducted concurrently (e.g., Red Sea, Great Barrier Reef and Vietnam, L.M. DeVantier unpublished; Socotra Islands [27]).
Taxonomic framework	Despite recent advances stabilizing coral taxonomy (e.g., taxonomic works cited above), substantial taxonomic uncertainty remains, as demonstrated by various recently published classifications and synonymies [2,53,55,61,62,64–66]. This has arisen, in part, because of differences between traditional morphology-based approaches and those employing molecular genetics. These nomenclatural issues are relevant mainly at taxonomic levels higher than species, although "name games" continue, and the placement of certain species within particular genera remains contentious. We have, as far as practicable, included species accepted in the major taxonomic revisions that preceded or were published over the period of this study (i.e., up to 2016), some minor specific nomenclatural differences notwithstanding. With some modification, our framework follows that of Veron et al. [3], as included in the open access website [1].
Species identification and inter-observer variability	Our dataset has been compiled by experienced surveyors, mainly Emre Turak and Lyndon DeVantier, working together or independently, with assistance in particular ERs from Terry Done, Mary Wakeford and Denise McCorry. Use of standard reference works, museum collections, extensive underwater photography and limited collection of specimens has minimized variability as far as practicable. Juvenile corals < 5 cm diameter, particularly in the speciose genera *Acropora*, *Montipora* and *Porites*, pose particular problems, and unless identity was certain, these were not recorded in our dataset. Having adopted a cautious approach to the issue of inter-observer variability, we have not tried to incorporate similar datasets from other researchers in the present study, although we have referred to them for comparison (Table S4).
Discrepancies between published ER species lists and abundance data	The abundance data were compiled during our site surveys, and as far as practicable subsequently updated from photography and specimens. Published records for certain species in particular ERs were also based on non-site observations, and hence may not be supported by our site abundance data.
Estimating rarity	Because of the taxonomic and survey difficulties noted above (see Table S1), we consider that our abundance estimates for a few species are unreliable. That is, their true abundance may be higher than documented here because of field identification issues and occurrence in cryptic locations or habitats poorly surveyed.
Sampling effort among ecoregions	With the notable exceptions of North Philippines (16 sites), Lakshadweep (14 sites), Gulf of Aden (13 sites) and the Pompey and Swain Reefs (3 sites) of Australia's Great Barrier Reef (GBR), sample sizes within ecoregions, although not standardized, were generally sufficient to approach asymptotic species richness (Figure 2). Our dataset is strongly focused on two of the main "centres of diversity" of reef corals, the CT and Arabia, and two nearby regions, notably eastern Australia and the central-western Pacific. Our dataset does not include two regions of major species' attenuation, be they latitudinal (e.g., Ryukyu Islands—Japan, Western Australia) or longitudinal (e.g., Central – Far Eastern Pacific). These host regional endemics not surveyed in the present study.
Ecoregion boundaries	Boundaries were based on the best information available, both published and unpublished [3], but have different levels of support. Our dataset can, however, be interrogated at much smaller geographic scales, an undertaking largely beyond the scope of the present analysis. This is a major objective for future development of the "Corals of the World" website [1].
Distribution ranges	Despite major recent advances in coral biogeography, range boundaries remain "fuzzy", disjunctions are poorly understood, and ranges are better documented for some species than others. Recently described species typically have highly restricted distributions initially, often only the type locality. Ranges may, or may not, be extended with further work.

Table 2. *Cont.*

Issue	Our Approach
Sampling effort across habitats	Our surveys were focused on reef slopes, crests and outer-mid reef flats, and typically limited to water depths of less than 50 m or to the base of the reef slope if shallower. We were unable to survey inner reef flats in water depths < 0.5 m.
True and false absences	We do not assume that a species missing from our inventories in a particular ER is actually absent there, even though our surveys covered a range of habitats.
Estimating individual species abundance ranks for massive *Porites*	Except where specimens were collected, we were unable to identify the large colony-forming massive *Porites* to species-level in the field. The approach taken here (Table 3) provides derived estimates at species level, the best that can be achieved from our dataset.

2.2. *Assessing Abundance of Massive* Porites

This important reef-building group is comprised of at least six species attaining very large colony sizes and ages in the Indo-Pacific [45,67]. These include *Porites lobata*, *P. lutea*, *P. australiensis*, *P. solida*, *P. mayeri* and *P. myrmidonensis*. Unless specifically identified from specimens, these species are particularly difficult to identify in a reliable manner to species level in the field, and hence were usually recorded as "massive *Porites*" in our dataset. Other massive species in the IWP (e.g., *P. murrayensis*, *P. densa*) do not attain large size, typically being < 20 cm colony width, and have distinct morphological characters facilitating field identification [2,25,45,52].

For the six large, colony-forming massive *Porites* species, we have estimated the species-specific abundance rank scores for all sites where specimen-based data were lacking. These were derived from the grouped massive *Porites* abundance score in each site in each ER in which each species is known to occur [3] (Table 3). The species-specific scores in Table 3 are based on published assessments of the relative abundance of each species, our specimen records, and on expert opinion [2,25,52] (Charlie (J.E.N.) Veron personal communication). For example, *P. lutea* and *P. lobata* are the most widespread and abundant of the group, often forming large mono-specific stands on reef flats and upper reef slopes, sometimes dominated by clones [67]. In the ERs where they occur, *Porites lobata* and *P. lutea* were considered the two most common species, followed by *P. australiensis*, *P. myrmidonensis*, *P. solida* and *P. mayeri*. The individual species scores are all within the range of the log 4 scale of the original grouped massive *Porites* abundance estimates.

Table 3. Rules for estimating specific abundances for 6 species of massive *Porites* in the ERs in which each species occurs [2,3]. The actual site abundance scores for Massive *Porites* (top row of table) were converted to the species-specific scores listed below.

Taxon	Site Abundance Score				
Massive *Porites*	1	2	3	4	5
Porites lobata	1	2	2	3	4
Porites lutea	1	2	2	3	4
Porites australiensis	0	1	2	2	3
Porites myrmidonensis	0	0	2	3	3
Porites solida	0	1	1	1	2
Porites mayeri	0	0	1	1	1

2.3. *Analysis*

To illustrate relations between sampling intensity and species richness, species rarefaction curves were plotted for selected ERs, using randomized reordering of sites [68].

Occurrence (O) of each species in each ER and across all 31 ERs was calculated as the percentage of sites in which that species was present. Mean abundance (MAbn) of each species in each ER and across all ERs was calculated as the sum of individual site abundance scores (1–5) divided by the number of sites in which that species was present. Overall abundance (OA) of each species was calculated as the product of their O and MAbn scores. Hypothetically if a species occurred in every site it would score 100 for O, and if it was locally dominant (abundance score of 5) in every one of those sites, it would have a MAbn of 5, and a maximum OA score of 500 in an ER or across the 31 ERs. In reality, no species achieves this level of ubiquity.

This simple OA metric provides a standard way of assessing species abundance across the IWP. As a measure of the overall distribution of relative abundance, each species was assigned to one of the following categories based on its IWP-wide OA score: Very Rare: OA < 0.1; Rare: OA of 0.1– < 1.0; Uncommon: OA of 1.0– < 10.0; Common: OA of 10.0– < 50.0; Very Common: OA of 50– < 100; Near ubiquitous: OA of 100–500.

Relations between species' occurrence and abundance were illustrated and trends assessed with linear regression. Differences in species richness and abundance between deep sites (typically from > 10– < 50 m depth) and shallow sites (typically < 1–10 m depth), and the depth preferences of individual species were also assessed. Tests of the significance of depth-related differences in richness and abundance were conducted using the paired sample non-parametric Wilcoxon signed-rank test in the XLSTAT statistical package. In this overview we have not assessed relations among alpha, beta and gamma diversity, a topic for future work.

Finally, we compared our abundance estimates with the findings of recent global and regional vulnerability assessments.

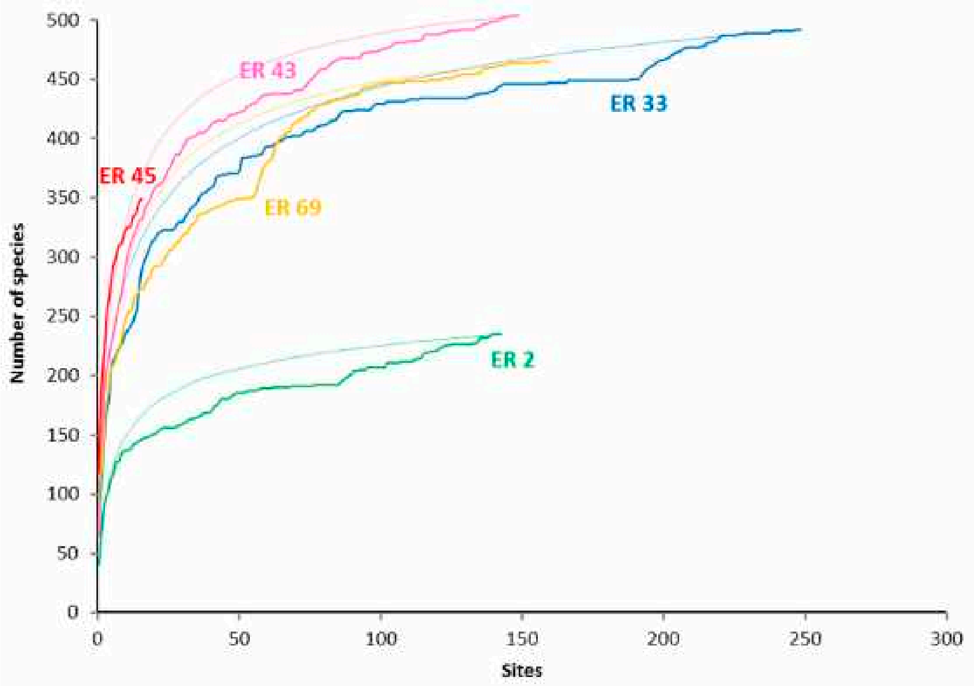

Figure 2. Species accumulation and rarefaction curves for selected Ecoregions. The accumulation curves reflect the order in which data were collected and added to the database, while the rarefaction curves (the thin lines) are based on repeated, randomized reordering of sites [68]. ER 2—Red Sea North-central; ER 33—Lesser Sunda Islands and Savu Sea; ER 43—Sulu Sea; ER 45 Philippines north; ER 69—Bismarck Sea (see Table 1 for details).

3. Results

3.1. Species Distributions

There was a broad range in the scale of species' distributions across the IWP. A large number of species were geographically restricted, with 157 species occurring in five or fewer of the 31 ERs, of which 47 species were found in only one ER. Conversely, 142 species were very widespread across the IWP, occurring in 25 or more ERs (Figure 3, Table S2). Of the 47 species restricted to only one ER, many are considered endemic to particular regions, notably the Red Sea (e.g., *Erythrastrea flabellata*, various *Echinopora* and *Montipora* spp.), Arabian Sea (*Fungia puishani, Parasimplastrea omanensis, Sclerophyllia maxima*), or ERs within the CT (Lesser Sunda Islands and Savu Sea for *Acropora suharsonoi* and *Euphyllia baliensis*, Cenderawasih Bay for three *Astreopora* spp.). These varied patterns of endemicity are consistent with speciation both at the periphery (e.g., Red Sea) and centre (e.g., CT) of diversity.

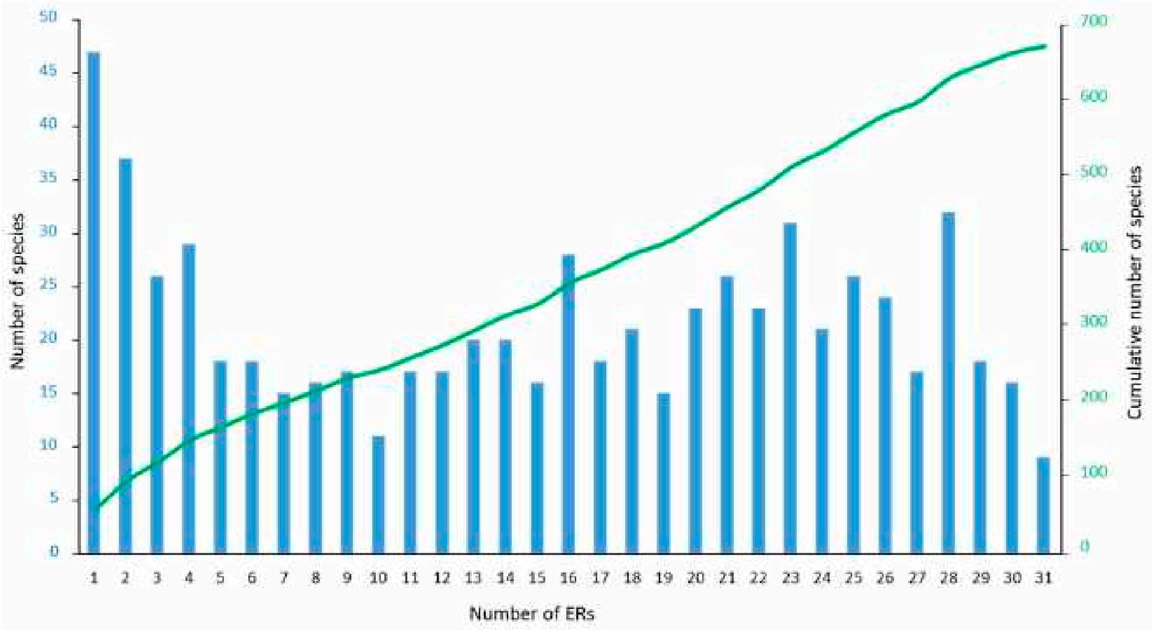

Figure 3. The number of species that were recorded in each of an increasing number of Ecoregions (e.g., 47 species were found in only one ER, while 9 species were found in all 31 ERs), and cumulative species tally across ERs.

