CARIBBEAN FISHERY MANAGEMENT COUNCIL
270 MUÑOZ RIVERA AVENUE, SUITE 401
SAN JUAN, PUERTO RICO 00918

PUBLIC HEARING ON DRAFT DOCUMENT TO DEVELOP COMPATIBLE REGULATIONS IN THE THREE AREAS OF ABRIR LA SIERRA, BAJO DE SICO AND TOURMALINE, IN THE WEST OF PUERTO RICO
HOLIDAY INN HOTEL
MAYAGÜEZ PUERTO RICO
JULY 18, 2014

SUMMARY MINUTES

The public hearing was held at the Holiday Inn Hotel, Mayagüez, Puerto Rico, and was chaired by Mr. Carlos Farchette, Council Chairman. Mr. Miguel A. Rolón and Mrs. Diana Martino, Council staff were also present.

Dr. Graciela García-Moliner gave a presentation on the proposed options. There were 62 people present at the public hearing, 44 signed in. Seventeen deponents commented on the Actions and Alternatives presented and 8 others included written comments on the sign-up sheets (Attachment A). A number of the deponents spoke on behalf of the members of fishing associations and/or clubs (Identified with an *). Written comments received (as of July 30 2014 are included as Attachment B.

Following are the comments provided:

1. Michelle Schärer – Marine Biologist. Department of Marine Sciences, Mayagüez, Puerto Rico

   -Written document handed and included as part of the minutes.
   -Action 1, Alternative 5b
   -Action 4, Alternative 3

2. Nelson Crespo* – Commercial Fisher. Representing "Villa Pesquera de Rincón" including fishers from the "Unión Asociación de Pescadores Comerciales de Rincón/Asociación de Pescadores Pargos Profundos". Rincón, Puerto Rico.

   -Written document handed and included as part of the minutes.
   -Action 1, Alternative 2 (Bajo de Sico, Tourmaline and Abrir la Sierra: December-February)
   -Action 3, Alternative 6
   -Action 4, Alternative 3
   -Action 5, Alternative 4
   -Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
   -Open the water column, surface area, for fishing and allow transit through these areas, as established in Bajo de Cico.

   -Red hind populations have increased and this fishery is of great economic importance
   -March and April are important months for tourism industry in the west coast, significant economic contribution

3. Andrés Maldonado – Commercial Fisher and Diver. Combate, Puerto Rico (See also written comment for clarification.)

   -In agreement with the comments provided and read by Nelson Crespo.
   -Action 1, Alternative 2 (Bajo de Sico, Tourmaline and Abrir la Sierra: December-February)
   -Action 3, Alternative 6
   -Action 4, Alternative 3
   -Action 5, Alternative 4
   -Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
   -Open the water column, surface area, for fishing and allow transit through these areas, as established in Bajo de Cico.

4. Félix Castro – Commercial Fisher – Aguada, Puerto Rico

   -In agreement with comments provided and read by Nelson Crespo.
   -Action 1, Alternative 2 (Bajo de Sico, Tourmaline and Abrir la Sierra: December-February)
   -Action 3, Alternative 6
   -Action 4, Alternative 3
   -Action 5, Alternative 4
   -Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
   -Open the water column, surface area, for fishing and allow transit through these areas, as established in Bajo de Cico.

5. Miguel Rivera – Commercial Fisher – Boquerón, Puerto Rico

   -In agreement with comments provided and read by Nelson Crespo.
   -Action 1, Alternative 2 (Bajo de Sico, Tourmaline and Abrir la Sierra: December-February)
   -Action 3, Alternative 6
   -Action 4, Alternative 3: Suggested that mooring buoys be deployed as an alternative for anchoring.
   -Action 5, Alternative 4
   -Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
   -Open the water column, surface area, for fishing and allow transit through these areas, as established in Bajo de Cico.
   -Opening the water column for fishing for mahi and wahoo does not impact with the aggregation

6. Robert Long- Recreational Fisher – Mayagüez, Puerto Rico

   -Does not agree with prohibiting the use of spear guns. It would be discriminatory when other fishing gears are allowed.

   -Requested that the current regulations be evaluated to determine their effectiveness.

-Apnea fishing is a very hard way of fishing and using spears would not hurt other species since this is a very selective manner of fishing with a directed target.

-Believes it seems reasonable to prohibit anchoring. (Action 4, Alternative 3)

-There is a need for enforcement and enforcement agents to give follow up to the current regulations.

-Marine resources are important and should be cared for, but the human resource is important as well and should be treated equally.

7. Fred Lentz – Commercial Fisher – Rincón, Puerto Rico.

-In agreement with:

-Action 1 – Alternative 2: The same for the three areas, December-February.
-Action 2 – Alternative 3.
-Action 3 – Alternative 6. The same for the three areas.
-Action 4 – preferred Alternative 3.
-Action 5 – preferred (Alternatives 2 and 4).
-Action 6 Alternative 6 (NEW): Prohibit fishing with spear guns of all species, no exception for HMS, and include wahoo.
Chumming is used while spear fishing in apnea for pelagics but other species can be speared fished (reef fish)

8. Victor Padilla – Commercial Fisher – El Seco, Mayagüez, Puerto Rico

- In agreement with comments provided and read by Nelson Crespo, Andy Maldonado and Fred Lentz.
-Action 1, Alternative 2 (Bajo de Sico, Tourmaline and Abrir la Sierra: December-February)
-Action 3, Alternative 6
-Action 4, Alternative 3
-Action 5, Alternative 4
-Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
-Open the water column, surface area, for fishing and allow transit through these areas, as established in Bajo de Cico.

-Eventually commercial fishers from the western area of Puerto Rico will be displaced and will not be able to earn a living by fishing as they have done for so many years if the government keeps putting more measures.
-Seasonal closures and these area closures are too much, these amount to too many closures.

9. Richard Jaeck – Recreational Fisher – Mayagüez, Puerto Rico

-There should be no more prohibitions or closures, what there needs to be is more education and enforcement for the current regulations in place. Ethical fishing.

-The catch should not be prohibited, but the number of specimens allowed to be caught regulated. Quotas established by sector (recreational and commercial separately).

-Educate, Manage, Enforce

-In agreement with:

- -Action 1, Alternative 2
- -Action 2, Alternative 1 (no action): Because we need to promote managing, which would promote diversity
- -Action 3, Alternative 6
- -Action 4, Alternative 3. If it applies to recreational and sports fishing vessels it should also include merchant vessels (which have big anchors) and there should be more enforcement regarding this also.
- -Action 5, Alternative 1: downriggers for wahoo, vertical jigging for wahoo, blackfin tuna, rainbow runner are some of the fishing techniques used by recreational fishers.
- -Action 6, Alternative 1

10. Alexis López - Independent Commercial Fisher

-An amendment should be made to Abril la Sierra and Tourmaline to:

- -Action 6, **Alternative 6: (NEW)** Allow spear fishing in all 3 areas (specifically in "boya 6", buoy 6, or Abrir la Sierra)
- -Action 5: Open the water column to fish for wahoo, mackerels, rainbow runner, tuna and dolphin fish
  - -Add an alternative that would open the use of spear gun for pelagic fishes in the area of "Boya 6" (Buoy 6 or Abrir la Sierra) and Tourmaline, as well as allowing "pesca de corrida" or trolling.
  - -Bajo de Sico may remain as it is, but spearfishing should also be allowed.

11. Pedro Silva – Commercial Fisher – Mayagüez, Puerto Rico

-Do not agree with the measure to not allow anchoring. He fishes during the night and needs to anchor in order to catch yellowtail, and also during the day when fishing for other species is it necessary that anchoring be allowed in the area to be able to fish. Use an anchor that can be retrieved easily.

-Large vessels anchor in these areas and cause much more damage.

-There are longliners and other large fishing vessels in the areas.

-The closures already in place are good and sufficient. There is no need for additional closures.

-Establish quotas for fishing in these areas.

-In disagreement with not being able to catch tuna.

-There should be no fish from other areas [imports] allowed during the closures.

-Enforcement is needed but if they intervene when fishing is going on, it ruins the day of fishing. These boats go by at very high speeds.

12. Luis Rodríguez – Commercial Fisher – Mayagüez, Puerto Rico

-To be able to fish in Tourmaline it is necessary to be able to anchor since the currents are too strong. The weights used for fishing in this area are 11 pound weights. He fishes during the night; therefore it is necessary to be able to anchor in that area.

-The anchor they use is not harmful to the bottom since it is not a dragging type anchor and is easily removed.

13. Alexis Loyola González – Commercial Fisher – Spear Gun Fisher

-In agreement with:

-Action 1 Alternative 2 for Abrir la Sierra which is especially important to his livelihood. If closed for six months this would add to the seasonal closure of the mutton snapper and in effect he would not be able to fish for 9 months. 75% of his fishing comes from the "Boya 6" (Buoy 6 or Abrir la Sierra) area: mutton snapper and other snappers.
-Action 2, ~~Alternative 3~~: Not in agreement with prohibiting possession – re-evaluated his position on this Action. Allow transit through the areas because it is needed when moving from Bajo de Sico to Buoy 8 (Tourmaline).
-Action 3, Alternative 6
-Action 4 (prohibit anchoring) he believes that the way of anchoring should be modified. USCG and FURA are patrolling Bajo de Sico, it is not for commercial fishing.
-Action 5, if we are not allowed to fish in this area then they will fish in the surrounding areas which will over exploit them.
-Action 6: if spear fishing is to be banned, then it should be for all fishing sectors, and not only penalize the commercial fishers. There is temptation to harvest what is prohibited and one has to decide if to obey the regulations or not. There is illegal queen conch fishing going on at Boya 6 (Buoy 6 or Abrir la Sierra).

-Wahoo is a recreational fish, not much money for the commercial fishers because of the cost of fishing for it.

14. José Conde – Commercial Fisher – Mayagüez, PR

-Why does the Council close areas and put in place regulations in the west coast area of Puerto Rico more than in the rest of the island?

15. Jairo Rosado – Commercial Fisher – Mayagüez, PR

-Action 6, **Alternative 6 (NEW):** Allow spear fishing in all 3 areas. There is no reason to ban the use of spear guns since this is a very selective fishing gear and you only catch what you target.

-Agrees with no action, leave closures as they are.

-The Tourmaline and Abril la Sierra areas should be opened.

-More enforcement of the regulations in place is needed.

16. Jaime Dávila Medina – Spear Fisher –Vega Baja, PR

    -The closures and regulations that are currently in place are enough. There is no need for more. What needs to be improved is the enforcement of the regulations and closures in place, and provide more education so that people better understand and comply; an educational campaign is needed.

    -No action. Things should be left as they are right now.

    -Spear gun fishing should not be eliminated, and it should be allowed in Tourmaline and Abril La Sierra. This is not a harmful gear. What is harmful are those who do not know the regulations.

    -Allow lobster fishing year round.

Additional comments received in writing at the public hearing (see Attachment A):

1. Natalia Lartigart –Independent
    a. Action 1, Alternative 2 (Bajo de Sico, Tourmaline, Abrir la Sierra: December - February)
    b. Action 2, Alternative 2
    c. Action 3, Alternative 6
    d. Action 4, Alternative 3
    e. Action 5, Alternative 5: allow trolling since there will no impact on the aggregations
    f. Action 6, **Alternative 5 (NEW):** Prohibit fishing with spear guns of all species during the seasonal closure established in Action 1 for the 3 (three) areas, meaning Bajo de Cico, Tourmaline and Abrir la Sierra.
2. Raymundo Espinoza –TNC
    a. Action 6, Alternative 3 but includes lionfish among the species whose harvest is allowed. Allow the harvest of lionfish with spear guns.
3. Evan Tuohy
    a. Same regulations for all three areasto simply management and enforcement areas
    b. This would also make regulations clearer for fishers.
4. Miguel Vargas Valle – Commercial Fisher, Rincón, PR
    a. Agrees with Nelson Crespo's comments
5. Chelsea Harns – Recreational Diver, Rincón, PR
    a. Supports further protection of spawning aggregations

Additional comments received:

1. Improve communication with fishers.
2. Keep mailing the information, best way to let the public present at the hearing know about meetings.
3. Keep providing information via Helena Antoun (CFMC-DNER staff).
4. Port Agents are needed.
5. Need for more education and information.
6. Enforce the regulations that are in place, including regulations that apply to recreational fishers.
7. Need to allow for young fishers to come into the fishery.

The public hearing adjourned at 9:14 pm.

#1

July 18, 2014

Good evening members of the Council, staff and public

My name is Michelle T. Schärer and I am a marine biologist graduated from the Department of Marine Sciences of Puerto Rico. I have been doing research in the west coast of Puerto Rico since 1996 and conducted studies in fisheries since the year 2000. My expertise is in the ecology of coral reef fish populations, spawning aggregations and marine protected areas of the Caribbean. I have been conducting evaluations of spawning aggregations of groupers in Puerto Rico and collecting data at Abrir la Sierra and Bajo de Sico since 2007.

I am here today to testify regarding the federal actions recommended for ABT as stated in the official documents. First of all I would like to propose that the Ecosystem Based Fisheries Management approach be implemented in this decision making process, which stresses the need for improved governance to ensure the success of the management measures decided. This includes transparency, stakeholder involvement and cooperation of all authorities involved in coral reef conservation and fisheries management. I believe we need to make this a priority in order to ensure the success and compliance of any management actions that come out of this process, given the lack of law enforcement in federal waters west of Puerto Rico.

Second, I would like to urge the Council to adopt a precautionary approach given the natural uncertainty and risk in attempting to manage fisheries of species that are considered data-poor, endangered and/or threatened. Management measures following the precautionary approach should be based on the best scientific advice available, taking into account the uncertainty in the advice and the risk that the fishing activity poses to the functioning of the ecosystem.

The reasons for the declines in our local reef fish species is undoubtedly very complex but it is clear that an ongoing history of overexploitation and habitat loss have played major roles in the current state of our local fish stocks. Evidence of this is the number of species that used to conform the coral reef community, which are currently rare, undersized and/or under threat of extinction worldwide, despite fishery bans and other management actions designated to protect them.

The areas under consideration today should be managed for the benefit of a variety of users including commercial fishers, recreational fishers, divers, underwater enthusiasts and the wildlife preservation community at large, not only the extractive users since it is a resource that is shared by all.

Local fishery experts in the 1990's identified ABT as three important spawning grounds for groupers, mainly red hind. Subsequent research conducted by Dr. García of the University of Puerto Rico has documented additional species of snappers and groupers in the mesophotic zones within ABT that are known to form spawning aggregations. It is widely recognized that spawning grounds are extremely vulnerable to fishing pressure and spawning aggregations can be decimated by the lack of identification, low compliance with seasonal regulations at these important sites.

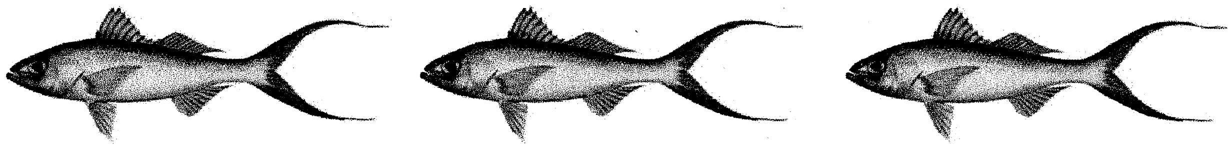
The scientific evidence from the US Virgin Islands suggests that the spawning stock of red hind has increased in abundance and size at the Red Hind Bank in St. Thomas, after it became a seasonally protected site and more recently a year-round no-take. Based on this example and building upon the scientific recommendations proposed by Dr. García in 2007 as well as the results of acoustic research from Bajo de Sico, which indicate habitat use by multiple species known to form spawning aggregations during most of the year I urge the Council to adopt alternative 5b (Action 1).

Maintaining a structurally complex coral reef within all three ABT areas is vital as this is essential fish habitat necessary for the productivity of coral reef fisheries. No anchoring or bottom tending gear should be allowed to come in contact with the benthic habitat at any time in order to minimize damage to corals.

The area of fishing grounds less than 30m in depth within Abrir la Sierra and Tourmaline together amount to 5.6% of the west coast insular platform. Preliminary results from research conducted at Abrir la Sierra indicate that the timing of the current three months closure designed for red hind is insufficient to protect the complete duration of the aggregation, which extended into March during 2013. Special attention should be given to the timing of seasonal closures and the recent data that suggest variability in the reproductive seasonality of fishery target species, which may be shifting due to climatic changes.

ms

#2



VILLA PESQUERA DE RINCON
CARR. 429 KM 1.1 INT. / BO. BARRERO / RINCON, P.R. 00677

Junio 18, 2014

Vista Publica

Desarrollo de Regulaciones Consistentes para Abrir la Sierra, Bajo de Sico y Tourmaline

Muy buenas noches a todos.
Mi nombre es Nelson Crespo y estoy en representación de los pescadores adscritos a la Villa Pesquera de Rincón que incluye Pescadores Comerciales de la Unión de Pescadores Comerciales de Rincón y de la Asociación de Pescadores de Pargos de Profundidad que a su vez tiene miembros adscritos de varios pueblos limítrofes del oeste y noroeste de P.R.

Después de una discusión intensa entre los miembros adscritos a nuestra Villa Pesquera esta es nuestra posición oficial.

Acción 1: Modificar la duración y los meses de las épocas de veda

La Alternativa 2: Modificar la época de veda del Bajo de Cico del 1 de diciembre hasta el ultimo día de febrero es la sugerida.

En cuanto al Bajo de Cico, no hay razón alguna que justifique una veda mayor para proteger especies que ya están protegidas y bajo manejo por el Consejo de Pesca y el Gobierno de P.R.

En cuanto al Tourmaline y Abrir la Sierra se debe quedar como esta de diciembre al último día de febrero. Alt 1

No estamos de acuerdo con la Alternativa Preferida del Consejo. Por qué?

Con cerrar los meses de octubre y noviembre no se compone nada. Aquí lo que se está buscando es la uniformidad en el manejo de las áreas y la protección de las agregaciones de Mero Cherna y Cabrilla las cuales esta evidenciado que sus picos de agregación son de diciembre a febrero.

Con las medidas que el Consejo de Pesca a tomado durante los pasados años hay más que protección para estas especies que son muy valiosas para el ecosistema y estamos de acuerdo que deben ser protegidas.

No podemos tapar el cielo con la mano y hacerles creer a las personas aquí presentes que en el pasado el Mero Cabrilla fue llevado al borde de la extinción comercial y que al presente continua así.

Hoy en día gracias a las acciones tomadas y vedas establecidas la población de Mero Cabrilla se encuentra recuperada y es una de gran importancia económica para la industria de la pesca.

Pero en esta discusión no podemos perder de vista no tan solo el aspecto socio-económico cultural y religioso del pescador si no también la sociedad puertorriqueña particularmente en el oeste de P.R. que depende de la gran actividad de turismo marino que viene a nuestras costas año tras año durante los meses de marzo a abril.

Esta bonanza económica es la que mantiene a flote no tan solo a los Pescadores Comerciales si no también a cientos de restaurantes, hospederías, pescaderías y comercio local en general que dependen precisamente del acceso al mar que ofrece la zona.

Ya los peces están siendo protegidos y el reclamo ambientalista ha sido atendido.

Vamos pues a proteger a nuestro recurso humano y económico permitiendo un acceso responsable al mar a los Pescadores Comerciales, Recreacionales y Operadores de Charters de P.R.

Acción 6: Modificar las Actividades de Pesca con Fisga

Entendemos que en esta Acción es pertinente proponer una quinta alternativa que debería leer de la siguiente forma:

Alternativa 5: Prohibir la pesca con fisga de todas las especies durante la época de veda establecida en la Acción 1 en las 3 áreas, entiéndase Bajo de Cico, Tourmaline y Abrir la Sierra.

Si los Pescadores Comerciales no pueden figar nadie debería hacerlo. Además esta acción eliminaría el riesgo y la tentación a figar peces de arrecife de no encontrar especies altamente migratorias en el área durante el periodo de veda.

Queremos hacer un aparte y recordarle al Consejo de Pesca que el propósito principal de estas acciones es que se abra uniformemente la columna de agua o sea la superficie, se permita el transito y la pesca en la superficie y a la misma vez proteger el fondo y las especies protegidas.

Esto ha funcionado en el Bajo de Cico y queremos una réplica de este manejo en el Tourmaline y Abrir la Sierra pero solamente con una veda durante los meses de diciembre hasta el último día de febrero en las tres áreas.

ATTACHMENT A

ATTENDEES

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

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VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 de julio de 2014

NOMBRE Alexis Loyola González

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL Urb. Valle Verde calle 4 D-9 00683

E-MAIL loyola668@gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☒ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

No estoy de acuerdo que aumenten los meses de veda de abrir la cierra soy pescado comercia con numero de licencia 6038 y vivo de la pesca de estos lugares en especial la sama y pargas si me sierra la ~~[illegible]~~ et abrir la sierra no puedo pescar la sama por 9 meses y que estaria cerrada desde octubre a junio que termine la veda de sama

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
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VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 julio 2014

NOMBRE Natalia Lartigaut

ORGANIZACION QUE REPRESENTA Independiente

DIRECCION POSTAL PO Box 658 Boqueron PR 00622

E-MAIL nlartigaut1@gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☐ **NO** ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Acción 1 Entiendo que las vedas deben ser de diciembre a febrero en las tres areas (Alt. #2.) Acción #2 la Alt. 2. Acción #3 Alternativa #4. Acción #4 No anclaje alt. 3. Acción #5 Alt. 5. Si debe permitir la pesca de corrida ya que no afectaría al agregamiento de las especies. Acción #6 De acuerdo con la proposición de el Sr. Nelson.

FIRMA Natalia

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

(14)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
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VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 de julio de 2014

NOMBRE Miguel G. Rivera

ORGANIZACION QUE REPRESENTA independiente

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DESEO HACER COMENTARIOS ORALES: SI ☒ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

sobre el cierre completo de la Baja 6,

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

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CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
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VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/Jul/2014

NOMBRE Raimundo Espinoza

ORGANIZACION QUE REPRESENTA TNC

DIRECCION POSTAL 806 Calle Lafayette
San Juan, PR 00909

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Accion 6 - Opcion preferida debe incluir al Pez Leon con las especies de HMS, que se permite pescar o con permiso especifico de pesca para Pez Leon.

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

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VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/14

NOMBRE EVAN TUOHY

ORGANIZACION QUE REPRESENTA Myself

DIRECCION POSTAL PO Box 828
Rincon, PR 00677

E-MAIL evantuohy@gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☐ **NO** ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Making regulation the same for all three areas in question would simplify management and enforcement actions. This would also make regulations more clear to area fishermen.

FIRMA
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

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CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
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VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/14

NOMBRE Miguel Vargas Valle

ORGANIZACION QUE REPRESENTA Pescador Comercial Villa Pesquera Rinco

DIRECCION POSTAL Apt 1071 Rincon
Barrio Barrero

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Estamos Total mente de acuerdo y respaldamos en su Totalidad las expreciones dadas por el pescador Nelson Crespo

FIRMA Miguel A Vargas Valle
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

(38)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18-07-2014

NOMBRE Jaime Dávila Medina

ORGANIZACION QUE REPRESENTA Pesca de Arpón

DIRECCION POSTAL 179 Jardín de Paraiso, Urb. Jardines de Vega Baja P.R. 00698

E-MAIL davilajaime30@yahoo.com

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Dejar vigente el reglamento que está actualmente.

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

NOTA: SUSTITUIR

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 de julio de 2014

NOMBRE Miguel G. Rivera

ORGANIZACION QUE REPRESENTA independiente

DIRECCION POSTAL P.O. Box 658, Boqueron, P.R. 00622

E-MAIL m-g-rivers @ Hotmail.com

DESEO HACER COMENTARIOS ORALES: SI ☒ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Total de acuerdo con los comentarios del companero Nelson, y Andres, Pero tener en cuenta que deven abrir la pesca de corrida entiendece petos, dorados. en las zonas no Fishing zone, Y dejar las vedas de dic/Feb.

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

⑳

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 | 7 | 14

NOMBRE Chelsea Harms

ORGANIZACION QUE REPRESENTA recreational diver

DIRECCION POSTAL PO BOX 828, Rincon 00677

E-MAIL chelsea.harms@upr.edu

DESEO HACER COMENTARIOS ORALES: SI ☐ **NO** ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Recreational diver & resident of Rincon. I've never seen a Nassau grouper and would like to. I support the further protection of the spawning aggregations.

FIRMA Chelsea Harms
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

⑮

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 17 de Julio 2014

NOMBRE Robert Long

ORGANIZACION QUE REPRESENTA Pueblo-Recreativo

DIRECCION POSTAL

E-MAIL abga17@yahoo.com

DESEO HACER COMENTARIOS ORALES: SI ☑ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

④

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18- Julio 2014

NOMBRE Felix M Castro Hndz

ORGANIZACION QUE REPRESENTA Pezcador comercial

DIRECCION POSTAL Bo. Espinel calle A B24-16
Aguada P.R. 00602

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☒ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

㉖

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7/18/2014

NOMBRE José B. Conde

ORGANIZACION QUE REPRESENTA ______

DIRECCION POSTAL #22 Calle Eugenio Cesani
Urb Reperto San Francisco, Mayagüez, P.R. 00682

E-MAIL josebconde@hotmail.COM

DESEO HACER COMENTARIOS ORALES: SI ☐ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA José B. C

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

㊴

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA ____________

NOMBRE Luis E Rodriguez (rodriguez)

ORGANIZACION QUE REPRESENTA ____________

DIRECCION POSTAL HC 5 Box 5830 mayagues

E-MAIL ____________

DESEO HACER COMENTARIOS ORALES: SI ☒ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA ____________

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

36

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/Jul/14

NOMBRE Pedro Silva

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL Calle Caracol #723 Mani
May. PR.

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☒ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Pedro E Silva

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

30

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 07/18/2014

NOMBRE Alexis Lopez

ORGANIZACION QUE REPRESENTA Independent

DIRECCION POSTAL 1135 AVE General Ramos san antonio
Aguadilla

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☑ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Alexis Lopez
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 JU/14

NOMBRE RICHARD JAECK

ORGANIZACION QUE REPRESENTA —

DIRECCION POSTAL EXT. LA RUEDA #44
MIRADERO - MAYAGUEZ PR 00682

E-MAIL BIGFISHJAECK@GMAIL.COM

DESEO HACER COMENTARIOS ORALES: SI ☑ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

㉖

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
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VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18-Julio-2014

NOMBRE Victor Padilla Santiago

ORGANIZACION QUE REPRESENTA Barrio El Seco

DIRECCION POSTAL Boulevard del Carmen #94
El Seco mayagüez P.R.

E-MAIL victor77Padilla@Gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☒ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA Fri 18 - July

NOMBRE Fred Lentz

ORGANIZACION QUE REPRESENTA Me Myself & I

DIRECCION POSTAL PO Box 1077
Rincon PR 00677

E-MAIL lobsterrancher @ AoL . com

DESEO HACER COMENTARIOS ORALES: SI ☒ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

②

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7-18-14

NOMBRE Andrés Mallonado

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL Hc-02 Box 2204
Boquerón PR 00622-

E-MAIL andres.scuba@Gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☑ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

③

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7-18-2014

NOMBRE Nelson Crespo

ORGANIZACION QUE REPRESENTA Villa Pesq. Rincón, Unión Pesc. Com. Rincón, Asoc. Pesc. Pargo Profun

DIRECCION POSTAL P.O. Box 533
Rincón, P.R. 00677.

E-MAIL RCFUNION@YAHOO.COM

DESEO HACER COMENTARIOS ORALES: SI ☒ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

①

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 2014

NOMBRE Michelle Schärer

ORGANIZACION QUE REPRESENTA MISMA

DIRECCION POSTAL P.O. Box 1442
Boquerón, PR 00622

E-MAIL m-scharer@hotmail.com

DESEO HACER COMENTARIOS ORALES: SI ☒ **NO** ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA MSchärer

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

(3)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7-18-14

NOMBRE Andrés Maldonado Phi

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL HC-02 box 2204
Boqueron Pr 00622

E-MAIL andresmanuel3773@gmail.com

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

6

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 2014

NOMBRE Eugenio Piñeiro-Soler

ORGANIZACION QUE REPRESENTA CFMC

DIRECCION POSTAL

E-MAIL GPSFISH@yahoo.com

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☑

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

7

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18-7-14

NOMBRE José E Altiery Nogueras

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL HC 02 Box 5553 Rincon PR

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA José Altiery

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

(10)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Jul. 2014

NOMBRE Hector Soto Soto

ORGANIZACION QUE REPRESENTA Pescador de aguada

DIRECCION POSTAL Bo. Espinar Buzón #119
Aguada P.R. 00602

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

11

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA ____________

NOMBRE Rafael Ramos Rivera

ORGANIZACION QUE REPRESENTA mani mayagüez

DIRECCION POSTAL elena segarra 86 mani mayaguez

E-MAIL ____________

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Rafael Ramos Rivera

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

12

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 17/07/2014

NOMBRE Joel Rodriguez Delestres

ORGANIZACION QUE REPRESENTA el mani Paola

DIRECCION POSTAL Barrio mani Calle Gaviota
Buzon # 2007 Mayagüez P.R.

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☑

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Joel Rodz
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

3

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 2014

NOMBRE Wilfredo Gerena Arroyo

ORGANIZACION QUE REPRESENTA ____________________

DIRECCION POSTAL 1138-2 AVE General Ramey SAN Antonio PR 00690

E-MAIL ____________________

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Wilfredo Gerena Arroyo

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

16

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 julio 2014

NOMBRE Ricardo López Ortiz

ORGANIZACION QUE REPRESENTA DRNA

DIRECCION POSTAL

E-MAIL rlopez@drna.gobierno.pr

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Sin comentarios hasta ahora

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

⑰

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Jul. 2014

NOMBRE José A. Melero

ORGANIZACIÓN QUE REPRESENTA Pescadores de Aguada

DIRECCION POSTAL Sector Caracol #2
Bo Espinal Aguada P.R. 00602

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☐

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

(18)

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/Julio/2014

NOMBRE JUAN L. Quiñones Hernandez

ORGANIZACION QUE REPRESENTA Pescador de Aguada

DIRECCION POSTAL Barrio Espinal Buzón 7-A
Aguada P.R. 00602

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DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☑

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Juan L Quiñones Hdz
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

19

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/14

NOMBRE William Badillo Jr

ORGANIZACION QUE REPRESENTA

DIRECCION POSTAL Bo Espinal aguada BB: 8B
00602

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DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

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41

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VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 /Julio /2014

NOMBRE Aurora Justiniano Santos

ORGANIZACION QUE REPRESENTA The Nature Conservancy

DIRECCION POSTAL ______

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DESEO HACER COMENTARIOS ORALES: SI ☐ **NO** ☑

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(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

2

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VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18-7-14

NOMBRE Noel Medina Doncell

ORGANIZACION QUE REPRESENTA pescador de Aguada

DIRECCION POSTAL P.O Box 1040
Aguada PR 00602

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☑

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

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(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

22

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/2014

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DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

25

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7/18/14

NOMBRE José A. Rivera

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

Vengo a escuchar opinion de pescadores principalmente

FIRMA J A Rivera
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

28

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18-7-14

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9

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 2014

NOMBRE Hector L. Benitez

ORGANIZACION QUE REPRESENTA Propia

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E-MAIL benitez4745@gmail.com

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

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CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

31

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/14

NOMBRE Noel Villanueva Valentín

ORGANIZACION QUE REPRESENTA Pescadería de Rincón y Aguadil

DIRECCION POSTAL 2740 playuela

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Noel Villanueva Valentín

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

37

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/14

NOMBRE alfredo morales Hernandez

ORGANIZACION QUE REPRESENTA Pescador de Rincon i aguadil

DIRECCION POSTAL 214 Playa India

E-MAIL

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA alfredo morales Hernandez
(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

33

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 14

NOMBRE Jossi O Altiery Carrert

ORGANIZACION QUE REPRESENTA Villa pesquera de Rincon

DIRECCION POSTAL Hc02 Box 5588 00677 Rincon

E-MAIL Mgc.diva@hotmail.com

DESEO HACER COMENTARIOS ORALES: SI ☐ NO ☒

COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

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(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

34

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
270 AVE. MUÑOZ RIVERA OFICINA 401
SAN JUAN PR 00918-1903

VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18 Julio 2014

NOMBRE [illegible]

ORGANIZACION QUE REPRESENTA Villa pesquera Rincón

DIRECCION POSTAL Box Barrio 5588; HC02 00622

E-MAIL

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

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(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
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VISTA PÚBLICA

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VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 18/7/014

NOMBRE Jonathon Muñiz

ORGANIZACION QUE REPRESENTA Villa pezquera Rincon

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA Jonathan Muniz

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

㊲

CONSEJO DE ADMINISTRACIÓN PESQUERA DEL CARIBE
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SAN JUAN PR 00918-1903

VISTA PÚBLICA

CONSIDERACIÓN DEL BORRADOR PARA DESARROLLAR REGLAMENTACIÓN CONSISTENTE EN LAS TRES ÁREAS CON VEDAS TEMPORERAS DE PESCA AL OESTE DE PUERTO RICO: ABRIR LA SIERRA, BAJO DE SICO Y TOURMALINE

VIERNES, 18 DE JULIO DE 2014

7:00 PM – 10:00 PM - MAYAGÜEZ HOLIDAY INN

FECHA 7-18

NOMBRE Hommy VELEZ (PulPO)

ORGANIZACION QUE REPRESENTA QuebraDilla SpeaHunterTeam (Pesca DE Arpon

DIRECCION POSTAL Villa Julia

Quebradillas

E-MAIL HommySub@HotMail.com

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COMENTARIOS ESCRITOS SOBRE ESTAS ALTERNATIVAS:

FIRMA

(PUEDE CONTINUAR SUS COMENTARIOS AL DORSO)

ATTACHMENT B

WRITTEN COMMENTS RECEIVED
AFTER THE PUBLIC HEARING

AS OF 7/30/14

Fw: comments ammendment #15 -RE: ABT
Graciela Garcia-Moliner
Jul 22 at 6:02 PM
To Britni LaVine - NOAA Federal Bill Arnold - NOAA Federal Miguel Lugo 2 More...
Hola
FYI!
====================
Graciela García-Moliner, Ph.D.
FMP and Habitat Specialist
Caribbean Fishery Management Council
270 Muñoz Rivera Avenue, Suite 401
San Juan, Puerto Rico 00918
Tel: 787-766-5926
Fax: 787-766-6239

----- Forwarded Message -----
From: javier privado <javiershdz@yahoo.com>
To: "graciela_cfmc@yahoo.com" <graciela_cfmc@yahoo.com>; "carlosfarchette@gmail.com" <carlosfarchette@gmail.com>; "rcfunion@yahoo.com" <rcfunion@yahoo.com>; "Lablanchard1st@gmail.com" <Lablanchard1st@gmail.com>; "gpsfish@yahoo.com" <gpsfish@yahoo.com>; "Roy.Crabtree@noaa.gov" <Roy.Crabtree@noaa.gov>; "phil.steele@noaa.gov" <phil.steele@noaa.gov>; "bill.arnold@noaa.gov" <bill.arnold@noaa.gov>; "alicia.barnes@dpnr.vi.gov" <alicia.barnes@dpnr.vi.gov>; "roy.pemberton@dpnr.vi.gov" <roy.pemberton@dpnr.vi.gov>; "cguerrero@drna.gobierno.pr" <cguerrero@drna.gobierno.pr>; "magarcia@drna.gobierno.pr" <magarcia@drna.gobierno.pr>
Sent: Tuesday, July 22, 2014 12:13 PM
Subject: comments ammendment #15

TO: Dra. Graciela García-Moliner, Carlos Farchette, Nelson R. Crespo, Louis Blanchard, Eugenio Pineiro, Roy E. Crabtree, Phil Steele, Bill Arnold, Miguel Garcia, Carmen Guerrero, Marcos Hanke, Ms. Alicia V. Barnesand Roy Pemberton.

VIA EMAIL: graciela_cfmc@yahoo.com,carlosfarchette@gmail.com, rcfunion@yahoo.com,Lablanchard1st@gmail.com, gpsfish@yahoo.com,Roy.Crabtree@noaa.gov, phil.steele@noaa.gov,bill.arnold@noaa.gov, alicia.barnes@dpnr.vi.gov,roy.pemberton@dpnr.vi.gov, cguerrero@drna.gobierno.pr, magarcia@drna.gobierno.pr

RE: Comments in the matter related to modifications of the areas known as Abrir la Sierra, Bajo de Sico andTorumaline

I would like to start in the matter of the complexity of the actions proposed. Since they are to become regulations their language has to be clear and their explanations simple. None of this is achieved with what is being proposed. Although uniformity of the 3 areas is what's best, this cannot be achieved by affecting negatively recreational and commercial fishermen. That adverse effect is what is the direct effect of the propose actions.