3.2. Species Richness

Across all 3075 sites, a total of 672 confirmed species of reef-building coral were recorded. The highest ER richness, 505 species from Sulu Sea, was compiled from two comprehensive surveys, of the Derawan area off the east coast of Indonesian East Kalimantan, and of the north-west and north-east coasts of Palawan Island in the Philippines (Table 1), both areas with high habitat diversity [1]. All the richest ERs, with more than 450 reef-building coral species present (Table 1), were in the CT, and also included Raja Ampat, Lesser Sunda Islands and Savu Sea, Celebes Sea, Cenderawasih Bay, Halmahera, Papua south-west coast, Bismarck Sea and Sunda Shelf.

Our score for ER richness for the North Philippines of 348 species is a significant underestimate (compare with [3,37]), affected by lack of sampling (Table 1, Figure 2).The opportunistic survey (16 sites) was undertaken during the IUCN reef coral Red List meeting at Batangas Bay, west Luzon and so focused on easily accessible local reefs (Table 1).

Both site and ER richness attenuated away from the CT (Table 1 and Figure 4), increasing again in Madagascar, Socotra and Northern Red Sea. The major latitudinal and longitudinal declines, north to Japan, south along Western Australia and east to Far Eastern Pacific, were not captured in our dataset.

3.3. Marginal ERs

Several ERs are comprised of marginal reef habitat, including the Gulf of Aden (Yemen), Moreton Bay (Eastern Australia) and Hong Kong (China). Despite their low species richness, these ERs play important roles in sustaining populations, respectively, of Arabian Sea endemics (Gulf of Aden) and otherwise rare taxa (e.g., *Platygyra acuta* and *P. carnosus* in Hong Kong, and *Acropora bushyensis* in Moreton Bay). These were also the most faunistically unusual ERs. For example, at Moreton Bay, the five most abundant corals were *Goniastrea australiensis*, *Plesiastrea versipora* and three species of *Turbinaria*. These species did not attain such high levels of abundance elsewhere in our study, but are common components of the coral fauna of other high latitude locations and turbid environments. Our ER richness tally of 114 species (Table 1) is a major increase on previous estimates [69], likely resulting from both successful recent recruitment into these subtropical waters from southern GBR, and our search methodology (Table 2).

Figure 4. Map showing species richness of Ecoregions. ER code numbers are inside or adjacent to circles (see Table 1 for details). Sizes of the inner and outer circles of each ER are scaled to indicate respectively the ER site mean and site maximum richness. For example, Halmahera ER (41) had the highest site richness (224 species). Overall ER richness is indicated by colour coding, as indicated in the Figure legend. Map courtesy of "Corals of the World" [1].

Local (site) richness peaked at 224 species at one shallow site in Halmahera ER. At that particular location, the richness tally for the adjacent deep and shallow sites combined topped 280 species ha^{-1}, representing more than one-third of all IWP reef-building corals on a small patch of one reef. The 10 richest sites, all with more than 190 species, were located in the CT, within Halmahera, Cenderawasih Bay and Papua south-west coast ERs. These three ERs, along with North Philippines, Sulu Sea and Sunda Shelf, had highest mean site richness scores of > 100 species, compared with an overall mean site richness of 71 spp. (SD 38 spp.). Approximately one-third of all sites had < 50 species present, two-thirds of sites had < 100 species and most of the remainder had < 150 species, with less than 3% of sites hosting > 150 species (Figure 5).

3.4. Effects of Depth on Richness and Abundance

For 1,808 sites that comprised adjacent deep–shallow pairs, there was little difference in site richness between shallow and deep sites (Figure 6A) with the mean for shallow sites being 89 spp. (SD = 35) and for deep sites being 88 spp. (SD = 31) (Wilcoxon P = 0.254). Mean site abundance (calculated as the sum of species' local abundance scores in each site) was, however, significantly higher in the shallower sites (Figure 6B) with mean abundance score for shallow sites being 144, (SD = 61) and for deep sites being 130 (SD = 52) (Wilcoxon $p < 0.0001$, Table S3).

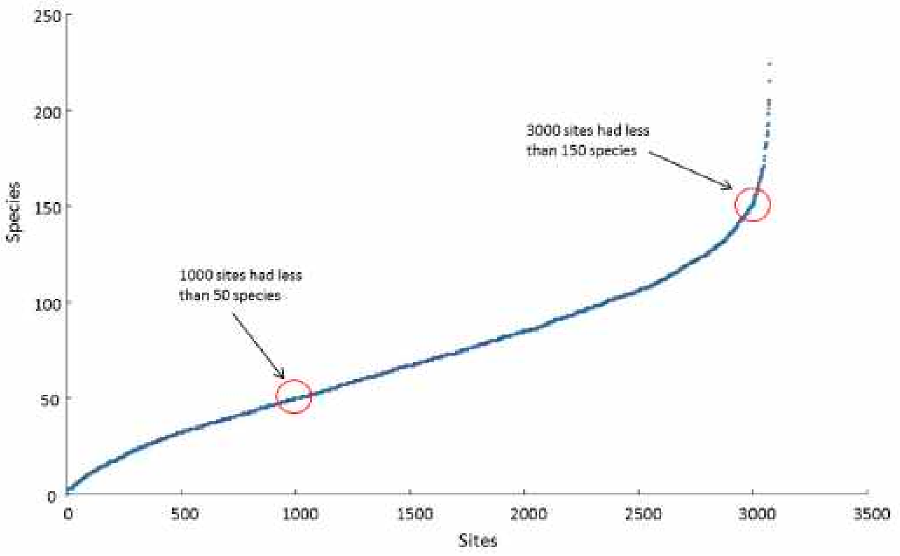

Figure 5. Spread of species richness across 3075 sites in the Indo-West Pacific (IWP), 1994–2016.

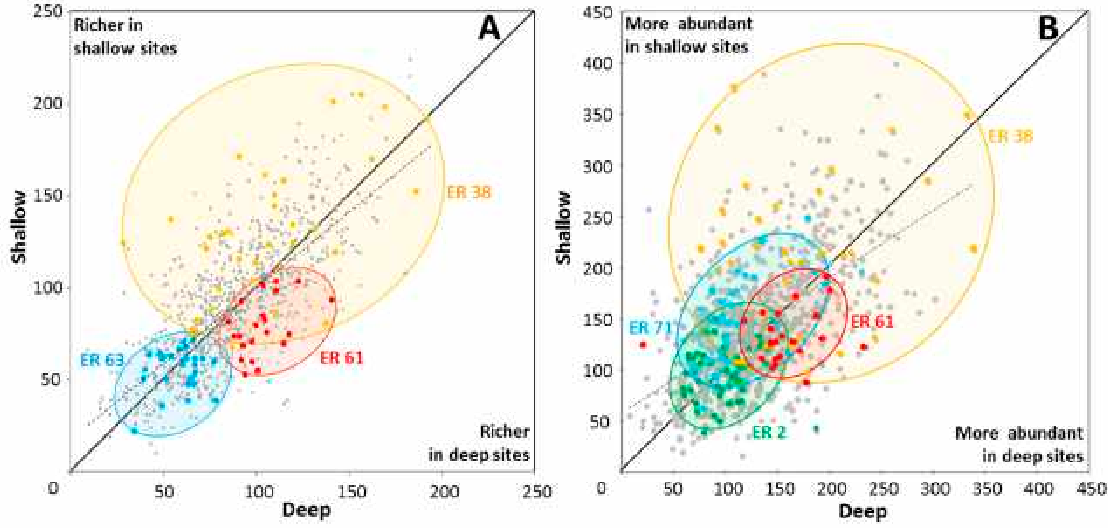

Figure 6. Scatterplots of (**A**) species richness (dotted trend line, $R^2 = 0.54$) and (**B**) abundance (sum of species' abundance scores for each site; dotted trend line $R^2 = 0.31$) in 904 pairs of shallow and deep sites. Site scores for selected Ecoregions are highlighted to illustrate intra- and inter-ER differences, where ER 2—Red Sea north-central; ER 38—Papua south-west coast; ER 61—Palau; ER 63—Yap Islands, Micronesia; ER 71—Milne Bay, Papua New Guinea (see Table 1 for ER details).

The strength of these depth-related differences in site abundance varied among different ERs (Figure 6B). For example, higher coral abundance was documented in shallow sites of Milne Bay and Papua south-west coast ERs, and higher abundance in deeper sites of Palau ER. Red Sea north-central ER showed little difference in site abundance with depth.

The vast majority of species in the paired sites, 622 species (representing 93% of total species pool), were found in both shallow and deep sites (Figure 7, Table S2), consistent with relatively broad tolerances to local ambient environmental conditions, notably illumination, wave energy and sediments. For 90 of these species there was little (<25%) difference in OA scores between deep and shallow sites. Most species of *Acanthastrea*, for example, exhibited this tolerance pattern. For most other species, however, there were substantial differences in OA scores, with 397 and 185 species preferring deeper or shallow sites respectively (>25% difference in OA scores). Overall, differences in species OA scores between shallow and deep sites were highly significant (Wilcoxon $p < 0.0001$, Table S3).

As would be expected, the speciose genera *Acropora*, *Montipora* and *Porites* were well represented in both depth ranges. Examples of *Acropora* species with strong preferences for shallow habitat included *Acropora aspera*, *A. digitifera* and *A. elseyi*. In deeper sites, *Acropora granulosa*, *A. plumosa* and *A. speciosa* were much more abundant. Notably, all recorded species of *Blastomussa*, *Caulastrea*, *Coscinaraea*, *Ctenactis*, *Diaseris*, *Echinophyllia*, *Euphyllia*, *Fungia*, *Galaxea*, *Merulina*, *Mycedium*, *Oulophyllia*, *Oxypora*, *Pachyseris*, *Pectinia*, *Plerogyra*, *Podabacia* and *Polyphyllia*, were more abundant in deeper habitats, as were most species of *Alveopora*, *Anacropora*, *Astreopora* and *Echinopora* (Table S2). Fifty species showed stronger niche differentiation, with 25 species being recorded only from shallow sites, and another 25 species only from deeper sites (Table 4), with implications for future population viability.

Of these 50 species, several have significant taxonomic issues or have major distributions outside our surveyed ERs (Table S1). In respect to their abundances, almost all were rare or very rare, with OA scores of <1. On the IUCN Red List, seven of these species have not yet been assessed and 16 species are Data Deficient. Of the remaining 27 species, three are considered of Least Concern, four are Near Threatened, 12 are Vulnerable and eight are Endangered (Table 4), their threatened status consistent with their apparent rarity and niche specialization.

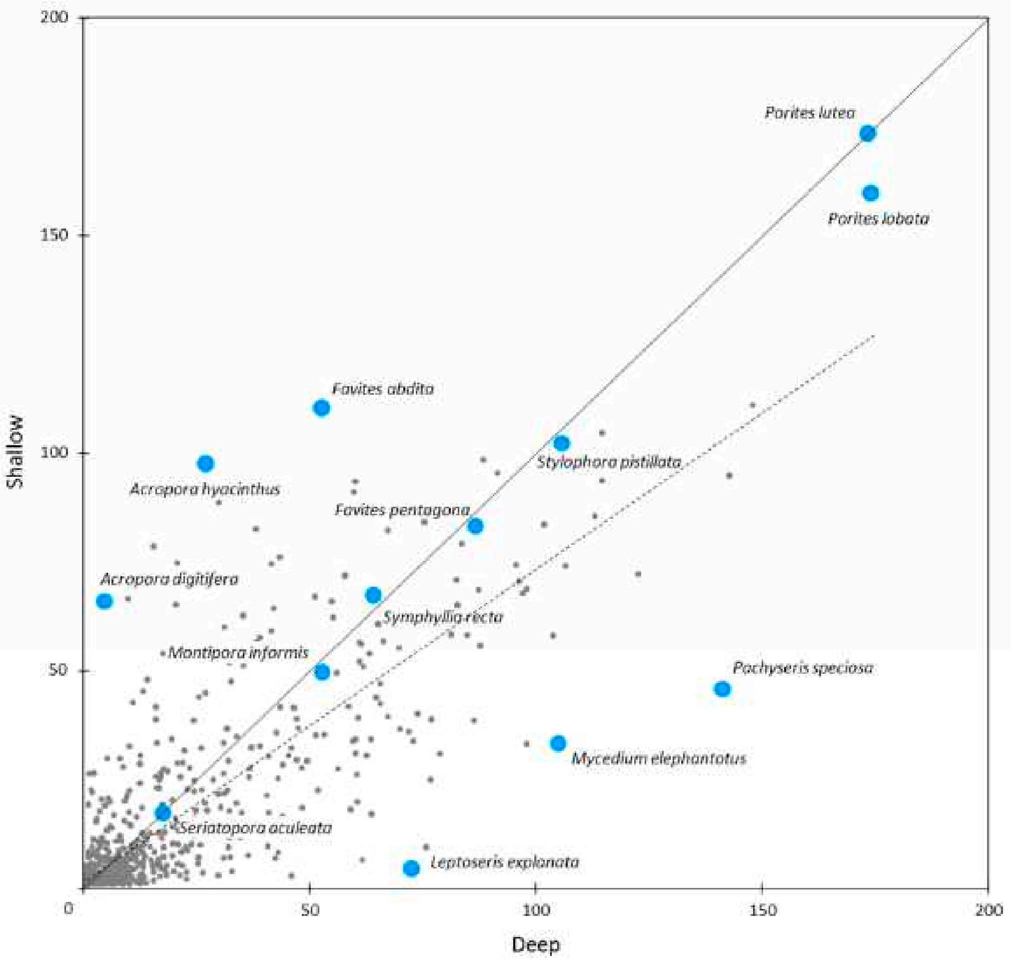

Figure 7. Scatterplot of species' Overall Abundance scores in all deep and shallow sites. Dotted trend line, $R^2 = 0.68$. Selected species with preferences for deep or shallow sites, or no apparent preference, are listed.

Table 4. Coral species recorded only from deep or shallow sites. * indicates taxonomic uncertainty and/or identification issue (see Table S1). Overall Abundance (OA) scores and International Union for Conservation of Nature (IUCN) Red List rankings are also listed, where NA—Not Assessed; DD—Data Deficient; LC—Least Concern; NT—Near Threatened; Vu—Vulnerable; En—Endangered. [1] Assessed in Red List as *Cynarina lacrymalis*. [2] Assessed in Red List as *Acropora rambleri*. [3] Assessed in Red List as *Lithophyllon ranjithi*. [4] Assessed in Red List as *Parasimplastrea sheppardi*. [5] Main distribution range outside surveyed ERs. Codes in parentheses are the IUCN Red List criteria [70].

Deep Sites	OA Score	IUCN Red List	Shallow Sites	OA Score	IUCN Red List
Acanthophyllia deshayesiana *,[1]	0.1	NT	*Acropora bushyensis*	0.23	LC
Acropora fragilis [2]	0.07	DD	*Acropora pruinosa*	1.27	DD
Acropora natalensis *	0.13	DD	*Acropora forskali* *	0.26	DD
Acropora pichoni	0.75	NT	*Acropora rufus* *	0.1	DD
Acropora rongelapensis	0.26	DD	*Acropora schmitti*	0.03	DD
Acropora roseni	0.03	En (A4ce)	*Acropora sirikitiae*	0.13	NA
Acropora rudis	0.16	En (A4ce)	*Acropora spathulata*	2.83	LC
Acropora russelli	0.52	Vu (A4c)	*Acropora torresiana*	0.62	DD
Acropora simplex	1.4	Vu (A4ce)	*Acropora tumida*	2.5	DD
Acropora stoddarti	0.07	DD	*Astreopora cenderawasih*	0.13	NA
Acropora tenella	0.72	Vu (A4ce)	*Echinopora irregularis*	0.03	DD
Craterastrea levis	0.16	NA	*Leptoseris kalayaanensis*	0.03	NA
Echinophyllia tarae *	0.03	NA	*Micromussa diminuta*	0.03	DD
Echinopora robusta	0.03	Vu (A4c)	*Montipora aspergillus*	0.03	DD
Echinopora tiranensis	0.03	DD	*Montipora echinata*	0.07	DD
Euphyllia baliensis	0.07	NA	*Montipora gaimardi*	0.52	Vu (A4c)
Horastrea indica [5]	0.13	Vu (A4c)	*Montipora pachytuberculata*	0.07	DD
Isopora togianensis	0.13	En (A4ce)	*Montipora saudii*	0.16	NT
Leptoseris amitoriensis	0.13	NT	*Pocillopora capitata* *,[5]	0.23	LC
Lithophyllon lobata [3]	0.46	En (A4c; B2ab (ii,iii))	*Pocillopora fungiformis*	0.39	En (A4c)
Montipora orientalis	0.03	Vu (A4c)	*Polycyathus chaishanensis* *	0.13	NA
Nemenzophyllia turbida	0.42	Vu (A4cd)	*Porites cocosensis*	0.16	Vu (A4cde)
Parasimplastrea omanensis [4]	0.39	En (A4c)	*Porites cumulatus*	1.6	Vu (A4cde)
Plerogyra discus	0.1	Vu (A4c)	*Porites eridani*	0.7	En (A4cde)
Stylocoeniella cocosensis	0.1	Vu (A4c)	*Porites ornata* *	0.7	En (A4cde)

3.5. Relative Abundance

At site level, more than 600 species were locally uncommon or rare overall (mean abundance scores of 2 or less), with only a few more locally common taxa (mean score > 2, Figure 8A). This result is also reflected in the shape of the OA species curve, with 67 species, only 10% of the total species pool, scoring OA > 50 (Figure 8B). Based on our classification of OA scores (Figure 9), approximately 62% of the total species pool were classified in the following categories: uncommon (40%), rare (19%) or very rare (3%); and 38% of species were classified in the following: common (29% of species), very common (8%) or near-ubiquitous (1%).

For individual species, IWP-wide OA scores ranged from <0.1 (six species) to 182.7 for *Porites* massive (compared to a possible maximum OA score of 500). Within the *Porites* massive species group, the two most common species were *Porites lutea* and *P. lobata* (Figure 10). These were the most abundant in our study, as reflected in their OA scores overall and for individual ERs (Table 5 and Table S2).

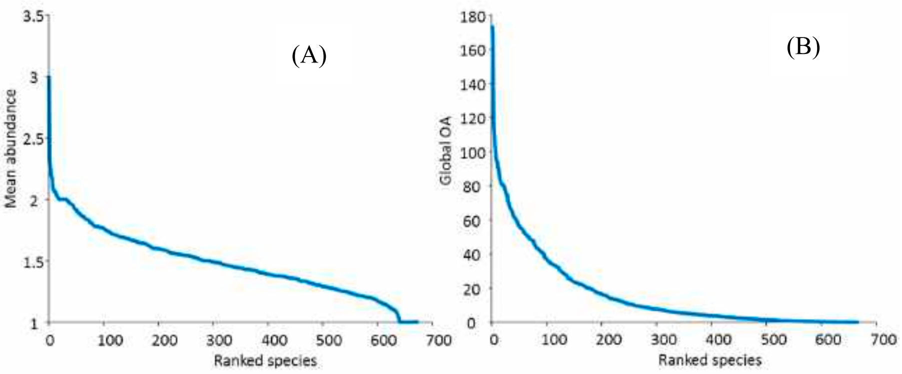

Figure 8. Abundances for 672 coral species. (**A**) Mean local abundance scores (on an approximately log 4 scale, see Methods). (**B**) Overall abundance scores across all sites (Global OA with possible maximum 500, see Analysis).

Other near-ubiquitous reef coral species included *Galaxea fascicularis*, *Goniastrea pectinata*, *Platygyra daedalea*, *Stylophora pistillata* and *Cyphastrea serailia*, all with IWP-wide OA scores > 100. These were followed closely by *Favia favus*, *Pocillopora verrucosa*, and *P. damicornis* (including cryptic species, Table S1, [63]), *Fungia fungites* and *Pavona varians*, all with IWP-wide OA scores > 90 (Table 5).

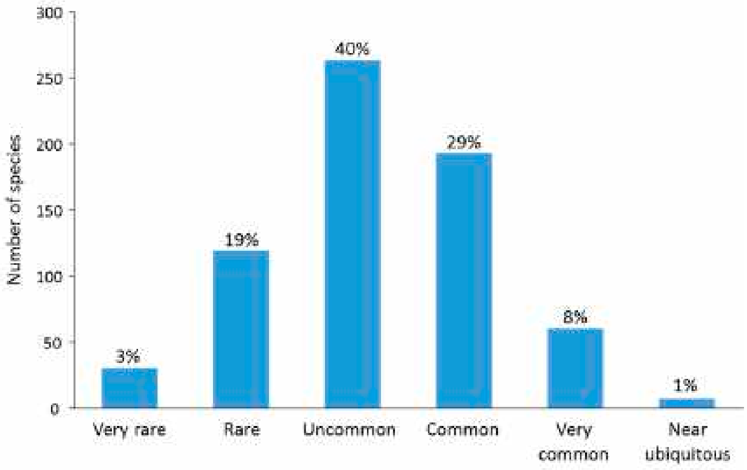

Figure 9. Number and percentage of species in each of six IWP Overall Abundance categories. Very rare—OA < 0.1; Rare—OA 0.1– < 1.0; Uncommon—OA 1.0– < 10.0; Common—OA 10.0– < 50.0; Very common—OA 50.0– < 100.0; Near ubiquitous—OA 100.0–500.0.

There was general concordance between our high OA scores for these species and their IUCN Red List categories (Table 5), with all 30 species being either of Least Concern (21 spp.) or Near Threatened (9 spp.), and with none in the more threatened categories.

Within individual genera, OA scores ranged widely (Table S2), one example being *Pectinia* (Table 6). Three species were common (OA scores of 20 to 46), four species were uncommon (scores between 1 and 8), and two species were rare (scores of 0.8). For *Pectinia* spp. there was much less concordance between OA scores and their Red List categories. For example, the two most common and widespread species, *Pectinia lactuca* and *P. alcicornis*, were listed as Vulnerable, and the third common species, *P. paeonia*, as Near Threatened. Three of the four uncommon species were listed as Near Threatened, the fourth, *P. maxima*, as Endangered. Of the two rare species, one, *P. africanus*, was listed as Vulnerable and the other, *P. pygmaeus* as Near Threatened.

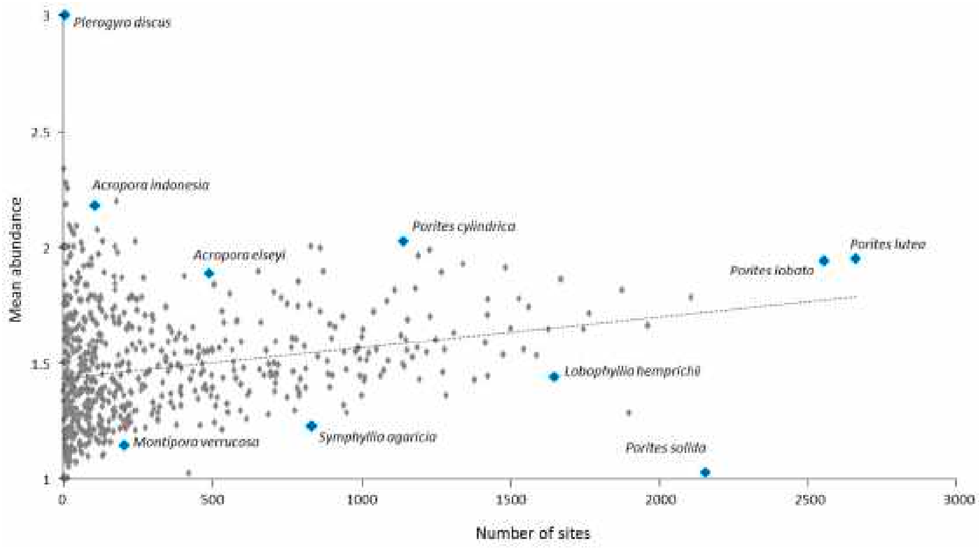

Figure 10. Scatter plot for 672 species of Mean Abundance vs. Occurrence (No. of sites), showing the weak relation (R^2 = 0.05) between increasing occurrence and abundance (i.e., more widespread species were only slightly more abundant). Selected species illustrate various abundance-occurrence relationships, e.g., *Plerogyra discus* and *Acropora indonesia* had relatively low levels of occurrence yet relatively high abundance in the sites in which they occurred.

Table 5. Overall Abundance score (from a maximum value of 500) for the 30 highest scoring reef-building corals over 3075 sites across the IWP ERs from 1994–2016. Means and SD were calculated for only those ERs in which each species was recorded. IUCN Red List assessments are also shown, where LC = Least Concern, and NT = Near threatened. * Assessed in Red List as *Acropora formosa*.