First of all the public hearings are to be an objective and neutral space for fishermen to express their views,opinions and points of interests, on the actions proposed. A public hearing cannot be a one side show. How can fishermen have an objective and real chance of having their opinions heard when some of the persons who spoke their opinions at the hearing arte the same persons the council uses for "scientific" data base for the documentDeveloping Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajode Sico, and Tourmaline Bank or when they are the same persons who are going to emit a vote as council member.A public hearing is for listening to the persons affected by what is proposed, not to hear what the council proposings' opinion is. The july 18th public hearing of the council did not comply with basic administrative standards, rules and regulations and by that any regulation decided in the future based on that meeting is null. The 18th of july public hearing did NOT take to account nor considered the opinions of the fishermen expressed on the scope meetings celebrated on the month of april 2014 by the council.

Second, the proposed actions specially the "preferred" ones by the council are to have a clear and adverse economic effect on recreational and commercial fishermen alike. That adverse economic effect is then to be added to our already damaged local economy. There is no scientific data base in the draft council document titledDeveloping Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajode Sico, and Tourmaline Bank that the actions proposed are really necessary for protection. Except; for the general prohibition on anchoring on the 3 areas and the more uniform regulatory process for law enforcement purposes.For example one of the "scientific" publications of "Sulka-Sullivan" cited (http://www.sefsc.noaa.gov/sedar/download/S19_RD11_Sluka%20and%20Sullivan%201998.pdf?id=DOCUMENT) of 1998, clearly establishe that prohibiting spear fishing exclusively on a certain area is not a solution for recovering fishing populations and on the other hand the council on Action 6's proposal recommends a ban on spear fishing exclusively on the 3 areas. When, the publication by "Sulka-Sullivan" concludes that spearfishing has not more nor less the same effect on fish populations that other fishing techniques.

I do believe that protecting reef fish for certain times a year is a most and should be the fundamental position for any action proposed by the council. By that I propose the following actions to be considered by the council: 1) Thesame closing dates for all 3 areas in which fishing (not possession) for reef fish is banned at the 3 areas. I do not endorse banning possession, because that could cause a higher risk or economic cost for vessels fishing the areas surrounding the protected ones. Closing date should be limited to 4 months only, January 1st to the 30th of april. This date is consistent with local state regulations and would create uniformity on state and federal regulations on the 3 areas and also takes in to consideration the economic impact of the closing on recreational and commercial fishermen, 2) Allow fishing for Higly Migratory Species and for coastal migratory pelagics year round on all 3 areas. There is no scientific base or data that suggests to the contrary. Fishing for Higly Migratory Species and for coastal migratory pelagics should allowed with any fishing technique not susceptible to affect reef fish (i.e. trolling, spear fishing, vertical jigging, etc.). Fishing techniques allowed should be considered to not have an effect on corals, the bottom habitat and reef fish,the 3 things the proposed actions are trying to protect, 3) Prohibit anchoring on the 3 areas year around, except for the use of moorings, 4)

Permit year round fishing for lobster with the prohibition of the use of nets, gillnets and bottom long lines.

With these proposed alternatives all interests are protected and the weight of the regulation considering the environment and the economic facto is well balanced.

RE: Comentarios en el asunto relacionado a modificaciones del las áreas conocidas como Abrir La Sierra, Bajo de Sico y Tourmaline

Quisiera comenzar con el expresar que las acciones propuestas resultan muy complejas para el entendimiento. Como van a ser regulaciones su lenguaje tiene que ser claro, preciso y simple al entendimiento. Ninguna de las acciones propuestas cumplen con estos propósitos antes mencionados. Aunque la uniformidad de las 3 areas es lo mas recomendado, este propósito no se puede lograr afectando adversamente a tanto Pescadores recreacionales como a comerciales. Las acciones propuestas por el consejo tienen un efecto demasiado adversos sobre los Pescadores recreacionales y comerciales.

Primero, las vistas públicas son espacios objetivos y neutrales para que los pescadores (que son quienes se van a ver adversamente afectados) expresen sus opiniones, puntos de vista y de interés sobre las acciones propuestas. Una vista pública no puede ser un espectáculo de un solo lado. Como los pescadores pueden tener una oportunidad objetiva y real de que sus opiniones sean escuchadas cuando las mismas personas que expresan su opinión en la vista son las mismas personas que el consejo utiliza como base científica para su documento borrador base, "Developing ConsistentRegulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and TourmalineBank" o cuando son las mismas persona que van a emitir su voto como miembros del consejo. Que parcialidad hay en una vista asi? Ninguna. El fin de una vista pública es para que las personas que se van a ver adversamente afectadas por lo propuesto expresen sus opiniones; no es para saber cuál es la opinión de la proposición del consejo. La vista del pasado 18 de julio de 2014 no cumplió con las regulaciones, estándares y reglas administrativas básicas y cualquier decisión que se tome en base a esta es nula. La vista del 18 de julio no tomo en consideración las opiniones de los Pescadores comerciales o recreacionales que fueron expresadas en los "scope meetings" celebrados en los meses de abril de 2014 por el consejo.

Segundo, las acciones propuestas, especialmente las "preferidas" por el consejo, van a tener un efectoeconómico claro y adverso sobre los pescadores comerciales y recreacionales. Ese efecto económicoadverso se añadirá a nuestra ya maltrecha economía local. No hay base científica en el borrador del documento del consejo titulado, "Developing Consistent Regulationsfor Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico and Tourmaline Bank que sustente que las acciones propuestas son realmente necesarias. Excepto, la prohibición general de anclaje y la regulación general uniforme para las 3 areas para propósitos de ejecución de la ley. Por ejemplo lapublicación científica utilizada por el consejo de "Sulka-Sullivan" de 1998(http://www.sefsc.noaa.gov/sedar/download/S19_RD11_Sluka%20and%20Sullivan%201998.pdf?id

=DOCUMENT)claramente establece que la prohibición exclusiva de la pesca con arpón (fisga) en un área especifica no es una solución para la recuperación de las poblaciones de pecesy por el otro lado el consejo en la propuesta Acción #6 recomienda la prohibición exclusiva de la pesca con arpon(fisga) en las 3 áreas. Esto, aun cuando la publicación de"Sulka-Sullivan" concluye que la pesca con arpón (fisga) no tiene ni más ni menos efecto en las poblaciones de peces en comparación con las otras artes de pesca.

Si creo que proteger los peces de arrecife por cierto periodos del año es algo positive y necesario y debe ser laposición fundamental para cualquier acción propuesta por el consejo. Por lo tanto propongo las siguientes acciones para ser consideradas por el consejo: 1) Las 3 áreas sean cerradas por el mismo periodo del año prohibiendo en este periodo la pesca (no posesión) de peces de arrecife. No sugiero la prohibición de la posesión porque esto puede ocasionar un riesgo de seguridad y económico sobre embarcaciones que se encuentren en las areasadyacentes a las cerradas. La fechas de cierre sugeridas son del 1 de enero al 30 de abril. Estas fechas son consistentes con las regulaciones estatales y federales y crearía una regulación uniforme tanto estatal como federal en las 3 áreas y también toma en consideración el impacto económico de los cierres en los pescadores comerciales y recreacionales, 2) Se permita la pesca de las especies altamente migratorias y de especies costeras migratorias durante todo el año en las 3 áreas. No existe evidencia o data científica que sustente lo contrario. La pesca de especies altamente migratorias y de especies costeras migratorias debe ser permitida con cualquier arte de pesca que no sea susceptible a afectar adversamente a los peces de arrecife (i.e. pesca de corrida, pesca con arpón (fisga) y "jigging" vertical). Las técnicas de pesca permitidas deber ser consideradas para que no tengan un efecto adverso sobre los corales, el fondo marino o los peces de arrecife; o sea las 3 cosas que las acciones propuestas intentan proteger, 3) Se prohíba el anclaje en las 3 áreas todo el año, salvo con el uso de "moorings", 4) Que se permita la pesca de la langosta en las 3 áreastodo el año, excepto su pesca mediante el uso de nasas, redes o "bottom long lines.

Con estas alternativas propuestas todos los intereses se protegen y el peso en la regulación tomando en consideración el factor ambiental y el factor económico queda balanceado.

Sent from my iPhone

Subject:	Fw: Carta abierta en respuesta a los porpuestos cambios en las pesquerias del area oeste de PR
From:	Graciela Garcia-Moliner (graciela_cfmc@yahoo.com)
To:	britni.lavine@noaa.gov; bill.arnold@noaa.gov; miguel.lugo@noaa.gov; maria.lopez@noaa.gov;
Cc:	iris_oliveras_cfmc@yahoo.com;
Date:	Thursday, July 24, 2014 10:22 AM

Comments - ABT

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Graciela García-Moliner, Ph.D.
FMP and Habitat Specialist
Caribbean Fishery Management Council
270 Muñoz Rivera Avenue, Suite 401
San Juan, Puerto Rico 00918
Tel: 787-766-5926
Fax: 787-766-6239

----- Forwarded Message -----
From: Hector Sanchez <hectormsanchez.cpa@gmail.com>
To: graciela_cfmc@yahoo.com; carlosfarchette@gmail.com; rcfunion@yahoo.com; Lablanchard1st@gmail.com; gpsfish@yahoo.com; Roy.Crabtree@noaa.gov; phil.steele@noaa.gov; bill.arnold@noaa.gov; alicia.barnes@dpnr.vi.gov; roy.pemberton@dpnr.vi.gov; cguerrero@drna.gobierno.pr; magarcia@drna.gobierno.pr
Sent: Thursday, July 24, 2014 9:36 AM
Subject: Carta abierta en respuesta a los porpuestos cambios en las pesquerias del area oeste de PR

OPEN LETTER ADRESSED TO PUBLIC OFFICIALS REPONDING TO THEIR PLANNED ACTIONS TO IMPACT AND RESTRICT RECREATIONAL AND COMMERCIAL FISHING AREAS IN PUERTO RICO BASED ON PREJUDICE AND DISCRIMINATORY PRINCIPLES AND NOT ON ANY FORMAL SCIENTIFIC STUDIES.

CARTA ABIERTA DIRIGIDA A OFICIALES PUBLICOS EN RESPUESTA A SUS ACCIONES PLANIFICADAS DE IMPACTAR Y RESTRINGIR AREAS DE PESCA RECREATIVAS Y COMERCIALES EN PUERTO RICO BASANDOSE EN PREJUICIOS Y PREMISAS DISCRIMINATORIAS Y SIN TENER NINGUNA BASE CIENTIFICA FORMAL PARA JUSTIFICAR SUS PROPUESTAS ACCIONES.

TO: Dra. Graciela García-Moliner, Carlos Farchette, Nelson R. Crespo, Louis Blanchard, Eugenio Pineiro, Roy E. Crabtree, Phil Steele, Bill Arnold, Miguel Garcia, Carmen Guerrero, Marcos Hanke, Ms. Alicia V. Barnes and Roy Pemberton.

VIA EMAIL: graciela_cfmc@yahoo.com, carlosfarchette@gmail.com, rcfunion@yahoo.com, Lablanchard1st@gmail.com, gpsfish@yahoo.com, Roy.Crabtree@noaa.gov, phil.steele@noaa.gov, bill.arnold@noaa.gov, alicia.barnes@dpnr.vi.gov, roy.pemberton@dpnr.vi.gov, cguerrero@drna.gobierno.pr, magarcia@drna.gobierno.pr

RE: Comments in the matter related to modifications of the areas known as Abrir la Sierra, Bajo de Sico and Torumaline

Dear Sir(s) or Maddam(s),

I would like to start in the matter of the complexity of the actions proposed. Since they are to become regulations their language has to be clear and their explanations simple. None of this is achieved with what is being proposed. Although uniformity of the 3 areas is what's best, this cannot be achieved by affecting negatively recreational and commercial fishermen. That adverse effect is what is the direct effect of the propose actions.

First of all the public hearings are to be an objective and neutral space for fishermen to express their views, opinions and points of interests, on the actions proposed. A public hearing cannot be a one side show. How can fishermen have an objective and real chance of having their opinions heard when some of the persons who spoke their opinions at the hearing arte the same persons the council uses for "scientific" data base for the document *Developing Consistent Regulations for Three*

Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank or when they are the same persons who are going to emit a vote as council member. A public hearing is for listening to the persons affected by what is proposed, not to hear what the council proposing' opinion is. The July 18th public hearing of the council did not comply with basic administrative standards, rules and regulations and by that any regulation decided in the future based on that meeting is null. The 18th of July public hearing did NOT take to account nor considered the opinions of the fishermen expressed on the scope meetings celebrated on the month of April 2014 by the council.

Second, the proposed actions specially the "preferred" ones by the council are to have a clear and adverse economic effect on recreational and commercial fishermen alike. That adverse economic effect is then to be added to our already damaged local economy. There is no scientific data base in the draft council document titled *Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank t*hat the actions proposed are really necessary for protection. Except; for the general prohibition on anchoring on the 3 areas and the more uniform regulatory process for law enforcement purposes. For example one of the "scientific" publications of "Sulka-Sullivan" cited (http://www.sefsc.noaa.gov/sedar/download/S19_RD11_Sluka%20and%20Sullivan%20 1998.pdf?id=DOCUMENT) of 1998, clearly established that prohibiting spear fishing exclusively on a certain area is not a solution for recovering fishing populations and on the other hand the council on Action 6's proposal recommends a ban on spear fishing exclusively on the 3 areas. When, the publication by "Sulka-Sullivan" concludes that spear fishing has not more or less the same effect on fish populations those other fishing techniques.

I do believe that protecting reef fish for certain times a year is a most and should be the fundamental position for any action proposed by the council. By that I propose the following actions to be considered by the council: 1) the same closing dates for all 3 areas in which fishing (not possession) for reef fish is banned at the 3 areas. I do not endorse banning possession, because that could cause a higher risk or economic cost for vessels fishing the areas surrounding the protected ones. Closing date should be limited to 4 months only, January 1st to the 30th of April. This date is consistent with local state regulations and would create uniformity on state and federal regulations on the 3 areas and also takes in to consideration the economic impact of the closing on recreational and commercial fishermen, 2) Allow fishing for Highly Migratory Species and for coastal migratory pelagics year round on all 3 areas. There is no scientific base or data that suggests to the contrary. Fishing for Highly Migratory Species and for coastal migratory pelagics should allowed with any fishing technique not susceptible to affect reef fish (i.e. trolling, spear fishing, vertical jigging, etc.). Fishing techniques allowed should be considered to not have an effect on corals, the bottom habitat and reef fish, the 3 things the proposed actions are trying to protect, 3) Prohibit anchoring on the 3 areas year around, except for the use of moorings, 4) Permit year round fishing for lobster with the prohibition of the use of nets, gillnets and bottom long lines.

With these proposed alternatives all interests are protected and the weight of the regulation considering the environment and the economic facto is well balanced.

RE: Comentarios en el asunto relacionado a modificaciones del las áreas conocidas como Abrir La Sierra, Bajo de Sico y Tourmaline

Estimados Señores y Señoras,

Quisiera comenzar con el expresar que las acciones propuestas resultan muy complejas para el entendimiento. Como van a ser regulaciones su lenguaje tiene que ser claro, preciso y simple al entendimiento. Ninguna de las acciones propuestas cumple con estos propósitos antes mencionados. Aunque la uniformidad de las 3 áreas es lo más recomendado, este propósito no se puede lograr afectando adversamente a tanto Pescadores recreacionales como a comerciales. Las acciones propuestas por el consejo tienen un efecto demasiado adversos sobre los Pescadores recreacionales y comerciales.

Primero, las vistas públicas son espacios objetivos y neutrales para que los pescadores (que son quienes se van a ver adversamente afectados) expresen sus opiniones, puntos de vista y de interés sobre las acciones propuestas. Una vista pública no puede ser un espectáculo de un solo lado. Como los pescadores pueden tener una oportunidad objetiva y real de que sus opiniones sean escuchadas cuando las mismas personas que expresan su opinión en la vista son las mismas personas que el consejo utiliza como base científica para su documento borrador base, *"Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank"* o cuando son las mismas persona que van a emitir su voto como miembros del consejo. ¿Qué parcialidad hay en una vista así? Ninguna. El fin de una vista pública es para que las personas que se van a ver adversamente afectadas por lo propuesto expresen sus opiniones; no es para saber cuál es la opinión de la proposición del consejo. La vista del pasado 18 de julio de 2014 no cumplió con las regulaciones, estándares y reglas administrativas básicas y cualquier decisión que se tome en base a esta es nula. La vista del 18 de julio no tomo en consideración las opiniones de los Pescadores comerciales o recreacionales que fueron expresadas en los "scope meetings" celebrados en los meses de abril de 2014 por el consejo.

Segundo, las acciones propuestas, especialmente las "preferidas" por el consejo, van a tener un efecto económico claro y adverso sobre los pescadores comerciales y recreacionales. Ese efecto económico adverso se añadirá a nuestra ya maltrecha economía local. No hay base científica en el borrador del documento del consejo titulado, "*Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico and Tourmaline Bank* que sustente que las acciones propuestas son realmente necesarias. Excepto, la prohibición general de anclaje y la regulación general uniforme para las 3 áreas para propósitos de ejecución de la ley. Por ejemplo la publicación científica utilizada por el consejo de "Sulka-Sullivan" de 1998 (http://www.sefsc.noaa.gov/sedar/download/S19_RD11_Sluka%20and%20Sullivan%20 1998.pdf?id=DOCUMENT) claramente establece que la prohibición exclusiva de la pesca con arpón (fisga) en un área especifica no es una solución para la recuperación de las poblaciones de peces y por el otro lado el consejo en la propuesta Acción #6 recomienda la prohibición exclusiva de la pesca con arpón (fisga) en las 3 áreas. Esto, aun cuando la publicación de "Sulka-Sullivan" concluye que la pesca con arpón (fisga) no tiene ni más ni menos efecto en las poblaciones de peces en comparación con las otras artes de pesca.

Si creo que proteger los peces de arrecife por cierto periodos del año es algo positive y necesario y debe ser la posición fundamental para cualquier acción propuesta por el consejo. Por lo tanto propongo las siguientes acciones para ser consideradas por el consejo: 1) Las 3 áreas sean cerradas por el mismo periodo del año prohibiendo en este periodo la pesca (no posesión) de peces de arrecife. No sugiero la prohibición de la posesión porque esto puede ocasionar un riesgo de seguridad y económico sobre embarcaciones que se encuentren en las áreas adyacentes a las cerradas. Las fechas de cierre sugeridas son del 1 de enero al 30 de abril. Estas fechas son consistentes con las regulaciones estatales y federales y crearía una regulación uniforme tanto estatal como federal en las 3 áreas y también toma en consideración el impacto económico de los cierres en los pescadores comerciales y recreacionales, 2) Se permita la pesca de las especies altamente migratorias y de especies costeras migratorias durante todo el año en las 3 áreas. No existe evidencia o data científica que sustente lo contrario. La pesca de especies altamente migratorias y de especies costeras migratorias debe ser permitida con cualquier arte de pesca que no sea susceptible a afectar adversamente a los peces de arrecife (i.e. pesca de corrida, pesca con arpón (fisga) y "jigging" vertical). Las técnicas de pesca permitidas deber ser consideradas para que no tengan un efecto adverso sobre los corales, el fondo marino o los peces de arrecife; o sea las 3 cosas que las acciones propuestas intentan proteger, 3) Se prohíba el anclaje en las 3 áreas todo el año, salvo con el uso de "moorings", 4) Que se permita la pesca de la langosta en las 3 áreas todo el año, excepto su pesca mediante el uso de nasas, redes o "bottom long lines.

Con estas alternativas propuestas todos los intereses se protegen y el peso en la regulación tomando en consideración el factor ambiental y el factor económico queda balanceado.

Sincerely/Sinceramente,

Hector M. Sanchez Ortiz, CPA, CGMA, CFE

7/24/14

Subject: Aclaración sobre mi posición en vista cambios en áreas 6-8 y bajo de Cico.

From: Andres Maldonado (andres.scuba@gmail.com)

To: graciela_cfmc@yahoo.com;

Date: Friday, July 25, 2014 4:58 AM

Coincido en que si se prohibe el uso del arpón a comerciales,también se prohíba a recreacionales en el periodo de los tres(3) meses de cierre en estas áreas antes mencionadas. De esas áreas fue lo discutido en esa vista. Nunca dije ni diré que se prohíba el uso del arpón en otras áreas y sólo estuve de acuerdo en la prohibición durante el periodo de cierre,no permanentemente. Gracias.

—

Sent from Mailbox

Subject: RIN 0648-XD325; Scoping Comments, Comprehensive Amendment to the U.S. Caribbean FMPs: Annual Catch Limit Control Rule -- Msg. 1

From: Andrea Treece (atreece@earthjustice.org)

To: graciela_cfmc@yahoo.com; roy.crabtree@noaa.gov;

Date: Friday, July 25, 2014 3:35 PM

Dear Graciela and Roy,

Thank you for accepting the attached comments. Please do not hesitate to contact me if you have any difficulty opening any of the attachments. I am sending 10 documents in all – one comment letter and nine scientific sources. I will likely send these in 2-3 emails to avoid making the messages too large.

Thank you for your work. Have a great weekend.

Best regards,

Andrea

Attachments:

EJ-CBD-CORALations Comment letter

IUCN report Exec. Summary

IUCN report Part I

Steneck et al 2014

Andrea A. Treece

Staff Attorney, Oceans Program

Earthjustice

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NORTHWEST ROCKY MOUNTAIN WASHINGTON, D.C. INTERNATIONAL

Via Electronic Mail

July 25, 2014

Mr. Miguel A. Rolón, Executive Director
Caribbean Fishery Management Council
270 Muñoz Rivera Avenue, Suite 401
San Juan, Puerto Rico 00918–1903
graciela_cfmc@yahoo.com

Dr. Roy Crabtree, Director
NMFS Southeast Regional Office
263 13th Avenue South
Saint Petersburg, Florida 33701
roy.crabtree@noaa.gov

Subj.: RIN 0648–XD325; Scoping Comments, Comprehensive Amendment to the U.S. Caribbean Fishery Management Plans: Annual Catch Limit Control Rule

Dear Mr. Rolón and Dr. Crabtree:

On behalf of the Center for Biological Diversity, CORALations, and Earthjustice, we submit these scoping comments regarding the U.S. Caribbean Fishery Management Council's ("Council") Comprehensive Amendment to the U.S. Caribbean Fishery Management Plans: Annual Catch Limit Control Rule. We offer the following comments and scientific information in the interest of restoring vital U.S. Caribbean coral reef ecosystems and securing a viable long-term future for the fisheries that depend on them.

Overall, we believe that the range of alternatives for establishing annual catch limit ("ACL") control rules for U.S. Caribbean fisheries needs to be expanded to include approaches that fully account for scientific uncertainty and ecological impacts of those fisheries, as required by Magnuson-Stevens Fishery Conservation and Management Act ("MSA"). With respect to the proposed parrotfish ACL control rule in particular, the Council must consider additional alternatives that reflect the best available science, which shows that the removal of parrotfish due to fishing – and the resulting increases in algal abundance – continues to be a major cause of the failure of Caribbean coral reef ecosystems to recover after disturbance.

Specifically, recent studies confirm that parrotfish grazing is essential to maintaining and restoring coral reef habitat, and that a significantly greater biomass of parrotfish than currently exists is required to control algal growth now that coral cover is low. The Council should therefore: (1) consider implementing further reductions in the parrotfish ACL based on the level of grazing needed to recover coral habitat; and (2) consider establishing a management system that prohibits the targeting of parrotfish in sensitive reef habitats while allowing it in other areas.

The Council Must Consider More Conservative ACL Control Rules for All Species

One of the overarching aims of the Council's ACL control rule proposal – to allow fishers to harvest more of the overfishing limit ("OFL") for stocks that are not determined to be undergoing overfishing – is fundamentally flawed. Specifically, the May 2014 scoping document expressed the concern that "fishers may be getting penalized because they cannot harvest the true OFL, resulting in unnecessary economic loss."[1] This concern seems to be the basis for the general approach in the scoping document, which is to provide alternatives for ACL control rules that consist of variations on maintaining the status quo ACL formulae or on making these formulae less restrictive on fishing. While the July 7, 2014 revised version of the scoping document tweaks this language to say that fishers "do not have the opportunity to harvest at higher sustainable levels,"[2] the rationale remains flawed. As explained below, the OFL is an outer limit, not a target, and leaving a small buffer between the OFL and ACL for stocks that are data poor and known to experience ACL overages is not sustainable.

Designing management measures to allow fishers to harvest up to or very close to the OFL is not consistent with National Standard 1 ("NS1") of the Magnuson-Stevens Fishery Conservation and Management Act ("MSA"). Notably, NS1 guidelines allow for ACLs and OFLs to be equal to one another only under very limited circumstances, and allows NMFS to presume that these measures are inadequate to prevent overfishing when they are set equal to one another.[3] In most cases, fishers should *not* be harvesting the true OFL or even close to the OFL, particularly for data poor stocks.

Substantial buffers need to be implemented between the OFL and acceptable biological catch level ("ABC") to account for the substantial scientific uncertainty in estimating the OFL for most Caribbean stocks. ACLs must additionally account for management uncertainty in order to prevent overfishing, and ecological and socioeconomic impacts of fishing in order to be consistent with optimum yield ("OY"). When setting catch limits, the Council "must take an approach that considers uncertainty in scientific information and management control of the fishery . . . such that there is a low risk that limits are exceeded . . ."[4] Designing control rules so as to allow fishers to harvest the OFL or very close to it will, in all likelihood, fail to prevent overfishing in the U.S. Caribbean and will have adverse effects on the ecosystem and long-term viability of the fisheries.

While we understand that the Council wishes to maximize fishing opportunities, the Council must ensure first and foremost that its management measures prevent overfishing and ensure that ecological, social, and economic reductions from MSY are accounted for (i.e. achieve OY). The alternatives that the Council has proposed thus far are not consistent with MSA

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[1] Draft Comprehensive Amendment to U.S. Caribbean Fishery Management Plans: Annual Catch Limit Control Rule (May 2014) at 3.

[2] Draft Comprehensive Amendment to U.S. Caribbean Fishery Management Plans: Annual Catch Limit Control Rule (July 2014) at 3.

[3] 50 C.F.R. § 600.310(f)(5).

[4] 50 C.F.R. § 600.310(b)(3).

National Standard 1. Therefore, the Council must consider a broader range of alternatives for setting ACLs in the U.S. Caribbean fisheries. That range of alternatives must consider alternatives that use greater buffers to account for uncertainty and ecological importance.

The Council Must Consider Additional, More Conservative Alternatives for Parrotfish Management

Under the Council's preferred alternative, ACLs for parrotfish would be maintained at their current levels based on the methodology used in Amendment 5 to the U.S. Caribbean Reef Fish Fishery FMP. Under the current methodology, ACLs are based on island-specific ABC levels recommended by the Council's Scientific and Statistical Committee ("SSC") minus a 15% buffer that is meant to account for scientific uncertainty in the estimate of the ABC. The ACL for St. Croix is then reduced by additional 5.8822% in an attempt to account for uncertainty regarding the effects of the fishery on essential settlement substrate for elkhorn and staghorn corals. This method yields commercial annual catch limits of 240,000 lbs in St. Croix, 42,500 lbs in St. Thomas/St. John, and 52,737 lbs in Puerto Rico.[5]

While these ACLs may have been sufficient to stop parrotfish from undergoing overfishing as it is currently defined under the MSA, they are likely not sufficient to end the ecosystem overfishing that has contributed to the rise of fleshy macroalgae that stresses corals and reduces their ability to recover after disturbance. In so doing, ecosystem overfishing of parrotfish can lead to a decline of critical fisheries habitat. Reef habitat around the U.S. Caribbean has been significantly degraded in recent decades, with less than 10% coral cover in most areas and a corresponding drop in the number, size, and diversity of fish species.[6] This trend is unlikely to stop unless fishery managers and water quality managers implement aggressive, forward-looking conservation measures. Restoring coral reef habitat is crucial not only for the corals themselves but for the fisheries they support.

Until now, NMFS has been operating under the assumption that fishing for parrotfish is a "moderate" threat to elkhorn and staghorn corals and their habitat, and that the main threats to these species are climate change, disease, and hurricanes. In point of fact, NMFS used this assumption as the fundamental basis for its determination in 2011 that continued fishing for parrotfish and other herbivores was not likely to jeopardize the continued existence of elkhorn and staghorn corals or adversely modify their critical habitat.[7]

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[5] Draft Comprehensive Amendment to U.S. Caribbean Fishery Management Plans: Annual Catch Limit Control Rule (July 2014) at 13, 32.

[6] J.B.C. Jackson, M.K. Donovan, K.L. Cramer and W. Lam (editors) (2014), Status and Trends of Caribbean Coral Reefs: 1970-2012, Global Coral Reef Monitoring Network, International Union for the Conservation of Nature, Gland, Switzerland, 304 pp. Available at: http://cmsdata.iucn.org/downloads/caribbean_coral_reefs___status_report_1970_2012 , Part I at 2.

[7] NMFS, Biological Opinion re Continued Authorization of Reef Fish Fishing Managed under the Reef Fish Fishery Management Plan (FMP) of Puerto Rico and the U.S. Virgin Islands (CRFFMP) (Oct. 4, 2011) at 175-79.

However, a new, comprehensive report issued by the International Union for Conservation of Nature ("IUCN") directly refutes NMFS's assumption. The IUCN report, which was co-authored by 90 experts, analyzed Caribbean coral reef data from more than 35,000 quantitative reef surveys and examined coral reef stressors and trends over time. Having undertaken this exhaustive analysis, the authors concluded:

> Our results contradict much of the rhetoric about the importance of ocean warming, disease, and hurricanes on coral reefs and emphasize the critical importance of historical perspective for coral reef management and conservation. The threats of climate change and ocean acidification loom increasingly ominously for the future, but *local stressors including an explosion in tourism, overfishing, and the resulting increase in macroalgae have been the major drivers of the catastrophic decline of Caribbean corals up until today.*[8]

Based on these findings, the IUCN recommended four major actions, including : "Adopt[ing] robust conservation and fisheries management strategies that lead to the restoration of parrotfish populations, including the listing of the parrotfish in relevant annexes of the Protocol concerning Specially Protected Areas and Wildlife (SPAW protocol) of the UNEP Caribbean Environment Programme."[9] The authors stressed that such measures were urgently necessary:

> We understand that action upon these recommendations will be a matter of local and national socioeconomic and political debate. But the implications of our scientific results are unmistakable: *Caribbean coral reefs and their associated resources will virtually disappear within just a few decades unless all of these measures are promptly adopted and enforced.*[10]

It has already been established that removing herbivores from a coral reef leads to increased algal growth and decreased coral cover, and that this in turn decreases herbivorous fish biomass, resulting in what has been dubbed a "death spiral."[11] Until recently, the precise mechanism by which this happens had not been studied in the wild. Notably, however, a recent study by Steneck et al. (2014) mimicked the effects of fishing for parrotfish by excluding larger parrotfish from grazing on particular areas; smaller parrotfish and other kinds of grazers were not excluded. The researchers measured algal growth and coral recruitment inside and outside the exclusion areas after one year. They found that "a modest reduction in grazing is sufficient to shut down coral recruitment."[12] They explained how fishing for parrotfish can switch a reef toward – or maintain a reef in – an algal-dominated state: "modest reductions only in herbivory from large parrotfish allow macroalgae to bloom, which creates a bottleneck in the process of

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[8] Jackson, et al. (2014), *supra* note 6, Exec. Summary at 14 (emphasis added).

[9] *Id.*

[10] *Id.* (emphasis in original).

[11] *See, e.g.,* M.E. Hay and D.B. Rasher (2010), Coral reefs in crisis: reversing the biotic death spiral, Biology Reports, 2:71, doi:10.3410/B2-71.

[12] R.S. Steneck, S.N. Arnold, and P.J. Mumby (2014) Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors, *Mar. Ecol. Prog. Ser.*, 506:115-127.

coral recruitment" and thereby drives condition that slow or stop coral recovery.[13] In other words – very importantly – parrotfish do not have to be "overfished" in order to be reduced to a level at which they can no longer effectively control algal growth enough to provide space for coral recruitment.

Moreover, maintaining parrotfish catch at historic levels, or even somewhat lower levels, is not sufficient to protect coral habitat and promote recruitment. This is particularly the case in areas such as the U.S. Caribbean where reefs are already in an algal-dominated state with relatively low coral cover. A number of scientists have noted that when coral cover is low, more herbivores are needed to reduce algal cover, create space for corals, and thus allow for coral recruitment, growth, and recovery.[14] In fact, Edwards et al. (2013) explained:

> Because of global declines in coral cover, benthic reef communities today probably have much more algae present than they did in the past. Thus, a much greater area needs to be grazed to maintain low algal standing stock and allow coral recruitment, survival and growth. *Resource managers therefore need to manage herbivore populations to be much larger than they ever were naturally, in order to effectively control algal abundance on degraded reefs.*[15]

The IUCN report further underscores that comparing current parrotfish and coral populations to the 1970s does not provide a meaningful baseline for healthy coral reefs and fish populations. "Most of the degradation of Caribbean reefs occurred between the 1970s to early 1990s[,]well before most ecological surveys began" and "[p]hase shifts from greater coral to greater macroalgal abundance happened early and geographically pervasive."[16] This observation further undermines the assumption in NMFS's 2011 Biological Opinion that *Diadema* was or is a more significant grazer than parrotfish on U.S. Caribbean reefs. To the contrary, the report authors found that *Diadema* was the predominant grazer on reefs that were already overfished by the 1970s. Had parrotfish populations been more robust at the time, the phase shift toward algal abundance and decline in elkhorn and staghorn corals might not have been so rapid.

Furthermore, the IUCN study supports existing scientific evidence that algal growth on coral reefs promotes the spread of disease on Caribbean coral reefs and renders corals less resilient to the effects of heat stress. The report noted that corals in the U.S. Virgin Islands and Puerto Rico suffered much greater coral mortality after milder episodes of thermal stress (measured as "degree heating weeks" or "DHW") than corals in other areas that experienced

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[13] *Id.*; *see also* S.N. Arnold, R.S. Steneck, and P.J. Mumby (2010), Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment, *Mar. Ecol. Prog. Ser.* 414: 91-105.

[14] Steneck et al. (2014), *supra* note 12; C.B. Edwards, et al. (2013), Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects, *Proc. R. Soc. B*, 281:20131835, *available at* http://rspb.royalsocietypublishing.org/subscriptions; I.D. Williams, et al. (2001), Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize, *Mar. Ecol. Prog. Ser.*, 222:187-196.

[15] Edwards et al. (2013), *supra* note 14. (emphasis added)

[16] Jackson, et al. (2014), *supra* note 6, Part I at 39.

more severe temperature events. The report concluded that "Coral mortality in the USVI and Puerto Rico after 2005 was due primarily to outbreaks of coral disease. . . . We postulate that these greater losses in the USVI and Puerto Rico may reflect regional differences in macroalgal abundance, which is generally considerably lower in the southern Caribbean."[17] The authors also noted that overfishing also appears to inhibit the capacity of reefs to recover from hurricane damage, noting that the locations where coral has failed to reestablish after major storms are also those that are most severely overfished.[18] On the other hand, increasing herbivorous fish populations may facilitate faster recovery of corals after climate-induced disturbances.[19]

NMFS and the Council have a duty under the Endangered Species Act and MSA to base conservation and management measures on the best available science, which these studies represent. As explained above, the best scientific information currently available runs directly counter to NMFS's prior assessment of status quo parrotfish ACLs on elkhorn and staghorn corals and their critical habitat. This is "new information [that] reveals effects of the action that may affect listed species or critical habitat in a manner or to an extent not previously considered."[20] Therefore, as mandated by its own regulations, NMFS must reassess whether the level of parrotfish removal it has authorized under status quo parrotfish ACLs is likely to jeopardize these corals or adversely modify their critical habitat.

Even more importantly, the Council and NMFS must pursue additional, science-based fishery management measures to recover U.S. Caribbean coral reefs and thereby ensure the long-term sustainability of the fishery. One option that has been successfully employed in Bonaire, Belize, and Turks and Caicos is to ban the harvest of all parrotfish. Such a measure would be fully justified by science and the experience of other islands, and simple to enforce. We recognize, however, that such a measure could have significant economic and social impacts on St. Croix. Another option is to significantly reduce catch limits for parrotfish to a level that allows sufficient grazing to significantly reduce algal cover and foster coral recruitment. A third option, presented by Dr. Peter Mumby to the Southeast Fisheries Science Center this spring, would be to prohibit the capture of parrotfish in *Orbicella* reefs but allow it in gorgonian plains, where grazing by parrotfish is not thought to be an important driver of algal cover or coral recruitment.[21] Such an approach merits further investigation, as it could provide an ecologically sound interim measure to reduce the impacts of parrotfish fishing on coral habitat while allowing some harvest of parrotfish to continue.

Finally, the Council must establish effective accountability measures to ensure that whatever ACLs or other management measures it develops achieve their purpose of preventing overfishing and promoting ecosystem health. To this end, the Council should require species-specific reporting of parrotfish catches as well as length data. This information would promote

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[17] *Id.*, Part I at 35.

[18] *Id.*, Part I at 45.