Coral Species	Overall Abundance Score	Mean OA Score Across ERs (SD)	Percent of 31 ERs	IUCN Red List
Porites lutea	173.7	178.0 (44.3)	100	LC
Porites lobata	165.1	179.2 (40.9)	97	LC
Galaxea fascicularis	125.0	141.1 (51.4)	94	NT
Goniastrea pectinata	113.3	134.3 (58.6)	97	LC
Platygyra daedalea	108.6	129.5 (49.5)	97	LC
Stylophora pistillata	103.5	123.0 (54.2)	94	NT
Cyphastrea serailia	100.8	106.5 (52.9)	100	LC
Favia favus	95.8	105.4 (42.3)	100	LC
Pocillopora verrucosa	94.7	111.0 (48.1)	90	LC
Pocillopora damicornis	94.3	111.0 (44.5)	97	LC
Fungia fungites	90.6	101.9 (38.7)	90	NT
Pavona varians	90.6	119.6 (57.3)	90	LC
Favites abdita	89.1	92.7 (49.0)	94	NT
Seriatopora hystrix	86.2	97.7 (59.1)	84	LC
Favites pentagona	84.2	92.9 (51.2)	100	LC
Favia matthaii	82.4	94.7 (51.8)	97	NT
Isopora palifera	81.5	95.4 (38.8)	87	NT
Porites australiensis	81.0	103.8 (30.9)	84	LC
Favia pallida	81.0	85.8 (44.9)	100	LC
Pachyseris speciosa	80.9	99.9 (47.2)	84	LC
Astreopora myriophthalma	80.2	99.2 (42.9)	94	LC
Acropora muricata *	79.9	87.8 (38.0)	94	NT
Lobophyllia hemprichii	79.9	96.2 (34.9)	94	LC
Porites rus	78.0	101.8 (54.2)	84	LC
Porites cylindrica	77.2	95.4 (36.2)	74	NT
Hydnophora exesa	75.5	85.6 (43.6)	100	NT
Merulina ampliata	75.0	103.0 (40.3)	81	LC
Porites solida	75.0	90.7 (34.3)	97	LC
Acropora hyacinthus	71.7	76.0 (53.9)	94	NT
Echinopora lamellosa	71.1	80.6 (37.4)	90	LC

Table 6. Abundance scores and IUCN Red List assessments for species of *Pectinia*. Codes in parentheses are the IUCN Red List criteria [70].

Species of *Pectinia*	Occurrence (% of sites)	Mean Abundance	Overall Abundance	IWP OA Category	IUCN Red List
Pectinia africanus	0.7	1.3	0.9	Rare	Vu (A4c)
Pectinia alcicornis	16.6	1.6	25.9	Common	Vu (A4c)
Pectinia ayleni	3.1	1.4	4.4	Uncommon	NT
Pectinia elongata	1.0	1.6	1.6	Uncommon	NT
Pectinia lactuca	31.7	1.5	46.5	Common	Vu (A4cd)
Pectinia maxima	3.9	1.5	5.7	Uncommon	En (A4cd)
Pectinia paeonia	15.7	1.5	23.0	Common	NT
Pectinia pygmaeus	0.5	1.8	0.8	Rare	NT
Pectinia teres	4.2	1.8	7.5	Uncommon	NT

3.6. Rare Taxa

At the opposite end of the OA spectrum, 91 species were recorded in 10 or fewer of the 3075 sites. Of these, some have taxonomic or other identification issues and their abundance estimates are not considered reliable (Table S1). The 40 rarest taxa, occurring in five sites or less (Table 7), represented a broad mix of geo-suffusive, habitat-suffusive and diffusive species. Geo-suffusive taxa, namely restricted range endemics, included recently described species, such as *Euphyllia baliensis*. This species may also be habitat-suffusive, favouring the upper mesophotic zone [60]. Other very rare, habitat-suffusive, mesophotic specialists included *Craterastrea levis*. This species could also be considered as diffusive, with a widespread distribution range across the Indian Ocean, although its true abundance has likely been underestimated, because its preferred habitat of > 35 m depth has not been well sampled. This species was also initially considered as geo-suffusive, a Red Sea endemic, prior to its discovery outside the Red Sea, in other parts of the western Indian Ocean [49,71,72] and in the CT (this study). Other apparently diffusive species included *Duncanopsammia axifuga*, *Echinopora ashmorensis* and *Micromussa diminuta* (Table 7).

These rarest taxa presently have a broad range of IUCN Red List assessments, with approximately half in Threatened categories: five species are Endangered; nine are Vulnerable; six are Near Threatened; four are Least Concern; 11 are Data Deficient; and five have not yet been assessed [70]. In respect of modeled vulnerability to climate change [22], all but three of the 35 assessed species scored highly under at least two of three broad criteria (Table 7). All species had high sensitivity, based on specific habitat preferences, life histories and symbiont associations. Twenty-one species also scored highly for "unadaptability", reflecting limited dispersal and adaptive capacity. Seventeen species had high exposure to climate impacts of bleaching and acidification, affecting range sizes through increasing habitat marginalization. Seven species, each of different genera, scored highly on all three criteria, and with their apparent rarity, must be considered at significant risk. Two are presently listed as Endangered, three as Vulnerable, one as Near Threatened and one as Data Deficient (Table 7).

Table 7. Species recorded from 5 sites or less, which may qualify under IUCN threatened category criteria (e.g., EN B1a, VU B1a, VU D2) in terms of extent of occurrence and population size (i.e., population very restricted in the number of locations, typically five or fewer, such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future). The IUCN Red List classification [19] is also provided, where: En—Endangered, Vu—Vulnerable, NT—Near Threatened, LC—Least Concern, DD—Data Deficient, NA—Not Assessed. Codes in parentheses are the IUCN Red List criteria [70]. Ratings for vulnerability to climate change [22], assessed under criteria of Sensitivity (Se), Unadaptability (Ua) and Exposure (Ex), are also provided, where H = high, L = low and U = unknown. * Species with main distribution ranges outside the present study. Species for which abundance estimates were considered unreliable (Table S1) were excluded.

Species	**O (% of sites)**	**Mean Abn.**	**OA**	**Form of Rarity**	**IUCN Red List Classification**	**Climate Change Vulnerability**		
						Se	**Ua**	**Ex**
Acropora bushyensis	0.1	2.3	0.23	Diffusive	LC	H	L	H
Acropora fragilis	0.07	1	0.07	Diffusive	DD (as A. rambleri)	H	L	L
Acropora roseni	0.03	1	0.03	Geo-suffusive	En (A4ce)	H	H	H
Acropora rudis	0.13	1.25	0.16	Geo-suffusive	En (A4ce)	H	H	L
Acropora sirikitiae	0.07	2	0.13	Geo-suffusive	NA	NA		
Acropora teres	0.03	1.5	0.1	Diffusive	DD	H	L	L
Alveopora viridis	0.13	1	0.13	Diffusive	NT	H	H	H
Anacropora pillai	0.13	1.5	0.2	Diffusive	DD	H	L	H
Astreopora cenderawasih	0.07	2	0.13	Geo-suffusive	NA	NA		
Astreopora scabra	0.13	1.25	0.16	Diffusive	LC	H	H	L
Craterastrea levis	0.16	1	0.16	Habitat-suffusive	NA	NA		
Duncanopsammia axifuga	0.16	1.2	0.2	Diffusive	NT	H	L	H
Echinopora ashmorensis	0.16	1.4	0.23	Diffusive	Vu (A4c)	H	L	H
Echinopora irregularis	0.03	1	0.03	Geo-suffusive	DD	H	H	U
Echinopora robusta	0.03	1	0.03	Geo-suffusive	Vu (A4c)	H	L	L
Echinopora tiranensis	0.03	1	0.03	Geo-suffusive	DD	H	H	U
Euphyllia baliensis	0.03	2	0.07	Geo- and habitat-suffusive	NA	NA		
Fungia puishani	0.16	1.6	0.26	Geo-suffusive	DD	H	H	L
Goniopora cellulosa *	0.07	1	0.07	Geo-suffusive	Vu (A4c)	H	H	H
Goniopora polyformis	0.13	1.5	0.2	Diffusive	Vu (A4c)	H	L	H
Goniopora sultani	0.13	1	0.13	Geo-suffusive	LC	H	H	U
Horastrea indica *	0.1	1.33	0.13	Geo-suffusive	Vu (A4c)	H	H	L
Isopora togianensis	0.07	2	0.13	Geo-suffusive	En (A4ce)	H	L	H
Leptoseris amitoriensis	0.13	1	0.13	Diffusive	NT	H	L	H
Leptoseris kalayaanensis	0.03	1	0.03	Geo-suffusive	NA	NA		
Micromussa diminuta	0.03	1	0.03	Diffusive	DD	H	H	H
Montipora aspergillus	0.03	1	0.03	Geo-suffusive	DD	H	H	U
Montipora echinata	0.07	1	0.07	Geo-suffusive	DD	H	H	U
Montipora orientalis	0.03	1	0.03	Diffusive	Vu (A4c)	H	H	H
Montipora pachytuberculata	0.07	1	0.07	Geo-suffusive	DD	H	H	U
Montipora saudii	0.13	1.25	0.16	Geo-suffusive	NT	H	H	U
Montipora verrilli *	0.07	1	0.07	Diffusive	DD	H	H	L
Plerogyra discus	0.03	3	0.1	Habitat-suffusive	Vu (A4c)	H	L	H
Pocillopora capitata *	0.13	1.75	0.23	Range extension to Fiji from Eastern Pacific	LC	H	L	L
Porites cocosensis	0.13	1.25	0.16	Diffusive	Vu (A4cde)	H	H	H
Porites eridani	0.07	1	0.07	Diffusive	En (A4cde)	H	L	H
Porites somaliensis *	0.07	1	0.07	Geo-suffusive	NT	H	H	L
Sclerophyllia maxima *	0.13	1.5	0.2	Geo-suffusive	NT (as *Acanthastrea maxima*)	H	H	U
Stylocoeniella cocosensis	0.1	1	0.1	Diffusive	Vu (A4c)	H	L	H
Stylophora madagascarensis	0.16	1.4	0.23	Geo-suffusive	En (A4c)	H	H	H

3.7. Centres of Abundance

The relative abundance of different coral species varied widely among different ERs (Table S2). This is illustrated by comparing different island groups within Micronesia and Polynesia (Table S4, incorporating data from [23] and Douglas Fenner and Peter Houk, unpublished). *Porites lutea* and *P. lobata* scored highly at most locations. *P. rus* ranked 24th on the IWP OA score, but was within the top 10 species at four Pacific locations, and was the most abundant coral at Pohnpei and Kosrae. *Galaxea fascicularis* ranked third on the IWP OA score, and its more localized rankings were 6th in Fiji, 12th in American Samoa, 18th in Palau, 29th on Pohnpei, 72nd on Kosrae, 161st on Marshall Islands, and not recorded at Yap. *Isopora palifera* ranked 17th on the IWP OA score, ranked first in Marshall Islands, and was also relatively common in Yap (ranking 21st). However it was lowly ranked at the other Micronesian islands of Kosrae, Pohnpei and Palau (57th, 58th and 77th respectively), and only 107th in American Samoa and 125th in Fiji. Among these same western Pacific locations, by contrast, *Goniastrea pectinata* and *Favia matthaii* showed relatively little variation in their ranking, although mostly scoring below their IWP-wide OA ranks.

Many reef-building coral species, even those with widespread IWP distribution ranges, had particular centres of abundance at time of survey, illustrated here with three widespread, distinctive species (Figure 11A–C).

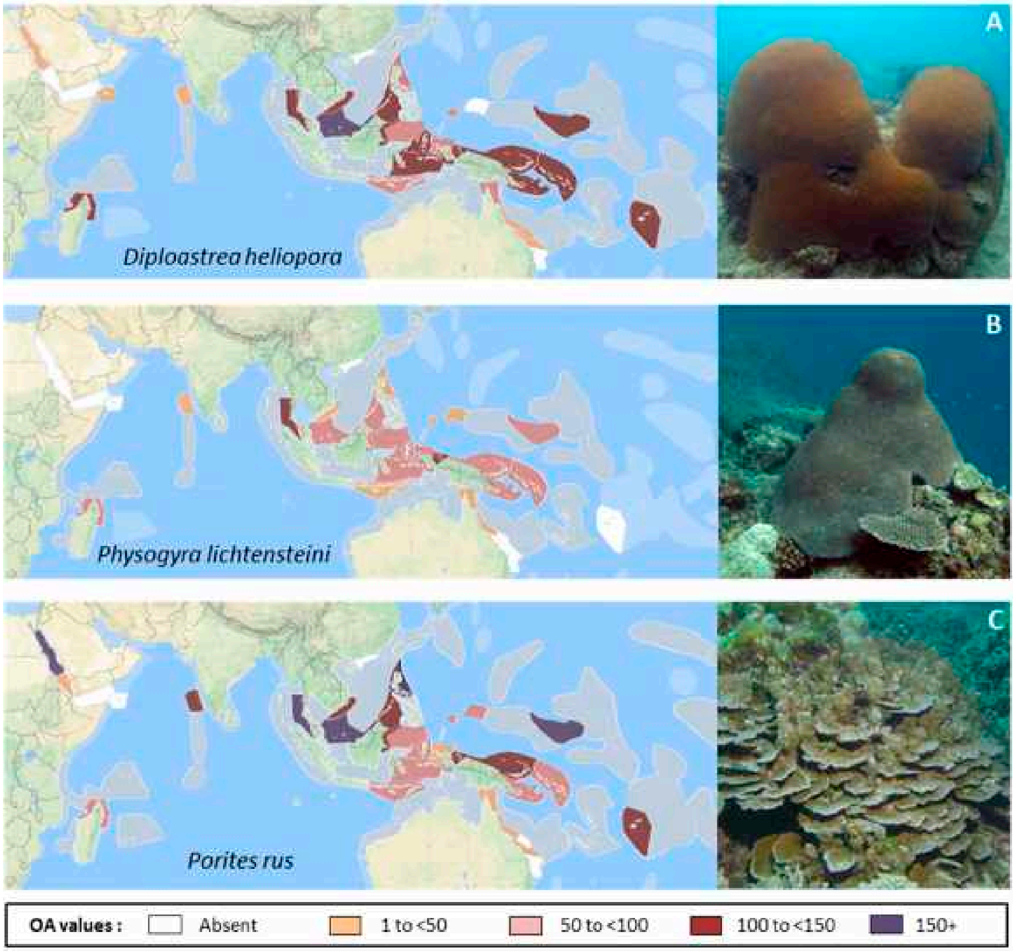

Figure 11. (**A**–**C**) Abundance maps of selected coral species, illustrated at right of maps. The darker the shading the higher the mean OA score in each ER. White shading indicates that the species was not recorded from that ER during our surveys, although it may occur there (see text for details). Grey shading indicates the known distribution range of the species [3], from "Coral of the World" [1]. Photos by Emre Turak.