[19] *See, e.g.*, P.J. Mumby and A.R. Harborne (2010), Marine reserves enhance the recovery of corals on Caribbean reefs, *PLoS ONE* 5(1): e8657, doi: 10.1371/journal.pone.0008657.

[20] 50 C.F.R. § 402.16(b).

[21] P.J. Mumby (2014), Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs, *Fish and Fisheries*, doi:10.1111/faf.12078.

compliance with existing bans on the capture of midnight, blue, and rainbow parrotfish, as well as size limits for other parrotfish species in St. Croix.[22] These requirements would also provide much-needed data to support stock assessments as well as analyses of the size and age structure of species' populations that could be compared to trends in algal growth and coral cover. Notably, the incidental take statement associated with the 2011 biological opinion stated that these data would be collected.[23] Including that requirement as an accountability measure would be helpful in implementing the terms and conditions of that opinion.

Conclusion

In order to maintain and restore U.S. Caribbean coral reefs – and the fisheries and other benefits they support – the Council and NMFS must take action to restore parrotfish populations to ecologically functional levels. Scientific evidence overwhelmingly points to the need to significantly increase the size and number of parrotfish grazing these reefs in order to reduce algal abundance and facilitate recruitment of corals that provide vital reef habitat. Restoring parrotfish populations and reducing algal abundance will also promote the resilience of U.S. Caribbean coral reefs to increasing threats of ocean warming, hurricanes, and disease. We recognize that significantly reducing parrotfish catches or prohibiting the targeting of parrotfish in certain areas may entail significant near-term economic effects on fishers. However, these measures could be the key to ensuring that coral reefs and the fisheries they support survive for the long term. We therefore request that the Council carefully consider alternatives to substantially increase parrotfish population and reduce fishery impacts, and that NMFS reassess the effects of this fishery on staghorn and elkhorn corals and their critical habitat.

Sincerely,

Andrea A. Treece
Staff Attorney, Oceans Program

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[22] Note that work remains to be done to address NMFS's recommendation in the ITS associated with the 2011 biological opinion that "NMFS, in collaboration with the CFMC, should implement escape vents in the trap fishery of the U. S. Caribbean to reduce bycatch of undersized herbivorous fishes in the trap sector of the reef fish fishery." NMFS, Revision to the Incidental Take Statement (ITS) of the 2011 Biological Opinion for the Caribbean Reef Fish Fishery (May 12, 2014) at 11.

[23] NMFS, Revision to the Incidental Take Statement (ITS) of the 2011 Biological Opinion for the Caribbean Reef Fish Fishery (May 12, 2014) at 9-10.

Status and Trends of Caribbean Coral Reefs: 1970-2012
EXECUTIVE SUMMARY

Jeremy Jackson

> ***"Perhaps the most striking aspect of plant life on a coral reef is the general lack of it. It seems anomalous to even the casual observer that tropical reefs, notable for their dazzling profusion of animal life, are almost devoid of conspicuous plants."***
>
> Sylvia Earle, 1972

INTRODUCTION

Sylvia Earle's early observations upon Caribbean reefs describe a forgotten world. Caribbean coral reefs have suffered massive losses of corals since the early 1980s due to a wide range of human impacts including explosive human population growth, overfishing, coastal pollution, global warming, and invasive species. The consequences include widespread collapse of coral populations, increases in large seaweeds (macroalgae), outbreaks of coral bleaching and disease, and failure of corals to recover from natural disturbances such as hurricanes. Alarm bells were set off by the 2003 publication in the journal *Science*[1] that live coral cover had been reduced from more than 50% in the 1970s to just 10% today. This dramatic decline was closely followed by widespread and severe coral bleaching in 2005, which was in turn followed by high coral mortality due to disease at many reef locations. Healthy corals are increasingly rare on the intensively studied reefs of the Florida reef tract, US Virgin Islands, and Jamaica. Moreover, two of the formerly most abundant species, the elkhorn coral *Acropora palmata* and staghorn coral *Acropora cervicornis*, have been added to the United States Endangered Species List. Concerns have mounted to the point that many NGOs have given up on Caribbean reefs and moved their attentions elsewhere.

It was against this gloomy backdrop that this study was undertaken to assess more rigorously than before the extent to which coral reef ecosystems throughout the wider Caribbean may have suffered the same fate, and if they have not, to determine what were the factors responsible. Various reports suggested that reefs in the southern Caribbean were in better ecological condition than elsewhere, with more live coral and reef fish. If this were true, understanding why some reefs are healthier than others would provide an essential first step for more effective management to improve the condition of coral reefs throughout the entire Caribbean region.

STRATEGY AND SCOPE OF THE PRESENT REPORT

Previous Caribbean assessments lumped data together into a single database regardless of geographic location, reef environment, depth, oceanographic conditions, etc. Data from shallow lagoons and back reef environments were combined with data from deep fore-reef environments and atolls. Geographic coverage was

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[1] T.A. Gardner et al. *Science* **301**, 958 (2003)

uneven, reflecting primarily the most studied sites with the most easily accessible data. Only total coral cover was recorded, with no attempt to assess the fates of different coral species. Nor was there any attempt to compile records of macroalgae, sea urchins, and fishes that are well known to have significant ecological interactions with corals.

We addressed these methodological problems by a detailed analysis of the status and trends of reef communities at distinct reef locations throughout the wider Caribbean. We also compiled essential metadata on the nature of the reef environment, depth, and history of human population growth, fishing, hurricanes, coral bleaching, and disease at each location. The quality of biological information varied among locations, but wherever possible data were obtained for coral and macroalgal cover, abundance of the critically important grazing sea urchin *Diadema antillarum*, and biomass of fishes, most importantly large grazing parrotfish.

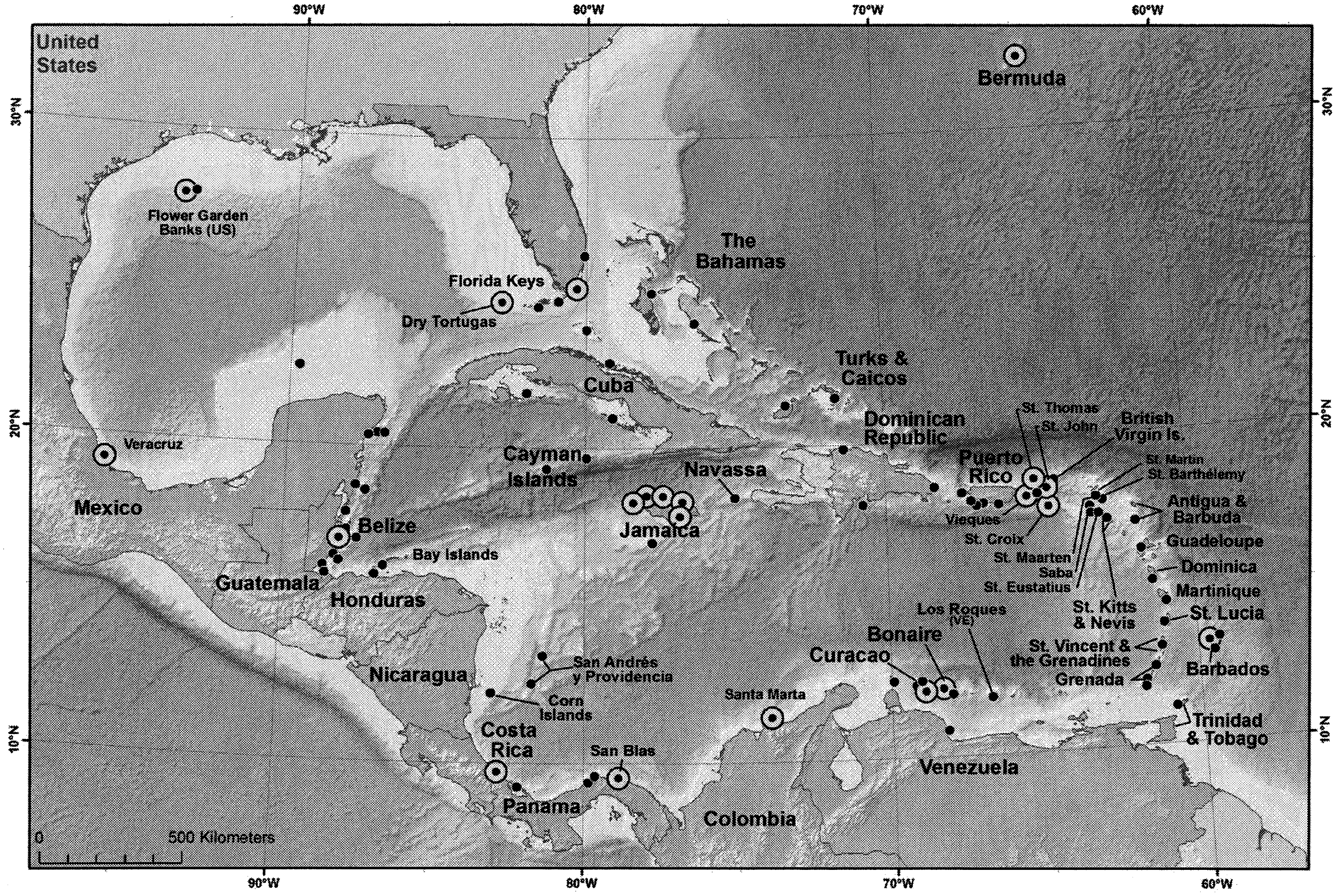

FIGURE 1. Distribution of 90 reef locations analyzed for this study. The large circles indicate 21 locations with the most complete time series data for analysis of long-term trends in coral cover.

Most of the quantitative data for Caribbean reefs is unpublished or buried in gray literature and government reports. To obtain these data, we contacted hundreds of people in all the countries of the Caribbean via several thousand emails, requests for data posted on relevant websites, and through presentations and interviews at international conferences. We also corresponded with managers of all the large monitoring programs in the region. In the end, we obtained data for corals, macroalgae, sea urchins, and fishes from a total of more than 35,000 quantitative reef surveys from 1969 to 2012. This is the largest amount of quantitative coral reef survey data ever compiled and exceeds by several fold that used for earlier Caribbean assessments.

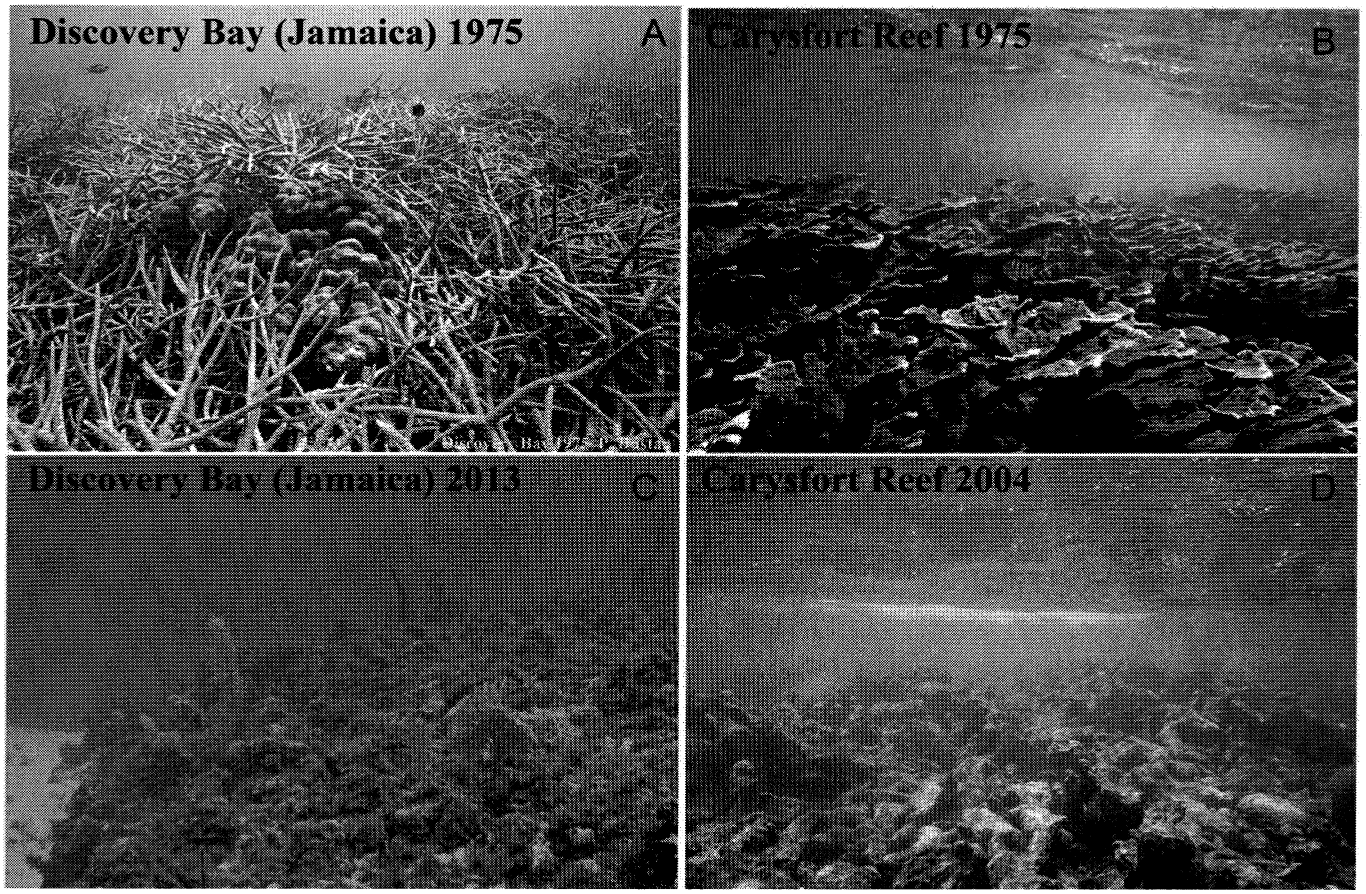

FIGURE 2. Phase shift from dominance by corals to dominance by macroalgae on the shallow fore-reefs in the northern Florida Keys and north coast of Jamaica. (A) Discovery Bay, Jamaica in 1975 and (C) the same location in 2013. (B) Carysfort Reef within the Florida Keys National Marine Sanctuary in 1975 and (D) in 2004 (All photos by Phillip Dustan).

Data are distributed among 90 reef locations in 34 countries (Fig. 1). Most of the data are from fore-reef and patch-reef environments in depths between 1-20 meters that are the focus of this study. Data are sparse up until the mass mortality of the formerly ubiquitous sea urchin *Diadema antillarum* in 1983-1984 when several monitoring programs first began. Data for corals are extensive and range from 1970 to the present. *Diadema* data are more limited up until mass mortality reduced its abundance to near zero and scientists realized what they had lost. Data for macroalgae are the most problematic because of inconsistent monitoring and taxonomy so that much of the data had to be discarded from our analysis. Quantitative data for both size and abundance of reef fishes needed to estimate fish biomass are unavailable until 1989 but are extensive after that.

The longest time series from the same reefs are large photo quadrats from 1973 to the present for fixed sites at Curaçao and Bonaire, with newer time series from the same islands beginning in the 1990s. Comparably long time series extending back into the early 1970s to early 1980s are available from the northern Florida Keys, Jamaica, St. John and St. Croix in the US Virgin Islands, and Panama. However, these records were compiled by different workers at different times and are therefore not as consistent or complete as data from the Dutch Caribbean.

Intensity of sampling varied greatly in time and space. We therefore partitioned the data into three time intervals of 12-14 years each based on major ecological events that extended throughout the wider Caribbean. These are:

1. 1970-1983: Interval from the oldest data up until and including the mass mortality of the formerly abundant sea urchin *Diadema antillarum* in 1983, as well as the first reports of White Band Disease (WBD) in the mid 1970s and early 1980s.
2. 1984-1998: From just after the *Diadema* die-off up to and including the widely reported 1998 extreme heating event.
3. 1999-2011: The modern era of massively degraded coral reefs.

PATTERNS OF CHANGE FROM 1970 TO 2012

Average coral cover for the wider Caribbean based on the most recent data for all the locations with coral data is 16.8% (range 2.8–53.1%). Taking into account the great variation among locations and data sets reduces this estimate to 14.3% (+2.0, -1.8). Even this more rigorously refined mean is 43% higher than the 2003 regional estimate of 10% cover. Nevertheless, coral cover declined at three quarters of the locations with the greatest losses for locations that were surveyed earliest and for the longest time.

Average coral cover for all 88 locations with coral data declined from 34.8% to 19.1% to 16.3% over the three successive time intervals, but the disparity among locations was great. In contrast, macroalgal cover increased from 7% to 23.6% between 1984-1998 and held steady but with even greater disparity among locations since 1998. The patterns were similar for the 21 locations with coral data from all three intervals highlighted by circles in Fig. 1. These opposite trends in coral and macroalgal cover constitute a large and persistent Caribbean phase shift from coral dominated to macroalgal dominated communities that has persisted for 25 years (Figs. 2 and 3), a pattern also strongly supported by ordination analyses of benthic community composition.

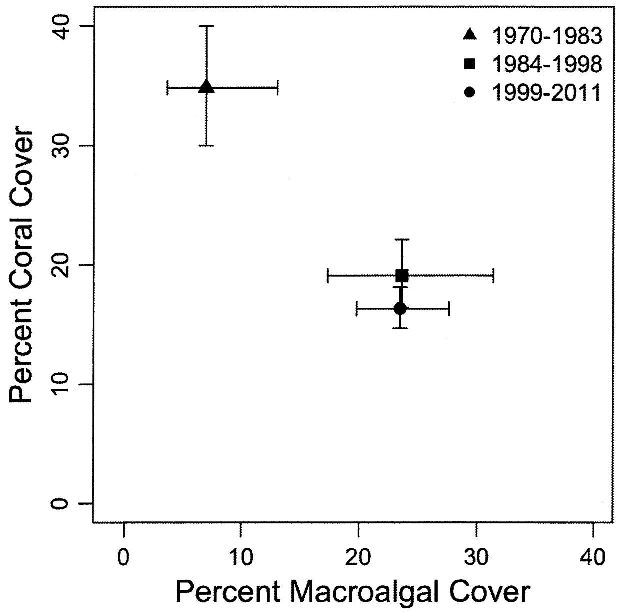

FIGURE 3. Large-scale shifts from coral to macroalgal community dominance since the early 1970s. Symbols and confidence intervals represent means and standard deviations for 3 time intervals that take into account variability due to location, and datasets using a mixed modeling framework.

The greatest overall changes in coral and macroalgal cover occurred between 1984 and 1998, after which there was little overall change at the great majority of locations except for places most strongly affected by the extreme warming events of 2005 and 2010. The same was true for formerly abundant elkhorn and staghorn *Acropora* that began to decline in the 1960s, the mass mortality of the sea urchin *Diadema antillarum* in 1983-1984, and the extreme overfishing of large parrotfish at most locations in the early to middle 20th century. Thus the largest and most damaging changes on Caribbean reefs occurred before most coral reef scientists and managers had begun to work on reefs, a classic example of the Shifting Baselines Syndrome and a harsh reminder that the problems of today are just the latest chapter in a much longer story of decline.

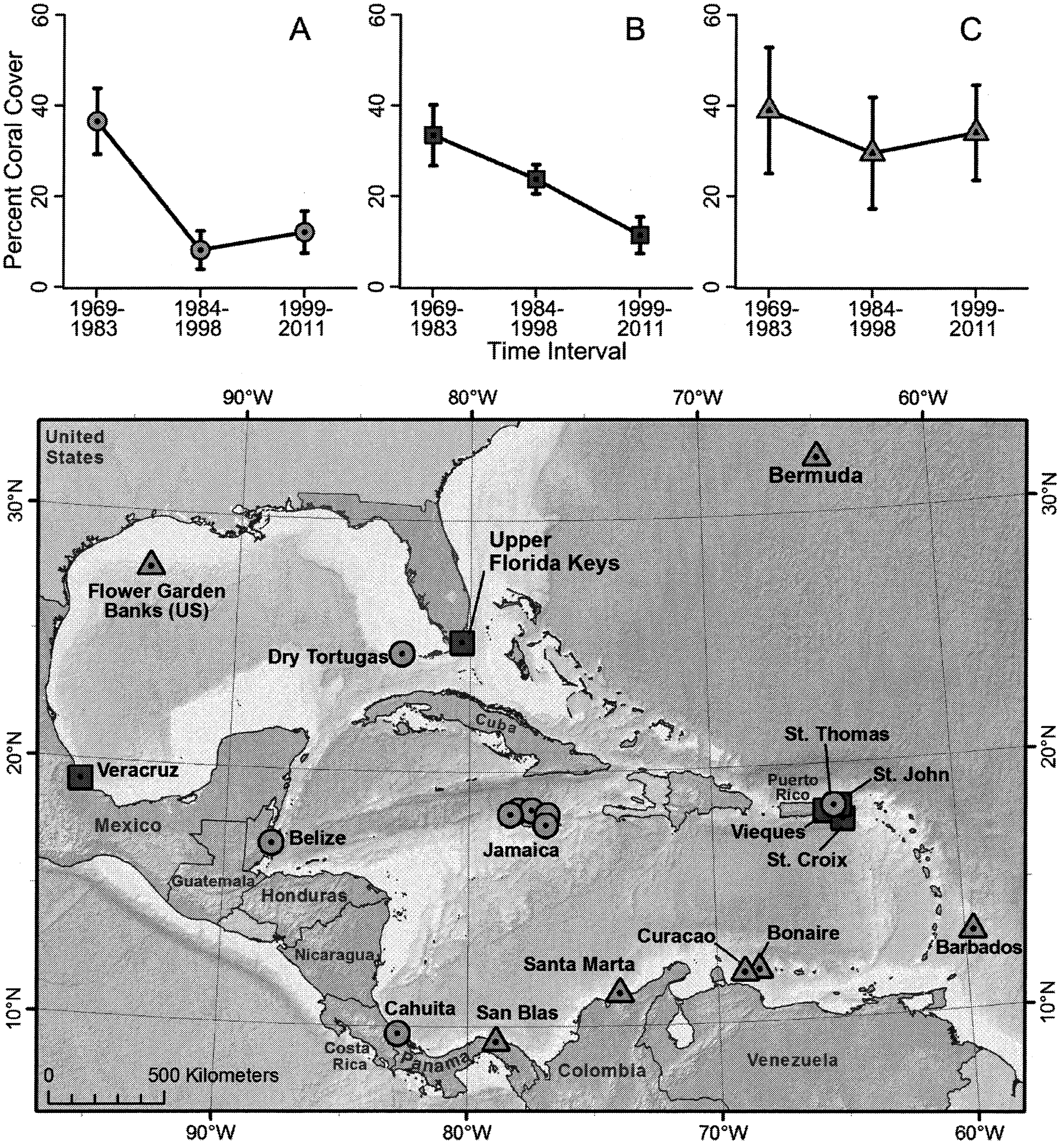

FIGURE 4. Trajectories of coral cover at 21 reef locations, grouped on the basis of the total amount of change over all three intervals and the tempo of change. (A) Hockey stick pattern with a steep decline between the first two intervals followed by little or no change. (B) Approximately continuous decline over all three intervals. (C) Comparative stability with smaller net changes in cover.

Looking beyond this general picture, however, long-term trends at the 21 highlighted locations in Fig. 1 exhibit three strikingly contrasting patterns of change in coral cover (Fig. 4). Trajectories for nine of the locations resemble a hockey stick with precipitous declines of 58-95% between intervals 1 and 2 followed by no change (Fig. 4A). In contrast, five other locations exhibited comparable decline that was spread out approximately equally between intervals 1 and 2 and between intervals 2 and 3 (Fig. 4B). The third group of seven locations exhibited much greater stability with overall changes (increase or decrease) of just 4-35% (Fig. 4C).

DRIVERS OF CHANGE

The drivers of the ecological degradation of Caribbean reefs need to be understood in the context of the highly unique situation of the Caribbean compared to other tropical seas. The Caribbean is effectively a Mediterranean sea that is the most geographically and oceanographically isolated tropical ocean on the planet. Isolation began tens of millions of years ago with the gradual break-up on the once circumtropical Tethys Seaway, the widening of the Atlantic Ocean, and ultimately isolation from the Eastern Pacific by the closure of the Panamanian Seaway 5.4 to 3.5 million years ago.

Consequently, Caribbean reef biotas are also highly distinctive. Many coral genera once combined with Pacific taxa have proven to belong to uniquely Atlantic evolutionary lineages based on molecular genetics. Moreover, acroporid corals that make up more than a third of Indo-Pacific coral diversity are represented by only two Caribbean species. Taxonomic diversity and ecological redundancy are low and the potential for rejuvenation from other regions is essentially nil. Caribbean species also have no evolutionary experience for dealing with exotic species and disease before the advent of people.

We focused on potential anthropogenic drivers of decline for which there were data for meaningful comparisons. Drivers were treated separately for ease of analysis and discussion, but they are inextricably linked. In particular, coral disease is a complex and poorly understood symptom of several forms of human disturbance rather than a direct driver of change. Thus disease is treated in relation to several different drivers including introductions of alien species, ocean warming, coastal pollution, and overfishing. Overall, results are stronger for evaluating effects of human population increase, overfishing, and ocean warming because there are more data, and less so for coastal pollution and invasive species.

FIGURE 5. Overpopulation: Mass tourism overcharges the Caribbean. (A) Large cruise ships with thousands of passengers arrive every day in the Caribbean, shown here is St. Thomas, the US Virgin Islands (Source: Calyponte, Wikipedia). (B) Numerous hotel resorts offer ever more tourists the opportunity to stay in the Caribbean Sea, as here at Cancún Island, Mexico (Source: Foto Propia, Photo by Mauro I. Barea G., Wikipedia). (C) High density of tourists line South Beach, Miami, Florida (Source: Photo by Marc Averette, Wikipedia).

Too many people

Tourism is the lifeblood of many Caribbean nations (Fig. 5). However, our evidence demonstrates that extremely high densities of both tourists and residents are harmful to reefs unless environmental protections are comprehensive, and effectively enforced. Unfortunately, this is only rarely the case. Numbers of visitors per square kilometer per year range from a low of 110 in the Bahamas to an astounding 25,000 at St. Thomas. All locations with more than the median value of 1,500 visitors per square kilometer per year have less than the median value of 14% coral cover except for Bermuda with 39% cover and Grand Cayman with 31%. The exceptional situation at Bermuda most likely reflects progressive environmental regulations in place since the 1990s and the infrastructure required to make them work. Otherwise, the harmful environmental costs of runaway tourism seem to be inevitable.

Overfishing

Artisanal fishing for subsistence is crucial to most Caribbean economies but the consequences have been catastrophic for coral reefs. Overfishing caused steep reductions in herbivores, especially large parrotfishes, which are the most effective grazers on Caribbean reefs but vulnerable to all gear types except hook and line.

Nevertheless, the consequences of overfishing parrotfish for coral survival were little understood until the abrupt demise of the sea urchin *Diadema antillarum* due to an unidentified disease in 1983-1984. Until then, *Diadema* had increasingly become the last important macro-herbivore on Caribbean reefs due to overfishing. *Diadema* and parrotfish strongly compete for food, and variations in their abundance were inversely proportional until 1983. This inverse relationship provides a rigorous proxy to assess the consequences of historical overfishing of parrotfish for coral cover in the absence of quantitative data for parrotfish biomass before 1989.

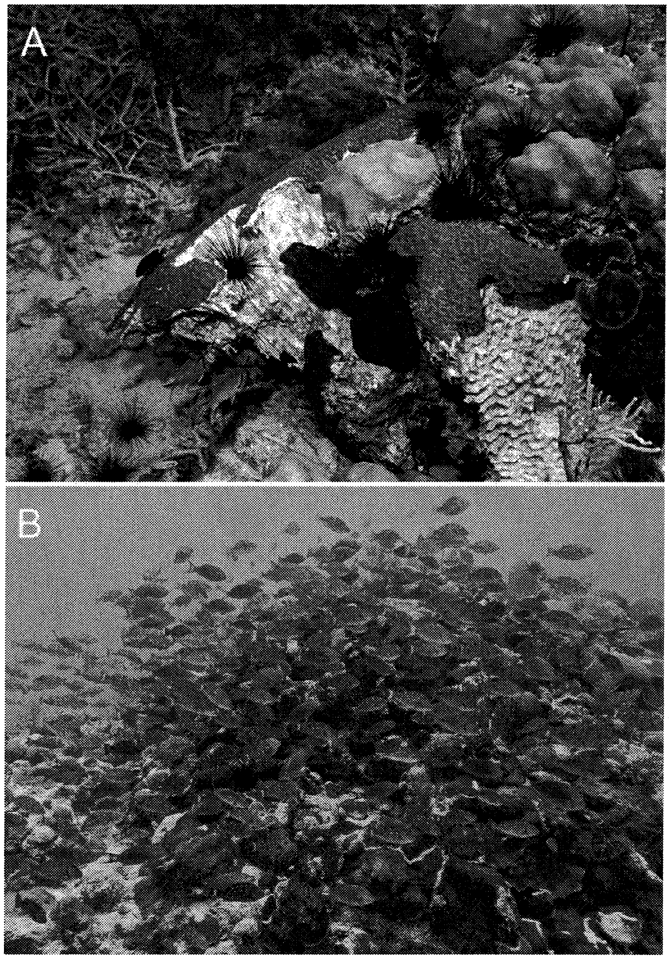

FIGURE 6. Formerly abundant grazers on Caribbean reefs. (A) Dense aggregation of the sea urchin *Diadema antillarum* on the west forereef at Discovery Bay, Jamaica in about 10 meters a year before the massive die-off in 1983/1984 (Photo by Jeremy Jackson). (B) Large school of Stoplight Parrotfish *Sparisoma viride* on the south shore of Bermuda where fishing on parrotfish is banned (Photo by Philipp Rouja). Such large numbers of parrotfish are rare to absent today on the great majority of Caribbean reefs.

Our analysis of overfishing focused primarily on 16 of the 21 highlighted reefs in Fig. 1 for which quantitative data on *Diadema* abundance were available before the die-off in 1983/84, in addition to coral cover for all three of the time intervals in Fig. 3. Nine of these reefs were classified as overfished for parrotfishes by 1983, with *Diadema* densities ranging from 6.9-12.4 per square meter, whereas the other seven reefs were classified as less fished with *Diadema* densities of just 0.5-3.8

per square meter. This ranking agreed well with the qualitative literature. Reefs where parrotfishes had been overfished before 1984 suffered greater subsequent decreases in coral cover and increases in macroalgae than reefs that still had moderately intact populations of parrotfish. Coral and macroalgal cover were independent of *Diadema* densities before 1984 when either the sea urchin or parrotfish grazed down macroalgae to extremely low levels. All that changed, however, after the *Diadema* die-off when coral cover declined in proportion to historical *Diadem*a abundance, a trend that has continued to the present day.

There is also strong field and experimental evidence for persistent indirect effects of the increase in macroalgae, including decreased larval recruitment and survival of juvenile corals and increased coral disease. Coral recruitment sharply declined after 1984, at least in part due to a decline in the parental brood stock. But there is also strong evidence for active interference by macroalgae. Larval settlement onto the tops of experimental panels in Curaçao declined five-fold between identical experiments in 1979-1981 and 1998-2004. Crustose coralline algae, that are a preferred substrate for larval settlement, covered the entire upper surfaces of the panels in the earlier experiment and macroalgae were absent. In contrast, upper surfaces in the later experiment were entirely covered by macroalgae.

Other experiments demonstrate that coral larvae actively avoid substrates where macroalgae are present and larval recruits suffer increased mortality and growth inhibition due to physical interference by macroalgae. But the strongest evidence for macroalgal interference comes from recent large increases in coral recruitment and juvenile survival on reefs where *Diadema* have partially recovered or parrotfish have increased in marine protected areas. Experiments also demonstrate that macroalgae induce a wide variety of pathological responses in corals including virulent diseases. Release of toxic allelochemicals by macroalgae also disrupts microbial communities associated with corals sometimes causing bleaching or death.

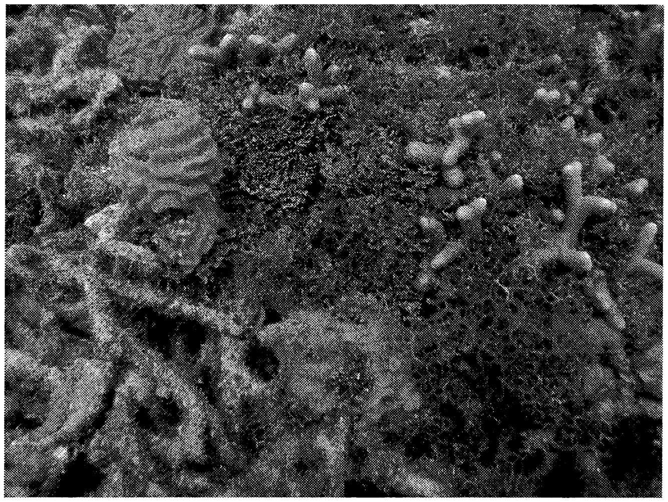

FIGURE 7. Dense growths of macroalgae with surviving branch tips of Porites protruding through the algal canopy in the top right corner and previously overgrown dead branches of Porites and Acropora cervicornis in the bottom left (Dry Tortugas, 2000, Photo by Mark Chiappone).

Overfishing may have also indirectly affected the capacity of reefs to recover from damage by hurricanes; something they have routinely done for millions of years before or reefs would not exist. Over the past few decades, however, corals have increasingly failed to become reestablished on many reefs after major storms. We investigated this apparent shift using data for the 16 reefs with coral and *Diadema* data from before 1984. Coral cover was independent of the long-term probability of hurricanes before 1984 but not afterwards. Overfishing of parrotfish may have decreased the ability of corals to recover after hurricanes. Reefs protected from overfishing at Bermuda experienced four hurricanes since 1984 with no loss in average coral cover, whereas recently overfished reefs on the Central Barrier in Belize declined by 49% after 3 hurricanes.

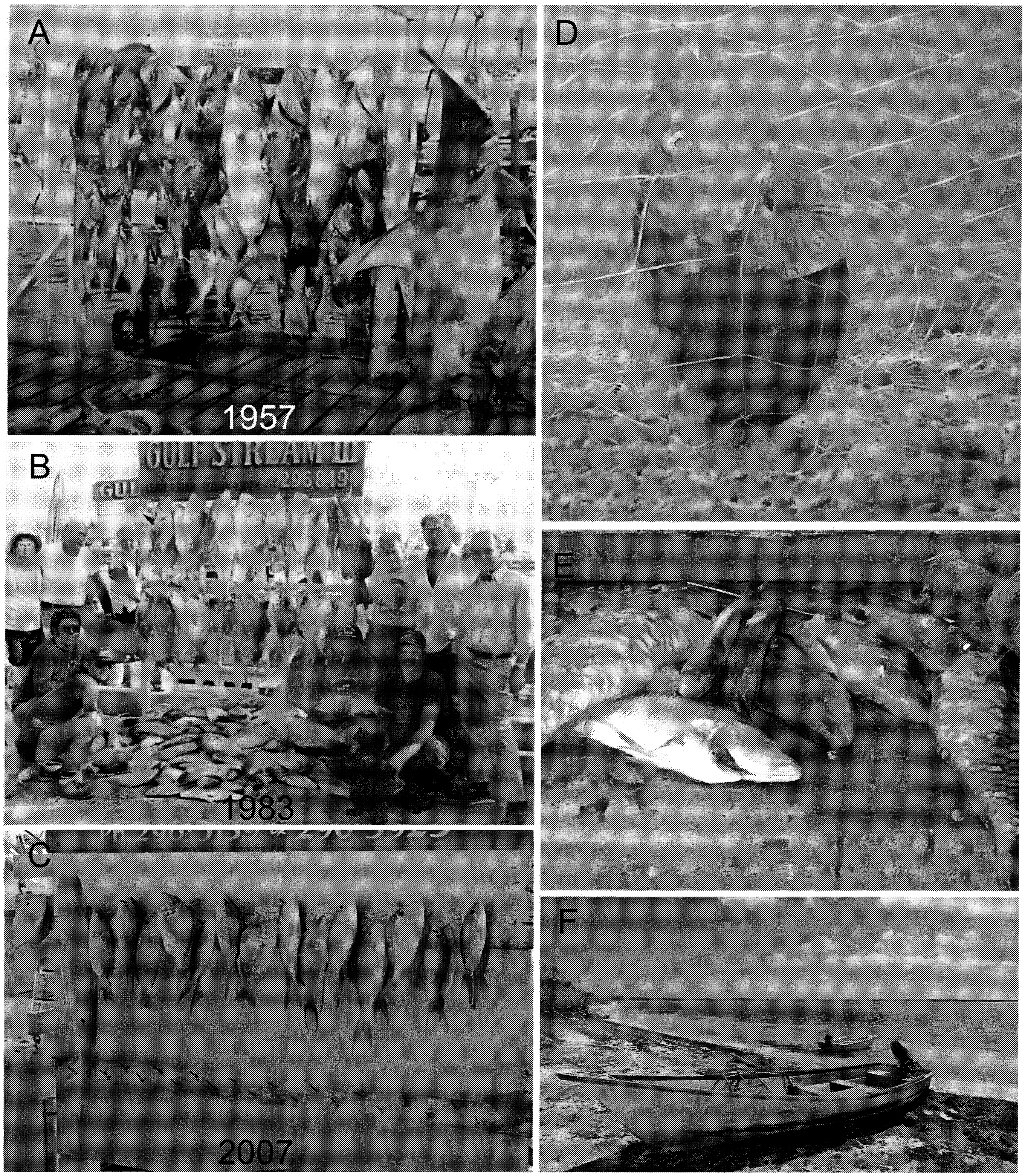

FIGURE 8. Overfishing severely reduced fish biomass and diversity in the Caribbean. (A – C) Decline in the composition and size of coral reef trophy fish in the Florida Keys since the 1950s (modified from McClenachan 2008). (D – F) Parrotfish were the most important grazers on Caribbean reefs: (D) Stoplight parrotfish (*Sparisoma viride*) caught in a gill net. (E) A typical day of spearfishing off southeast Curaçao. (F) Fishing boats at Barbuda's Coco Point (Photos by Ayana Elizabeth Johnson).

Coastal pollution

Limited comparative data for water transparency based on secchi disk observations at three CARICOMP sites (Caribbean Coastal Marine Productivity Program by UNESCO) show that water quality is declining in areas of unregulated agricultural and coastal development. In particular, water transparency steeply declined over 20 years at Carrie Bow Cay in Belize due to huge increases in agriculture and coastal development from Guatemala to Honduras such as illustrated in Fig. 9C. A similar pattern was observed at La Parguera on the west coast of Puerto Rico. In contrast, water quality improved in Bermuda.

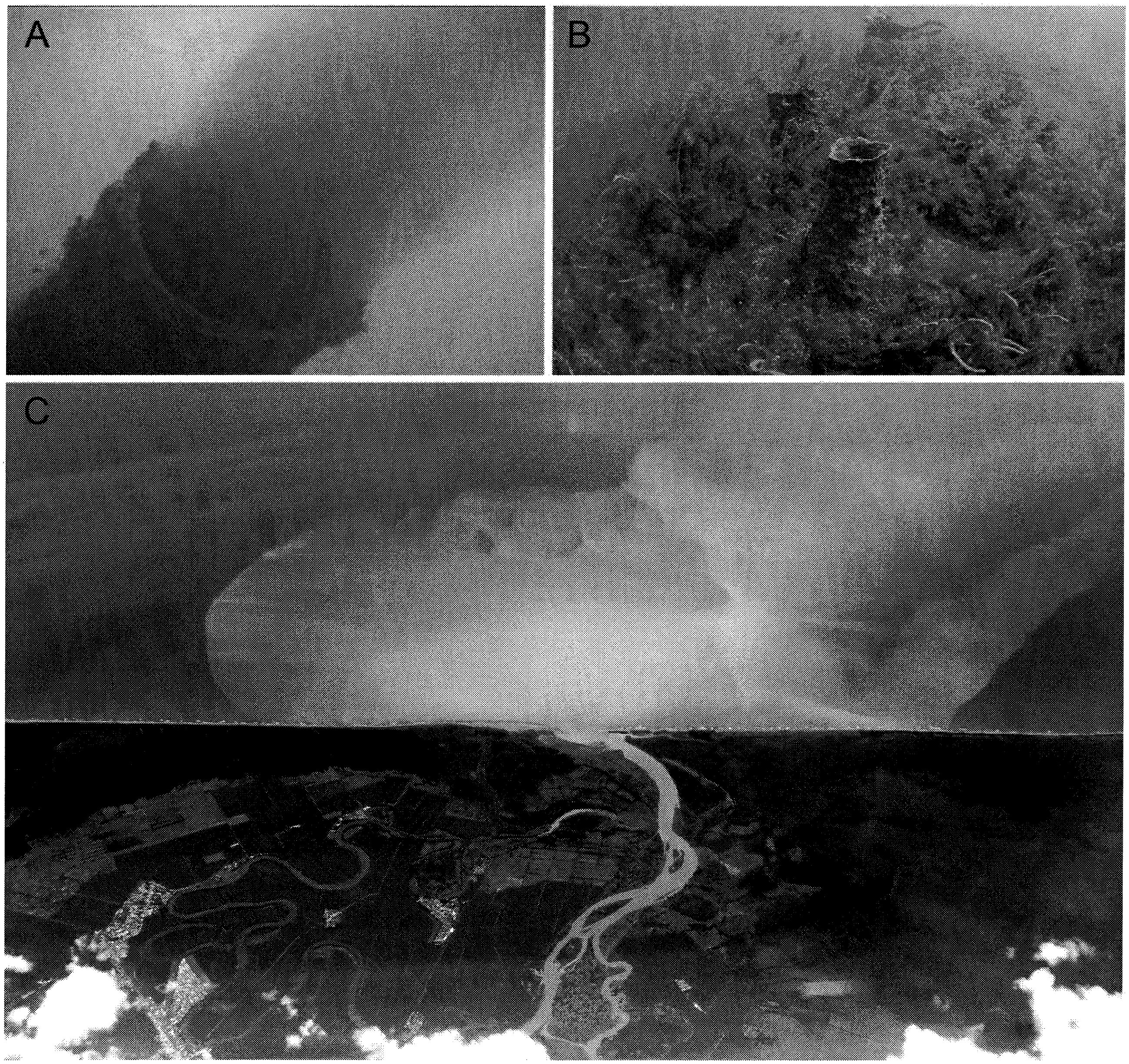

FIGURE 9. Impacts of coastal pollution on Caribbean reefs. (A) Sewage outfall in Delray Beach, Florida that discharges 13 million gallons per day of treated sewage up-current of a coral reef. (B) Macroalgae carpeting dead corals near the sewage outfall (Photos by Steve Spring, Marine Photobank). (C) Massive discharge of sediment loads by a river entering the Caribbean Sea off the Meso-American Coast (Photo by Malik Naumann, Marine Photobank).

Coral disease has been linked to excessive organic pollution but the data are spotty and limited in scope. In general there is a pressing need for more systematic and extensive monitoring of water quality throughout the wider Caribbean.

Ocean warming

Our first analyses were based on the Reefbase compilation of extreme bleaching events that showed no significant relationship between the numbers of extreme events per locality and coral cover at locations across the wider Caribbean, Gulf of Mexico and Bermuda. Because of the subjectivity of such bleaching assessments, however, we obtained data for degree heating weeks (DHWs) for all 88 localities with coral cover from NOAA Coral Reef Watch.

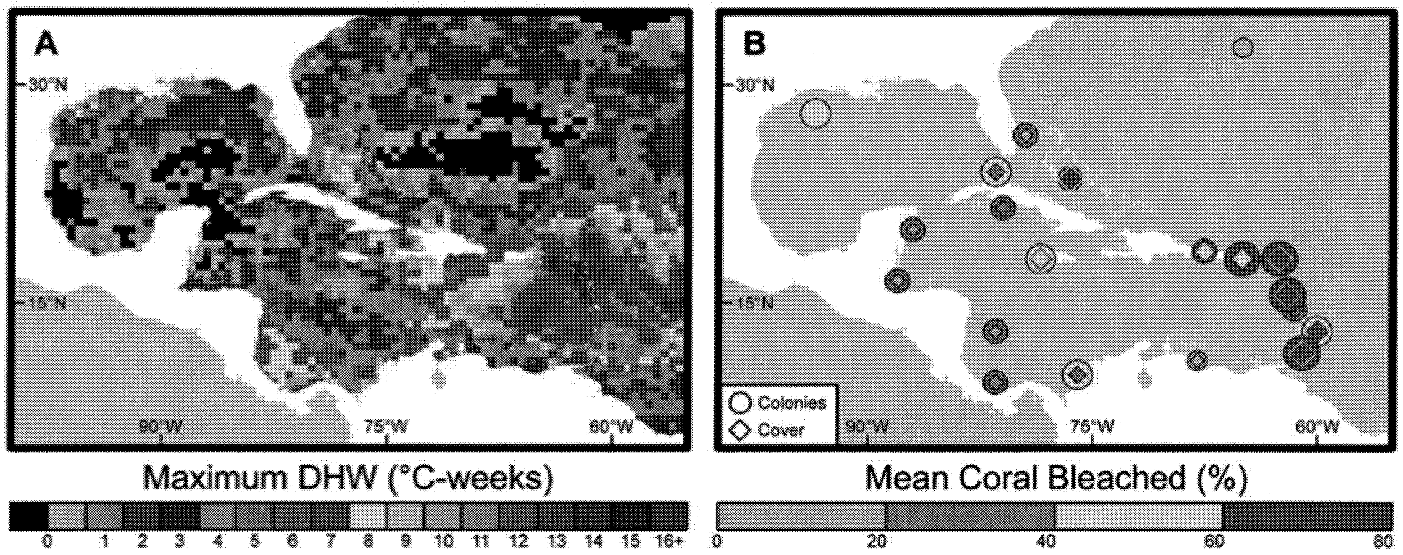

FIGURE 10. Extreme heating event and associated coral bleaching that most severely impacted the eastern Caribbean in 2005. (A) Degree heating weeks from Pathfinder Satellite observations. (B) Reports of the intensity of coral bleaching compiled from field observations (Courtesy Mark Eakin and colleagues).

We then used these data to assess the effects of the 1998, 2005, and 2010 extreme warming events on coral cover by calculating the proportional changes in coral cover for the two years following each event in relation to the two years before the event, and then plotting the proportional change in relation to the numbers of degree heating weeks (DHWs) experienced at each locality. There is a weak but insignificant negative correlation between losses in coral cover and numbers of DHWs, regardless of whether the data were analyzed for each warming event or combined, or whether we included all the localities or restricted the analysis to include only localities that experienced at least 8 DHWs. Moreover, the greatest losses in coral cover occurred at reef locations with less than 8DHWs.

We caution that our results do not men that extreme heating events are unimportant drivers of coral mortality due to coral bleaching and disease, as they clearly have been in the USVI, Puerto Rico, Florida Keys, and elsewhere. Moreover, increasingly severe extreme heating events will pose an even greater threat to coral survival in future decades. But our results do belie any regionally consistent effects of extreme heating events up to now and strongly imply that local stressors have been the predominant drivers of Caribbean coral decline to date.

Potentially deleterious effects of ocean acidification have not been treated here because of the lack of comparative data. If present trends of decreased pH continue, however, the ability of corals and other calcareous reef species to deposit skeletons will be increasingly compromised.

Diadema and *Acropora*. This interpretation is also consistent with the apparent lack of any major environmental shift in the 1970s that might have triggered the outbreak of disease. Most importantly, the emergence of these diseases occurred many years before the first reported extreme heating events.

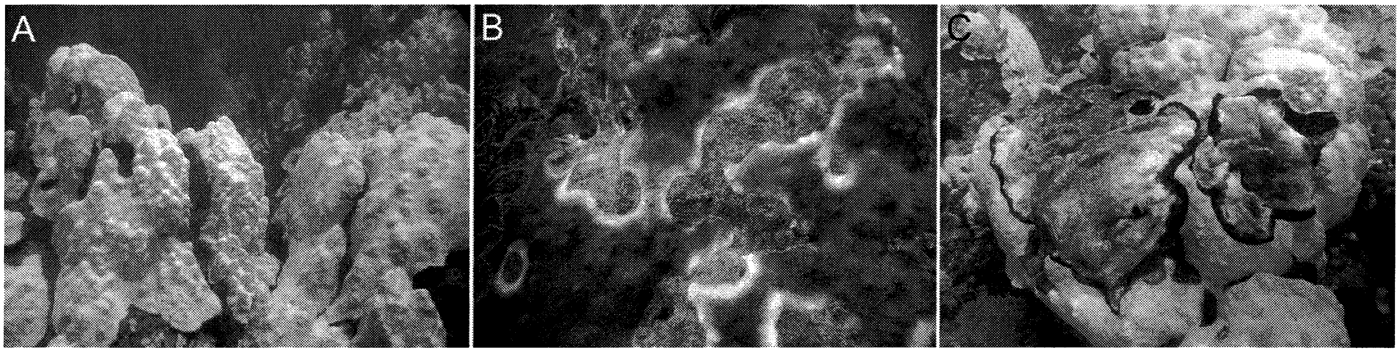

FIGURE 11. Effects of coral bleaching and disease on the formerly abundant coral *Orbicella faveolata*. (A) Bleached corals (Turrumote, Puerto Rico, 2005). Extensive partial colony mortality due to infection by (B) Yellow Band Disease (Turrumote, Puerto Rico, 2005) and (C) Black Band Disease (Los Roques Venezuela, 2010). (Photo A by Ernesto Weil; C & B by Aldo Cróquer).

Invasive species

The explosion of exotic Pacific lionfish throughout the wider Caribbean (Fig. 12) has wreaked havoc in Caribbean fish communities. But as serious as the potential long-term consequences may be, they pale in comparison to the introduction of the unidentified pathogen that caused the die-off of *Diadema antillarum* or the effects of "White-band disease" (WBD) on acroporid corals. *Diadema* mass mortality began only a few km from the Caribbean entrance of the Panama Canal. That, coupled with orders of magnitude increases in bulk carrier shipping in the 1960s and 1970s, strongly suggests that *Diadema* disease was introduced by shipping. The same may be true of coral diseases although their earliest occurrences were widespread throughout the Caribbean.

Because of their isolation for millions of years, and by analogy to the fates of Native Americans after their first contact with Europeans, Caribbean species should be exceptionally prone to the impact of introduced diseases. And this appears to be the case. We know of no examples of the virtual elimination due to disease of any marine species throughout the entire extent of the Indian or Pacific oceans comparable to the demise of Caribbean

It would be possible to test this introduced species hypothesis for WBD since the pathogen is known and available for DNA-sequencing. It may also be possible for *Diadema* even though the pathogen is unknown by genetic analysis of entire frozen specimens of *Diadema* that died from the disease. This is not an entirely academic exercise: the two pivotal events in the demise of most Caribbean reefs are as much a mystery today as they were when they first occurred 30 or more years ago.

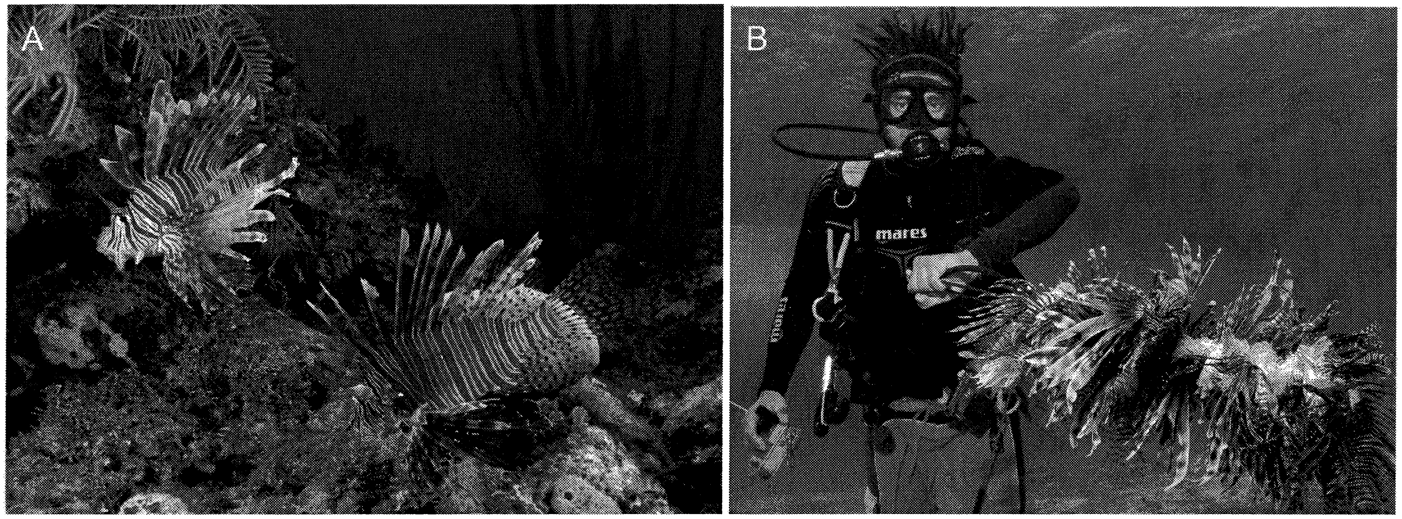

FIGURE 12. Population explosion of the highly successful Pacific lionfish (*Pterois volitans*) introduced into the Caribbean sometime between the 1980s and the early 1990s. (A) Abundant invasive lionfish on the reefs in the Cayman Islands (Photo courtesy of Niel Van Niekerk, with permission from IFAS, University of Florida). (B) Lionfish speared as part of a widespread effort to control the populations in the Dry Tortugas (Photo courtesy of ICRI).

SUMMARY

Outbreaks of *Acropora* and *Diadema* diseases in the 1970s and early 1980s, overpopulation in the form of too many tourists, and overfishing are the three best predictors of the decline in Caribbean coral cover over the past 30 or more years based on the data available. Coastal pollution is undoubtedly increasingly significant but there are still too little data to tell. Increasingly warming seas pose an ominous threat but so far extreme heating events have had only localized effects and could not have been responsible for the greatest losses of Caribbean corals that had occurred throughout most of the wider Caribbean region by the early to mid 1990s.

In summary, the degradation of Caribbean reefs has unfolded in three distinct phases:

1. Massive losses of *Acropora* since the mid 1970s to early 1980s due to WBD. These losses are unrelated to any obvious global environmental change and may have been due to introduced pathogens associated with enormous increases in ballast water discharge from bulk carrier shipping since the 1960s.

2. Very large increase in macroalgal cover and decrease in coral cover at most overfished locations following the 1983 mass mortality of *Diadema* due to an unidentified and probably exotic pathogen. The phase shift in coral to macroalgal dominance reached a peak at most locations by the mid 1990s and has persisted throughout most of the Caribbean for 25 years. Numerous experiments provide a link between macroalgal increase and coral decline. Macroalgae reduce coral recruitment and growth, are commonly toxic, and may induce coral disease.

3. Continuation of the patterns established in Phase 2 exacerbated by even greater overfishing, coastal pollution, explosions in tourism, and extreme warming events that in combination have been particularly severe in the northeastern Caribbean and Florida Keys where extreme bleaching followed by outbreaks of coral disease have caused the greatest declines.

IMPLICATIONS FOR MANAGEMENT

Our results contradict much of the rhetoric about the importance of ocean warming, disease, and hurricanes on coral reefs and emphasize the critical importance of historical perspective for coral reef management and conservation. The threats of climate change and ocean acidification loom increasingly ominously for the future, but local stressors including an explosion in tourism, overfishing, and the resulting increase in macroalgae have been the major drivers of the catastrophic decline of Caribbean corals up until today.

What this means is that smart decisions and actions on a local basis could make an enormous difference for increased resilience and wellbeing of Caribbean coral reefs and the people and enterprises that depend upon them. Thus, four major recommendations emerge from this report:

1. **Adopt robust conservation and fisheries management strategies** that lead to the restoration of parrotfish populations, including the listing of the parrotfish in relevant annexes of the Protocol concerning Specially Protected Areas and Wildlife (SPAW protocol) of the UNEP Caribbean Environment Programme. A recommendation to this effect was passed unanimously at the October 2013 International Coral Reef Initiative Meeting in Belize (see Box).

2. **Simplify and standardize monitoring** of Caribbean reefs and make the results available on an annual basis to facilitate adaptive management.

3. **Foster communication and exchange of information** so that local authorities can benefit from the experiences of others elsewhere.

4. **Develop and implement adaptive legislation and regulations** to ensure that threats to coral reefs are systematically addressed, particularly threats posed by fisheries, tourism and coastal development as determined by established indicators of reef health.

We understand that action upon these recommendations will be a matter of local and national socioeconomic and political debate. But the implications of our scientific results are unmistakable: *Caribbean coral reefs and their associated resources will virtually disappear within just a few decades unless all of these measures are promptly adopted and enforced.*

RECOMMENDATION
on addressing the decline in coral reef health throughout the wider Caribbean: the taking of parrotfish and similar herbivores

Adopted on 17 October 2013, at the 28th ICRI General Meeting (Belize City)

Background

The latest report of the Global Coral Reef Monitoring Network (GCRMN), entitled: *Status and Trends of Caribbean Coral Reefs: 1970-2012* is the first report to document quantitative trends of coral reef health based on data collected over the past 43 years throughout the wider Caribbean region.

The results of the study clearly show:

- Coral reef health requires an ecological balance of corals and algae in which herbivory is a key element;
- Populations of parrotfish are a critical component of that herbivory, particularly since the decline of *Diadema* sea urchins in the early 1980s;
- The main causes of mortality of parrotfish are the use of fishing techniques such as spearfishing and, particularly, the use of fish traps.

The Report further identifies that overfishing of herbivores, particularly parrotfish, has been the major drivers of reef decline in the Caribbean to date, concluding that management action to address overfishing at the national and local levels can have a direct positive impact on reef health now and for the future. *In some areas of the wider Caribbean (for example Bermuda and the Exuma Cays Land and Sea Park in the Bahamas, and more lately in Belize and Bonaire), active management including bans on fish traps, has led to increases in parrotfish numbers and consequent improvement in reef health and resilience to perturbations including hurricanes. This is in contrast to other areas within the Caribbean, where heavily fished reefs lacked the resilience to recover from storm damage.*

Positive impacts on reef health demonstrably have spill over effects on local economies, including the potential for alternative livelihoods to fishing, thanks to increased tourism revenues, replenishment of fish stocks and restoration of ecosystem services such as shoreline protection.

It is recognised that in the Caribbean there are varying levels of community reliance on fishing in general and the taking of parrotfish in particular. However, in light of the evidence now available, and in accordance with ICRI's Framework for Action cornerstone of 'integrated management' (which includes fisheries management), the International Coral Reef Initiative would like to highlight the benefits of strong management to protect reefs from overfishing, and urges immediate action to effectively protect parrotfish and similar herbivores.

Accordingly, the International Coral Reef Initiative urges Nations and multi-lateral groupings of the wider Caribbean to:

1. ***Adopt*** conservation and fisheries management strategies that lead to the restoration of parrotfish populations and so restore the balance between algae and coral that characterises healthy coral reefs;

2. ***Maximise*** the effect of those management strategies by incorporating necessary resources for outreach, compliance, enforcement and the examination of alternative livelihoods for those that may be affected by restrictions on the take of parrotfish;

3. ***Consider*** listing the parrotfish in the Annexes of the SPAW Protocol (Annex II or III) in addition to highlighting the issue of reef herbivory in relevant Caribbean fisheries fora;

4. ***Engage*** with indigenous and local communities and other stakeholders to communicate the benefits of such strategies for coral reef ecosystems, the replenishment of fisheries stocks and communities' economy.

PART I: OVERVIEW AND SYNTHESIS FOR THE WIDER CARIBBEAN REGION

Jeremy BC Jackson, Mary K Donovan, Katie L Cramer, Vivian YY Lam, Rolf PM Bak, Iliana Chollett, Sean R Connolly, Jorge Cortés, Phil Dustan, C. Mark Eakin, Alan M Friedlander, Benjamin J Greenstein, Scott F Heron, Terry Hughes, Jeff Miller, Peter Mumby, John M Pandolfi, Caroline S Rogers, Robert Steneck, Ernesto Weil, Jahson B Alemu I, William S Alevizon, Jesús Ernesto Arias-González, Andrea Atkinson, David L Ballantine, Carolina Bastidas, Claude Bouchon, Yolande Bouchon-Navaro, Steve Box, Angelique Brathwaite, John F Bruno, Chris Caldow, Robert C Carpenter, Bernadette H Charpentier, Mark Chiappone, Rodolfo Claro, Aldo Cróquer, Adolphe O Debrot, Peter Edmunds, Douglas Fenner, Ana Fonseca, Marcia C Ford, Kirah Forman, Graham E Forrester, Joaquín R Garza-Pérez, Peter MH Gayle, Gabriel D Grimsditch, Hector M Guzmán, Alastair R Harborne, Marah J Hardt, Mark Hixon, Joshua Idjadi, Walter Jaap, Christopher FG Jeffrey, Ayana Elizabeth Johnson, Eric Jordán-Dahlgren, Karen Koltes, Judith C Lang, Yossi Loya, Isaias Majil, Carrie Manfrino, Jean-Philippe Maréchal, Croy MR McCoy, Melanie D McField, Steven Miller, Thaddeus Murdoch, Ivan Nagelkerken, Richard Nemeth, Maggy M Nugues, Hazel A Oxenford, Gustavo Paredes, Joanna M Pitt, Nicholas VC Polunin, Pedro Portillo, Héctor Bonilla Reyes, Rosa E Rodríguez-Martínez, Alberto Rodriguez-Ramirez, Benjamin I Ruttenberg, Rob Ruzicka, Stuart Sandin, Myra J Shulman, Struan R Smith, Tyler B Smith, Brigitte Sommer, Chris Stallings, Rubén E Torres, John W Tunnell, Jr., Mark JA Vermeij, Ivor D Williams, Jon D Witman

Caribbean coral reef ecosystems are severely degraded due to human overfishing, pollution, climate change, and the synergies among them. Coral cover has reportedly declined by more than 80% since the 1970s (Fig. 1), virtually all the large fishes, sharks, and turtles are gone (Fig. 2), and the threats of global climate change loom increasingly ominous for the future (Fig. 3) (Hughes 1994; Jackson 1997; Aronson and Precht 2001; Jackson et al. 2001; Gardner et al. 2003; Pandolfi et al. 2003; McClenachan 2008; Eakin et al. 2010). The severity of the situation has raised serious questions about the future of Caribbean reefs and indeed reefs worldwide (Knowlton 2001; Hughes et al. 2003, 2010; Bellwood et al. 2004; Pandolfi et al. 2005; Hoegh-Guldberg et al. 2007; Hughes et al. 2010).

FIGURE 1. Estimates of annual percent coral cover for the entire wider Caribbean region (re-plotted from Gardner et al. 2003).

FIGURE 2. Overfishing significantly reduced fish biomass and diversity in the Caribbean. (A - C) Decline in the composition and size of coral reef trophy fish in the Florida Keys since the 1950s (modified from McClenachan 2008). (D - F) Parrotfish were the most important

grazers on Caribbean reefs: (D) Stoplight parrotfish (*Sparisoma viride*) caught in a gill net. (E) A typical day of spearfishing off southeast Curaçao. (F) Fishing boats at Barbuda's Coco Point (Photos by Ayana Elizabeth Johnson).

FIGURE 3. Effects of coral bleaching and disease on the formerly abundant coral *Orbicella faveolata*. (A) Bleached corals (Turrumote, Puerto Rico, 2005). Extensive partial colony mortality due to infection by (B) Yellow Band Disease (Turrumote, Puerto Rico, 2005) and (C) Black Band Disease (Los Roques Venezuela, 2010). (Photos A and B by Ernesto Weil; C by Aldo Cróquer).

Nevertheless, there are reasons for hope based upon the remarkable abundance and resilience of corals at some remote Pacific island reefs that are protected from local impacts of overfishing and pollution (Friedlander and DeMartini 2002; Knowlton and Jackson 2008; Sandin et al. 2008a; Pandolfi et al. 2011; Gilmour et al. 2013). Despite increased warming and coral bleaching throughout the Pacific, these reefs have recovered from past episodes of bleaching and still support extraordinarily abundant and resilient populations of fishes and corals.

There are also reports of considerable variability in the condition of Caribbean reefs (Kramer 2003; Newman et al. 2006; Schutte et al. 2010) that is obscured by plotting a single line for reef condition over time, regardless of location, reef type, depth, environmental conditions, and human impact as in Fig. 1 (Gardner et al. 2003). For example, live coral cover is less than the reported Caribbean average of 10% in the Florida Keys (Dustan 2003; DuPont et al. 2008) and the US Virgin Islands (Edmunds 2002; Rogers and Miller 2006; Miller et al. 2009), but commonly exceeds 30% on reefs in Curaçao and Bonaire (Bak et al. 2005; Sandin et al. 2008b; Steneck et al. 2011; Vermeij 2012), the Flower Gardens Banks (Aronson et al. 2005; Hickerson et al. 2008), and Bermuda (Murdoch et al. 2008; Smith et al. 2013).

The causes of these regional differences are poorly understood despite their obvious significance for conservation and management. Caribbean reefs with the highest coral cover tend to be characterized by little land-based pollution; some degree of fisheries regulations and enforcement; lower frequencies of hurricanes, coral bleaching, and disease; and moderate economic prosperity. However, these apparent trends have not been rigorously investigated.

There is also a fundamental methodological problem in the common failure to distinguish between the potential anthropogenic drivers of reef degradation such as human overpopulation, overfishing, coastal pollution, introductions of alien species, and ocean warming and acidification due to the burning of fossil fuels, versus their effects such as losses of corals and increases in macroalgae, coral bleaching, and disease (Hughes et al. 2010). This confusion is compounded by scientific provinciality. Most scientists study reefs in a geographically limited area and then project their results to the entire Caribbean. This tendency for over generalization is further compounded by an overall lack of comparative data to address multiple factors in a unified analysis (Hughes et al. 2010).

New insights in science commonly emerge from examining exceptions to general patterns rather than the norms (Knowlton and Jackson 2008). Thus the major goal of this report is to document the variable condition of Caribbean reefs as a means towards better understanding of the factors driving Caribbean reef decline and what actions might be adopted to prevent their demise.

To this end, Part I of the report is divided into five main sections:

1. data, methods, and analysis;

2. description of quantitative changes in the status and trends of major components of Caribbean coral reef ecosystems (corals, macroalgae, sea urchins, and fish) since 1970 throughout the tropical western Atlantic;

3. analysis of the different potential drivers of change to attempt to determine their comparative impact on reefs to the present day and likely impacts in the future;

4. synthesis of results; and

5. recommendations for management.

1. DATABASE, METHODOLOGY, AND ANALYSIS

Most of the quantitative data for Caribbean reefs is unpublished or buried in gray literature and government reports that have not been systematically exploited in previous long-term assessments of changing conditions throughout the region. We contacted hundreds of people in all the countries of the Caribbean via several thousand emails, requests for data posted on relevant websites, and through presentations and interviews at the 64th Gulf and the Fisheries Institute (GCFI) annual conference in Puerto Morelos, Mexico in 2011 and the 12th International Coral Reef Symposium (ICRS) and ICRI meetings in Cairns, Australia in 2012. We also corresponded with managers of large monitoring data sets, including the National Oceanic and Atmospheric Administration (NOAA) Center for Coastal Monitoring and Assessment Biogeography Branch, Caribbean Coastal Marine Productivity Program (CARICOMP), Atlantic and Gulf Regional Reef Assessment (AGRRA), Caribbean Adaptation to Climate Change Mainstreaming Adaptation to Climate Change (CPACC MACC) programs, Coral Reef Evaluation and Monitoring Project (CREMP) carried out by Florida Fish and Wildlife (FWC), and the Inventory and Monitoring Program (I&M) conducted by the National Park Service South Florida Caribbean Network (NPS SFCN).

1a. SCOPE OF THE DATA

We obtained data from 78 principal investigators supplemented by data from 143 published scientific papers and reports. In total, these include data from more than 35,000 surveys of corals, macroalgae, the sea urchin *Diadema antillarum*, and reef fish from 287 data sets, distributed among 90 reef locations in 34 countries, states, or territories (Tables 1 and 2, Fig. 4). This is by far the largest amount of quantitative coral reef survey data ever compiled and exceeds several fold the data employed for previous analyses of Caribbean reefs (Gardner et al. 2003; Schutte et al. 2010).

Sampling units are defined as follows:

Survey: A set of replicate data points collected at a unique reef site, date, depth, or range of depths. Individual surveys are replicates or averaged values for a series of replicates within datasets at a unique site, date and depth.

Data Set: An individual data collection by a single researcher or research team in a particular country, territory, or state.

Site: One or more surveys at the same depth and GPS coordinates on the same reef.

Location: A geographic cluster of exact survey coordinates (sites) revealed by GIS and further defined by prevailing oceanographic conditions (windward or leeward, onshore or offshore, etc.) and political boundaries.

Country, State, or Territory: An independent nation (Cuba, Curaçao, Jamaica, Panama) or political entity attached to or within a single country (Bonaire, Florida, Guadeloupe, Puerto Rico), either of which may be further subdivided to reflect geographic isolation (St. Thomas, St. Croix, and St. John within the US Virgin Islands within the USA).

TABLE 1. Summary of numerical extent of data collected for the wider Caribbean, Gulf of Mexico, and Bermuda. For definitions of terms see text.

FIGURE 4. Geographic distribution of the 90 reef locations analyzed for this study and listed in Table 2. Large circles indicate 21 reef locations with the most complete time series data for analysis of long-term trends in coral cover.

TABLE 2. List of coral reef locations used for this study with extent of sampling, range of years sampled, depth, changes in coral cover for locations sampled more than once, and recent biomass of parrotfish. Locations without percent coral cover were included for data for macroalgae, sea urchins, or fish.

Compilation of the great majority of the data presented very substantial challenges for organization and management. We obtained two types of ecological data: (1) raw data provided directly by researchers and (2) summarized data extracted from peer-reviewed articles and government or gray literature reports. The datasets were based upon various sampling designs and methodologies, reported widely variable ecological and environmental parameters, utilized differing codes and groupings for reported variables, and were presented in a unique format. Consequently, we had to convert each database into a standardized, uniform format with accompanying crucial meta-data on precise geographic locations for GIS, sampling methodology, reef environmental parameters, and reef management history and status. To accomplish this, we developed a data template (Appendix 1) by soliciting input from study collaborators at the workshop in Panama, the ICRS and ICRI meetings in Cairns Australia, and countless additional emails. Compiling and organizing this information required a coordinated and extremely time-consuming effort to evaluate each dataset individually and to edit, reformat, and check for data consistency and quality before merging datasets into a master database.

The great majority of the data are for reef corals, macroalgae, *Diadema*, and fishes from fore-reef and patch-reef environments in depths between 1-20 m (Fig. 5). Therefore, all of the analyses for this report are restricted to these types of reefs and depths. Data are sparse and geographically limited until the mass mortality of *Diadema antillarum* in 1983. This striking event, combined with growing awareness of the severity of *Acropora* mortality due to White Band Disease (WBD), stimulated a surge of monitoring efforts. Numbers of surveys for corals and *Diadema* are about 12,000, for reef fish about 20,000, but only about 4,000 for macroalgae.

FIGURE 5. Frequency of surveys by depth for (A) corals ($\bar{X}$ = 9.5 ± 8.34), (B) macroalgae ($\bar{X}$ = 11.3 ± 10.7), (C) *Diadema antillarum* ($\bar{X}$ = 7.7 ± 4.9), and (D) reef fishes ($\bar{X}$ = 8.8 ± 6.3).

There are no quantitative survey data for reef fish biomass prior to 1989. Data for *Diadema* abundance and macroalgal cover are also rare until the sea urchin began to die *en masse*. Most of the coral data are for total coral cover, but there are also considerable data broken down by genus or species since the early 1970s. Many of the fish surveys only recorded certain groups such as parrotfish or groupers, but the identification and recording of these charismatic taxa appears to be generally good. The greatest problems of data quality are with macroalgae, which were not recorded consistently except by a small number of experts in algal ecology and systematics. We defined macroalgae as erect calcareous or fleshy algae greater than 2 cm tall. These include, but are not limited to species of the genera *Cladophora*, *Dictyota*, *Halimeda*, *Liagora*, *Microdictyon*, and *Sargassum*. In many cases macroalgae were recorded as turf and vice versa, and the CARICOMP protocol distinguished macroalgae by such different criteria that we could not use their algal data in our analysis. Considerable energy was invested in vetting the algal data to throw out all of the questionable data sets, which explains why the numbers of surveys for macroalgae are so much smaller than the other groups.

Most of the surveys employed haphazardly placed or fixed transects or quadrats. Examples include the remarkable nearly 40-year data set provided by Rolf Bak for fixed quadrats in Curaçao and Bonaire, larger scale transect surveys for particular reefs by individual scientists, and large monitoring programs such as CARICOMP, CREMP, and FWC. Surveys were varyingly conducted with widely varying frequency and consistency from 1970 to the present, although the numbers of surveys were small and restricted to only a few locations until the 1980s, and coverage did not substantially increase until the 1990s (Fig. 6A).

FIGURE 6. Number of surveys by year for coral, macroalgae, *Diadema*, and fishes for (A) all permanent or haphazardly collected data, (B) data from the AGRRA program, and (C) data collected from locations randomly selected for each census so that there are no repeated observations from the same geographic point.

Two other major survey programs beginning in the 1990s employed entirely different sampling approaches. AGRRA began in 1997 and used widely varying rapid sampling protocols that have changed throughout the history of the project and also differ among regions surveyed (Fig. 6B). In contrast, data are collected from stratified random sites for the NOAA Biogeography Program surveys in Puerto Rico and the US Virgin Islands, and by the Florida Keys Coral Reef Monitoring Assessment team (PIs: S. Miller and M. Chiappone) and Southeast Florida Coral Reef Monitoring and Evaluation Project (PI: Gilliam) in the Florida Reef Tract (Fig. 6C). In this latter case, surveys include sandy and rocky bottoms in addition to actual reef habitat so are not directly comparable to the other data.