Diploastrea heliopora (IWP OA 68.5) was recorded from 25 ERs, occurring in 48% of all sites, with centres of abundance in Madagascar and from the Andaman Sea to Fiji. It was uncommon to very rare in the Red Sea and NW Indian Ocean. The relative ubiquity of this species, occurring in nearly half of all sites, countered its typically low local abundance scores, being rare, or uncommon, in most sites in which it occurred. We did not find it in Red Sea south, Gulf of Aden or Yap Islands ERs, although it is confirmed or expected to occur there [1].

Physogyra lichtensteini (IWP OA 41.3) was recorded from 22 ERs, in 31% of all sites. It was not recorded from marginal ERs of the NW Indian Ocean, Hong Kong and Moreton Bay. It had highest levels of abundance in the Andaman Sea, and was common across the CT, in Pohnpei and in Madagascar. We did not find it in Red Sea north-central, Great Barrier Reef south or Fiji ERs, although it is confirmed to occur there [1].

Porites rus (IWP OA 78.0) was recorded in 26 of the 31 ERs and 40% of all sites. It ranged from 0 to 282.9 in OA scores, ranking as the most abundant species in several ERs, and with widespread centres of abundance from the Red Sea to the Sunda Shelf to Fiji. It was less common throughout much of the CT, with ER OA scores of < 100. We did not find it in Gulf of Aden or Great Barrier Reef south-east ERs, although it is confirmed to occur there [1].

4. Discussion

4.1. Species Richness

Our tally of 672 species across 31 ERs, although substantial, is some 50 species less than the total species pool for these ERs listed in the most recent global compilation of species distributions [1]. The latter study includes all confirmed records from numerous authors [3]. At the level of individual ERs, our tallies are also lower, to be expected given the wealth of additional studies [3].

For comparison, a large coral biogeographic study ranging from the CT to the western-central Pacific that employed sets of replicate 10 m line transects recorded a total of only 333 reef-building coral species [30,32,73]. The last study considered that transects are sufficient to adequately characterize regional richness, yet their IWP tally of 333 species is much lower than the number of species that occur within a single island group in many ERs of the CT. For example, Bunaken National Park (Celebes Sea ER, Table 1) was sampled using transects in the above study [30,32,73] and by the present method [29]. Our study recorded 390 species there, 57 species more than the total IWP-wide species pool of the transect study. This again illustrates the major differences in richness estimates that can arise from different sampling methods (Table 2).

The richest ERs and individual sites were all found in the CT, consistent with other studies [3,40]. This biogeographic province hosted more than 75% of species recorded here, and a significant number of species that remain undescribed (Emre Turak, Lyndon DeVantier unpublished). Within the CT, the richest ER, Sulu Sea, is highly habitat-diverse. It was also well sampled (Table 1). Despite its highest score, we do not consider this ER to be the centre of reef coral diversity; rather it is one of several ERs with high local and regional richness. Similarly, the richest individual site was found in Halmahera ER, but we do not consider that this is the "bulls-eye" of local richness. Processes governing population dynamics, including complex interactions among episodic and/or chronic disturbances and individual coral tolerances, reproduction, dispersal and recruitment, together ensure that such sites are ephemeral in space and time. What can be concluded, however, is that over the two decadal period of this study the CT hosted both sites and ERs of exceptional species richness, and showed attenuation away from the centre. The reasons for this have been long debated, and will not be addressed here (but see e.g., [30,37,38,40,74]).

4.2. Relative Abundance

Our study also documents major differences in the relative abundance of different coral taxa across the IWP. Most species ranged widely in abundance among different ERs (Table S2). This manifests as differential contributions to the assembly of coral communities and reef-building at local and regional scales across each species' range (Table S4). Although such differences have been well known, at least at local scales, the reasons why certain corals are much more abundant or rare than others, locally, regionally or globally, remain perplexing. It would appear to be contingent on specific sets of life history traits that confer advantage to a population in particular ecological circumstances [22].

These traits may provide tolerance to a broad range of ambient environmental conditions, including fluctuations in temperature, turbidity, salinity and alkalinity, as exemplified by *Porites* spp., massive forms of which were the most abundant taxa, occurring commonly in all ERs. Other traits may confer regular reproductive success (e.g., brooding and planulae release) and rapid recruitment (growth to reproductive maturity). Such traits [22] are exemplified by some pocilloporids (*Stylophora pistillata, Pocillopora damicornis, P. verrucosa*, Table 5), and other near-ubiquitous species, ensuring continued local—meta-population viability. These traits, when linked with successful dispersal and recruitment, would appear crucial.

Yet even among these two taxonomic groups, only certain species attained near ubiquity, while other highly abundant species represented numerous other scleractinian genera (Table 5). These exhibit a very broad range of life histories, with different morphologies, growth rates, reproductive modes, symbiont associations and other traits [22,25,51,75–77]. These species also display a broad range across the autotrophy-heterotrophy spectrum [78], indicating that no strategy or taxonomic affiliation confer universal advantage.

Conversely a large number of species were rare to very rare (Table 7, Figure 9 and Table S2). These also represented a broad range of genera and life histories. Many have relatively restricted global distributions [1,3], some in regions poorly sampled in this study, while others prefer habitats not well sampled (Table 2), notably the mesophotic zone [79].

4.3. Different Forms of Rarity

Highly diverse ecosystems, including coral reefs, have many species that are locally and regionally rare, well-illustrated by our ER species accumulation curves, which continued to increase, albeit slowly, over the duration of our surveys (Figure 2). Such rarity can be categorized as diffusive, geo- or habitat-suffusive (Table 7). Major recent revision of distribution range mapping [1,3] has enabled improved understanding of geo-suffusive species. The habitat-suffusive nature of some species is also relatively well understood. Examples of apparently geo-suffusive taxa include *Acropora suharsonoi* and *Euphyllia baliensis*. Both are morphologically distinctive (Figure 12A, B) with highly restricted distribution ranges, presently known only from Lesser Sunda ER. We recorded *A. suharsonoi* from six sites in all, always locally rare. The more recently described *E. baliensis* is known only from the type locality, in the upper mesophotic zone of a clear-water reef. Habitat-suffusive species include those that prefer shallow or deeper reef slopes (Table 4), some of which were never found in high local abundance (but see later).

Diffusive and habitat-suffusive rarity were exemplified in our study by *Craterastrea levis*, a mesophotic species (Figure 12C) originally described from the Red Sea (reviewed by [72]). We did not find it in the western Indian Ocean, but did record it in Halmahera and Papua south-west coast ERs in the CT, a major range extension. Another apparently diffusive species, at least in the surveyed reef habitats, is *Duncanopsammia axifuga* (Figure 12D). This species is also widespread across the IWP, occurring rarely on sandy edges of reef slopes. It may be more abundant in sandy inter-reefal habitats, not surveyed during the present study.

The number and identity of truly diffusive species remains to be determined, a task hindered by the significant limitations of underwater survey. All dedicated surveys, since the advent of SCUBA, would cover much less than one-thousandth of one percent of available reef habitat. It may well be that species presently considered as diffusive have locations of high local abundance yet to be discovered. Two examples are the widespread *Caulastrea tumida* and *Echinomorpha nishihirai*. *C. tumida* was recorded from 10 ERs, with a mean OA score of 4.21 (Table S2). In eight ERs it was uncommon or rare (OA between 0.63 and 9.28), and in one ER it was common (Sunda Shelf, OA 22.33). *E. nishihirai* was recorded from nine ERs, with a mean OA score of 5.12 (Table S2). In eight ERs it was uncommon or rare (OA between 0.65 and 7.22), and in one ER it was common (Fiji, OA 28.26).

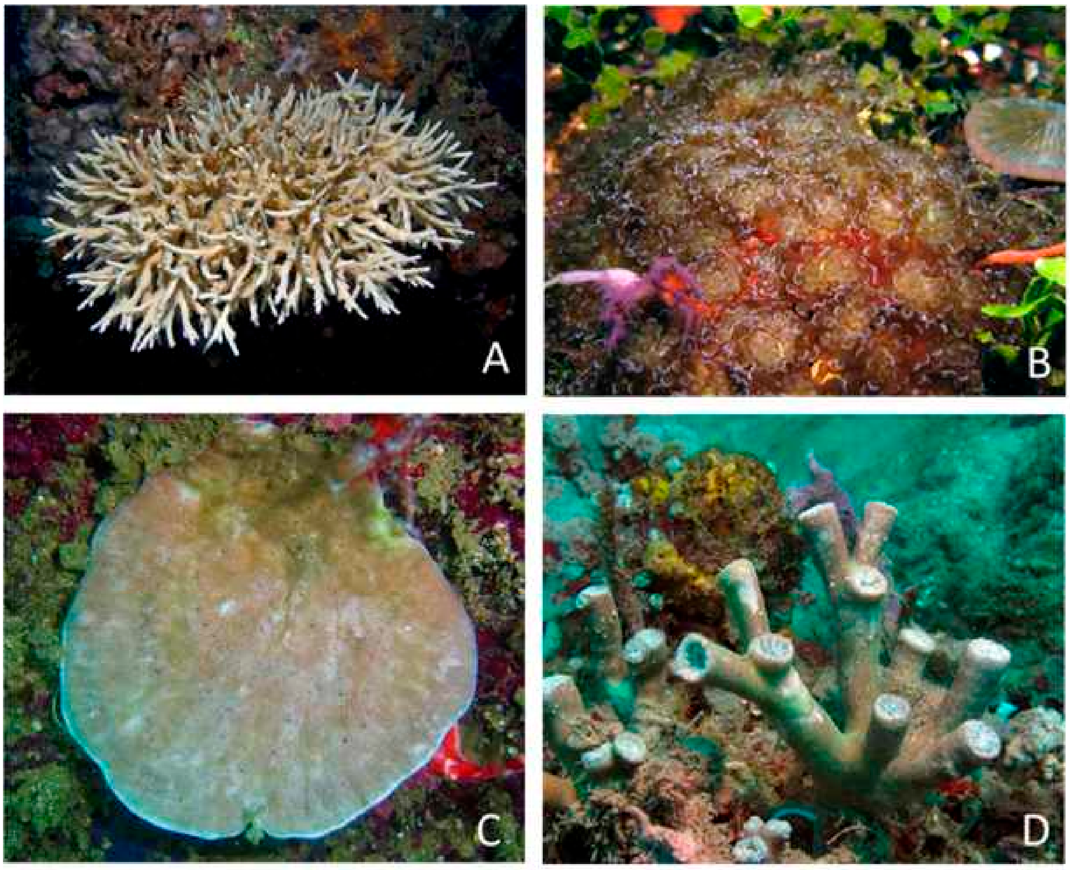

Figure 12. (**A**) Coral species displaying different forms of rarity. *Acropora suharsonoi*, Bali (geo-suffusive); (**B**) *Euphyllia baliensis*, Bali (geo- and habitat-suffusive); (**C**) *Craterastrea levis*, Halmahera (diffusive and habitat-suffusive); (**D**) *Duncanopsammia axifuga*, Timor Leste (diffusive and habitat suffusive). Photos by Emre Turak.

Other apparently rare species were described long ago but were not recorded during our surveys. For example, *Simplastrea vesicularis* and *Boninastrea boninensis* were not found, despite considerable search effort within their known distribution ranges [2]. These species are either exceedingly rare, highly cryptic or occur in habitats not well sampled (inner reef flats, reef slopes > 40 m depth). Both species were described from ERs (Java Sea and Bonin Islands respectively) not sampled during the present study, and may be geo-suffusive, although both have been found elsewhere, albeit rarely [1]. Hence, although we are confident that our method records most reef-building coral species present at site and ecoregion levels (Figure 2), some species were not found in ERs where they were found in prior studies, including initial taxonomic descriptions.