The longest time series with consistent data are Rolf Bak's study beginning in 1973 for large fixed photo quadrats at 4 stations and 4 depths at Curaçao and Bonaire totaling 243 m^2 (Bak et al. 2005). Photographs were taken annually, but data for corals and macroalgae identified from the photographs have been analyzed so far only for 5-year intervals. An additional site in east Curaçao was added starting in 1993. Robert Steneck also began monitoring reefs at Bonaire in 1999 (Steneck and Arnold 2009). Comparably long time series extending back into the early 1970s to early 1980s are available from the northern Florida Keys (Dustan 1977, 1985; Porter and Meier 1992), Jamaica (Hughes and Jackson 1985; Liddell and Ohlhorst 1986, 1992; Hughes 1994; Loya, unpublished data), St. John and St. Croix in the United States Virgin Islands (Rogers et al. 1991, 2008; Edmunds 2002; Rogers and Miller 2006; Miller et al. 2009), and Panama (Guzmán et al. 1991; Shulman and Robertson 1996; Guzmán 2003). However, these records were compiled by different workers at different times and are therefore not as consistent or complete as data from the Dutch Caribbean.

1b. ANALYSIS

Trends in percent cover were assessed for total corals and macroalgae. Trends in density were assessed for *Diadema antillarum* and reef fishes. Analyses were based on a hierarchal structuring of the data and were summarized based on means of surveys within individual datasets for each location. Each survey was assigned to a "location" so each dataset contributed one value to each location unless that dataset covered more than one location. Finally, means were calculated for each location. All statistical analyses were conducted using the software program R version 2.15 (R Development Core Team 2011).

Because the intensity of sampling varies so greatly in time and space, we partitioned the data into three 12 to 14-year time intervals based on major ecological events that extended throughout the wider Caribbean. These are:

1. 1970-1983: Interval from our oldest data until the massive die-off of the sea urchin *Diadema antillarum* in 1983 including the first reports of White-Band Disease (WBD) from the mid 1970s to early 1980s.
2. 1984-1998: From the end of the *Diadema* die-off up to and including the widely reported 1998 extreme heating event.
3. 1999-2011: The modern era of massively degraded coral reefs including the extreme heating events in 2005 and 2010.

We also selected a subset of 21 reef locations for more detailed statistical analyses (large circles in Fig. 4) based upon availability of coral cover data for all three time intervals as well as associated metadata important for the interpretation of the possible drivers of reef degradation.

General and generalized linear mixed effects models (Pinheiro and Bates 2000) were used to test explanatory variables across time and with response variables (R packages lme4: Bates and Maechler 2010, and glmmADMB; Skaug and Fournier 2013). Where the response variable was percent cover we used generalized linear mixed models assuming a beta distribution since the response variable is a percentage. Otherwise, general linear mixed models were used on square-root transformed response variables to reduce the mean-variance relationship and meet the assumptions of linear modeling. We accounted for temporal and spatial autocorrelation by adding random components of year nested within survey and dataset (for definitions see previous section), thus each survey within each dataset was treated as a repeated measure. The model accounted for differences in sampling by location by further nesting within location. For each model 95% confidence intervals were calculated for means that accounted for variation due to dataset and location based on 5000 simulations (R package arm: Gelman et al. 2010). Criteria for comparing model fits were based on minimizing the Akaike Information Criterion (AIC). An estimate of restricted maximum likelihood was used to fit the models. Bonferroni-adjusted pair-wise multiple comparisons were conducted for specific post-hoc hypotheses where appropriate.

Means were modeled for time bins defined above, as well as the values for the oldest (first) year and most recent year a location was studied. In most cases, the oldest or most recent year for a given location was comprised of a single dataset, but in the case of multiple datasets per year the datasets were averaged. Current coral cover was estimated by considering, for 88 locations, the most recent estimate of cover per location as long as the most recent survey was after 1998. Analyses across time bins were conducted for each location with mixed effects models including random effect of dataset. Tukey Honest Significant Differences for post-hoc pairwise comparisons of means were conducted with adjustments for multiple means.

To assess trends in *Acropora* abundance over time, frequency of occurrence and dominance across various time bins were constructed. Because sample sizes are small before 1950, and the locations represented in various time bins are not consistent, care should be taken when interpreting results. Thus we constructed confidence intervals for proportions assuming a binomial distribution with the Pearson-Klopper method. Temporal trends in *Acropora* species percent cover were also examined for data after 1975 in the GCRMN database where means and standard deviations were calculated as for trends discussed above.

Multivariate ordination was conducted to investigate temporal trends in benthic community composition. Locations were included in the ordination if data were available for percent cover of corals at the species (or species group) level as well as for total macroalgae for the same replicate. Coral species were combined into 19 groups by species or genera, and by growth form, to reduce zero occurrences for rare species, especially for species with limited geographic range.

We used two forms of ordination analysis to assess changes in coral and macroalgal assemblage composition. Principal Components Analysis (PCA) uses Euclidean distances to compute a similarity matrix projected on a PCA ordination graph that illustrates the total amounts of the variance "explained" along the first, second, and third PCA axes. PCA has the advantage that results are easily interpretable with taxa represented by arrows that indicate increasing abundance in the direction of the arrow. In contrast, non-metric, multidimensional scaling (MDS) is based on rank order correlation and uses a Bray-Curtis similarity matrix to generate an ordination (Clarke et al. 2005). MDS has the important advantage of not treating zeros as values of occurrence since multiple zero occurrences common in ecological data can play havoc with resemblance based on Euclidean distance. But, the order of the axis does not necessarily imply importance, which renders the results less intuitive and more difficult to interpret.

PCA and MDS were performed on square root transformed mean percent cover data across two time bins to explore the change in benthic assemblage composition over time (R package vegan: Oksanen et al. 2013). Species were scaled proportional to the eigenvalues for graphical purposes, so angles reflect correlations in multidimensional space (Legendre and Legendre 1998).

Relationships between coral and macroalgal cover and anthropogenic drivers were explored using various methods depending on the question and data structure (see text of relevant sections for detailed methodological information). Wherever relevant, we employed generalized linear mixed effects models with a beta distribution as described above to test the relationship between coral cover and drivers.

2. OVERALL CHANGES IN BIOLOGICAL ABUNDANCE

We first discuss status and trends of corals and macroalgae, which are the two major sessile components of Caribbean reef communities. Next we consider the demise of three major taxa that have severely declined over the past 40 years: the branching coral genus *Acropora* that once overwhelmingly dominated most shallow reefs, the sea urchin *Diadema antillarum*, and parrotfishes. The latter two are (or were) the most important macroscopic herbivores on Caribbean reefs.

2a. PATTERNS OF CHANGE FOR CORALS AND MACROALGAE

Mean live coral cover for the tropical western Atlantic based upon the most recent estimates of cover for each of the 88 locations in Table 2 is 16.8% (median 14.5%, range 2.8% for southeast Florida to 53.1% for the Flower Garden Banks). The mean is 68% higher than the mean of 10% cover reported previously for 2001 (Gardner et al. 2003) but almost identical to the mean of 16.0% cover for the years 2001-2005 from a more recent and more rigorous assessment (Schutte et al. 2010).

We further refined the estimate of mean percent coral cover using statistical methods to take into account the great variation among locations and datasets, resulting in a mean of 14.3% (+2.0, -1.8) This lower value reflects the skewed shape of the variation in coral cover across the region, wherein most locations fall well below the mean with several notable exceptions of locations with considerably higher than average coral cover (Fig. 7). This variation is further apparent when the quantiles of current coral cover are considered. The upper quartile is 21.2%, while the 95% quantile is 31.5%. Five locations fall above the 95% quantile including Bermuda, the leeward coast of Bonaire, the southwest coast of Curaçao, the Flower Garden Banks in the northern Gulf of Mexico, and Morrocoy National Park on the mainland coast of Venezuela (However, the high value for Morrocoy resulted from the relocation of the CARICOMP study site to a different reef after all the corals at the original location had died.).

FIGURE 7. Histogram of current estimates of percent coral cover from 88 locations across the Caribbean with box plot reflecting 0, 25%, 50%, 75% quantiles.

Coral cover declined at 52 of 71 (73%) locations in Table 2 for which time series data are available (Fig. 8). The decline was greatest for locations with the oldest estimates of percent cover (Fig. 8A) and the longest periods of observation (Fig. 8B). This is the now classic pattern of "shifting baselines" for fisheries management (Pauly 1995; Jackson and Jacquet 2011; Jackson et al. 2012). Another striking example of the Shifting Baselines Syndrome in the Caribbean concerns the status and trends of green turtle populations on nesting beaches that have been surveyed for varying lengths of time (Jackson 1997; McClenachan et al. 2006). Beaches observed for less than 40 years exhibit a wide mixture of positive and negative trends, whereas all beaches observed for more than 40 years have suffered very large declines of 75-95%.

FIGURE 8. Percent change in coral cover at 71 locations in Table 2. Change in percent cover of corals in relation to (A) cover measured in the earliest year of observation ($R^2 = 0.63$, $p < 0.01$) and (B) the duration of the study period for that location ($R^2 = 0.17$, $p < 0.01$).

Long-term changes in corals and macroalgae

Average changes in coral and macroalgal cover over the three time intervals are presented in Table 3 for all locations and the 21 long-term data locations in Fig. 4. Mean coral cover in depths of 0-20 m for all locations declined from 33.0% before 1984, to 18.6% from 1984-1998, and 16.4% from 1999 to today (Fig. 9A, Table 3). The average pattern of decline did not vary greatly with depth. Coral cover before 1984 was 33.2% on reefs from 0-5 m depth versus 32.6% cover in depths of 5.1-20 m (Table 3). After 1999 coral cover declined slightly more on reefs shallower than 5 m. *Acropora palmata* once overwhelmingly dominated reefs in 0-5 m with cover as great as 50 to 85% (Woodley et al. 1981; Gladfelter 1982). Thus, our data suggest that the decline of *Acropora palmata* had begun before the first quantitative surveys at most reef locations. In contrast, a locally variable mix of species including the *Orbicella* (formerly *Montastraea*) *annularis* species complex, other massive and plating corals, and *Acropora cervicornis* formerly dominated reefs from 5 to 20 m (Goreau 1959; Kinzie 1973; Bak 1977; Bak and Luckhurst 1980; Liddell and Ohlhorst 1986, 1988).

TABLE 3. Corrected values of percent cover of corals and macroalgae by depth for 3 time periods for all locations and for the subset of 21 circled locations in Fig. 4. Values are means with 95% confidence intervals in parentheses calculated with mixed-effect beta regression that takes into account variability due to location and datasets

FIGURE 9. Distribution of coral cover among all the locations in Table 2 for all three time intervals and depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

Changes in coral cover were similar on the 21 reefs in Fig. 4 except that coral cover was lower in shallow depths before 1984 and the subsequent declines were more abrupt between time intervals 1 and 2 (Table 3, Fig. 10).

FIGURE 10. Distribution of coral cover for the 21 long-term data locations (large circles in Fig. 4) for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

Macroalgal cover in 0-20 m was 7.0% prior to the mass mortality of *Diadema antillarum* in 1983 and then tripled to 23.6% afterwards (Fig. 11A, Table 3). However, the patterns vary strongly with depth. Macroalgal cover from 0-5 m depth averaged 12.1% before 1984 and increased afterwards to 40.1% (Table 3). In contrast, macroalgal cover was only 4.0% on reefs in 5.1-20 m before 1984, and then increased 5-fold after the *Diadema* died (Fig. 11C, Table 4). Macroalgal cover since 1999 has averaged about 23.2% but varied enormously among the 67 locations from 1-69%. Changes in macroalgae on the 21 reefs were similar to that for the entire dataset (Table 3, Fig. 12).

FIGURE 11. Distribution of percent macroalgal cover among all the locations in Table 2 for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

FIGURE 12. Distribution of percent macroalgal cover for the 21 long-term data locations (large circles in Fig. 4) for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent uncorrected means within locations for each time bin. Vertical line indicates mean, and N is the number of locations.

The clearly opposite trends in coral and macroalgal cover (Figs. 9 and 10 versus Figs. 11 and 12) demonstrate a highly significant and persistent shift throughout the wider Caribbean from reef communities where corals were the most abundant occupiers of space to reef communities where macroalgae are more abundant than corals (Fig. 13). Such a striking reversal from coral to macroalgal dominance is commonly referred to as a phase shift (sensu Hughes et al. 2010); a pattern first documented in even more extreme form from Jamaica between the 1970s and 1990s (Hughes 1994).

FIGURE 13. Large-scale shifts from coral to macroalgal community dominance since the early 1970s at (A) all locations and (B) the 21 long-term data locations (large circles in Fig. 4). Symbols and confidence intervals represent corrected means and standard deviations for 3 time intervals that take into account variability due to location and datasets using a mixed modeling framework.

Geographic Variation in Reef Degradation

The preceding histograms demonstrate very large geographic differences in the status and trends for coral cover at different reef locations. To document the nature of this variability in greater detail, we constructed two different kinds of timelines for the status and trends in coral cover for two different subsets of reefs presented below. The focus here is on documenting the patterns of variation among sites. Implications and insights derived from the timelines are discussed in the following section of the report on anthropogenic drivers of change.

<u>Timelines for specific reef sites</u>: These document detailed patterns of variation in coral cover and rates of change on a local scale for 40 particularly well-studied reef sites for which data were available over a span of at least eight years (Table 4, Appendix 2). The earliest of the timelines begins in 1972 but the great majority of sites were not surveyed quantitatively until the 1990s. Average net change in coral cover for the 40 sites is -21% but variation was extreme among sites (range +1 to -64%). Eight sites exhibited remarkable stability with a net change of only +1 to -5%

cover. In contrast, four sites declined by $\geq$ 55% and another six sites by 32% or more.

TABLE 4. Geographic locations, depths, year span, availability of coral taxonomic data, and net changes in coral cover for detailed timelines for 40 reefs. [1] T. P Hughes original site, now a CARICOMP site.

Whenever possible we chose reefs for plotting timelines for which taxonomic data were available for reef composition at the specific or generic level. Taxa were lumped into eight taxonomic and morphological groups for ease of graphing the data: acroporids (*Acropora palmata* and *A. cervicornis*), other branching corals (principally *Porites* and *Madracis*), agaricids (*Agaricia* and *Helioseris*), *Orbicella* (formerly *Montastraea*) *annularis* species complex, *Montastraea cavernosa*, *Porites astreoides*, and other corals (principally massive species of *Diploria*, *Siderastrea*, and *Colpophyllia*).

Taxonomic data were available for at least some of the surveys from 32 of the 40 sites. The fates of different taxa varied considerably. Species that suffered the greatest proportional losses include most of the former ecologically dominant taxa on Caribbean reefs, including *Acropora palmata* and *A. cervicornis*, branching *Porites* and *Madracis*, the *Orbicella annularis* species complex, and the large plate-like *Agaricia* species. However, most acroporid mortality occurred long before the first surveys at most of the sites. Species that declined the least include species that form massive colonies including the genera *Diploria*, *Siderastrea*, and some *Porites*. Shifts in taxonomic composition are analyzed further in the section on ordination analyses.

<u>Timelines for reef locations with coral cover data for all three time intervals:</u>
Twenty-one of the reef locations (clusters of nearby reef sites) enumerated in Table 2 were surveyed at least once before 1984, from 1984 through 1998, and from 1999 to 2011 (Fig. 4,Table 5).

TABLE 5. Changes in coral and macroalgal cover at the 21 long-term data locations indicated by large yellow circles in Fig. 4. Coral cover data are available for all three time intervals at all 21 locations. Macroalgal data are available for all three of the time intervals for just 9 of the 21 locations. Percent change over the three intervals is expressed as both the absolute change in cover and the proportional change (cover in time interval 3 minus cover in interval 1/cover in interval 1). The pattern of change refers to Fig. 14. P-values are the result of post-hoc comparison of means between the 1st and 2nd time interval and the 2nd and 3rd time interval with significance at the 95% level in bold.

Long-term trends in coral abundance varied greatly among these 21 locations (Table 5) that are grouped into three contrasting patterns of change to highlight their different histories (Fig. 14). Trajectories for nine of the 21 locations (Belize, Costa Rica, Florida Dry Tortugas, Jamaica, and St. Thomas) resemble a hockey stick with steep declines in coral cover between intervals 1 and 2 followed by little change thereafter (Fig. 14A). Proportional losses in coral cover between 1984 and 1998 ranged from 58 to 95% (average 73%). Coral cover at five additional locations (Florida Upper Keys, St. Croix, St. John, Veracruz Mexico, and Vieques Puerto Rico exhibited comparable proportional decline (50-80%, average 65%) that was spread out more evenly among the three time intervals (Fig. 14B). The third group of seven locations exhibited greater overall stability, although overall mean abundance among these locations differed nearly three fold (Fig. 14C). Coral cover at six of these locations including Barbados, Bonaire, Curaçao, Flower Gardens Bank, San Blas, and Santa Marta declined by just 4-35% over the three time intervals and increased at Bermuda by 35% (Fig. 14C). However, the increase at Bermuda is largely due to more comprehensive sampling of a wider diversity of habitats in recent years rather than an increase at earlier monitored sites.

FIGURE 14. Disparate trajectories of coral cover at 21 mapped locations for which data for coral cover are available for all three time intervals (1 = before 1984, 2 = 1984-1998, 3 = 1998-2011). Values are means of percent coral and macroalgal cover averaged over all the data for each location within each time interval. Locations are grouped by eye into thee general categories based on the total amount of change in coral cover over the three time intervals and the tempo of change. (A) hockey stick pattern of 49-90% decline between intervals 1 and 2 followed by little or no change. (B) approximately constant and continuous decline ranging from 50-80% over all three intervals. (C) comparative stability of +35% to -35%. Note that the trajectory for Bonaire is a hybrid of patterns A and C. (D) map showing geographic distribution of the three patterns of change. For further details see text.

The geographic distribution of the three different patterns of change overlap broadly throughout the wider Caribbean but there are also differences (Fig. 14D). Locations that exhibited the hockey stick pattern of dramatic early decline followed by no change (orange circles) are distributed very widely from Florida in the north to Costa Rica in the south and from Belize in the west to St. Thomas in the east. Locations where coral cover declined progressively through all three intervals (blue squares) are more constrained in latitude and distributed in a band from Veracruz in the west to Vieques, St. Croix, and St. John in the east. Lastly, locations that exhibited the greatest stability in coral cover (green triangles) are concentrated in the extreme south and north of the wider Caribbean plus Bermuda.

The disparate reef histories in Fig. 14 clearly demonstrate the folly of attempting to understand the causes of coral reef decline for the entire Caribbean as a single ecosystem, an approach that ignores the enormous heterogeneity in environments and history of human and natural disturbance among different reef locations. This is even more apparent in timelines of coral cover compiled for individual reef sites (Table 4, Appendix 2). Moreover, locations that suffered the greatest proportional loss in coral cover over the three time intervals (cover interval 1- cover interval 3/cover interval 1) also suffered the greatest absolute loss in cover (cover interval 1-cover interval 3) (Fig. 15). The strong correlation between proportional and absolute decline further strengthens the conclusion that trajectories of change at different locations reflect their unique histories of events rather than some pervasive force throughout the entire wider Caribbean.

FIGURE 15. Absolute change in percent cover of corals from before 1984 to after 1999 versus the proportional change in coral cover ($R^2 = 0.65$, $p < 0.01$).

Ordination of coral and macroalgal community composition:

We used PCA and MDS to investigate patterns of change in community composition of corals and macroalgae for the entire dataset and the 21 reef locations in Table 5 (Fig. 16-17). Coral taxa were grouped based on an analysis of their average abundance and frequency of occurrence in the overall dataset to minimize zero occurrences in the ordination matrix. The resulting nineteen taxa include: *Acropora cervicornis, Acropora palmata, Agaricia tenuifolia,* other *Agaricia, Colpophyllia, Diploria, Eusmilia, Helioseris, Madracis, Meandrina, Millepora, Montastraea cavernosa, Mycetophyllia, Orbicella* [formerly *Montastraea*] "*annularis*" complex, *Porites astreoides,* other (overwhelmingly branching) *Porites, Siderastrea, Stephanocoenia,* and other corals. Macroalgae were considered as a single taxon.

Results are presented here for the PCA analyses only. The best results are for the 21 locations with data for coral and macroalgae in the same analysis in which the first three principal components explain more than 70% of the total variance. (Table 6, Fig. 16A-B). The strongest separation along PCA 1 is between macroalgae versus corals. PCA 2 accounts for an additional 20% of the variance reflecting the opposite trends in occurrence of branching *A. palmata* and the *Orbicella annularis* species complex. The same analysis based on all the localities produces a similar pattern but explains less of the total variability (Fig. 16C-D), a difference we attribute to the lack of consistency of locations among time intervals due to very limited sampling at most of the locations in Table 2 and greater variety in reef environments compared to the more restricted analysis.

TABLE 6. Summary statistics for PCA analyses of coral and macroalgal community composition.

FIGURE 16. Principal components analysis of coral taxa and macroalgae. (A-B) PCA based on all available data for the 16 of 21 locations in Table 5. (C-D) PCA based on all available data for the 44 locations with coral data from more than a single year in Table 2.

Ordinations based only upon coral taxa without macroalgae yielded consistently poorer results, underlining the fundamental importance of the phase shift between corals and macroalgae that dominates patterns of change (Fig. 17).

FIGURE 17. Principal components analysis of coral taxa without macroalgae. (A-B) PCA based on all available data for 18 of the 21 locations in Table 5. (C-D) PCA based on all available data for the 64 locations with coral data available at a fine taxonomic level.

2b. EXTREME DECLINE OF FORMERLY DOMINANT SPECIES

Three taxa of formerly great ecological significance on Caribbean reefs suffered massive declines up to several decades before the first quantitative surveys at most of the 90 locations in Table 2. Losses were so great that the species are virtually ecologically extinct; meaning they no longer play any significant ecological role in determining the distribution and abundance of surviving species. Understanding the subsequent decline of Caribbean reefs hinges upon a clear understanding of the magnitude of these early changes that in most places have hardly left a trace.

Decline of *Acropora palmata* and *A. cervicornis*

Acropora palmata and *A. cervicornis* were among the most abundant and ecologically dominant corals on Caribbean reefs in depths down to 20 m for the last one million years until the 1970s and 1980s (Goreau 1959; Geister 1977; Adey 1978; Jackson 1992, 1994; Pandolfi 2002; Pandolfi and Jackson 2001, 2006). Distribution and abundance were highly variable. Nevertheless, the former ecological dominance of *Acropora* is obvious from the composition of Holocene and Pleistocene reef rock, the coral fraction of which is 80-90% *Acropora* by volume in the majority of shallow-water sections (Mesolella 1967; Macintyre and Glynn 1976; Lewis 1984; Liddell et al. 1984; Jackson 1992 and references within; Pandolfi and Jackson 2001, 2006; Aronson and Precht 2001).

Both species experienced intense mortality due to White-Band Disease (WBD) since the mid to late 1970s until today (Gladfelter 1982; Porter and Meier 1992; Aronson and Precht 2001; Porter et al. 2001; Patterson et al. 2002; Weil and Rogers 2011). Hurricanes and outbreaks of predators also devastated acroporids in Jamaica and the USVI in the 1980s (Knowlton et al. 1981, 1990; Woodley et al. 1981; Rogers et al. 1991; Rogers and Miller 2006), and there is strong paleontological evidence for die-offs several decades earlier in Barbados (Lewis 1984), Bocas del Toro, Panama (Cramer et al. 2012), and more broadly throughout the region (Jackson et al. 2001).

Unfortunately, there are remarkably few quantitative data on the abundance of either species until they were already greatly diminished by disease, a spate of hurricanes in close succession, and degrading water quality to be reviewed in the next section. To address this, we compiled a very large qualitative database on the occurrences of both species back into the 19th century to supplement the quantitative data (Appendix 3). The proportion of reef sites with presence and dominance of *Acropora palmata* and *A. cervicornis* was computed for the time period from 1851-2012. Data include qualitative and quantitative information from the primary peer-reviewed scientific literature, government reports, and less commonly historical literature as well as quantitative data received directly from contributors to this study and compiled in the larger GCRMN database. Quantitative data include percent cover for either *Acropora* species, while qualitative data include presence/absence and relative abundance data, as well as descriptions of relative abundance categories (Appendix 3). Data are primarily from underwater field surveys, although a small number are from boat-based observations and high-resolution aerial photographs. Data from the literature were extracted from texts, tables, figures, and maps.

Only data from "reef crest" and "midslope" reef zones were included in the analysis. Generally, reef crest data spanned 0-6 m water depth and midslope data spanned between 6-20 m, as 6 m was the depth at which dominance typically shifted from *A. palmata* to *A. cervicornis* in the quantitative data. However, the distinction between reef crest and midslope was made on a reef site-by-site basis, taking into account additional information on reef zone or reef morphology, if available. For some locations, the cutoff was closer to 10 m, the same value used in Jackson et al. (2001). Data were not included if determination of the reef zone could not be made. Data were recorded at the reef site level and computed by averaging over replicates within the same reef site and reef zone. In total, 1,855 reef sites from 67 locations were compiled for the reef crest zone and 4,543 reef sites from 80 locations for the midslope zone. These included locations that were not represented in the master GCRMN quantitative database (Table 2).

Results are presented in Fig. 18. Sample size is small before 1950, and the locations represented in various time bins are not consistent. Nevertheless, the data confirm the remarkably great abundance of both species before the 1970s. *Acropora palmata* was present at more than 80% of all areas surveyed in depths less than 10 m throughout the wider Caribbean region and was recorded as "dominant" at 60% of these localities Fig. 18 A-C. The data also suggest that the decline in *A. palmata* occurrence and dominance began in the 1960s in accord with the paleontological data (Lewis 1984; Cramer et al. 2012). The patterns for *A. cervicornis* are similar to *A. palmata* (Fig. 18D-F). The species was present at 60% of all localities surveyed before 1959 and dominant at nearly 40% of them. As for *A. palmata*, there is a suggestion that dominance began to decline before the 1970s but there are less data than for *A. palmata*. Quantitative data are extremely sparse showing a maximum average percent cover of just over 1% although some reefs were still blanketed by about 50% cover, emphasizing the dearth of quantitative data before the late 1980s.

FIGURE 18. Decline in *Acropora palmata* and *A. cervicornis* throughout the wider Caribbean region based on qualitative and quantitative data. (A) frequency of occurrence of *A. palmata*; (B) frequency of reefs at which *A. palmata* was described as the dominant coral; (C) changes in percent cover recorded in the GCRMN quantitative database; (D) frequency of occurrence of *A. cervicornis*; (E) frequency of reefs at which *A. cervicornis* was described as the dominant coral; (F) changes in percent cover recorded in the GCRMN quantitative database. Sample size (numbers of sites) indicated adjacent to points. Confidence intervals are 95% binomial intervals for A, B, D, and E and standard errors for C and F.

Decline of *Diadema antillarum*

Diadema antillarum was variably abundant on Caribbean reefs until 1983 when it rapidly suffered mass mortality from an unidentified pathogen throughout its range in the tropical western Atlantic (Lessios et al. 1983; Lessios 1988). Reported densities before the die-off ranged from a low of about 1/m^2 to a spectacular 90/m^2 in a harbor at Discovery Bay Jamaica. Hughes et al. (2010) compiled all the available data from the literature for trends in *Diadema* abundance since the earliest quantitative surveys to present. We supplemented their analysis with additional data from the GCRMN database with essentially similar results (Fig. 19). Average density throughout the region was about 8-10/m^2, declining to near zero between 1983 and 1984. Average density remained extremely low throughout the second time interval (1984-1998), and then rose almost imperceptibly during the third period. However, some locations have densities today back up to 3-5/m^2 (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Idjadi et al. 2010; Vardi 2011).

FIGURE 19. Abundance of *Diadema antillarum* throughout the wider Caribbean from 1972 to 2012. Densities of > 25 /m^2 before 1983 are not shown and are not included in average densities. Studies that intentionally surveyed aggregations were not included.

Parrotfish abundance and biomass

Reef fishes were overfished before the middle of the 20th century throughout large areas of the Caribbean including especially Jamaica and the USVI (Duerden 1901; Thompson 1945; Randall 1961, 1963; Munro 1983; Hughes 1994; Hay 1984; Jackson 1997). This was decades before the first underwater quantitative surveys in the late 1970s and 1980s. Reef fishes were still reported to be abundant at many remote localities such as the Belize Barrier Reef (Lewis and Wainwright 1985; Lewis 1986), but the once large schools of large bodied groupers and parrotfishes had mostly disappeared. Fishing prior to the 1970s was mostly artisanal using small nets and fish traps. Parrotfish were not specifically targeted but their wide bodies made them particularly vulnerable to traps (Johnson 2010).

We examined parrotfish abundance since 1988 in two ways. In the first case, we compiled all the quantitative data on parrotfish biomass in the GCRMN database after the year 2000 to examine the frequency distribution of biomass (Table 2; Fig. 20). Mean parrotfish biomass taking into account differences among locations and datasets was only 14g/m^2, a small fraction of the highest Caribbean value recorded of 71 g/m^2 and an even smaller percentage of their abundance on protected Indo-Pacific reefs (Sandin et al. 2008a).

FIGURE 20. Frequency distribution of parrotfish biomass based on all available data after the year 2000 in the GCRMN database (1988-2012) with box plot reflecting the median and the first and third quantiles and dots for outliers.

Time series of parrotfish biomass longer than ten years are available for only three locations at St. John USVI, Guadeloupe, and Bonaire (Fig. 21). Values at St. John have been extremely low, hovering around 5-10 g/m^2 since the beginning of the surveys in 1988 in accordance with Randall's (1961) much earlier work in the 1950s when he observed the USVI were already severely overfished (Fig. 21A). In contrast, parrotfish biomass at Guadeloupe also started off at around 10 g/m^2, but has since gradually increased for unknown reasons to between 25-30 g/m^2 (Fig. 21B). Bonaire exhibits a strikingly different pattern (Fig. 21C). Parrotfish biomass in 2003 was similar to the highest recorded in the Caribbean (71 g/m^2) but has since plummeted to less than 30 g/m^2 due to recent targeted fishing on parrotfishes (Fig. 24C; Steneck and Arnold 2009; Steneck et al. 2011).

FIGURE 21. Trends in parrotfish biomass since 1988 at (A) St. John, (B) Guadeloupe, and (C) Bonaire. Error bars represent one standard error.

3. ANTHROPOGENIC DRIVERS OF CORAL REEF DEGRADATION

The ultimate driver of environmental degradation is human population growth coupled with inevitable increases in resource consumption, pollution, and habitat degradation as humanity clamors to feed, clothe, and satisfy 7 billion people and counting (Meadows et al. 1972; Vitousek et al. 1997; Wackernagel et al. 2002). But population alone is seldom a good predictor of environmental condition because of enormous disparities in consumption, cultural traditions, and the ways people exploit, pollute, and directly physically impact their natural environment.

Another major difficulty in deciphering cause and effect is the common failure to distinguish between potential drivers of coral decline (overpopulation, overfishing, coastal pollution and development, rising temperatures due to the burning of fossil fuels, introduced species, etc.) and their effects (increases in macroalgae, coral bleaching, coral disease) (Hughes et al. 2010). This problem is especially vexing in the case of coral diseases that have exploded since the first reports of their occurrence in the 1970s (Antonius 1973; 1977; Gladfelter 1982).

Coral diseases have taken a dreadful toll and it is easy to forget that their sudden emergence is almost certainly the result of some combination of anthropogenic stressors (introductions of exotic pathogens, eutrophication, warming, increases in macroalgae, etc.) rather than a natural force. Nevertheless, because of their great and increasing importance, we have treated coral diseases separately in section 3f. A similar confusion exists for the role of hurricanes that are natural phenomena but have been hypothesized to have increased in occurrence and intensity due to climate change. This postulated increase has been blamed for the failure of reefs to recover from the storms. We therefore treat the role of hurricanes separately in Section 3g.

Here we attempt to identify the major drivers of Caribbean coral reef decline by analyzing different anthropogenic stressors one at a time. The results are obviously a work in progress, but we believe they are remarkably clear in identifying the major factors responsible for reef degradation to date and ways in which the nature of stresses on Caribbean reefs are likely to change over the next few decades. Future analyses for publication in the scientific literature will examine all of the drivers together by multivariate analysis.

3a. POPULATION DESITY OF RESIDENTS AND VISITORS (TOURISTS)

We compiled data from the World Wide Web on the average numbers of residents and visitors per year over the past decade at 34 and 29 Caribbean reef locations respectively (Table 7). Considerable effort was invested in locating data for coral reef regions and not for entire countries, as has been the general practice for studies of the impact of people on coral reefs. It is meaningless to compare an ecological metric such as coral cover for an archipelago like Los Roques Venezuela to the entire population of Venezuela, or the condition of the Florida Keys to the population of the entire State of Florida. In general, data for numbers of residents was more forthcoming than for visitors, and in several cases numbers of visitors were combined for two or more different locations such as St. Thomas and St. John because of the lack of an international airport on St. John. Population densities were calculated for land area rather than reef area because the topographic data for land area are more reliable and precise due to satellite mapping. In contrast, published estimates of reef area commonly vary several-fold for the same location because of different definitions of what constitutes a reef and different technologies and methods of observation employed.

TABLE 7. Numbers of visitors and residents and the numbers/km^2 for 34 Caribbean locations plus Bermuda. Data compiled from the World Wide Web based on censuses of residents and tourist board and industry data for numbers of visitors. Most data are for the past five to seven years.

Population densities of residents varied 165-fold, from a low of 8 persons/km^2 at Little Cayman to a high of 1,316/km^2 at San Andrés Colombia with 24 of the locations between 100-1000/km^2 (median = 264/km^2). Variations in numbers of visitors per year are even more extreme, ranging 229-fold from 110 persons/km^2 in the Bahamas to an astounding 25,196/km^2 at St. Thomas. Seventeen of the 29 locations have between 1001 to 10,000 visitors/km^2/year (median = 1500/km^2/year). Nine of the locations had less than 1000 visitors/km^2 and 2 have more than 20,000/km^2.

Coral cover is plotted against the density of residents and annual density of visitors in Fig. 22. We used 2 by 2 contingency table analysis to test to explore the relationship between human population density and coral cover. Boundaries of the four quadrants were determined by median values of coral cover and by median densities of residents and tourists. Coral cover is significantly negatively correlated with both the density of residents ($N = 34$, $X^2 = 7.5$, df = 1, $p = 0.01$) and the density of visitors per year ($N = 29$, $X^2 = 5.99$, df = 1, $p = 0.01$). Moreover, all the locations with more than 2,635 visitors/km^2/year have only 6.1 to 13.6% cover.

Most tourists to Caribbean locations never get beyond the swimming pool to even see a coral reef so their impact on reefs is indirect. The most important indirect effects include runoff of sediments due to unregulated coastal development of roads and hotels, dredging harbors for yachts and gargantuan cruise ships, and nutrient pollution from runoff from golf courses and untreated or minimally treated sewage from hotels, cruise ships, and cesspits (see references in the section on water quality below). In this light, the remarkably high coral cover at Bermuda despite very high densities of visitors and residents is almost certainly a result of strongly enforced environmental and fisheries regulations as discussed below.

FIGURE 22. Coral cover in relation to human population density. (A) Numbers of residents/km^2, (B) numbers of visitors/km^2/year. B = Bermuda, C = Cayman Islands, N = Corn Islands Nicaragua

3b. FISHING

Artisanal coral reef fisheries are traditionally among the most important sources of protein and livelihood throughout Caribbean coastal communities (Jackson 1997; Hardt 2009). As populations have grown, however, overfishing has resulted in the widespread collapse of reef fish stocks with dire consequences not only for peoples' livelihoods and nutrition but also the ecological condition of coral reefs (Duerden 1901; Thompson 1945; Munro 1983; Hughes 1994; Hawkins and Roberts 2003). The ecological consequences of overfishing are complex and depend on a host of factors including the types of fishing gear employed, the variety of species exploited, trophic cascades, interactions with other kinds of human disturbance, and the unique environmental characteristics of different reefs (Jackson et al. 2001; Mumby et al. 2006, 2007, 2012; Estes et al. 2011). Nevertheless, overfishing is strongly correlated with ecological collapse of reef ecosystems as defined by decrease in coral cover and recruitment and increases in macroalgal abundance and coral disease (Hughes 1994; Sandin et al. 2008a).

The ecological consequences of overfishing in the Caribbean for coral reef communities are most clearly associated with reductions in the abundance and sizes of herbivores, most importantly parrotfishes, surgeonfishes, and sea urchins. Innumerable experiments have shown that exclusion or removal of these grazers results in explosive increases in the abundance of macroalgae (Randal 1961; Lewis 1986; Lirman 2001; Hughes et al. 2007) that potentially compete with corals in numerous ways discussed below. This is perhaps most obvious in the Caribbean where the mass mortality of the sea urchin *Diadema antillarum* coupled with the overfishing of parrotfishes has resulted in the large increases in macroalgal abundance documented in the previous section (Table 3; Figs. 11-13).

Fishing pressure and the state of reef fish populations varied greatly among Caribbean reef locations in the 1970s due to a complex mix of fishing practices, economic well being, and cultural traditions that are beyond the scope of this report. Nevertheless, certain patterns are clear. Densely populated West Indian islands with a long tradition of sugar economies based upon slavery (e.g., Jamaica, Barbados, Hispaniola, the Virgin Islands, and most of the Lesser Antilles) developed labor intensive artisanal fisheries based largely on the use of fish traps and small nets that resulted in extreme overfishing by the early 20th century (Duerden 1901; Thompson 1945; Randall 1963; Munro 1983; Jackson 1997; Hawkins and Roberts 2003; Hardt 2009). In contrast, continental reefs along the coasts of Florida, Mexico, the Mesoamerican Barrier Reef, and northern South America were generally less densely populated and less heavily fished until the 1970s to 1990s (Goode 1887; Jackson 1997; McClenachan 2008).

Diadema abundance before 1984 as a proxy for historical fishing pressure

Most of the historical information on overfishing is anecdotal or qualitative and there were very few hard scientific data to back them up until Mark Hay (1984) conducted a comparative study from 1980-1982 on the intensity of grazing by the sea urchin *Diadema antillarum* versus grazing by parrotfishes and surgeonfishes at several locations across the wider Caribbean. Densities of *Diadema* on eight heavily fished reefs ranged from 5-20/m^2 (median = 10) versus 0 to 8/m^2 (median = 1) on less fished reefs (Hay 1984, his Table 2, $F_{1,12} = 20.7$, $p < 0.01$).

Hay did not count herbivorous fishes but instead used strips of the seagrass *Thalassia testidinum* as standardized "baits" to measure rates of herbivory. Rates of consumption of *Thalassia* bait by fishes and *Diadema* were inversely proportional in relation to the extent of overfishing on the reefs. Fish consumption of bait on lightly fished reefs in Belize, Panama, Honduras, and a protected area in the US Virgin Islands was 5-10 times higher than on heavily overfished reefs in Haiti and the US Virgin Islands. Consumption and abundance of *Diadema* showed the opposite pattern, with very little consumption on less fished reefs and high consumption exceeding that by grazing fishes on overfished reefs.

There is also considerable evidence from ecological surveys and from natural and manipulative experiments for intense competition for food between *Diadema* and grazing fishes, especially parrotfish. Abundance of *Diadema* and grazing fishes were inversely proportional across a depth gradient on reefs near Carrie Bow Cay in Belize (Lewis and Wainwright 1985). *Diadema* were most abundant in the high spur and groove habitat (4.3/m^2) where the high habitat relief likely provided better protection from predators than less complex habitats. In contrast, parrotfish abundance was only 0.07/m^2, the lowest in any of the five reef habitats surveyed. *Diadema* abundance was extremely low (0.1 to 0.7/m^2) in all the other reef zones where parrotfish abundance ranged from 0.09-0.32/m^2.

Hay and Taylor (1985) strengthened the evidence for strong competition between *Diadema* and parrotfish in two *Diadema* removal experiments at St. Thomas and St. Croix that were conducted just before the *Diadem*a die-off occurred. Numbers of parrotfish at two control (non-removal) sites at St. Thomas were 0.02 and 0.04/m^2 versus 0.18/m^2 at the removal site (Kruskal-Wallace Test, $p < 0.05$). Similarly at St. Croix, there were 0.08 parrotfish/m^2 at the single control site versus 0.29/m^2 at the removal site (Kruskal-Wallace Test, $p < 0.05$). These patterns were confirmed by surveys before and after the die-off of *Diadema* within four reef zones at Tague Bay, St. Croix (Carpenter 1990b). Numbers of parrotfish increased 3.9-fold from 0.17/m^2 transect before the die-off to an average of 0.66/m^2 afterwards on the backreef and reef crest. Similar comparisons for the three forereef zones surveyed showed a 2.8-fold increase from 0.29 to 0.81 parrotfish/m^2 at 2 m; a 2.3-fold increase from 0.25 to 0.57/m^2 at 5 m; and a 4.1-fold increase from 0.17 to 0.67/m^2 at 10 m. All of these differences were significant by 1-way ANOVA at $p < 0.0001$.

Summarizing the above, Hay's (1984) study confirmed that overfishing on many Caribbean reefs occurred before the mass mortality of *Diadema* in 1983, a fact consistent with Jack Randall's (1961, 1963) pioneering investigations in the 1950s and all of the historical data (Duerden 1901; Thompson 1945; Munro 1983; Jackson 1997; McClenachan 2008; Hardt 2009). But this is difficult to document beyond Hay's and the other specific study sites because there are virtually no quantitative survey data on the biomass of Caribbean herbivorous reef fishes prior to 1988 (Tables 1 and 2, Fig. 6).

What we can do, however, is to use the patterns of *Diadema antillarum* abundance prior to 1984 as a proxy for historical fishing pressure based upon (1) the well-documented inverse correlation between *Diadema* abundance and herbivorous fish abundance prior to the mass mortality of *Diadema* in 1983 (Ogden et al. 1973; Hay 1984, Lewis and Wainwright 1985), (2) the increase in herbivorous fish abundance after the die-off of *Diadema* in 1983 (Carpenter 1990a, b; Robertson 1991), and (3) Hay and Taylor's (1985) *Diadema* removal experiments. Besides all of the above, we know of no evidence to suggest that *Diadema* abundance was not inversely proportional to fishing pressure. Thus the proxy relationship is robust.

Contrasting fates of reefs since 1984 in relation to historical fishing pressure

Data on *Diadema* density/m^2 before 1984 were available for 16 of the 21 reef locations in Table 5 and Fig. 14 (Table 8, Appendix 4). *Diadema* densities ranged from a low of 0.5/m^2 at San Blas, Panama to a high of 12.4/m^2 at the Port Royal Cays, Jamaica. There is a clear break in the values between reefs in San Blas, Bermuda, the Upper Florida Keys, Bonaire, Belize, Curaçao, and Cahuita Costa Rica (0.5/m^2 to 3.8/m^2, median = 1.5/m^2, classified here as "less fished" reefs) versus reefs in Barbados, Jamaica, and the US Virgin Islands (6.9/m^2 to 12.4/m^2, median - 9.1/m^2, classified here as "overfished" reefs, t-test: t = 9.0, df = 13.6, $p < 0.01$). These values correspond closely with what is known qualitatively about fishing pressure at these locations before 1984 (Appendix 5).

TABLE 8. Data for the analysis of the effects of historical and recent fishing pressure on coral cover for the 16 locations in Table 5 with *Diadema* data from before the die-off.

We conducted a linear mixed-effects model analysis to compare median coral cover between "less fished" versus "overfished" reefs based on the density of *Diadema* at the 16 locations before the 1983 die-off (see methods section for model formulation). As expected, there was no significant correlation between coral cover at less fished and overfished locations before 1984 (Fig. 23A; GLMM p=0.19) because high *Diadema* abundance compensated for the low abundance of herbivorous fish. But this changed after the 1983 mass mortality of *Diadema* when median values of coral cover significantly diverged between less fished and overfished reefs (Fig. 23B-C; GLMM p<0.01). Similar results were found for coral cover since 2005 (Fig. 23D; GLMM p=0.01). There is also a significant difference between time periods 1 and 3 in the proportional loss in coral cover between "less fished" locations (median = -35%, range +35% to -80%) and "overfished" locations (median = -65%, range -22% to -90%) ($F_{1,14}$ = 4.96, p = 0.04). Comparisons between time periods 1 and 2 and 1 and 4 are not significant but all of the trends are in the same direction.

Data for macroalgae are too incomplete for meaningful statistical comparison of changes in macroalgal abundance between "less fished" and "overfished" reefs although the trends are consistently in the expected direction with two to three times higher macroalgal cover at locations that had been earlier overfished (Table 8, Fig. 23 D-E).

FIGURE 23. Percent coral (A-D) and macroalgal (D-E) cover in relation to the abundance of *Diadema antillarum* before the die-off in 1983 for the 16 reef locations in Table 8. (A) coral cover 1970-1983 (N = 16, median = 39.2/m^2 versus 34.1/m^2, p = 0.19), (B) coral cover 1984-1998 (N = 16, median = 21.0/m^2 versus 8.4/m^2, W = 53, p < 0.01), (C) coral cover 1999-2011 (N = 16, median = 28.8 versus 11.8, p = 0.02), and (D) coral cover since 2005 (N = 15, median coral cover 31.5/m^2 versus 10.1/m^2 p = 0.01). (E) macroalgal cover 1970-1983 (N = 8, median MA cover 1.0 versus 1.6%), (F) from 1984-1998 (N = 11, median MA cover = 11.7 versus 22.4%), (G) from1999-2011 (N = 14, median MA cover = 15.2% versus 43.6%), and (H) since 2005 (N = 14, median MA cover = 14.8% versus 35.1%).

The role of parrotfish today

Further support for the harmful consequences of overfishing herbivorous fishes upon coral cover is apparent from the positive and negative correlations on reefs today between the abundance of grazing parrotfishes and the percent cover of corals and macroalgae for all of the locations in Table 9 with paired data (Fig. 24). The non-parametric correlation is significant for coral cover versus parrotfish (Fig. 24A) but not for macroalgae versus parrotfish due to the smaller sample size for macroalgae and considerably greater scatter in the data (Fig. 24B). Results were opposite for the smaller dataset of 16 reefs (Fig. 24 C-D).

FIGURE 24. Percent coral cover and macroalgal cover versus parrotfish biomass since 1998 for all reef locations with paired data Table 9: (A) N = 67, r_s = 0.31, p = 0.02; (B) N = 46, r_s = -0.19, p = 0.20. The same analysis for only the16 locations in Table 8: (C) r_s = -0.36, p = 0.21); (D) r_s = -0.81, p = 0.01).

Generally speaking, the few reefs in the upper quartile of parrotfish biomass today (locations with > 15.6g/m^2) have significantly more coral than reefs where parrotfish are less abundant (t = 2.24, df = 60.7, p = 0.03). This is especially evident when the relationship between parrotfish biomass and macroalgal cover is compared with a linear-mixed model between locations that had been overfished before 1984 (high *Diadema* abundance) and those that were not (Fig. 24D). All of the historically overfished localities have low parrotfish biomass and low coral cover (Fig. 24C), and macroalgal cover is significantly greater than at less fished locations ($t = -2.12$, $df = 36.2$, $p = 0.03$), and strongly negatively correlated to parrotfish abundance (Fig. 24D, $\beta = -1.14$, $SE = 0.40$, $p < 0.01$).

Indirect effects of fishing due to increased macroalgal abundance

Reduction in coral recruitment

Approximately one quarter of Caribbean corals are brooding species that produce comparatively small numbers of large planula larvae that disperse short distances from their parents. Larval mortality is lower than for broadcasting species and populations may be effectively self-seeding (Jackson 1991). In contrast, the remaining broadcasting species spawn gametes that are fertilized in the ocean and larvae disperse farther and suffer higher mortality before settlement than brooding species so that there is little or no correlation between adult abundance and recruitment at different sites (Jackson 1991).

Numbers of coral recruits before the *Diadema* mortality were overwhelmingly dominated by brooding species that comprised > 90% of all recruits (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al. 1984; Hughes and Jackson 1985). Recruits of brooding species are still more abundant than broadcasting species, but rates of coral recruitment have greatly declined. The most extensive long-term data are from Jamaica and Curaçao (Hughes and Tanner 2000; Vermeij 2006). Cover of two brooding species in Jamaica (*Agaricia agaricites* and *Leptoseris cucullata*) declined 83% between 1977 and 1993 while the average number of recruits/year declined 75%. Thus the decline in recruitment was similar to the loss in coral cover. This was not the case in Curaçao, however, where coral cover declined by 50% but coral recruitment in identical settlement panel experiments declined by more than 80% between 1979-1981 and 1998-2004 so that the decline in recruitment cannot be attributed entirely to a simple decline in the abundance of parental colonies.

The differences on the upper surfaces of the settlement panels were even greater and provide a clue to the factors responsible. Upper surfaces in 1979-1981 were almost entirely dominated by crustose coralline algae that favor coral recruitment (Morse et al. 1988; Hughes et al. 2007; Arnold and Steneck 2011) and macroalgae were absent, whereas from 1998-2004 the upper surfaces were covered by macroalgae. Total numbers of recruits after each following year were > 500 in the 1979-1981 experiments compared to about 25 in the 1998-2000 experiments. These included a total of 981 recruits of *Agaricia* and *Porites* in the earlier experiment versus none of these taxa in 1998-2000. Numbers of "juvenile" corals (< 4 cm) on the reefs at Curaçao decreased by only 55% but these small corals can be as much as 13 years old (Vermeij et al. 2011). There was also a dramatic shift in juvenile coral composition: mean density of juveniles of brooding species decreased on average by about 10 recruits/m^2 whereas that of spawning species increased by 1-2 recruits/m^2.

The data from Curaçao strongly suggest that increased macroalgal abundance is a major factor in the reduced recruitment of corals, an observation consistent with earlier observations of Rogers et al. (1984) who concluded: "High rates of coral recruitment tended to be associated with low [non-calcareous] algal biomass and relatively high grazing pressure by urchins and fishes." Recent experiments strongly support this hypothesis. Recruitment of *Porites astreoides* larvae in Florida was inhibited by a variety of the most abundant macroalgae and cyanobacteria on Caribbean reefs (Kuffner et al. 2006). All of the macroalgal and cyanobacterial species tested caused recruitment inhibition or avoidance behavior by larvae and several species also significantly increased mortality of recent recruits. Behavioral avoidance reactions by the coral larvae suggest some form of chemical inhibition. There is also experimental evidence for more direct physical inhibition of recruitment by macroalgae at Roatán, Honduras (Box and Mumby 2007). Shading by *Lobophora* and *Dictyota* caused considerable losses in juvenile coral tissues and increased mortality of recruits and presence of *Dictyota* around the periphery of coral recruits decreased their growth rates by as much as 99%, and decreased cohort survival. Additional settlement experiments in Belize confirm that crustose coralline algae are strongly favorable to coral recruitment whereas macroalgae and turf algae inhibit recruitment (Arnold and Steneck 2011).

The role of macroalgae in inhibiting coral recruitment is even more strongly supported by striking increases in coral recruitment following reductions in macroalgae by recovering populations of *Diadema* and parrotfish. *Diadema* have begun to recover in increasingly large areas across the Caribbean (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006) reaching densities of 1.7/m^2 to 8.9/m^2 on a spatial scale of several km at sites in Belize, Jamaica, St. Croix in the northern Caribbean and Bonaire, Grenada, and Barbados in the south. Juvenile coral densities ranged from 4.5/m^2 to 32.3/m^2 in areas where *Diadema* have recovered versus 2.5/m^2 to 12.9/m^2 where they have not. A more recent study at Discovery Bay, Jamaica corroborated these results (Idjadi et al. 2010). Macroalgae were reduced from 68% to 6% cover. A combination of crustose corallines, turf algae, and bare space constituted 74% of the reef surface following grazing instead of 16%, and corals more than doubled from 4 to 11% cover in urchin zones compared to areas where urchins were absent.

A similar result emerges from the partial recovery of parrotfish in marine protected areas in the Bahamas (Mumby et al. 2006, 2007; Mumby and Harborne 2010). Increased parrotfish abundance and size in the Exuma Cays Land and Sea Park resulted in a 2- to 3-fold increase in parrotfish grazing intensity compared with unprotected sites. This increase in grazing further resulted in a decrease in macroalgal cover from 20-25% to about 1-5% and a 2- to 3-fold increase in coral recruitment. Moreover, size-adjusted rates of change in cover of five dominant coral species increased in areas within the marine park and decreased outside. The tipping point between positive and negative effects on coral growth occurred at about 10% macroalgal cover. Finally, the benefits of marine protected areas for increasing herbivory on reefs greatly exceed the potentially harmful effects of increased predator abundance on parrotfish (Mumby et al. 2006). This is because large bodied parrotfish can achieve an escape in size from predators.

Thus all of the evidence to date strongly supports the hypothesis that high macroalgal cover strongly reduces the recruitment of juvenile corals into the coral reef community. The negative effects of macroalgae far exceed the effects of decreased parental populations.

Increases in coral disease

There is also increasingly strong experimental evidence that high macroalgal abundance due to overfishing may induce outbreaks of coral disease as will be discussed in Section 3f on coral disease.

3c. COASTAL POLLUTION

It has long been understood that areas of greater sedimentation, seawater turbidity and light attenuation are less favorable to corals than clearer waters (Odum and Odum 1955; Sheppard et al. 2009). Low light affects photosynthesis by microbial symbionts, and sediments and oil interfere with ciliary feeding and may require increased production of mucus for sediment removal (Dodge et al. 1974; Bak and Elgershuizen 1976; Loya 1976; Dodge and Vaisnys 1977; Bak 1978; Rogers 1983b, 1990; Jackson et al. 1989; Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993; Wolanski et al. 2003; D'Croz et al. 2005; Cramer et al. 2012). All of these different forms of stress may decrease coral growth rates and survival

Several factors contribute to increased turbidity including unregulated coastal development, dredging, other forms of coastal pollution such as oil spills, re-suspension of bottom sediments by storms, proximity to areas of naturally heavy rainfall and erosion, and excess nutrients from sewage, agriculture, and clearing of land. Nutrient pollution may be especially problematic because of excess production by phytoplankton and benthic algae that further reduce light levels (D'Croz et al. 2005) and may promote macroalgal growth and disease. The resulting positive feedback loop has negative impacts on coral survival including increased growth of macroalgae that may overgrow, abrade, or poison corals as well as inhibit their recruitment (Section 3b) and promote coral disease (Kline et al. 2006; Section 3f).

Most of the evidence regarding nutrient pollution versus grazers for the increased abundance of macroalgae implicates top down control by fishes, sea urchins, and smaller invertebrates (Hughes and Connell 1999; Aronson and Precht 2000; Burkepile and Hay 2006, 2008, 2009). However, nutrient and chlorophyll data are unavailable for most Caribbean reef locations because optical data from satellites cannot yet reliably determine chlorophyl levels in reef waters and there is a dearth of systematically collected data from water samples at different reef locations. Thus it not yet possible to systematically explore whether there is a strong case for the role of bottom-up processes except in the most heavily polluted locations such as parts of the Florida Reef Tract (Lapointe 1997; Leichter et al. 2003). There is also no consistent monitoring of toxic substances released into Caribbean waters although some of the toxic effects of oil spills suggest that, just as for the Exxon Valdez spill (Peterson et al. 2003), chemical toxins of all sorts may be a greater problem for Caribbean reefs than is generally understood (Jackson et al. 1989; Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993; Fernandez et al. 2007; García et al. 2008; Ramos et al. 2009).

Fortunately, simple measurements of water clarity/transparency are an excellent measure of several aspects of water quality including the effects of sediments, nutrients, and organic matter (Fabricius et al. 2012). There are also limited comparative data to examine trends in water transparency based upon secchi disk measurements that record the distance through the water column in meters at which the secchi disk is no longer visible from the surface or along a horizontal plane at depth (CARICOMP). Measurements were made at only seven of the CARICOMP sites and were made consistently for more than ten years at only three: inside the lagoon and on the fore reef at Carrie Bow Cay, Belize and at a single forereef site at La Parguera Puerto Rico (Table 9).

TABLE 9. Average secchi disk depths, degree heating weeks in 1998, 2005, and 2010, changes in coral cover in the two years following the extreme heating events of 1998, 2005, and 2010, and parrotfish abundance and coral cover since 1998 for 88 Caribbean reef locations (numbers same as in Table 2). See the text for the different drivers sections for further details.

Trends in water transparency were assessed by testing the linear relationship of secchi distance to year while assuming an AR-1 autocorrelation (R package *nlme*; Pinheiro and Bates 2013). Water transparency significantly declined at all three consistently monitored sites, while coral cover has declined by approximately two thirds (Fig. 25; Koltes and Opishinski 2009; K. Koltes, personal communication; E. Weil, personal communication). The decline in transparency at Carrie Bow Cay is related to the conversion of lands bordering the Gulf of Honduras to agriculture and urban development. Massive amounts of sediments, primarily from Guatemala and Honduras, were introduced to the Gulf following the 2 m rainfall during Hurricane Mitch (Smith et al. 2002). These sediments became entrained in the gyre of the Gulf and continue to be re-suspended. More recent rapid conversion of the Belize coastline to intensive agriculture and tourism is also a major factor. Coastal development is also responsible for the downward trend at La Parguera (Hertler et al. 2009).

FIGURE 25. Decline in water transparency over time at the CARICOMP at fore-reef and lagoonal sites at Carrie Bow Cay and a fore-reef site at La Parguera, Puerto Rico. All of these trends are highly significant (GLMM, $p < 0.01$). See text for details.

Coral cover declined by approximately two thirds at both Carrie Bow Cay and La Parguera, but the declines were episodic and uncorrelated with the gradual decline in water quality. Most of the decline at Carrie Bow Cay occurred before the transparency data began and coral cover increased by approximately 10% between 1994 and 2003 before declining precipitously by > 25% cover between 2003 and 2007 (Appendix II).

In contrast, water transparency did not change appreciably over 7 years at Morrocoy, Venezuela, but there were very large increases in heavy metals and hydrocarbons in relation to Venezuela's massive oil production (Bastidas et al. 1999; García et al. 2008; Ramos et al. 2009) that may have been a major factor in the dramatic losses in coral cover along the Venezuelan coast. Water transparency increased by about 50% over eight years at Bermuda.

3d. OCEAN WARMING

Reef corals host endosymbiotic photosynthetic dinoflagellates (*Symbiodinium*) that provide sugar to their coral host and are essential for coral growth and survival. Coral bleaching results from the ejection of the symbiotic dinoflagellates from the host coral due to stress. The most common form of bleaching occurs in response to extended increases in sea-surface temperature (SST) that are routinely measured in terms of Degree Heating Weeks (DHWs), defined as numbers of weeks during which SSTs exceed 1°C above the local climatological thermal maximum (Brown 1997; Hoegh-Guldberg 1999; Knowlton 2001; Hughes et al. 2003; Baker et al. 2008; Donner et al. 2007). However, different types of *Symbiodinium* are more or less resistant to elevated temperatures so that the bleaching response can be exceedingly varied and complex (Rowan et al. 1997; Knowlton and Rohwer 2003; Baker et al. 2008).

Mass mortality of corals commonly occurs when such high temperatures persist for more than one month. Bleaching events were rare before 1980 (Glynn 1993) but have since increased greatly in intensity and frequency due to rising temperatures that are in turn due to burning of fossil fuels and increases in other greenhouse gas emissions (Hoegh-Guldberg et al. 2007; Donner 2009, 2011). Increasingly severe coral bleaching events occurred in the Caribbean in 1995, 1998, 2005, and 2010 (Wilkinson and Souter 2008; Eakin et al. 2010).

Much progress has been made in prediction of coral bleaching events using long-term records of SST variability and the duration of heating events in association with the ReefBase compilation (http://www.reefbase.org) of coral mass bleaching events (Donner 2011; Chollett et al. 2012a,b). However, the ReefBase dataset has been criticized for three reasons: (1) bias towards reporting the occurrence of mass bleaching events, but less frequently their non-occurrence, (2) uneven spatial distribution of reports, and (3) absence of data from many of the large, well organized monitoring programs (Oliver et al. 2009; Donner 2011).

A major step forward has been provided by NOAA Coral Reef Watch (CRW) that has conducted near real-time global monitoring of thermal stress (http://coralreefwatch.noaa.gov) since 2000 based on satellite SST data at a resolution of 0.5-degree (~50km). These data have the important advantage of measuring the strength of the driver rather than the ecological response and complement observations *in situ*. They also provide an independent and consistent measure of thermal stress over the entire ocean rather than a hodgepodge of scattered measurements using different instruments and methodologies. As such, they provide an invaluable tool for managers and scientists to alert them of likely severe bleaching events before they occur and to facilitate preparations for essential in situ observations of ecosystem response. The DHWs product has been associated with significant coral bleaching (≥4 DHWs), and with widespread bleaching and significant coral mortality (≥8 DHWs; Liu et al. 2003; Eakin et al. 2009). However, extreme bleaching events do not always result in massive coral mortality, as evidenced by very large variations in mortality among locations that were comparably heated following the extreme heating event in 2005 (Eakin et al. 2010). CRW has also produced historical thermal stress products based on retrospective SST data as far back as 1985.

For this study, CRW extended these thermal stress products historically based on retrospective SST satellite data prior to 2000. SST data at 0.5-degree resolution were developed from the Pathfinder version 5.2 dataset (Casey et al. 2010), mimicking the methodology used for the operational CRW near real-time SST product (as described in Eakin et al. 2009). These data were combined with the near real-time SST data to extend the time-series back to 1985. Annual maximum DHW values for 1985-2011 (0.5-degree) were calculated for reef-containing pixels corresponding to each location in Table 9. Data were then combined for each location by taking the median number of DHW per location for 1998, 2005, and 2010. Pathfinder SST data were provided by GHRSST and the US National Oceanographic Data Center, supported in part by a grant from the NOAA Climate Data Record (CDR) Program for satellites. Our use of these data solely reflects the opinions of the authors of this report and do not constitute a statement of policy, decision, or position on behalf of NOAA or the US Government.

We analyzed changes in coral cover for the two years following each of the prolonged and extreme heating events in 1998, 2005, and 2010 relative to the two years preceding the event in relation to the numbers of DHWs experienced (Table 9). There was also a significant heating event across the southern Caribbean in 1995 with numbers of DHWs ranging from > 10 to 19.5 in a broad swath from mainland Colombia and San Andres in the west to Venezuela in the east, and with slightly lower numbers of DHWs in Panama and Barbados (CARICOMP 1997). Unfortunately, coral cover data are too sparse for detailed before and after comparisons around this event. Nevertheless, the timelines for these reefs that go back before 1995 show little decline or even increases in coral cover after 1995, suggesting low coral mortality. Support for this inference comes from the timelines for Morrocoy and Los Roques in Venezuela that begin a few years after 1995 with exceptionally high coral cover of 55% and 44% coral cover respectively (Table 4, Appendix 2). There are also scattered reports of bleaching events at Florida before 1995 (Billy Causey, personal communication) but we lack the quantitative data for comparative analysis.

We explored the relationship between degree heating weeks and proportional changes in coral cover for the 1998, 2005, and 2010 heating events both separately and for all three events combined using non-parametric correlations. Linear statistics are not appropriate in this case due to spatial and temporal autocorrelation causing residual variation to be correlated. Correlations were calculated for proportional changes in coral cover (decreases or increases) as a function of numbers of DHWs using two data sets. In the first case we used all of the data regardless of the numbers of DHWs experienced at any location. The purpose of this broader analysis was to determine the extent to which extreme heating events may have been responsible for changes in the abundance of corals throughout the wider Caribbean in comparison with other drivers of change. In contrast, the second analysis only employed data above the postulated critical threshold of 8 DHWs to examine more closely the impact of extreme heating events on coral cover. We also assessed the extent to which proportional changes in coral cover were related to numbers of DHWs above and below 8 DHWs by constructing contingency tables.

There is a small, non-significant negative correlation between proportional changes in coral cover and numbers of DHWs for the entire data set (Fig. 26A). We also examined the same data using 2 x 2 contingency table analysis for changes in coral cover at locations that experienced < 8 or $\geq$ 8 DHWs with marginally significant results ($X^2 = 3.11$, df = 1, $p = 0.07$). Remarkably, however, the trend is *opposite to the expected pattern* because the two locations that experienced the highest numbers of DHWs experienced a substantial proportional *increase* in coral cover. Moreover, the proportion of locations that lost coral cover is not different for places that experienced more or less than 8 DHWs (74% and 73% respectively), and six of the eight locations that suffered losses in coral cover > 50% coral were exposed to < 8 DHWs. Finally, and even more remarkably, there is a significant *positive* correlation between proportional changes in coral cover and numbers of DHWs using only the data for locations that experienced > 8 DHWs ($r_s = +0.66$, $p = 0.01$).

FIGURE 26. Proportional changes in coral cover in the two years following major heating events in relation to the number of degree heating weeks (DHWs) at all the locations for which paired data are available (Table 9) (A) all three events combined, $r_s = -0.10$, $p = 0.34$); (B) in 1998, $r_s = -0.07$, $p = 0.71$; (C) in 2005, $r_s = -0.20$, $p = 0.25$, and (D) in 2010: $r_s = -0.20$, $p = 0.29$. See text for details of the analysis.

Graphs of the loss of coral cover against the number of DHWs after 1998, 2005, and 2010 vary in their relationship between coral cover and thermal stress (Fig. 26B-D). For the earliest event in 1998, there are very few Caribbean reef locations that experienced ≥ 8 DHWs, and overall no relationship was found to proportional loss of coral cover (Fig. 26B). Similarly, no regional correlation between DHW and proportional loss in coral cover was found in 2005 (Fig. 26C) and 2010 (Fig. 26D). Contingency table analyses for 2005 and 2010 were also non-significant (2005: $X^2 = 0.78$, df = 1, $p = 0.38$; 2010: $X^2 = 1.92$, df = 1, $p = 0.17$). Contingency table analysis could not be done for 1998 because of the lack of data in the upper right quadrant.

Lack of an overall regional correlation between numbers of DHWs and changes in coral cover does not mean that bleaching is an unimportant cause of coral mortality because numerous studies have clearly demonstrated mass mortality following coral bleaching (Hoegh-Guldberg et al. 2007). Moreover, even greater rising temperatures in the future will almost certainly have increasingly severe effects. But the data do belie any strong, regionally consistent effects of coral bleaching upon coral cover *up to the present*. Instead, mortality due to bleaching has been highly localized. At Belize, for example, coral cover dropped precipitously from about 35-45% to zero after the massive bleaching event at two cays on the leeward side of the southern barrier reef (Aronson et al. 2002), but mortality was negligible at Glovers Atoll farther offshore (Mumby 1999). A similar drop occurred at Carrie Bow Cay from the combined effects of coral bleaching and Hurricane Mitch (K. Koltes, personal communication). Mortality was also very extensive after the 2005 massive bleaching event at St. John, with proportional losses in coral cover of up to 60% on some reefs (Miller et al. 2009), and at La Parguera, Puerto Rico (Weil et al. 2009). In both of these cases, however, mortality may have been largely due to a major outbreak of disease that closely followed the thermal stress (see Section 3f).

3e. INVASIVE SPECIES

The Caribbean is effectively a Mediterranean sea and has been the most isolated tropical ocean on the planet ever since the final closure of the Central American Seaway by the rise of the Isthmus of Panama between about 5 to 3 million years ago severed its connection with the eastern tropical Pacific (Coates and Stallard 2013; Jackson and O'Dea 2013). Isolation from the tropical Indian Ocean to the east occurred even earlier due to the movements of the continents of Africa and Asia, the subtropical Mediterranean, and the inhospitable eastern Atlantic. Thus, by analogy to the fates of the myriad island birds and reptiles decimated to the point of extinction by introduced species of snakes, rats, cats, and goats (Fritts and Rodda 1998; Pimentel et al. 2005), Caribbean marine species should be exceptionally prone to the impact of introduced competitors and predators. Moreover, by analogy to the fates of the original Americans after their first contact with European diseases (Crosby 1986; Mann 2005), Caribbean corals should be especially vulnerable to introduced diseases.

Most of the recent focus on introduced marine species has concentrated on highly visible macro-organisms, such as the explosive increase in the abundance of the Pacific lionfish *Pterois volitans* throughout the entire wider Caribbean over the past decade (De Leon et al. 2011; Hackerott et al. 2013) or the uncontrolled spread of the alga *Caulerpa taxifolia* in the northern Mediterranean (Meinesz et al. 1993, 2001). The potential effects of lionfish on Caribbean invertebrates and fishes may be severe, especially in exacerbating the consequences of overfishing by depleting juvenile parrotfishes and surgeonfishes (Albins and Hixon 2018, 2013). However, it is too soon to tell whether native predators might eventually have an impact of lionfish, especially in marine reserves where predators could regain their former abundance (Mumby et al. 2013).

Far too little attention has been paid, however, to the introduction of the myriad marine organisms we cannot see, including virtually all microorganisms and pathogens. The case of the unidentified pathogen that caused the mass mortality of *Diadema antillarum* in 1983-1984 is a case in point. *Diadema* mortality began next door to the Caribbean entrance to the Panama Canal, whence it spread like wildfire on ocean currents eastward to Trinidad and Tobago and northward throughout the western Caribbean, Greater Antilles, and Florida all the way to Bermuda, with mortality in the eastern Caribbean arriving from both the north and the south in 1984 (Lessios et al. 1984; Lessios 1988). Introduction via ballast water from the Pacific is seemingly the most reasonable explanation.

This begs the question of why so many marine diseases first appeared in the 1970s and early 1980s, a pattern for which there is no compelling environmental explanation. Temperatures were not excessively warm in the 1970s and heating in relation to El Nino in 1983 was small compared to the episodes in 1995, 1998, 2005, and 2010. There is also no evidence of a pervasive decline in Caribbean water quality before the 1980s or later.

In contrast, the volume of international shipping exploded in the late 1960s with the advent of bulk carriers and enormous cruise ships that discharged untold volumes of ballast water into coastal waters before stricter regulations may have begun to take effect (Carlton 1996). Greater speed of transport among distant ports may also be a contributing factor. Many introduced species have been transported by ballast water, and this is especially true for microbes that have been calculated to be transported in numbers on the order of 10^{20}/year into the lower Chesapeake Bay alone (Ruiz et al. 2000; Drake et al. 2007). None of this proves that *Diadema* disease or WBD were introduced into the Caribbean from another ocean. But given the numbers of microbes in ballast waters, it is remarkable that all marine diseases have not been introduced throughout the global ocean. Introductions of aquarium species and so-called "live rock" for aquaria are another potentially major avenue for incidental introductions of pathogens.

Once introduced, different environmental factors may retard or promote the growth of introduced species including species that cause disease. But it is important not to confuse the causes of an initial outbreak from factors that may subsequently promote or inhibit its spread and increase.

3f. INCREASING INCIDENCE OF CORAL DISEASE

Corals are complex ecological communities (holobionts) comprising the coral host and an extraordinary diversity of associated eukaryotic and prokaryotic microorganisms (Rohwer et al. 2001, 2002; Knowlton and Rohwer 2003; Rosenberg et al. 2007). These associates include a great diversity of intracellular, endosymbiotic dinoflagellates (*Symbiodinium*) and a bewildering variety of bacteria, archaea, and viruses that confer essential nutritional and immunological benefits to the host coral by photosynthesis, provision of nutrients, nitrogen fixation, and resistance to infection. The ecological balance among all of these mutualistic ecological components of the holobiont community is essential for coral health. Breakdown in that balance due to a change in the environmental or genetic landscape of the holobiont or the invasion or increase in a pathogen compromises the health of the holobiont in the form of myriad forms of coral bleaching or disease. Understanding of the underlying mechanisms of these ecological interactions that compromise coral health is in its infancy, so that scientists are required to describe phenomena in terms of their gross phenotypic expression (e.g., bleaching, White-Band Disease, Black-Band Disease, Yellow-Band Disease, etc.) rather than the precise underlying ecological components of cause and effect (Weil and Rogers 2011).

In recognition of this complexity, disease is commonly defined as "any impairment to health resulting in physiological dysfunction" due to a pathogen (virus or microorganism), environmental perturbation, toxic substance, or genetic changes in the affected organism (Weil and Rogers 2011). Defined so broadly, coral bleaching, mercury poisoning, or smothering by sediments can be treated as a disease – a definition so broad as to be of little use. For this report, therefore, we define coral diseases more narrowly as impairments to coral health caused by a demonstrable or presumptive infectious pathogen that results in varying pathological responses or death (see Martin et al. 1987; Wobeser 1994 for further discussion of these criteria).

Coral diseases so defined occur in a bewildering variety of forms that may affect a few or many coral taxa (Weil and Rogers 2011). In most cases the diseases are identified by the pathological expression exhibited by the affected coral. The actual pathogens have been identified in only a few cases, and similar manifestations of disease in the changing appearance of the affected coral may be caused by different pathogens in different circumstances. Failure to identify pathogens is the major impediment to any real advance in understanding the causes and consequences of coral disease. Little is known about transmission, but there is evidence that various predators of corals including fishes, polychaete worms, and snails may transmit diseases from one coral prey to the next, as well as transport by currents (Williams and Miller 2005; Rosenberg et al. 2007; Weil and Rogers 2011) or in the ballast water of ships (Drake et al. 2007).