This is a function of sampling effort, which was not equal across ERs (Table 1), detectability and rarity. For sampling effort, even our most comprehensive surveys covered only a tiny fraction of available reef habitat (<< 0.001%). Detectability is influenced by inter-specific differences in morphological "plasticity", with some species showing little variation across their ranges (e.g., *Diploastrea heliopora*) while others are remarkably "protean" or cryptic, closely resembling sibling taxa in phenotypic expression (e.g., many species of *Acropora*). With colleagues, we have recently categorized species based on their ease and reliability of identification, and some species recorded here are considered difficult, and hence their abundance estimates are not considered reliable (Table S1).

4.4. Centres of Abundance

Many, if not all, coral species have centres of abundance within their meta-populations - particular locations hosting significant sub-populations, likely crucial for maintenance and replenishment. Conversely, other ERs within a species' range hosted only sparse sub-populations (Figure 11 and Table S2), in some cases only a single record. In the latter locations, such species may not achieve effective population sizes, their presence being dependent on the vagaries of long-distance dispersal.

We have identified such contemporary centres of abundance and rarity for numerous IWP species during a period of significant ecological change. Of the three examples illustrated in Figure 11, *Porites rus* and *Diploastrea heliopora* had similar overall patterns of distribution, yet *D. heliopora* was uncommon to rare in the Red Sea and NW Indian Ocean, whereas *P. rus* was abundant in the northern Red Sea, one of several major centres of abundance for this species. *Physogyra lichtensteini* has both a more restricted IWP distribution range and lower OA scores across most of its range, with contemporary centres of abundance in the Andaman Sea and Cenderawasih Bay.

Such centres have shifted, and presumably will continue to shift, through ecological and geological time, in an analogous, although not necessarily similar, way to centres of diversity [80]. For example, studies combining contemporary surveys of coral communities with shallow reef coring have demonstrated significant changes in community structure on decadal to millennial time scales [81], the result of differential survivorship and recovery following disturbance.

4.5. Refugia

It is not likely, however, that there will be significant shifts into more temperate regions in response to global warming, given the latitude-limiting effects of light, among other factors [82–85]. This is not to discount the present increase in richness at latitudinal edges of reef development and in non-accretional coral communities, including Moreton Bay ER, where our tally of 114 species is a major increase on previous surveys [69]. Rather it is to recognize the latitudinal limits to reef growth [18,84].

There has been considerable recent discussion over the role that depth may play in providing refuge for corals from high sea temperatures and other disturbances [79,86]. During the period of our study, highest coral abundances occurred in shallow sites (Figure 6B). This will likely change in coming decades, with increasing disturbance focused on shallow reef habitat causing loss of corals and their replacement by other taxonomic groups, particularly algae. Most common IWP reef-building corals have a broad tolerance for different ambient environmental conditions, their populations extending from shallow reef slopes to the upper mesophotic zone. Of the 672 species surveyed here 622 spp. occurred in both deep and shallow sites.

This apparent lack of niche-specialization is one reason for the application of neutral theory to coral reefs [87,88]. Yet even among these tolerant taxa, most had greater abundances either on shallow or deeper reef slopes. Of these species, more than twice as many exhibited apparent preference for deeper rather than shallow sites, suggesting that preferred habitat for most IWP coral species is the mid to lower reef slope, below 10 m depth. Even among the 90 species that did not show strong depth preferences, 54 species were more common in deeper than shallower sites (Table S2). In 50 species, these depth preferences are sufficiently strong to be considered a form of niche specialization (Table 4). Species with strong preferences for shallow habitats, such as *Acropora aspera*, *A. digitifera* and *A. spathulata* (Table S2), may be at particular risk from predicted future change, given that the impact of disturbance, including coral bleaching from elevated sea temperatures or other stressors (e.g., freshwater influx), is often most severe in shallow waters. Mitigating against such risk is the inherent phenotypic and genotypic capacity of such species to acclimate and/or adapt, contingent in part on the complex relation between the coral host, zooxanthellae and other symbionts.

4.6. Species Vulnerability

Several recent analyses, using markedly different approaches, have assessed coral vulnerability at global [19,21,22,89] and regional scales ([17]—western Indian Ocean; [20]—Caribbean Sea; [23]—Marshall

Islands). Given the continuing predicted decline in area, extent and/or quality of reef habitat globally [16,19,90], some 40 species could potentially qualify in an IUCN Threatened category (Table 7), under the Red List geographic range criterion (extent of occurrence or area of occupancy). This criterion requires a species to be known to exist at no more than five locations.

Qualification under IUCN criteria of small geographic range and small and reducing population size is, however, contingent on the assumption that there are no unsampled populations. Clearly this is a difficult, if not impossible, criterion to meet for reef-building corals. Indeed, the general utility of these criteria for corals is limited by several important caveats:

1. our surveys, or indeed any work to date, have not sampled the entire ranges of many species, not even the main distribution ranges of some, with the most accurate and up-to-date compilation of such data being shown in the distribution maps of "Corals of the World" [1].
2. most corals have the potential for widespread dispersal as planktonic larvae or via rafting [75] on the decadal time scales relevant to assessing extinction risk, both within and among ecoregions.
3. some species prefer habitats not well sampled, by us or others, including the mesophotic zone (e.g., *Craterastrea levis*) or deep sandy areas (e.g., *Heterocyathus aequicostatus* and *Heteropsammia cochlea*), or live cryptically under boulders on shallow reef flats (e.g., *Stylaraea punctata*), limiting assessment of their true abundance.

These limitations may become of less concern, however, as the spatial and temporal scales of disturbances continue to increase throughout this century, with expected concomitant reductions in ranges, as suggested by projections of future habitat marginalization [16,90]. These studies found that suitable habitat will become increasingly restricted, from the combined effects of high sea temperatures and acidification (among other impacts) by mid-21st century. This will test the inherent capacities of different coral species for acclimation and adaptation, in respect of their life histories, notably physiological tolerances and flexibility in symbiosis.

Some of the rarest corals in this study (Table 7) also qualified as highly vulnerable to future climate change impacts, using a traits-based approach, and incorporating habitat marginalization under various scenarios of bleaching and acidification [22]. That study found that up to 253 species were highly vulnerable, 73 species of which are listed in threatened categories on the IUCN Red List. Conversely, up to 150 coral species could qualify as "potential adapters". These do not have the high sensitivity and low adaptability traits that, in combination, could otherwise render them highly vulnerable [22].

For most species, increasing disturbance will likely reduce sub-population connectivity, increasing isolation and risk of local extinction. A regional analysis of the Marshall Islands [23] used IUCN Red List criterion (VU D2). In this criterion, a population is considered vulnerable if it is very restricted in the number of locations (typically five or fewer) such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future. As these authors noted, this criterion can be employed at regional scales provided that the population to be assessed is isolated from conspecific populations. Notably, only one of the species identified as regionally vulnerable from the Marshall Islands (*Acropora bushyensis*) qualified as potentially threatened in our broader scale study under VU D2, contrasting with its Least Concern ranking in the IUCN Red List assessment [19]. As shown herein, many coral species have pronounced centres of abundance, whilst otherwise being uncommon or rare across much of their distribution ranges, an important consideration when applying IUCN geographic range criteria.

In the initial Red List assessment, approximately half of the species listed in Table 7 fulfilled threatened species criteria [19]. Some, the geo-suffusive taxa, have restricted distributions, all are rare, and all are predicted to suffer major loss of suitable habitat in coming decades [16,19,90]. A case in point, *Euphyllia baliensis*, is a highly distinctive species discovered during this study (Figure 11B). It is only known from the type locality, which is threatened by development proposals including sand mining and a port. The corollary, that more widespread and abundant species are less at risk, at least to regional impacts, is also true, as reflected in the IUCN rankings of Least Concern or Near Threatened for the most abundant and widespread corals (Table 5).

Yet there are increasingly important exceptions that may well override these criteria in respect to corals. These include epidemic disease outbreaks in otherwise non-threatened species, or other global impacts at meta-population scales [91]. Density-independent effects of global changes to sea temperature and ocean chemistry that cause physiological stress and resultant mortality across the meta-population can decouple stock abundance from recruitment. This may induce a downward spiral in reproductive rates, even in the most widespread and abundant taxa [91]. This is a pertinent warning as sea temperatures continue to warm and oceans acidify and become increasingly depleted of oxygen, with a concomitant increase in diseases [92]. Any major reductions in population sizes and reproductive output will limit the capacity for dispersal in and among heavily impacted reef tracts. In this situation, the approach [23] of assessing vulnerability at regional scale clearly holds merit.

4.7. Extinction Risk

There is little argument that corals, and the reefs they build, continue to decline, even in managed marine protected areas [5,13–16,18]. Both proximate and ultimate causes for the declines are well understood, and include a wide array of local, regional and global impacts, some acting in synergy, some antagonistic (see e.g., [92–94]). Coral species, and indeed individual populations and sub-populations, vary in their specific response(s) to impact. At present, we know little of this intra- and interspecific variability, resistance and resilience. Nor do we have any clear indication of the meta-population sizes required for each species to meet these impacts.

Yet the Scleractinia as an Order has a long evolutionary history dating some 200 million years, having successfully survived several of earth's mass extinctions. It seems probable that future extinctions will differ among species groups and regions, at least initially [17,20–22]. A pertinent example is provided by the relatively high levels of endemism and long evolutionary history of some geo-suffusive western Indian Ocean corals [4]. Several Arabian and western Indian Ocean endemics, including *Sclerophyllia maxima*, *Montipora saudii*, *Horastrea indica*, *Fungia puishani* and *Stylophora madagascarensis*, ranked among the rarest of corals in this study (Table 7), and must be considered at particular risk. Another suite of very rare species is, as far as is known, endemic to particular ERs within the CT. These include the aforementioned *Acropora suharsonoi* and *Euphyllia baliensis* (Lesser Sunda Islands and Savu Shelf) and *Astreopora acroporina*, *A. cenderawasih*, and *A. montiporina* from Cenderawasih Bay (Table S2). All have very small populations and must be considered particularly vulnerable.

Extinctions of the most evolutionarily distinct corals, exemplified by the monotypic genera, will also increase the loss of evolutionary diversity [21]. In the present study, this risk is demonstrated by the apparent rarity of the monotypic *Duncanopsammia axifuga* and *Horastrea indica* (Table 7), or indeed by *Simplastrea vesicularis* or *Boninastrea boninensis*, neither of which was recorded. Concern over some other evolutionary distinctive taxa, such as *Diploastrea heliopora* [17,41], is however alleviated to some degree by their higher OA score, and their widespread centres of abundance in different regions (Figure 11A). *D. heliopora* has a long evolutionary history dating to the Oligocene [2], is tolerant of a wide variety of disturbances, with life history traits [22], including reproductive mode, that presumably provide it with a level of evolutionary "insurance against extinction" that is greater than some other taxa. And yet our present understanding of the roles that different life histories will play in influencing coral demography and hence vulnerability under changing environmental conditions in coming decades remains rudimentary.

In conclusion, this study provides an overview and baseline (albeit a shifted one), of the richness and abundance of reef-building corals on increasingly endangered IWP reef systems at the end of the 20th and beginning of the 21st century. This should contribute to future sub- and meta-population analyses examining vulnerability, resistance and resilience of species to disturbance. Future collaborative work will also address potential refugia, including the upper mesophotic zone, relations among abundance, range size and life history traits, alpha, beta and gamma diversity and community assembly. Together, it is hoped these will inform appropriate policy and contribute to successful conservation action.

Supplementary Materials: The following are available online at www.mdpi.com/1424-2818/9/3/25/s1: Table S1: Species with taxonomic issues; Table S2: Species abundance summary; Table S3. Effects of depth on richness and abundance; Table S4. Comparison of the Overall Abundance (OA) ranking of the 30 most abundant IWP corals in various NW and SW Pacific ERs and areas.

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Author Contributions: L.D. and E.T. conceived, designed and conducted the surveys that form the basis of this study; both also analyzed the data; and wrote the paper.

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Coping with Commitment: Projected Thermal Stress on Coral Reefs under Different Future Scenarios

Simon D. Donner*

Department of Geography, University of British Columbia, Vancouver, Canada

Abstract

Background: Periods of anomalously warm ocean temperatures can lead to mass coral bleaching. Past studies have concluded that anthropogenic climate change may rapidly increase the frequency of these thermal stress events, leading to declines in coral cover, shifts in the composition of corals and other reef-dwelling organisms, and stress on the human populations who depend on coral reef ecosystems for food, income and shoreline protection. The ability of greenhouse gas mitigation to alter the near-term forecast for coral reefs is limited by the time lag between greenhouse gas emissions and the physical climate response.

Methodology/Principal Findings: This study uses observed sea surface temperatures and the results of global climate model forced with five different future emissions scenarios to evaluate the "committed warming" for coral reefs worldwide. The results show that the physical warming commitment from current accumulation of greenhouse gases in the atmosphere could cause over half of the world's coral reefs to experience harmfully frequent ($p \geq 0.2$ year^{-1}) thermal stress by 2080. An additional "societal" warming commitment, caused by the time required to shift from a business-as-usual emissions trajectory to a 550 ppm CO_2 stabilization trajectory, may cause over 80% of the world's coral reefs to experience harmfully frequent events by 2030. Thermal adaptation of 1.5°C would delay the thermal stress forecast by 50–80 years.