The first report of coral disease in the Caribbean was for BBD in Belize, Florida, and Bermuda in the early 1970s and throughout the western Atlantic soon after (Antonius 1973, 1977; Weil and Rogers 2011). BBD appears as a dark microbial mat and infects 19 species of Caribbean corals. BBD was followed closely by a virulent outbreak of WBD that caused mass mortality of *Acropora palmata* in the US Virgin Islands in the late 1970s, and spread throughout the western Atlantic to cause mass mortality of both *A. palmata* and *A. cervicornis* in the early 1980s to the present (Gladfelter 1982; Goreau et al. 1998; Aronson and Precht 2001; Weil and Rogers 2011). In total, about 13 different diseases of corals have been identified whose distribution and prevalence varies greatly among different locations within the wider Caribbean (Weil and Cróquer 2009; Cróquer and Weil 2009; Weil and Rogers 2011).

Despite numerous breakthroughs in documenting the agents of coral disease we do not understand why outbreaks of disease occur. The two most likely explanations are (1) introduction of a pathogen to an area where it was previously absent, as in the case of bubonic plague, and (2) increase in the abundance of a previously rare pathogen due to changes in the physical or biotic environment as with outbreaks of cholera in polluted waters. A third possibility is the evolution of a new pathogen that sweeps through host populations with devastating effects. Such an explanation is extremely unlikely for Caribbean corals because it would require the synchronous evolution of more than a dozen major coral pathogens within one or two decades.

Data are so far inadequate to identify whether invasions or environmental change were the major factor in the emergence of particular Caribbean coral diseases, but there are valuable hints related to the timing of appearance and severity of diseases. This is especially true for the first outbreaks in the 1970s and early 1980s, most notably WBD, BBD, and the pathogen that caused the massive die-off of the sea urchin *Diadema antillarum* in 1983/84 (Lessios et al. 1984; Lessios 1988; Weil and Rogers 2011). In each case, mass mortality approaching 95-100% occurred 15-25 years before the first episodes of extreme heating events due to global warming or any other documented regional environmental change. It is therefore of considerable interest that the effects of WBD and *Diadema* disease have been so much more extreme than in other tropical seas. Nothing like the mass mortality of *Diadema* has affected any echinoderm throughout the entire Indian Ocean or tropical Pacific, nor has any genus of Indo-Pacific acroporid suffered such broad and lasting extirpation as Caribbean *Acropora palmata* and *A. cervicornis*.

More progress has been made in understanding the causes of more recent and seemingly chronic disease outbreaks in relation to rising temperatures and the increased abundance of macroalgae after the demise of *Diadema* (Table 3; Figs 12-14). Evidence for a temperature effect comes from increases in the incidence in disease after extreme heating events and coral bleaching (Weil and Rogers 2011). However, such outbreaks of disease may result either from a general weakening of coral due to the physiological distress caused by bleaching or thermal stress per se. Experiments are needed to help resolve these alternatives.

In contrast, numerous recent experiments have demonstrated that physical contact or even close proximity to various macroalgae may also trigger the outbreak of a wide variety of pathological responses including virulent diseases in corals (Nugues et al. 2004; Kline et al. 2006; Smith et al. 2006; Rosenberg et al. 2007; Knowlton and Jackson 2008; Barott and Rohwer 2012; Morrow et al. 2012; Rasher et al. 2012; but see Vu et al. 2009 for somewhat contrary results). Toxic allelochemicals from macroalgae also disrupt the complex microbial communities present on the surface of coral colonies, and may cause bleaching and death of coral tissues when in direct contact (Rasher and Hay 2010; Rasher et al. 2011).

In summary, increases in macroalgae principally due to overfishing can disrupt the ecological balance of reef coral assemblages in many ways. Macroalgae inhibit coral growth and may cause direct mortality by shading or abrasion. They also inhibit coral recruitment and disrupt symbiotic assemblages resulting in outbreaks of disease and coral death. These are all testable hypotheses in marine protected areas and wherever else that populations of herbivores may recover and graze down macroalgae to previously low levels of abundance. If the macroalgal disease hypothesis is correct, incidence of coral disease should decline in concert with the decline in macroalgae.

Bleaching and disease are increasingly closely associated in their occurrence but the reasons are obscure because coral cover at some reefs *increased* or was stable after experiencing very high numbers of DHWs (Table 9; Fig. 26). For example, the leeward coast of Bonaire experienced < 1, 5.8, and 13.7 DHWs in 1998, 2005, and 2010 with a proportional *increase* in coral cover of 11, 13, and 0.1% respectively in the two years thereafter. The southwest coast of Curaçao also experienced > 10 DHWs during all three events and percent coral cover *increased* proportionately by 25% after 1998, by 47% after 2005, and declined by just 2% after 2010. Northwest Curaçao and nearby Los Roques experienced 2.3 and 2.9 DHWs in 2005 with 2% and 4% change in coral cover. However, these same locations experienced a precipitous proportional decline in coral cover of 55% and 14% respectively after experiencing 8.3 and 12.5 DHWs in 2010. The decline in NW Curaçao was due to a combination of factors including exceptional storms, increased coastal development, and coral bleaching (Mark Vermeij, personal communication), but the decline at Los Roques was due to massive coral bleaching followed by disease (Bastidas et al. 2012).

In contrast, coral cover on reefs in the USVI and at La Parguera and Vieques in Puerto Rico declined proportionately by 47-53% after enduring 7 to 8.3 DHWs in 2005. These much greater losses in coral cover after experiencing less heat stress than in NW Curaçao and Los Roques strongly imply that the consequences of extreme heating stress are somehow mediated by other environmental factors than heat stress alone. Coral mortality in the USVI and Puerto Rico after 2005 was due primarily to outbreaks of coral disease (Rogers and Miller 2006; Muller et al. 2008; Rogers et al. 2009; Miller et al. 2009; Weil et al. 2009). We postulate that these greater losses in the USVI and Puerto Rico may reflect regional differences in macroalgal abundance, which is generally considerably lower in the southern Caribbean. Support for this hypothesis comes from the experiments discussed above and the anomalous increase in total algal cover at Los Roques of 34 to 54% before and after the 2010 extreme heating event when coral cover declined precipitously, versus the minor proportional losses in coral cover in SW Curaçao where macroalgal cover is much lower.

3g. THE ROLE OF HURRICANES

Strong hurricanes have been a natural occurrence on coral reefs for millions of years and are potentially highly destructive to corals (Woodley et al. 1981; Rogers et al. 1982, 1991). Reefs have routinely recovered from hurricane damage in the past or reefs would not exist. The occurrence of hurricanes varies greatly throughout the wider Caribbean region (Chollett et al. 2012a). Hurricanes are frequent and intense in a broad swath from the northern Lesser Antilles across Puerto Rico, eastern Cuba, Jamaica, and the Cayman Islands to eastern Yucatan as well as southern Florida. In contrast, hurricanes are rare all across the southern third of the Caribbean from Barbados to Nicaragua and points south. Despite these differences, however, average coral cover from 1970 through 1983 was remarkably similar among the 16 locations with old *Diadema* data in Tables 5 and 8. Corals differ greatly in their rates of recruitment, growth, and reproduction. These differences in life history characteristics are believed to have been responsible for a natural pattern of succession of reef communities extending for up to several decades after a storm had passed (Woodley et al. 1981; Rogers 1983a).

Nevertheless, the frequency and intensity of hurricane occurrence have been proposed as important drivers of coral decline on Caribbean reefs, especially since the 1980s when corals have failed to recover in many cases due to some combination of human stressors (Gardner et al. 2005). We therefore examined this hypothesis in two ways using the 16 reefs in Table 8. The first analysis addresses the null hypothesis that coral cover at the 16 locations prior to the mass mortality of *Diadema antillarum* in 1983 was independent of the long-term annual probability of hurricane occurrence at each location over the past 160 years. The second analysis addresses the null hypothesis that the changes in coral cover after 1983 were independent of the numbers of hurricanes that actually occurred at each location after 1983. Hurricanes vary in intensity and the details of their tracks through an area that affect their potential impact on reefs (Fabricius et al. 2008), but such detailed data are available for only a small proportion of hurricanes. Nevertheless, the long-term probability of hurricane occurrence, and their actual frequency since 1983, should provide a good first order estimate of the impact of hurricanes on coral cover both in the past and on reefs today.

Hurricane incidence was measured using the Atlantic Hurricane data set (1851-2012), which tracks the location and intensity of the eye of tropical cyclones every six hours (Jarvinen et al. 1984). Hurricane force winds may extend several kilometers from the hurricane track. We captured the spatial influence of hurricanes by using the buffering system described by Keim et al. (2007) and Edwards et al. (2011). Buffers capture the area of influence of each hurricane by taking into account the intensity of the storm, its asymmetry, and the reduction in wind speed away from the track (Keim et al. 2007; Edwards et al. 2011). The hurricane dataset was used previously by Chollett (2012a) but is here updated to include Bermuda and four more years of data from 2009-2012 (Table 8). Hurricane incidence was extracted for each pixel within the polygon drawn for each reef location in Table 5 (Fig. 27). The number of pixels extracted and the average and standard deviation of hurricane incidence were reported for each of four time periods: (1851-2012, 1970-1983, 1984-1998, and 1999-2012).

FIGURE 27. Example of the methodology for extraction of the incidence of hurricanes for the Upper Florida Keys.

Coral cover on reefs before 1984 is negatively correlated with the long-term probability of hurricane occurrence but the relationship is not significant (Fig. 28A). This suggests that hurricane frequency was not a major determinant of coral cover on reefs prior to 1984.

FIGURE 28. Coral cover versus hurricane occurrence for the 16 reef locations in Table 8. (A) There is no relation between the long-term probability of hurricane occurrence at the 16 reefs in Table 5 up to 1983 ($r_s = -0.4, p = 0.15$). (B) Since 1984, the number of hurricanes is also uncorrelated with coral cover ($r_s = -0.25, p = 0.38$) except when the protected reefs at Bermuda are removed from the analysis ($r_s = -0.57, p = 0.04$).

The number of hurricanes that have occurred at the 16 locations since 1984 is highly positively correlated with the long-term probability of hurricane occurrence at the same locations, demonstrating that the incidence of hurricanes over the past 30 years has not departed from the normal pattern ($r_s = 0.67, p = 0.01$). Average coral cover since 2005 is negatively but insignificantly correlated with the numbers of hurricanes that have occurred since 1984, due to the very high coral cover at Bermuda despite four hurricanes since 1984 (Table 8, Fig. 28B). Removal of Bermuda from the analyses had no effect on the results for the years prior to 1984, but the negative correlation between coral cover and number of hurricanes since 1984 was significant (Fig. 28B). It is important in this context to remember that acroporids have always been absent from Bermuda where reefs are overwhelmingly dominated by massive corals, which are more resistant to hurricanes than branching species (Woodley et al. 1981).

Fish traps were banned in Bermuda in 1990 and parrotfish are still abundant. In contrast, reefs on the Belize Central Barrier have been overfished since the 1990s (Mumby et al. 2012) in addition to having experienced three hurricanes. Coral cover declined proportionately by 49% (Table 5). Coral bleaching was extensive at Carrie Bow Cay ten days after the passage of Hurricane Mitch (K. Koltes, personal communication), but the reason(s) for bleaching are obscure because of a huge influx of sediments and freshwater due to > 1 m of rain within 24 hours (Koltes and Opishinski 2009; K. Koltes, personal communication). Massive influxes of freshwater have been previously shown to have caused nearly 100% coral bleaching in Jamaica following hurricane Flora in 1963 (Goreau 1964). Jamaica was already overfished in the 1960s (Jackson 1997) but *Diadema* were extremely abundant and macroalgae virtually absent. These are only isolated examples but suggest that protection of herbivores and wiser land use as in Bermuda may have conferred greater resilience of reefs to hurricanes.

3h. THE SPECIAL CASE OF THE FLORIDA REEF TRACT (FRT)

The ecological situation of the FRT is unique due to its particular environmental setting and the unprecedented scale of human impacts that include all of the drivers discussed in this report (Ault et al. 2005; Keller and Causey 2005; Causey 2008; Kruczynski and Fletcher 2012).

The FRT is a predominantly continental reef system in south Florida and the Florida Keys that is situated towards the northern geographic occurrence of Atlantic coral reefs. Fluctuations in environmental conditions and the long-term probability of hurricane occurrence are among the highest in region. The FRT is also positioned at the junction of Caribbean waters from the south, Gulf of Mexico waters from the West, and the subtropical western Atlantic. Moreover, the reefs of the Florida Keys sit just offshore of Florida Bay into which the Everglades drain. For all of these reasons, the assemblages of species and habitats of the FRT were considerably different from anywhere else in the wider Caribbean region long before human impacts intensified.

Unprecedented increases in land use, coastal development, and pollution of south Florida occurred over the past half century as human populations exploded. The hydrology of the Everglades and Florida Bay has drastically changed and nutrient and sediment influx greatly increased with direct impacts on coastal estuarine habitats and water quality in the Florida Keys. These local dynamics have combined with regional and global environmental change to impact reefs along most of the FRT.

Today the FRT is adjacent to the major metropolitan area of greater Miami with a rapidly growing human population exceeding 5 million while also serving as a popular tourist destination with unparalleled access to the reefs for recreation and exploitation. Intensity of human use and environmental impacts greatly exceeds that of any other region in the wider Caribbean, if not the world Numbers of fishers, boaters, and divers increase every year. Nearly a million vessels are registered in Florida with a majority in the southern portion of the state. Damage due to boat groundings, propeller scour, anchoring, and shipwrecks is extensive and wastewater runoff enormous. Overfishing has virtually eliminated formerly abundant Goliath and Nassau Groupers and stocks of other target species such as snappers, lobsters, and conchs are overfished.

Establishment of the nearly 10,000 square kilometer Florida Key's National Marine Sanctuary (FKNMS) in 1997 led to the creation of a modest network of no-take marine reserves with a total protected area of only 6% of the total area of the Keys. This action, combined with increasingly restrictive fishing regulations, has led to small increases in a limited number of stocks, and a general slowing of the decline in fish stocks overall. The FKNMS has also been successful in encouraging collaborative management strategies allowing Florida to successfully document and implement corrective actions to improve wastewater and storm water treatment and disposal.

In conclusion, the FRT epitomizes a kind of worst-case scenario in which unprecedented population growth and inadequate governance and regulations have resulted in the critical endangerment of an entire coral reef ecosystem. Despite the positive and courageous actions of the Sanctuary, coral cover is well under 10% and declining. Much more stringent actions will be required for any hope of coral survival.

4. SYNTHESIS

We first review the major results of the analyses of pattern and then focus on the apparent importance of the different drivers of coral reef decline.

4a. PATTERNS OF CHANGE

The three overarching results of this report are that

1) Most of the degradation of Caribbean reefs occurred between the 1970s to early 1990s well before most ecological surveys began.
2) Phase shifts from greater coral to greater macroalgal abundance happened early and are geographically pervasive.
3) Geographic disparity in the fates of reefs at different locations was and is truly enormous.

Timing and rates of reef degradation

Average coral cover throughout the wider Caribbean, Gulf of Mexico, and Bermuda declined by 49% from an overall average of 33.0% before 1984 to 17.7% since 2005 (Tables 2 and 3, Fig. 7). Refinement of our 2005 estimate to take into account the great variation among locations and datasets lowers the 2005 estimate to 14.3% coral cover with an overall decline of 59%. These estimates of loss are considerably lower than Gardner and colleagues' estimate of an 80% decline from 50% to 10% (Gardner et al. 2003) but in good agreement with the estimate of Schutte et al. (2010) of a 60% decline from about 40% to 16% cover. The earlier estimates were based on considerably less data and were disproportionally dominated by surveys from the Florida Reef Tract, US Virgin Islands, and Jamaica that are among the most severely degraded reefs in the entire region.

Coral cover declined at 73% of locations with time series data (Fig. 8). The declines were greatest for locations that began to be studied earliest and over the longest period of time. Indeed, 88% of the total overall Caribbean decline in coral cover occurred between 1984 and 1998, and this increases to 100% for the 21 reef locations with long-term data extending back before 1984 (Table 3). Likewise, 99% of the overall Caribbean increase in macroalgal cover occurred before 1998, with a somewhat lower value of 81% for the 21 long-term reefs.

The same was true for the dramatic declines of iconic species. *Acropora palmata* and *A. cervicornis* began to decline in the 1960s and were virtually ecologically extinct at most Caribbean locations by the mid 1980s (Fig. 18). *Diadema antillarum* was the most important grazer on overfished Caribbean reefs and common elsewhere until 1983-1984 when more than 95% of all Caribbean *Diadema* died due to an unidentified pathogen (Lessios 1988; Fig. 19). Parrotfish had been extremely reduced at Jamaica, the USVI, and other overfished locations by the 1960s or before (Randall 1961, 1963; Munro 1983; Hay 1984; Lewis and Wainwright 1985), and are rare on most Caribbean reefs today (Fig. 20).

These sobering results of very early decline long before most coral reef ecologists today had ever seen or read about a coral reef are a classic example of the Shifting Baselines Syndrome (Pauly 1995; Jackson and Jacquet 2011; Jackson et al. 2012) and a harsh reminder that what is going on today is the end of a much longer story.

Phase shifts

The dramatic reversal between coral and macroalgal abundance (Fig. 13) occurred over about a decade and is strong evidence for a phase shift in coral reef community structure (Done 1992; Knowlton 1992, 2004; Hughes 1994; Hughes et al. 2010; Schutte et al. 2010). Forty-one percent of the total variation in the PCA ordination of coral and macroalgal community composition at the 21 long-term locations is explained by the shift from coral to macroalgal dominance (Fig. 16).

Some have questioned the generality of phase shifts on coral reefs claiming that the Caribbean example of corals to macroalgae is unrepresentative of the general pattern of overall change (Aronson and Precht 2006; Bruno et al. 2009). However, our results are based on vastly more data and greater geographic coverage than any previous analysis and overwhelmingly support the occurrence of a phase shift at most Caribbean locations from coral to macroalgal dominance. The question is not whether a phase shift occurred, but what might be done about it to return reefs to their thoroughly documented former dominance by abundant corals.

Geographic variation in reef decline

Clues to the possible recovery of Caribbean reefs lie in the enormous variability among Caribbean reef locations today (Table 3 and 5; Figs. 9-12, 14; Appendix 1). Coral cover for 53 locations since 2005 varies from a low of < 3% off of Port Royal, Jamaica to a high of 53% at the east Flower Garden Banks in the northern Gulf of Mexico (Table 9). Seventeen locations have < 10% coral cover and another 21 between 10 to < 20%. Thus, three quarters of all the Caribbean locations for which we could find data have degraded by at least 50% below the average coral cover before 1984. But 15% of the locations have > 20% cover and another 13% have > 30% cover including Bermuda, Grand Cayman, Jardines de la Reina on the south coast of Cuba, southwest Curaçao, the leeward coast of Bonaire, Flower Garden Banks, and Los Roques Venezuela. This pattern is virtually identical to the distribution of cover in the third time interval of 1999-2011 (Fig. 7). The obvious question is why these reefs with > 30% cover are doing so well compared to all the rest?

4b. DRIVERS OF CORAL REEF DECLINE

Our analyses focused on potential drivers of decline for which there were adequate data for meaningful comparisons. The results are particularly strong for evaluating the effects of overpopulation, overfishing, and global warming, and less so for coastal pollution and invasive species.

Too many people

Tourism is the lifeblood of many Caribbean nations but our evidence strongly suggests that extremely high densities of tourists and residents are harmful to reefs unless environmental regulations to protect reefs are comprehensive, stringent, and effectively enforced. All locations with > 5,000 visitors/km^2/year have < 14% coral cover except for Bermuda with 39% (Table 7, Fig. 22). Likewise, islands with substantially > 500 residents/km^2 have < 15% coral cover except for Bermuda. The situation at Bermuda reflects exceptionally effective regulations and the infrastructure to enforce them, as well a greater level of economic well being that obviates the need for subsistence fishing. But without similar protections, the harmful environmental costs of runaway tourism and population growth seem inevitable.

Overfishing

Artisanal fishing for subsistence is crucial to most Caribbean economies but the consequences have been catastrophic for coral reefs. Overfishing caused steep reductions in herbivores, especially parrotfishes, which are vulnerable to all gear types except hook and line. The greatest reductions occurred where fish traps were the favored gear, although low catches today are resulting in increased spearfishing and larger nets.

The severe consequences of the overfishing of parrotfishes for coral survival were generally unappreciated until the abrupt demise of the sea urchin *Diadema* in 1983-1984 that had increasingly become the last important herbivore on Caribbean reefs (Fig 19; Hay 1984; Hughes 1994; Jackson 1997). *Diadema* and parrotfish compete intensely for food (Randall 1961; Lewis and Wainwright 1985; Hay and Taylor 1985; Carpenter 1990b), and their abundance was inversely proportional until 1983. This inverse relationship provides a rigorous proxy for the assessment of the consequences of historical overfishing of parrotfish in the absence of quantitative data for reef fish abundance before 1983 (Table 8).

Most of our analysis of overfishing focused on the fates of 16 reefs for which we have quantitative data on *Diadema* abundance before the die-off, plus coral cover for the three time intervals 1970-1983, 1984-1998, and 1999-2011 (Tables 3, 5, 8). Nine of the 16 reefs were classified as overfished for parrotfishes by 1983, with *Diadema* densities ranging from 6.9-12.4/m^2, whereas the other seven reefs were classified as less fished with *Diadema* densities of 0.5-3.8/m^2. These classifications agreed well with what we could glean from the qualitative literature (Appendix 4).

Reefs where parrotfishes had been overfished before 1984 suffered greater decreases in coral cover (Fig. 23 A-D) and increases in macroalgae (Fig. 23 E-H) than reefs that still had functional populations of parrotfish. Coral cover was independent of *Diadema* densities before 1984 (Fig. 23A) when either *Diadema*, or parrotfish, or both managed to graze down macroalgae to extremely low levels. But all that changed dramatically after the *Diadema* die-off when coral cover became negatively correlated with historical *Diadem*a abundance right up to the present day (Fig. 23B, C, D). Conversely, macroalgal cover became positively correlated with historical *Diadema* abundance since there were no longer any abundant herbivores to hold it in check, but the scatter was much greater and correlations weaker and generally not significant (Figs. 23 E-H).

There is also compelling field and experimental evidence for persistent indirect effects of increased macroalgal abundance that strongly impede coral recovery through decreased recruitment and increased disease (Box 1). Coral recruitment has greatly declined since 1984, at least in part due to a decline in the parental brood stock, but there is also strong evidence for active interference by macroalgae. Macroalgae also induce a wide variety of pathological responses including virulent diseases and may release toxic allelochemicals that disrupt microbial communities associated with corals causing bleaching or death.

Box 1. Harmful effects of increased macroalgal (MA) abundance on larval recruitment and outbreaks of disease of Caribbean reef corals (for further details see text).

Type of study	Observation	Reference
Reduction of coral recruitment and survival of juvenile corals		
Field surveys in St. Croix	Coral recruits most abundant in locations of high grazing pressure and low abundance of non-calcareous (fleshy) algae	Rogers et al. 1984
Fouling panel experiments in Curaçao	20-fold reduction in larval recruitment onto upper surfaces of panels in 1998-2000 compared with 1979-1981 (after versus before mass mortality of Diadema) due to blanketing of the panels by MA	Vermeij 2006
Settlement experiments in Belize	Greater larval recruitment onto substrates covered by crustose coralline algae and low recruitment onto surfaces covered by MA	Arnold and Steneck 2006
Laboratory experiments on Larval behavior	Larval avoidance of substrates with all species of MA or cyanobacteria tested	Kuffner et al. 2000
Field observations in the Bahamas	2 to 3-fold increase in coral recruitment at sites where parrotfishes have increased and MA have decreased in protected areas	Mumby et al. 2006, 2007; Mumby and Harborne 2010

Field observations at numerous sites around the Caribbean where Diadema have recently recovered to densities >1/m2	Reduction of MA to very low percent cover and several-fold increases in juvenile corals and coral cover	Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Idjadi et al. 2001
Pathological responses of corals to proximity to macroalgae		
Laboratory experiments with corals and macroalgae from numerous Caribbean locations	Close proximity or contact with MA results in coral death[1]	Nugues et al. 2004; Smith et al. 2006; Rosenberg et al. 2007; Barott and Rohwer 2012; Morrow et al. 2012
Laboratory experiments at various Caribbean locations	Toxic allelochemicals from macroalgae disrupt microbial communities on coral surfaces and may cause bleaching or death on contact with corals	Rasher and Hay 2010; Rasher et al. 2011

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[1] But see Vu et al. 2009

Finally, overfishing may have also indirectly affected the capacity of reefs to recover from damage by hurricanes; something they have routinely done for millions of years (Woodley et al. 1981; Jackson 1991). Over the past few decades, however, corals have increasingly failed to become reestablished on many reefs after major storms (Gardner et al. 2005). We investigated the causes of this apparent shift using the data for the 16 reefs with data from before 1984 in Tables 5 and 8. Coral cover was independent of the long-term probability of hurricane occurrence before 1984 (Fig. 28A), but not afterwards (Fig. 28B). The reasons are obscure because the locations that have experienced the most hurricanes since 1984 were also among the most extremely overfished (Table 8; median for overfished locations = 3 hurricanes since 1984, median for less fished locations = 0 hurricanes since 1984). But it is unlikely to be just a coincidence that the greater vulnerability to storms began just after the *Diadema* die-off, especially given the extraordinary resilience of coral cover at Bermuda after 4 hurricanes since 1984.

Coastal pollution

Almost everyone agrees that coastal pollution is an increasingly serious problem for coral reefs but there are precious few rigorously and consistently collected data comparable to that for Degree Heating Weeks (Table 9). Thus, it is difficult to do more than compile a list of local situations on coral reefs and attempt to generalize as has been done for sedimentation stress (Rogers 1990; Fabricius 2005) and oil spills (Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993), but not yet for nutrients.

Nevertheless, limited comparative data for water transparency at three CARICOMP sites at based on simple secchi disk observations suggest that water quality on Caribbean reefs may be declining significantly (Table 9; Fig. 25). Water transparency declined significantly over 20 years at Carrie Bow Cay due to steep increases in the clearing of land for agriculture and for coastal development in Belize and continued deforestation of the high coastal mountains along the Gulf of Honduras in Guatemala and Honduras (Burke and Sugg 2006; Fig. 25 A-B). Similar declines were observed at La Parguera, Puerto Rico (Fig. 25C). Secchi disk measurements were a standard part of the CARICOMP protocol and it is unfortunate that the measurements were made at so few CARICOMP sites. The results from strongly suggest a very serious decline in water quality that is being widely ignored.

Global climate change

We began our study expecting to document very large and pervasive consequences of coral bleaching but that was resoundingly not the case. Our first analyses were based on the ReefBase compilation of extreme bleaching events that showed no significant relationship between the numbers of extreme events/locality and coral cover at locations across the wider Caribbean, Gulf of Mexico and Bermuda. We next requested and obtained Pathfinder Sea Surface Temperature data from the National

Oceanographic Data Center through the assistance of Mark Eakin and Scott Heron. The result is the comprehensive data for degree heating weeks (DHWs) for all 88 localities with coral cover in Table 9.

Graphs of the proportional loss in coral cover in relation to numbers of DHWs in the two years following the 1998, 2005, and 2010 major heating events are surprisingly flat, essentially mirroring our earlier results (Fig. 26). All the slopes are weakly negative but non-significant in spite of the well-documented cases of extreme coral bleaching followed by disease that has severely affected reefs in the USVI and Puerto Rico after 2005 and elsewhere (Miller et al. 2009; Weil et al. 2009). Repeating the analyses using only the data for locations that suffered ≥ 8 DHWs gives even weaker and anomalous results.

The reason for the general lack of correlation is that coral cover at several locations has substantially increased or held steady after extreme heating events (points on or above the lines of zero percent change in Fig. 26. Many of these exceptional locations have either high parrotfish abundance or low macroalgal cover, or both (Fig. 26, Tables 2 and 5). This implies that high grazing pressure and/or low macroalgal abundance may have somehow increased the resilience of corals to the otherwise fatal combination of massive bleaching followed by disease, which has been the generally accepted pattern for the consequences of extreme heating events. Our results do not imply that coral bleaching is unimportant or that it will not become even more dangerous in the future (Hoegh-Guldberg et al. 2007). But they do belie any regionally consistent effects of coral bleaching up to now, and suggest that strong measures to protect parrotfish and other grazers could make an important difference for the survival of corals in an increasingly warmer world.

None of this would necessarily apply to the deleterious effects of ocean acidification which has not been treated here because it is too soon to know what the effects are now much less in the future. If present trends of decreased pH continue, however, the ability of corals and other calcareous reef species to deposit skeletons will be increasingly but perhaps not fatally compromised (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011).

Invasive species

The explosion of exotic Pacific lionfish throughout the wider Caribbean has wreaked havoc in Caribbean fish communities. But as serious as the potential consequences may be, they pale in comparison to the introduction of the pathogen that caused the die-off of *Diadema antillarum* or the effects of WBD on acroporid corals. The first occurrence of *Diadema* mass mortality at the Caribbean entrance of the Panama Canal (Lessios 1988) coupled with the enormous increases in bulk carrier shipping and the salt water aquarium trade in the 1960s and 1970s (Carlton 1996; Drake et al. 2007) can hardly be a coincidence.

The Caribbean is effectively a Mediterranean sea and has been the oceanographically and geographically most isolated tropical ocean on the planet since the continuous emergence of the Isthmus of Panama 3-5 million years ago (Jackson and O'Dea 2013). This strongly suggests that, by analogy to the fates of the original Americans after their first contact with Europeans (Crosby 1986; Mann 2005), Caribbean species should be exceptionally prone to the impact of introduced diseases. And this appears to be the case. We know of no other examples of the virtual elimination due to disease of any marine species throughout the entire extent of the Indian or Pacific oceans comparable to the demise of Caribbean *Diadema* and acroporids. This interpretation is also consistent with the failure to discern any environmental shift in the 1970s that could have triggered the outbreak of disease.

Concluding remarks

Overpopulation in the form of too many tourists and overfishing appear to be the two best predictors to date of the overall decline in Caribbean coral cover over the past 30 or more years. Coastal pollution is undoubtedly increasingly significant but there are too little data. Increasingly warming seas have caused extensive coral bleaching and mortality and pose an increasingly ominous threat in the future. But so far extreme heating events appear to have been of surprisingly limited and local significance.

5. RECOMMENDATIONS FOR MANAGEMENT

Our results challenge much of the conventional wisdom about the relative importance of global climate change versus more local impacts of overdevelopment, coastal pollution, and overfishing as the primary drivers of coral reef degradation to date and emphasize the critical importance of historical perspective for coral reef management and conservation (Jackson et al. 2001; Pandolfi et al. 2005; Knowlton and Jackson 2008; Hughes et al. 2010). The threats of climate change and ocean acidification loom very large for the future but have not been the major drivers of the decline of Caribbean corals up to now.

Overemphasis on climate change distracts attention from acute local to regional problems about which much could be done to improve conditions on reefs. It also provides an excuse for managers and governments not to make the hard decisions required to stop overfishing, coastal pollution, and unsustainable development and to do the simple, basic monitoring essential for adaptive management.

Smart decisions can make an enormous difference for the wellbeing of coral reefs and the people and enterprises that depend upon them. No place is close to perfect and everywhere is threatened, but the higher coral cover and comparative resilience to extreme heating events or frequent hurricanes on most reefs in Bermuda, Bonaire, Curaçao, the Venezuelan parks, the Flower Garden Banks, and the Jardines de la Reina in Cuba provide clear examples of what could begin to be achieved by strong and effective environmental regulation (albeit that the regulations greatly differ among these different sites).

Four major recommendations emerge from this report:

1. Adopt robust conservation and fisheries management strategies that lead to the restoration of parrotfish populations, including the listing of the parrotfish in relevant annexes of the Protocol concerning Specially Protected Areas and Wildlife (SPAW protocol) of the UNEP Caribbean Environment Programme. A recommendation to this effect was passed unanimously at the October 2013 International Coral Reef Initiative Meeting in Belize (see Box 2 below).

The most important recommendation based on the evidence of this report is the urgent and immediate need to ban fish traps and fishing of any kind for parrotfish and to severely restrict and regulate all other kinds of fishing throughout the wider Caribbean including spearfishing, gill nets, long lines, and all other destructive fishing practices.

The need for strong fisheries regulations has been obvious for decades (Thompson 1945; Randall 1963; Munro 1983; Hay 1984; Hughes 1994; Jackson 1997; Jackson et al. 2001), but only the managers of Bermuda, Los Roques, the Flower Gardens Banks, Bonaire, Jardines de la Reina, and most recently Belize have taken effective action. Given current trends, reef corals can be expected to become ecologically extinct in the Florida Keys, US Virgin Islands, and most of Jamaica within a decade.

With a few local exceptions, reef associated fish stocks are severely overfished and depleted throughout the wider Caribbean. The market value of remaining fisheries is miniscule compared to the damage fishing does to reefs in terms of lost tourist revenues, coastal protection, and the other ecosystem services reefs provide (Pandolfi et al. 2005). Without effective management and welfare, subsistence fishing of ever-depleted stocks will remain vitally important for the very survival of artisanal fishers living on the edge, but the costs of providing alternative dignified livelihoods for these fishers pale in comparison to the enormous losses of coral reef resources and biodiversity caused by continued overfishing.

2. Simplify and standardize monitoring of Caribbean reefs and make results freely available in real time to promote adaptive management.

There is an urgent need to develop *simple, standardized* monitoring protocols to assess in real time the condition of reefs throughout the wider Caribbean. CARICOMP and AGGRA made important progress but protocols were not consistently followed. Highly elaborate and costly programs in the US Virgin Islands and Florida are impractical to achieve elsewhere.

Most of the information for this report came from individual scientists who generously shared their data. But it took nearly two years to begin to use it reliably because of the diversity of metrics, formatting errors, and internal inconsistencies. Much of the data was unusable because we could not verify locations, depths, and missing metadata. The situation is inexcusable and no one should ever have to go through such an exercise again. In contrast, the Center for Tropical Forest Science and partners monitor 48 standardized forest plots in 22 countries containing 4.5 million trees that are routinely surveyed with up-to-date data readily accessible online (Losos and Leigh 2004).

The results of this report further suggest that regular and consistent monitoring of a small number of key variables would be sufficient to establish status and trends for well-informed adaptive management:

1. Percent cover of corals and macroalgae,
2. Abundance and biomass of parrotfish and *Diadema* abundance,
3. Coral recruitment measured as the density of small colonies < 40 mm,
4. Prevalence of coral disease, and
5. Water transparency measured by a secchi disk

Additional information including abundance of other herbivores and outbreaks of bleaching and coral disease are also highly informative. The bottom line, however, is that reefs with abundant coral, little macroalgae, abundant herbivores, strong coral recruitment, and clear water are healthy by any standard, and those that depart from that pattern are not. We should make sure that all Caribbean nations have all of this simple, basic information before embarking on more complex and challenging endeavors of greater interest to scientists than any value to the managers on the ground.

3. Foster communication and exchange of information

Resources are needed to revitalize the Caribbean node of the GCRMN and other mechanisms to foster exchange of information and cooperation. The GCRMN Workshop in Panama was the first time most of the participants had met or interacted with each other. Ignorance of the work of participants from different countries was great and participants expressed frustration about working in isolation of what was going on elsewhere.

4. **Develop and implement adaptive legislation and regulations** to ensure that threats to coral reefs are systematically addressed, particularly threats posed by fisheries, tourism and coastal development as determined by established indicators of reef health.

We understand that action upon these recommendations will be a matter of local and national socioeconomic and political debate. But the implications of our scientific results are unmistakable: *Caribbean coral reefs and their associated* *resources will virtually disappear within just a few decades unless all of these measures are promptly adopted and enforced.*

Box 2. Recommendation passed unanimously at the 28th General Meeting of ICRI in Belize City, Belize, 17 October 2013.

RECOMMENDATION on addressing the decline in coral reef health throughout the wider Caribbean: the taking of parrotfish and similar herbivores

Adopted on 17 October 2013, at the 28th ICRI General Meeting (Belize City)

Background

The latest report of the Global Coral Reef Monitoring Network (GCRMN), entitled: *Status and Trends of Caribbean Coral Reefs: 1970-2012* is the first report to document quantitative trends of coral reef health based on data collected over the past 43 years throughout the wider Caribbean region.

The results of the study clearly show:

- Coral reef health requires an ecological balance of corals and algae in which herbivory is a key element;
- Populations of parrotfish are a critical component of that herbivory, particularly since the decline of *Diadema* sea urchins in the early 1980s;
- The main causes of mortality of parrotfish are the use of fishing techniques such as spearfishing and, particularly, the use of fish traps.

The Report further identifies that overfishing of herbivores, particularly parrotfish, has been the major drivers of reef decline in the Caribbean to date, concluding that management action to address overfishing at the national and local levels can have a direct positive impact on reef health now and for the future. *In some areas of the wider Caribbean (for example Bermuda and the Exuma Cays Land and Sea Park in the Bahamas, and more lately in Belize and Bonaire), active management including bans on fish traps, has led to increases in parrotfish numbers and consequent improvement in reef health and resilience to perturbations including hurricanes. This is in contrast to other areas within the Caribbean, where heavily fished reefs lacked the resilience to recover from storm damage.*

Positive impacts on reef health demonstrably have spill over effects on local economies, including the potential for alternative livelihoods to fishing, thanks to increased tourism revenues, replenishment of fish stocks and restoration of ecosystem services such as shoreline protection.