Conclusions/Significance: The results suggest that adaptation – via biological mechanisms, coral community shifts and/or management interventions – could provide time to change the trajectory of greenhouse gas emissions and possibly avoid the recurrence of harmfully frequent events at the majority (97%) of the world's coral reefs this century. Without any thermal adaptation, atmospheric CO_2 concentrations may need to be stabilized below current levels to avoid the degradation of coral reef ecosystems from frequent thermal stress events.

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* E-mail: simon.donner@ubc.ca

Introduction

Anthropogenic climate change threatens the function of coral reef ecosystems and the millions of people across the tropics depending on those ecosystems for food, income and shoreline protection [1–4]. Approximately one quarter of the carbon dioxide emitted by human activity is absorbed by the oceans. The rise in oceanic carbon dioxide threatens to reduce rates of calcification by corals and other reef organisms and could eventually limit reef accretion [4,5]. In addition, ocean temperatures of 1–2°C greater than the usual summer maximum can cause mass coral bleaching, a paling of the reef-building animals caused by a breakdown of the symbiosis with the colourful dinoflagellates *Symbiodinium* [1,6]. Episodes of mass coral bleaching have led to coral mortality, declines in coral cover and shifts in the population of other reef-dwelling organisms [1,2,4,7–11].

The degradation of coral reefs due to ocean warming is expected to progress faster than many other prominently researched impacts of climate change, including ice sheet melting, Amazonian forest dieback, migration of tropical diseases and declines in agricultural productivity [12, see Fig SPM.2]. Anthropogenic forcing is likely (>90%) to have already played a role in recent mass bleaching events, including the 2005 event in the Eastern Caribbean [13]. Past analyses have concluded that ocean warming over the next three to four decades may make mass coral bleaching a frequent occurrence worldwide, depending on assumptions about thermal adaptation [1,13–15]. The marine science and conservation community has responded with calls to stabilize greenhouse gas emissions at a level which would such avoid frequent, severe mass bleaching events [3,4,16].

The extent to which greenhouse gas mitigation can alter the long-term forecast for coral reefs is limited by the time lag between greenhouse gas emissions and the physical climate response. The thermal inertia of the deep ocean and other components of the climate system delay the physical response to changes in external forcings like greenhouse gases. This physical commitment is calculated by the difference between the transient response and the equilibrium response of an atmosphere-ocean general circulation model to a change in atmospheric greenhouse gas concentrations. In addition to this physical commitment, the expected lag between a decision to reduce greenhouse gas emissions and the implementation of mitigation activities imparts a societal warming

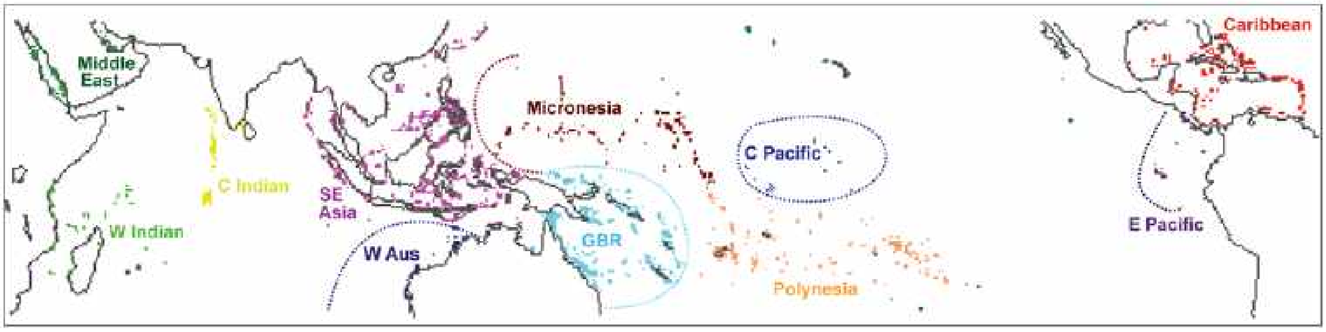

Figure 1. Map of the 0.5°×0.5° coral reef "cells" grouped into eleven ocean provinces. The map depicts the 1687 cells which contain warm-water coral reefs and are described as ocean in the CM2.0 and CM2.1.
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commitment. For example, the slow turnover of capital stock in the energy industry is likely to preclude a very rapid shift from carbon-intensive forms of power generation like conventional coal to alternative options like solar, wind or coal with carbon capture and storage.

This study specifically examines the implications of "committed warming" for coral reef ecosystems worldwide (Fig. 1) for the first time. The likelihood of severe mass coral bleaching occurring at reefs worldwide over the next two centuries is estimated by integrated satellite-observations of sea surface temperatures and thermal stress indices with output from simulations of the Geophysical Fluid Dynamics Laboratory (GFDL) climate models CM2.0 and CM2.1 [17]. The analysis is conducted for five different future scenarios including i) the stabilization of atmospheric greenhouse gas concentrations at year 2000 levels ("Commit"), ii) the SRES B1 mitigation scenario, in which atmospheric CO_2 concentrations could stabilize at 550 ppm in the year 2100, and iii) the SRES A1b "business-as-usual" scenario, in which atmospheric CO_2 concentrations reach 700 ppm in the year 2100 (Fig. 2). Comparison of projections from the different scenarios provides a measure of physical and societal mass bleaching "commitment" given different assumptions about the adaptability of coral reef ecosystems. The results provide insight into the level of atmospheric greenhouse gas concentrations necessary to avoid degradation of coral reef ecosystems worldwide and the need for coordinated efforts to maximize coral reef resilience.

Results

Sea surface temperature

This section summarizes the projected change in sea surface temperatures averaged across the tropical oceans and across the eleven ocean provinces that contain coral reef ecosystems (see Materials and Methods). The simulated increase in annual mean SST for each of the coral reef provinces over the 21st century ranges from lows in the Commit scenario to highs in the fossil-fuel intensive A2 and A1F1 scenarios (Table 1). The CM2.0 and CM2.1 ensemble results for the Commit scenario indicate that 0.4–0.6°C of the simulated regional SST increase by 2090–2099 in the SRES scenarios is due to the physical commitment from atmospheric greenhouse gas accumulation until the year 2000.

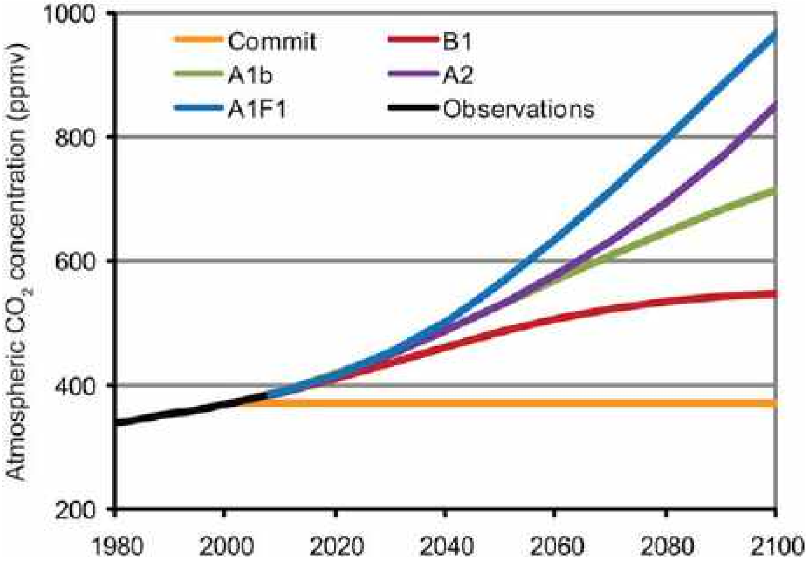

Figure 2. Annual globally averaged atmospheric carbon dioxide concentration (in ppm) from 2000 to 2100 in the five future scenarios considered in this study. The observed global mean concentration from 1980 to 2007 is displayed for comparison. The concentration stabilizes at 370 ppm in the year 2000 in the Commit scenario. The concentration reaches at 550 ppm and 700 ppm by the year 2100, in the B1 and A1b scenarios respectively.
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Table 1. Annual mean SST anomaly averaged across each ocean province.

Region	SST anomaly 2030–2039					SST anomaly 2090–2099				
	Commit	B1	A1b	A2	A1f1	Commit	B1	A1b	A2	A1f1
Caribbean	0.4	0.8	0.9	0.9	1.1	0.6	1.5	2.4	2.7	3.4
Middle East	0.4	0.9	1.0	0.9	1.1	0.6	1.6	2.5	3.0	3.5
W Indian	0.4	0.7	0.8	0.8	1.0	0.6	1.4	2.2	2.8	3.4
C Indian	0.4	0.7	0.9	0.8	1.0	0.6	1.4	2.3	2.9	3.5
W Australia	0.3	0.8	0.9	0.8	1.0	0.5	1.3	2.1	2.8	3.4
SE Asia	0.3	0.7	0.8	0.8	0.8	0.5	1.3	2.1	2.7	3.2
GBR+Melanesia	0.4	0.6	0.8	0.8	1.0	0.5	1.2	2.1	2.7	3.3
Micronesia	0.4	0.5	0.8	0.7	1.1	0.5	1.4	2.5	3.0	3.6
Central Pacific	0.4	0.6	0.8	0.7	1.1	0.6	1.4	2.5	3.0	3.6
Polynesia	0.3	0.6	0.6	0.7	0.9	0.4	1.1	1.9	2.3	2.8
East Pacific	0.4	0.8	0.9	0.9	1.1	0.6	1.5	2.4	2.8	3.5
All tropics	**0.3**	**0.6**	**0.7**	**0.6**	**0.8**	**0.5**	**1.1**	**1.8**	**2.3**	**2.8**

The anomaly for each region is the difference between the projected CM2.0 and CM2.1 ensemble decadal mean SST models and the 1980–2000 ensemble mean SST.
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There is an additional 0.7–0.9°C increase in regional mean SST in the B1 scenario, in which atmospheric CO_2 concentrations stabilize at 550 ppm by 2100. The difference between the emissions path of B1 scenario and the "business-as-usual" A1b scenario results in an additional 0.8–0.9°C increase in regional mean SST.

The projected SST anomalies in the different future scenarios do not diverge for several decades. The difference between the mean projected warming for 2030–2039 in the B1, A1b and A2 scenarios is $\leq 0.1^\circ$C for seven of the eleven reef provinces, and $\leq 0.3^\circ$C for the remaining four reef provinces (Table 1). For example, the nine-year running mean SST anomaly for the Central Indian Ocean reef province shows a similar trend between B1 and A1b until after the 2030s (Fig. 3). The results of the Commit scenario indicate that roughly half (0.3–0.4°C) of the 0.5–1.0°C warming projected for the reef provinces in the B1, A1b and A2 scenarios is due to the physical commitment in the climate system. The remainder of the warming by 2030–2039 is similar between the SRES scenarios because of the overlap in emissions trajectories (the "societal" commitment) in the scenarios and the lagged response of the climate system to greenhouse gases emitted during the intervening years (the "physical" commitment). The 0.5–0.9°C SST increase by 2030–2039 in the B1 scenario is a possible measure of the combined physical and societal warming commitment. A lower amount of mean surface ocean warming would require a near-term effort to reduce greenhouse gas emissions below the B1 trajectory.

Mass Coral Bleaching

The occurrence of mass coral bleaching is commonly predicted by the accumulation of sea surface temperatures above the maximum value in the monthly climatology (e.g., the highest value in a long-term average of monthly temperatures). This baseline above which thermal stress accumulates is typically referred to as the maximum monthly mean (MMM). Here, the annual accumulation of "degree heating months" (DHM, in °C-month)

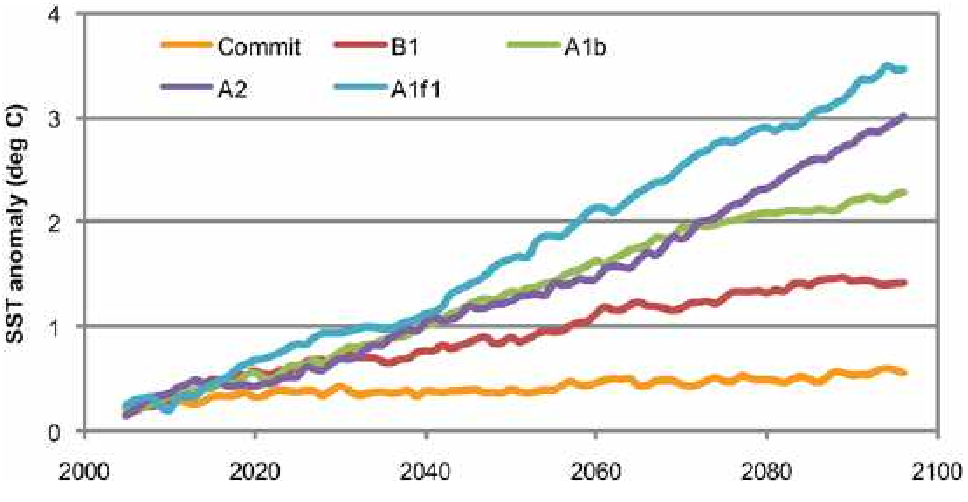

Figure 3. Nine-year running mean annual sea surface temperature anomaly (in °C) for the Central Indian Ocean. The anomaly is calculated from the ensemble of the CM2.0 and CM2.1 annual sea surface temperatures.
doi:10.1371/journal.pone.0005712.g003

above the MMM from 2001–2100 is calculated in each coral reef cell for each of the future scenarios by integrating model output with observed SST data (see Materials and Methods). A DHM value of 2°C-month is employed as an indicator of thermal stress which can lead to severe mass coral bleaching [13,15]. The likelihood of a severe mass coral bleaching event ($DHM \geq 2°C$-month) occurring in a given year from 2005–2095 in each coral reef cell is calculated using a ten-year running period of results from both the CM2.0 and CM2.1 simulations (i.e. $n_{years} = 20$) for each future scenario.

For the purposes of analysis, the results are used to determine the year in which severe mass coral bleaching begins to occur more than once every five years ($p = 0.2$). The arbitrary five year return period represents a simple estimate of the shortest acceptable time between severe bleaching events. It is based on the minimum time required for hard coral cover to recover to pre-bleaching levels reported in the literature (e.g. [14,18–21]). In reality, recovery can vary widely in space and time due to factors like coral community structure, *Symbiodinium* diversity, other stressors, and bleaching experience [21–26]. Recovery can also be difficult to define; even if hard coral cover returns to pre-bleaching levels, changes in the community composition and age structure may affect ecosystem function and the diversity of reef organisms [7–10]. A single minimum acceptable return period is applied here in order to facilitate spatial comparison of the climate projections and to avoid the model uncertainty caused by including results the field studies which used a variety of different methods and metrics to characterize recovery.

The results of the Commit scenario indicate that severe coral bleaching becomes a five-year event for over half the world's coral reefs by 2080 due solely to the physical commitment from the accumulation of greenhouse gases in the atmosphere until the year 2000 (Fig. 4). The annual average DHM across each reef provinces in the different scenarios demonstrates the regional variation in current and projected frequency of thermal stress (Table 2). The results suggest the physical warming commitment poses less of a threat to reefs in the Caribbean, Middle East, Great Barrier Reef and Melanesia than to reefs in other regions. Alternatively, parts of the equatorial Pacific are expected to already experience $DHM \geq 2°C$-month almost once every five years. Coral reefs in the central and eastern equatorial Pacific experience high background SST variability due to the Southern Oscillation. The persistence of coral reefs in a region subject to frequent thermal anomalies may indicate that those ecosystems possess a naturally higher resistance to thermal anomalies or are capable of rapid recovery from thermal stress.

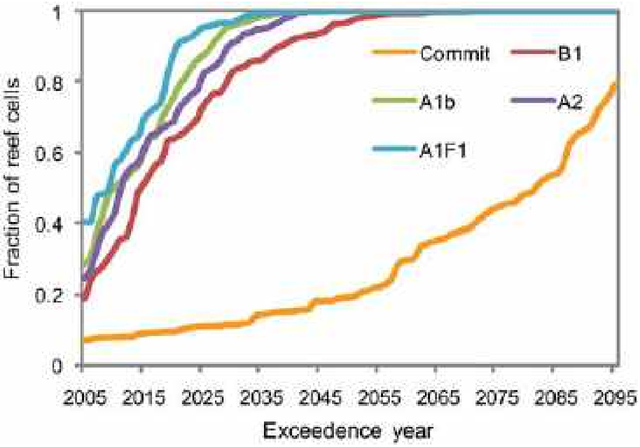

Figure 4. Frequency distribution of the year in which the probability of severe mass bleaching events ($DHM \geq 2°C$-month) exceeds 20% for each the 1687 coral reef cells. The probability of mass bleaching in each scenario is estimated from running 10-year intervals of both the CM2.0 and CM2.1 simulations.
doi:10.1371/journal.pone.0005712.g004

In the B1 scenario, the five year frequency threshold is surpassed by 80% of the world's reefs by 2030, fifty years earlier than in the Commit scenario and ten years later than in the higher emissions A1b scenario (Fig. 4). The fraction of reefs expected to have surpassed the five year frequency threshold by 2005 increases from 7% in the Commit scenario to 19% in the B1 scenarios and 29% in the A1b scenario. This result varies between the scenarios, despite the small differences in simulated SSTs over the current decade (e.g., Fig. 3), because the projected and observed warming since the beginning of this study's 1985–2000 climatological baseline period may have already elevated the frequency of severe thermal stress close to or past the five year threshold in many locations.

The difference between the projected exceedence year in the B1 and in the A1b scenario is less than 10 years in 70% of the coral reef cells and less than 20 years in 90% of the coral reef cells. Differences of 20 years or more occur only in parts of Melanesia, Polynesia, West Australia and the Western Indian Ocean (Fig. 5). The projections are similar in the two scenarios because the combination of the physical warming commitment and the likely societal warming commitment is sufficient to regularly cause DHM accumulation in excess of the upper bleaching threshold in the next several decades. Therefore, absent any adaptation or acclimation by corals and their symbionts, the majority of the world's coral reefs could experience frequent mass bleaching events by 2030, even if the world is able to shift greenhouse gas emissions from a business-as-usual emissions path (A1b) to a 550 ppm stabilization path (B1).

Effect of adaptation

The IPCC defined adaptation as measures that reduce the vulnerability of a system to climatic stress [12]. Using this broad definition of the term adaptation, there are several ways in which coral reefs may adapt to increasing thermal stress. Corals and their

Table 2. Year that the probability of $DHM > 2°C$-month exceeds 20%.

	Commitment		**SRES B1**		**SRES A1b**	
	Base	**+1.5 K**	**Base**	**+1.5 K**	**Base**	**+1.5 K**
Caribbean	n/a	n/a	2016	n/a	2018	2074
Middle East	n/a	n/a	2033	n/a	2023	2070
W Indian Ocean	2063	n/a	2024	n/a	2013	2088
C Indian Ocean	2063	n/a	2019	n/a	2012	2082
Western Australia	2071	n/a	2024	n/a	2016	2086
SE Asia	2061	n/a	2021	n/a	2012	2074
GBR+Melanesia	2095	n/a	2028	n/a	2017	2092
Micronesia	2009	n/a	2010	n/a	2005	2065
Central Pacific	2005	n/a	2005	2062	2005	2051
Polynesia	2072	n/a	2016	n/a	2015	2094
East Pacific	2048	n/a	2014	n/a	2012	2073

The results are taken from CM2.0 and CM2.1 ensemble projections under different future emissions scenarios.
doi:10.1371/journal.pone.0005712.t002

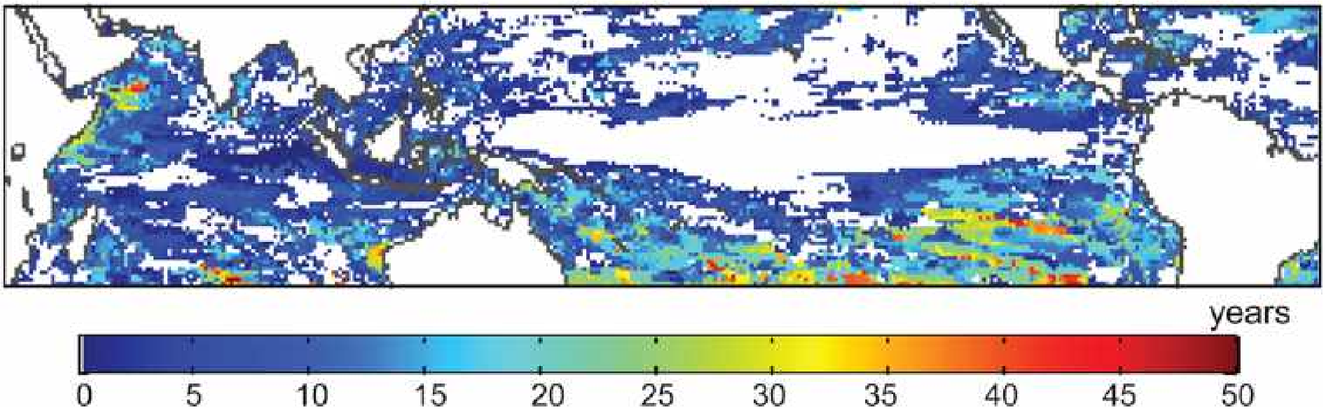

Figure 5. Positive difference in the exceedence year between the A1b and B1 scenarios, assuming no thermal adaptation. The exceedence year in each scenario is the ensemble mean of the year in which the probability of DHM≥2°C-month exceeds 20%. In grid cells where the probability is not reached before 2100, the difference is calculated as 2100 – exceedence year for A1b. For the purposes of presentation, results are displayed for all grid cells, rather than only coral reef cells.
doi:10.1371/journal.pone.0005712.g005

symbionts may be able to biologically adapt or acclimate to thermal stress via a range of mechanisms including symbiont shuffling and switching [27–30] and heterotrophic plasticity [31]. At the community level, selective coral morbidity and mortality during bleaching events may lead to dominance of more resistant and resilient growth forms and species, thus reducing vulnerability to future thermal stress events. Finally, management interventions like reducing fishing pressure and protecting thermally resistant micro-environments may be able to increase resistance to thermal stress and enhance the rate at which coral reef ecosystems recover from a mass bleaching event [32].

The effect of adaptation on the probability of severe mass bleaching events is calculated for each scenario, again using a ten-year running period of both the CM2.0 and CM2.1 simulations ($n_{years} = 20$). A potential increase in thermal tolerance of 1.5°C is employed, based on the outer bound of increased thermal tolerance observed in the common Indo-Pacific species *Acropora millepora* [33] and *Acropora Aspera* [34]. This value is employed as a benchmark because the genus *Acropora* encompasses one-quarter to one-third of one-quarter of scleractinian coral diversity [35], dominates shallow coral cover in parts of the Indo-Pacific [34], and is typically bleaching sensitive [23,24,33]. In reality, the thermal flexibility of corals should vary widely between species, growth forms and environments. The assumption of a 1.5°C thermal flexibility is a best guess of what could be achieved by some common corals through biological mechanisms and management efforts based on existing literature.

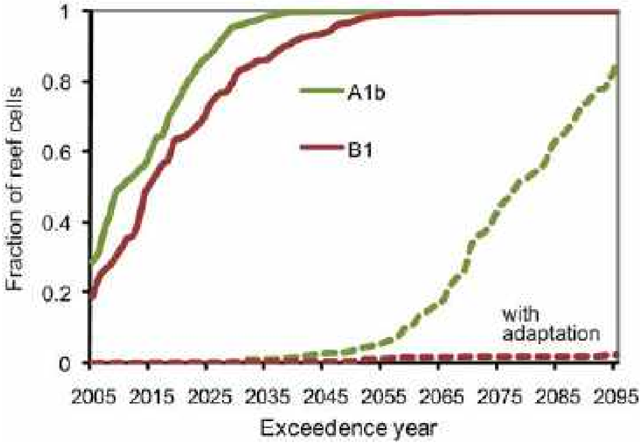

Figure 6. Frequency distribution of the year in which the probability of severe mass bleaching events (DHM≥2°C-month) exceeds 20% for each the 1687 coral reef cells. The frequency of mass bleaching in each scenario is estimated from running 10-year intervals of both the CM2.0 and CM2.1 simulations. Shown are results for SRES A1b and SRES B1, assuming no thermal adaptation (thick lines) and 1.5°C thermal adaptation (dashed lines).
doi:10.1371/journal.pone.0005712.g006

A 1.5°C increase in thermal tolerance postpones the passage of the five year return period until at least the latter half of the century for almost all of the world's coral reefs in each scenario (Fig. 6). No coral reef cells pass the threshold before 2050 in the Commit scenario or the B1 scenario, and only 4% pass the threshold before 2050 in the A1b scenario. By the end of the century, over 80% of the coral reef cells experience bleaching at least once every five years in the A1b scenario. In the B1 scenario, however, less than 3% of coral reef cells experience bleaching once every five years by the end of the century. Examining the results by region, only the Central Pacific passes the five year bleaching threshold during this century in the B1 scenario (Table 2). The increase in thermal tolerance delays the bleaching threshold the longest in regions like Polynesia, where the models project lower warming relative to the global mean warming, as in [15].

The divergence between A1b and B1 bleaching trajectories (Fig. 6) in the adaptation case occurs essentially because the increase in thermal tolerance exceeds the total physical and societal warming commitment, roughly depicted by the B1 scenario, but not the additional warming expected under the business-as-usual A1b scenario. The difference between the trajectories suggest sustained 1.5°C increase in the thermal tolerance of corals and their symbionts would, at minimum, postpone severe mass bleaching from becoming a five-year event for the majority of the world's reefs until the latter half of the century. If, in addition to the sustained increase in thermal tolerance, mitigation efforts shift atmospheric CO_2 concentrations from the "business-as-usual" trajectory depicted in the A1b scenario to the 550 ppm stabilization trajectory depicted in the B1 scenario, the models results indicate that severe mass bleaching would become a five-year event for a small minority (<3%) of the world's coral reefs this century.

The analysis of climate change impacts under future emissions scenarios often ends in the year 2100, even though the climate