It is recognised that in the Caribbean there are varying levels of community reliance on fishing in general and the taking of parrotfish in particular. However, in light of the evidence now available, and in accordance with ICRI's Framework for Action cornerstone of 'integrated management' (which includes fisheries management), the International Coral Reef Initiative would like to highlight the benefits of strong management to protect reefs from overfishing, and urges immediate action to effectively protect parrotfish and similar herbivores.

Accordingly, the International Coral Reef Initiative urges Nations and multi-lateral groupings of the wider Caribbean to:

1. ***Adopt*** conservation and fisheries management strategies that lead to the restoration of parrotfish populations and so restore the balance between algae and coral that characterises healthy coral reefs;

2. ***Maximise*** the effect of those management strategies by incorporating necessary resources for outreach, compliance, enforcement and the examination of alternative livelihoods for those that may be affected by restrictions on the take of parrotfish;

3. ***Consider*** listing the parrotfish in the Annexes of the SPAW Protocol (Annex II or III) in addition to highlighting the issue of reef herbivory in relevant Caribbean fisheries fora;

4. ***Engage*** with indigenous and local communities and other stakeholders to communicate the benefits of such strategies for coral reef ecosystems, the replenishment of fisheries stocks and communities' economy.

Annex: *Executive Summary - Status and Trends of Caribbean Coral Reefs; 1970-2012, GCRMN Report*

Vol. 506: 115–127, 2014
doi: 10.3354/meps10764

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 23

Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors

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ABSTRACT: Dominance shifts in ecosystems can occur rapidly, resulting in alternative stable states. While some coral reef ecosystems shift and recover relatively quickly, others recover slowly or not at all over periods of centuries. We explore the role of large (fishing-susceptible) parrotfish in triggering algal phase shifts as alternative attractors that may lock reefs into coral-depleted alternative stable states. We designed an experiment to modestly reduce herbivory only from large parrotfish in the immediate vicinity of experimental coral settlement nursery habitats. We used vertical pegs ('parrotfish deterrents' or PDs) around coral settlement plates on 2 Belizean forereefs. Time-lapse videos and a year's accumulation of bite-marks on plates confirmed that only herbivory from large parrotfish declined significantly due to PDs. Patches of macroalgae developed around PDs reducing coral recruitment in this treatment only. Two dominant reef-dwelling coral genera (*Porites* and *Agaricia*) recruited to our settlement plates. The fast-growing, high-light requiring, reef-building coral *Porites* was more negatively affected by phase shifts; this coral failed to recruit at and above mid-levels of algal abundance. We illustrate the direct roles ecological processes such as herbivory from large parrotfish play in regulating algal abundance, which in turn reduces the recruitment potential of reefs and thus the ecosystem's capacity to recover. Combining our empirical results with an individually-based ecological simulation model, we determined that these processes cascade to drive alternative states and create a 'hysteresis' effect delaying or preventing recovery of the coral reef ecosystem.

KEY WORDS: Alternative attractors · Alternative stable states · Coral recruitment · Herbivory · Hysteresis · Parrotfish · Phase shift · Reinforcing feedback

INTRODUCTION

Coral reefs are complex and often highly diverse ecosystems that can rapidly flip between coral-dominated and alternative states. These systems can lock into alternative stable states (Knowlton 1992) or rapidly recover to their former structure (e.g. Golbuu et al. 2007). Contrasting ecosystem states on coral reefs are often called 'phase shifts' (Done 1992, Hughes 1994). Phase shifts were initially defined as a shift between a 'coral-dominated' and 'coral-depleted and/or algal dominated' state (Done 1992). When reef-corals die, dominance of the ecosystem shifts to other organisms (e.g. Norström et al. 2009) but most commonly to benthic marine algae. Thus, anything that kills most corals on a reef, by definition, creates a phase shift. The conspicuous shift to foliose macroalgae is now synonymous with phase shifts on most Caribbean coral reefs (e.g. Hughes 1994).

Coral mortality has increased globally over the last several decades (Gardner et al. 2003, Bruno & Selig 2007) due to disease, predator out-breaks, climate-induced bleaching and hurricanes. Mortality events are often sudden and may involve thresholds such as well-known thermal thresholds that trigger coral bleaching and death (Lesser 2004). However, we know much more about what kills corals and drives phase shifts towards coral-depletion, than we do

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*Corresponding author: steneck@maine.edu about what drives coral recruitment and the recovery phase of these ecosystems back to coral dominance. While some reef ecosystems recover rapidly (i.e. decade scale; Golbuu et al. 2007), others, especially Caribbean reef ecosystems, are notoriously slow to recover or have shown no signs of recovery from disturbances (Connell 1997). Invariably, massive (or near complete) coral mortality requires the recruitment of reef corals to initiate recovery. This is especially true for Caribbean reefs today after the mass mortality of primarily clonally-propagating acroporid corals shifted dominance to smaller, primarily recruiting poritid-corals (Pandolfi & Jackson 2006, Mumby & Steneck 2008).

Deficient coral recruitment and poor recovery of reef ecosystems may result from myriad sources. There may be too few reproductive corals to maintain high fertilization success and therefore too few larvae (i.e. Allee effects; Knowlton 1992). Too few larvae may arrive to nursery habitats from reproductive populations (i.e. connectivity effects; Jones et al. 2009). Arriving larvae may fail to find nursery habitats or detect necessary triggers for metamorphosis and settlement (facilitation effects; Harrington et al. 2004). Finally, it is possible that rates of post settlement mortality are too high for any coral to survive, negating all earlier events (Harrington et al. 2004, Arnold et al. 2010).

The existence of phase shifts does not necessarily imply that the contrasting states are stable or reinforced by feedbacks that slow recovery. While this topic remains hotly debated (e.g. Dudgeon et al. 2010), it has long been known that coral reefs are nonequilibrial systems (Connell 1978), so they do not necessarily lock into one state versus another indefinitely. However, many previous studies have suggested that ecological feedbacks could create a hysteresis lag that slows or seemingly stops ecosystem recovery (e.g. Mumby et al. 2013b). Accordingly, we explore what drives the trajectory of coral reef community composition. Specifically, we study how herbivory may drive contrasting states in a phase shift in ways that interfere with coral recruitment. If this happens, it can change the trajectory of ecosystem structure in what Scheffer & Carpenter (2003) call alternative attractors. Our understanding of phase shifts and the role of herbivores as a driver of ecosystem structure on coral reefs has focused on (1) small-scale herbivore exclusion experiments (Lewis 1986), (2) natural field experiments where fishing levels have manipulated herbivory (Dulvy et al. 2002), (3) large-scale correlations between herbivores and macroalgal cover (Williams & Polunin 2001), and (4) ecological models of processes (Mumby et al. 2007). Despite this broad range of studies, we lack experimental evidence of the mechanism by which depletion — but not exclusion — of herbivores leads to a loss of coral. In other words, how does the depletion of herbivory, mostly by fishing larger and most vulnerable parrotfish (Hawkins & Roberts 2004), foster an increase in algae and a depletion of coral? We designed a small-scale experiment to manipulate herbivory and quantify the impact on algal structure and the recruitment of corals. We then placed our results in an ecosystem-context by incorporating the manipulation in an ecological model. We found that our observed decline in coral recruitment under reduced herbivory is consistent with the mechanism predicted by ecological models to drive and lock reinforcing feedbacks on the shift from coral to algal dominance.

Specifically, our experiments used terra-cotta coral settlement plates to standardize recruitment habitat architecture, substrate composition and succession. We controlled for changes due to larval connectivity effects by clustering treatments and controls in the same small (i.e. 1 to 2 m diameter) footprint on coral reefs. We used stainless steel pegs to physically impede the largest herbivorous fish (i.e. parrotfishes) from the microhabitat surrounding coral nursery habitats. We excluded large fish because they are frequently most vulnerable to fishing pressure on coral reefs (Hawkins & Roberts 2004), and large herbivores may play a disproportionately large functional role in coral reef ecosystems (Mumby et al. 2006). Explicitly, we sought to determine if modest alterations at small-scales in the frequency and intensity of herbivore-induced disturbances could result in localized phase shifts to macroalgal abundance sufficient to affect the recruitment of corals and at larger scales to the recovery of coral reef ecosystems.

MATERIALS AND METHODS

All experiments were placed at 10 m water depth on wave-exposed fore reefs (i.e. facing eastward) at Glovers Reef and Carrie Bow Cay on the Belizean Barrier Reef (Fig. 1A). Physically the 2 sites are similar in terms of sea temperatures (27 to 29°C; Mumby et al. 2014) and water clarity (horizontal secchi disk distances exceed 20 m at both sites); however, wave exposure is greater at Glovers (log of wave exposure is 8 J m^{-3} versus 6 J m^{-3} at Carrie Bow; Chollett & Mumby 2012).

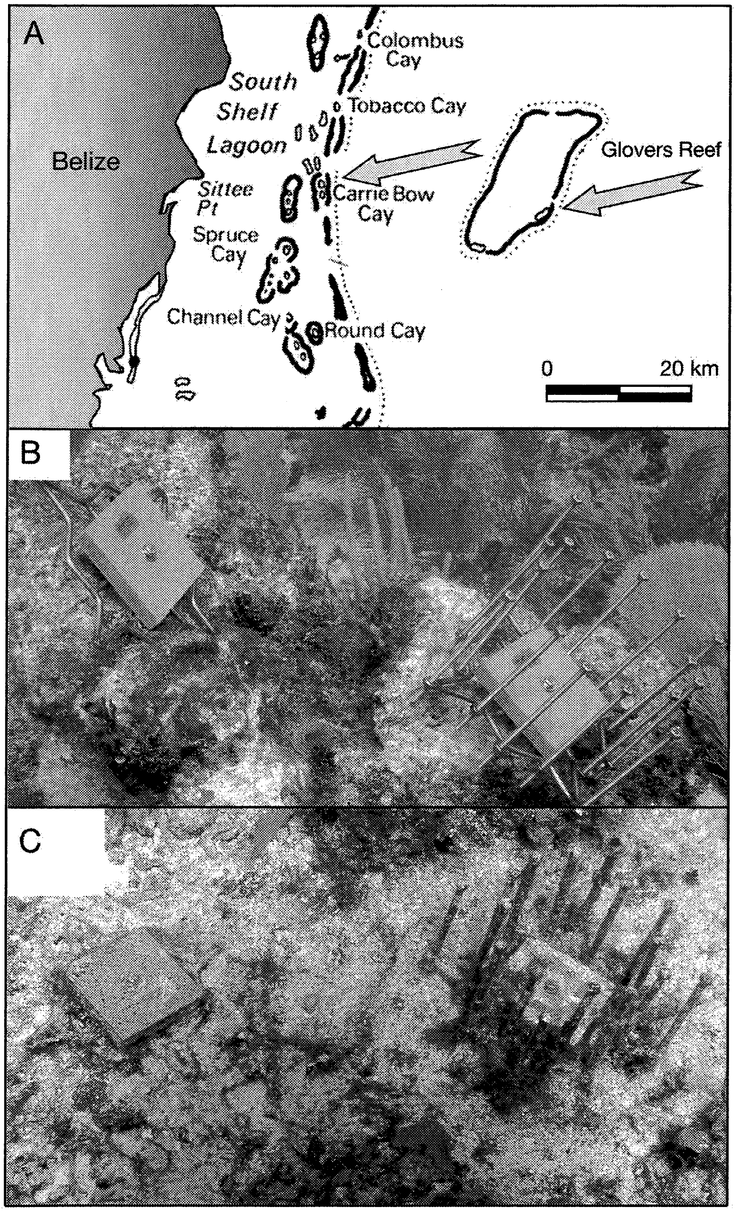


Fig. 1. (A) Belize: Glovers Reef and Carrie Bow Cay study sites. Arrows: average wind direction. Parrotfish deterrents (PDs) and PD-control (B) on deployment and (C) after 1 yr at Glovers Reef

Standardized coral settlement substrata and parrotfish deterrents

We used terra-cotta coral settlement plates to quantify coral recruitment in a standardized way (methods of Arnold et al. 2010). Specifically, unglazed terra-cotta ceramic tiles (10 × 10 × 1 cm) were affixed to the reef with sheetrock wall anchors. All settlement tiles were elevated above the reef surface by a 1 cm spacer. This method of quantifying coral recruitment has been used throughout the world's coral reefs (reviewed in Ritson-Williams et al. 2009).

To determine the effect of macroalgae on coral recruitment, we designed a simple means of reducing herbivory in ways having least effect on light and water motion (2 key factors driving benthic algal productivity). To impede herbivory specifically from large bodied grazing fishes in the immediate vicinity of our coral settlement plates, we installed a 20 cm diameter stainless steel wire frame under the plates that was bent into an 8-point star with stainless steel nuts welded to each point and valley. Into each nut we screwed a 15.2 cm stainless steel bolt. These parrotfish deterrents (PDs) thus consisted of a 16-point crown of spikes with 4 cm gaps surrounding the elevated terra-cotta coral settlement plate (Fig. 1B). Control frames bent identically but without any stainless steel bolts represented the PD control (Fig. 1B). A second control of 'naked' settlement tiles (i.e. without PDs or PD control frames) was deployed in equal numbers.

In March 2007, PDs, PD controls and naked plates were deployed in 24 sets of the 3 setups (1 treatment and 2 controls for a total of 72 settlement tiles) at Glovers Reef, with an identical array of treatments and controls nearly 20 km to the west on the Belizean Barrier Reef adjacent to Carrie Bow Cay (Fig. 1A). The experiment was terminated 1 yr later in March 2008.

Quantifying herbivory

We used 2 independent methods to quantify herbivory on and around the 144 experimental coral settlement plates 1 yr after placement so succession of reef organisms would be complete and in order to minimize novelty effects. First, species-specific and size-specific rates of grazing were quantified using stationary video cameras, and second, the size and density of parrotfish bite marks on the settlement plates were quantified.

Rates of grazing by all fish were recorded from 37 videos of 1 to 2 h duration during March 2008. Cameras were placed in areas distant from diver activity, and often no humans were in the water for the duration of the video observations. Dominant fish groups were parrotfish (Scaridae), tangs (Acanthuridae) and damselfishes (Pomacentridae). Since only the former 2 families are known to create net reductions in algal biomass (Steneck 1988), we quantified all species and size-specific bite rates on them.

To estimate the frequency and intensity of parrotfish grazing, we measured the size (nearest mm) and number of bite marks on each edge of the terra-cotta tiles. For this, after plates had been analyzed for coral spat, substrate colonization and photographed, they were decalcified in hydrochloric acid to remove all calcified epibionts. The plates themselves were unaffected by the acid digestion. The bite mark method quantified the annually accrued frequency and intensity of grazing. This analysis was only applied at the Carrie Bow site because the Glovers Reef plates were unavailable.

Quantifying algal abundance

We quantified algal abundance within the 10 cm perimeter surrounding coral settlement plates. The perimeter, rather than the plate itself, was examined because nearly all settling corals are found on the distal portion of the underside of the tiles (e.g. Arnold et al. 2010; discussed further in 'Results'). Percent cover of fleshy macroalgae was visually assessed within 25 × 25 cm quadrats, and canopy heights were measured to the nearest mm. The product of these 2 measurements is a nondestructive proxy for algal biomass (Steneck & Dethier 1994, Mumby et al. 2013b).

To determine if the PD posts increase algal abundance by their mere presence (e.g. creating an algal friendly habitat) or by deterring herbivores, we measured macroalgal abundance around each post so the algal extent outside the PD crown can be compared to that growing inside the crown. If herbivores have no effect, the algal abundance should have an isodiametric pattern.

Quantifying coral recruitment and rates of growth

Coral spat recruit primarily to the underside of terra-cotta plates at 10 m (Arnold et al. 2010). A pilot study at the same location using the same settling plate method examined coral spat on all surfaces and found that over 80% of the coral spat were on the distal portion of the underside of the plates (Arnold & Steneck 2011).

To quantify coral recruitment, plates were retrieved from the field by unbolting them from the reef surface and sliding the plates onto a threaded rod with 1 cm spacers placed between them to prevent abrasion and damage of organisms (including corals) living on them (methods of Arnold et al. 2010). In the laboratory, we examined the underside of each plate with a dissecting microscope. Each coral was identified to genus (if possible), and measured for size and distance from the outer edge of the plate. The abundance of all other colonizing organisms and their proximity to the coral spat were quantified, but these data were not used in this study. We used differences in the diameter of newly settled corals to estimate intraspecific differences in growth rates relative to where they settled on the underside of terra-cotta plates. Previous studies on identical settlement plates determined coral recruitment with distance from the edge of the plate does not change over the course of the year (Arnold 2011 and unpubl. data); therefore differences in size reflect differences in growth rates rather than simply older spat being larger.

Modeling PD effects to ecosystem scale resilience

To investigate the wider ecosystem-level impacts of the PD manipulation, we incorporated the observed effects of the PDs on parrotfish grazing into an existing model of a Caribbean reef system (Mumby et al. 2007). The model is a spatial simulation of ecological processes including the recruitment, growth, mortality, competition and disturbance of corals and algae on forereef environments. All parameters have an empirical justification and the model behavior has previously been tested (and found to follow) an independent 20 yr time series of reef dynamics in Jamaica (Mumby et al. 2007). The model makes no *a priori* assumptions about the existence of alternative stable states, yet these emerge from simulations. We estimated the impact of the PDs on grazing in 3 steps. First, we determined the instantaneous grazing intensity of the entire parrotfish community at the Glovers Reef site. Parrotfish community structure was surveyed at the beginning and end of the study using ten 30 × 4 m transects per sampling period. Data were pooled across census periods, and the grazing behavior of each fish was converted to a grazing intensity based on allometric scaling relationships between the species, body size, and life phase of a parrotfish and its grazing rate and bite area (Mumby 2006). This resulted in the mean total grazing intensity (GIR) of the fish community (% of the reef h^{-1}). The second step disaggregated the total grazing intensity by each fish size class so that the direct bite rate observations on PDs, for which fish were placed into 4 size classes, could be related to the wider reef-scale GIR measurements derived from the fish census. This was done using Eq. (1),

$$\mathrm{GI_{PD}} = \sum_{i=1}^{C}\left(\frac{\mathrm{BR\_PD}_i}{\mathrm{BR\_PC}_i}\right)\mathrm{GIR}_i \tag{1}$$

where $\mathrm{GI_{PD}}$ is the grazing intensity on reefs whose herbivores have been depleted by the level simulated using PDs; BR_PD and BR_PC are the observed bite rates of parrotfishes on the PDs and PD controls respectively; GIR is the modeled grazing intensity from fish census on reefs without PDs, and i is the ith parrotfish size class (C), from 1 to 4 (i.e. <10, 11–15, 16–20, and >20 cm).

Lastly, the effect of PDs on the instantaneous grazing intensity of the fish community was scaled to a longer-term, 6-monthly measure of grazing used by the ecological model, PRG (Proportion of Reef Grazed). The PRG effectively represents the net outcome of algal production and the integrated action of fish grazing over a 6 mo period, which is the time interval of the model. Previous studies at Glovers Reef concluded that the entire parrotfish community was able to maintain ~0.30 of the reef in a grazed state over time (Mumby 2006). Eq. (2) was then used to adjust the PRG to that expected on a reef whose herbivores had been depleted by the level simulated by the PD manipulation. $\mathrm{PRG_{PD}}$ denotes the proportion of the reef grazed with depleted herbivores:

$$\mathrm{PRG_{PD}} = 0.3\left(\frac{\mathrm{GI_{PD}}}{\mathrm{GIR}}\right) \tag{2}$$

The ecosystem impact of a PD-like reduction in fish grazing was investigated by superimposing the change in reef state upon a plot of the system's state equilibria and thresholds. Coral cover at the sites was determined using 5 line intercept transects of 10 m length.

RESULTS

Herbivory

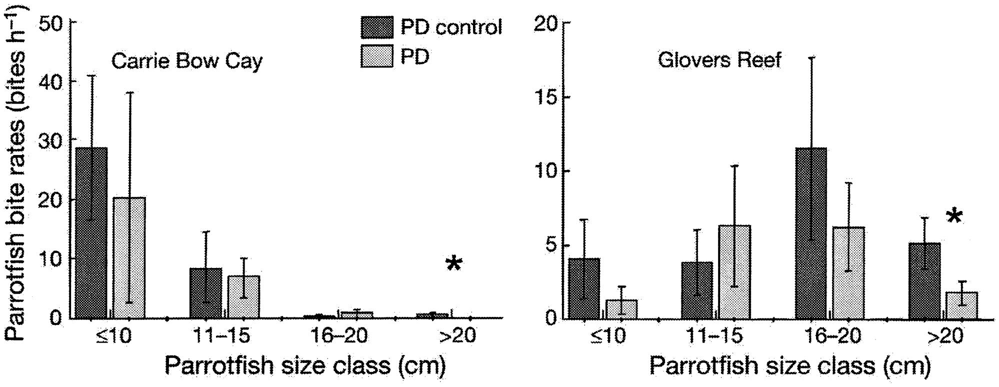
The frequency and intensity of herbivore-induced disturbance differed between the 2 study reefs. We recorded 293 grazing events among 7 species of herbivorous fishes in the 37 videos (1 h duration) trained on PDs or PD controls (often both were in the same field of view) that had been in place for 1 yr on the 2 reefs. Parrotfishes (Scaridae) were the dominant herbivores comprising 92 and 69% of the grazing fish fauna on videos taken at Carrie Bow and Glovers reefs, respectively. Surgeonfishes, the Acanthuridae, accounted for the rest of the observed herbivory. Of surgeonfishes, 2 size classes grazed the areas of the PD and PD controls but showed no significant effect of site or treatment ($p > 0.37$); thus, they will not be considered further.

Grazing parrotfishes were larger (Fig. 2A) at Glovers than at Carrie Bow Cay. Striped and redband parrotfishes (*Scarus iserti* and *Sparisoma aurofrenatum*, respectively) predominated, comprising 92% of grazing fish observed at Carrie Bow compared to 54% of the grazing at Glovers. Three other parrotfish species grazed around PDs at Glovers, including the large and powerful stoplight parrotfish, *Sparisoma viride*.

Observed fish bite rates were analyzed with generalized linear models (GLM) with quasipoisson errors (to allow for over-dispersion of the data). A separate model was created for each size class of fish (Fig. 2A) where each model attempted to predict number of bites per plate h^{-1} based on 2, potentially-interacting predictors: the site (Glovers versus Carrie Bow) and treatment (PDs versus PD control). We found site effects for body size with bite rates from small parrotfish (≤10 cm) being greater at Carrie Bow than Glovers (Fig. 2A, $p = 0.01$). Parrotfishes >15 cm appeared to graze more at Glovers than at Carrie Bow (marginal significance, $p = 0.08$; Fig. 2A). However, significant treatment effects were only found in the largest size class of parrotfishes (>20 cm), such that grazing was significantly greater in PD controls ($p = 0.029$; see Fig. 2A) than PDs (e.g. PDs had no bites from large parrotfish at Carrie Bow yet a modest bite rate of 0.3 on PD controls).

The size and number of bite marks etched onto the terra-cotta plates during the year (Fig. 2B) effectively recorded the intensity (amount removed per bite) and frequency (number of bites per time) of parrotfish-induced disturbance, respectively. We subdivided measured bite marks on plates into small (≤5 mm) and large (>5 mm) and examined effects for all treatments (Fig. 2B). While small and large bites looked suppressed in the PD treatments, only the decline of bite marks from large parrotfish was significant (quasipoisson GLM intercept based on naked plates: 2.09 with coefficient for PD at −0.87 and $p = 0.03$). PD effects on small bites were only marginally significant ($p = 0.07$).

A) Bite rates (videos)



B) Bite marks (plates)

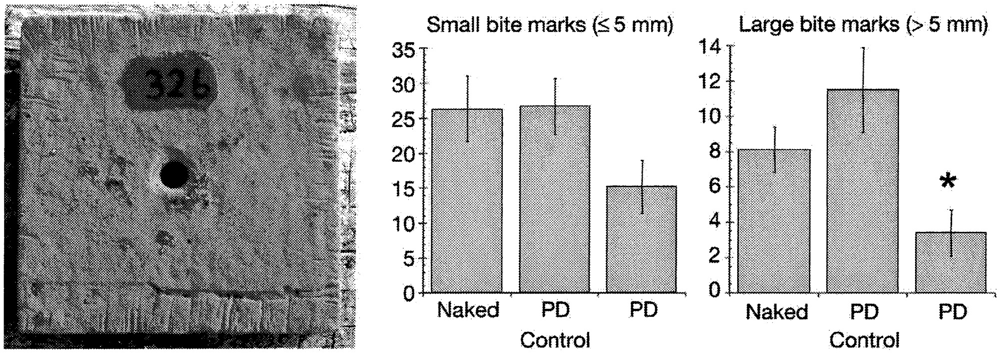


Fig. 2. (A) Parrotfish bite rates per size class at Glovers and Carrie Bow Cay reef sites recorded from videos. (B) Bite marks on terra-cotta settlement plate after 1 yr at Carrie Bow Cay reef (left), and bite rates (# marks yr^{-1}) for small and large scrapes for the parrotfish deterrents (PDs) treatment, PD control, and 'naked' settlement tiles control. *Significant reduction only exists for large parrotfish bites compared to controls (see text)

Algal abundance

At both sites, algal abundance increased in the perimeter space around the PD terra-cotta tiles (Fig. 3). These localized phase shifts to macroalgae were clearly visible and often in stark contrast with the lower algal abundance evident on the adjacent PD controls (photo in Fig. 1C). Erect fleshy macroalgae were dominated by brown algae of the genus *Dictyota*. Other macroalgae included the genera of *Padina, Liagora, Sargassum, Gelidium* and *Zonaria*. We quantified macroalgae abundance by spatial coverage (i.e. percent cover), canopy height and algal index (a product of percent cover and canopy height used as a proxy for algal biomass; Mumby et al. 2013b). All were significantly more abundant in the PD treatments compared to PD control and naked plates (Fig. 3, linear models of arc-sin transformed data with site and treatment as fixed effects found significant negative coefficients for the PD with $p = 0.004$ for macroalgal cover, 0.0016 for canopy height, and 0.0004 for the algal index).

To test for algal retention effects of the stainless steel posts in the PD, we measured the linear distance of macroalgae away from the posts towards the plate (inside the PD crown) versus away from the plate (outside the PD crown). If algae simply grow readily on stainless steel independently of herbivore effects, the algal growth should be radially equidistant. However, macroalgae consistently extended asymmetrically towards the inner portion of the PD (i.e. towards the coral settlement plate). The average contiguous extent of macroalgae away from the PD posts was 2.3 mm (±0.61 SE) outside the PD crown and 10.69 (±0.59 SE) towards the inside. This pattern is consistent with higher rates of herbivory outside the PD crown.

There was no consistent site effect across treatments; however, macroalgal cover was significantly greater on the PDs at Glovers compared to Carrie Bow (linear model intercept with naked plates at Carrie Bow = 28.1, PD coefficient = 10.2, $p = 0.004$, interaction between PD and Glovers coefficient = 11.7, $p = 0.01$; model $r^2 = 0.41$, $p < 0.0001$). Macroalgal canopy heights had a significant treatment effect ($p = 0.0016$) but no site effect. The algal index had a significant treatment effect for PDs ($p = 0.0004$) and marginally-significant differences in the PDs between Glovers and Carrie Bow ($p = 0.06$).

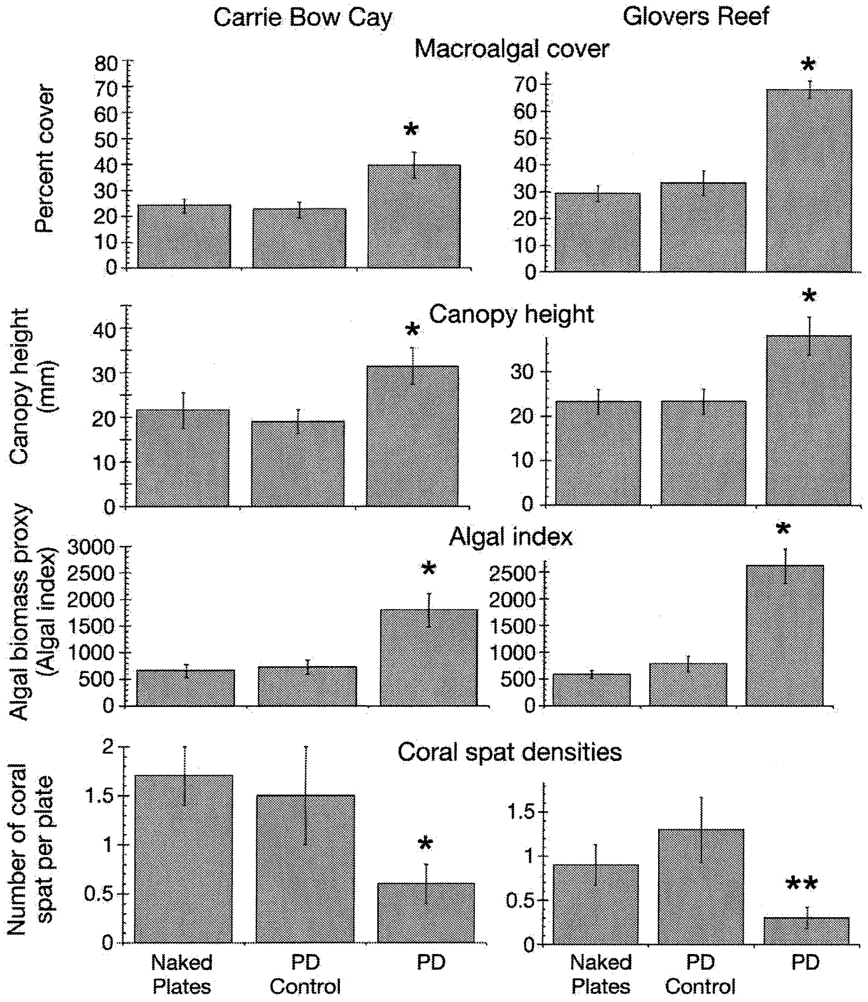


Fig. 3. Fleshy macroalgae abundance as percent cover, canopy height and biomass proxy 'algal index' (% cover × canopy height in mm) on the benthos surrounding coral settlement plates. Coral recruitment densities on the underside of the terra-cotta settlement plates (pooling all taxa). *p < 0.05, **p < 0.01 compared to naked plates and PD controls. See Fig. 2 for definitions

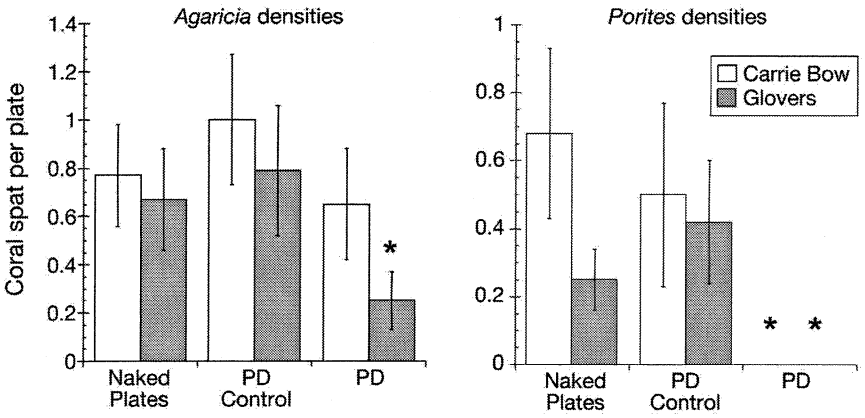


Fig. 4. Population density of newly settled corals for the 2 most abundant genera: *Agaricia* and *Porites* at both study reefs. *Significant differences compared to parrotfish deterrent (PD) control and 'naked' control

Coral recruitment and growth

Newly settled coral ('spat') were more abundant on the undersides of naked plates and PD controls than on the surface of PD plates surrounded by localized algal phase shifts at both study locations (Fig. 3, quasipoisson GLM with site and treatment as fixed effects, significant negative coefficient for PDs with $p = 0.008$).

The 2 coral genera comprising most of the spat identified on the terracotta titles, *Agaricia* and *Porites*, differ ecologically and geologically, and they displayed different treatment effects. The most common *Agaricia* species to recruit to settlement plates (and found on the reef as juvenile corals) were *A. agaricites* and *A. humilis* but not *A. tenuifolia* (Arnold 2011). *Agaricia* spp. recruited to all treatments at all sites but its probability of occurrence was only significantly retarded on PDs at Glovers (Fig. 4; binomial test assigning its observed prevalence of 0.42 on both naked plates and PD controls to that of 0.16 on PDs, yielded a probability of 0.008). *Porites astreoides*, the most probable *Porites* species recruiting to the settlement plates, is a reef building coral (Pandolfi & Jackson 2006) that now dominates Caribbean reef frameworks (Pandolfi & Jackson 2006). Although species determinations are impossible among newly recruited corals, we confirmed the presence of *P. astreoides* on other longer-duration settlement plates placed at these sites. Importantly, *Porites* failed to recruit to any of the PD treatments (Fig. 4). The probability that *Porites* would fail to recruit to PDs by chance was less than 0.001 at each site (i.e. binomial test assigning the observed prevalence on either naked plates or PD controls to the observed prevalence on PDs).

On those treatments that *Porites* spat were able to settle, their distribution was confined to the outer edge of the underside of the settle-

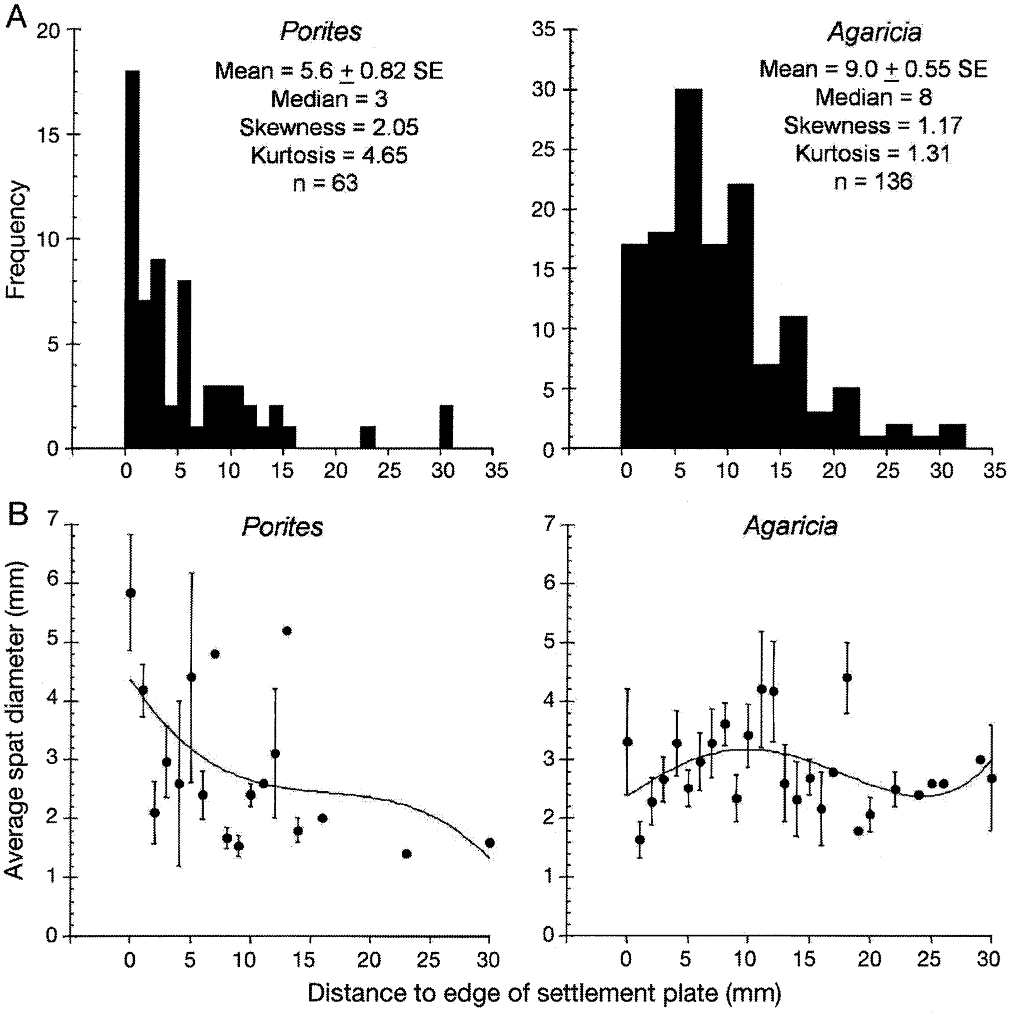


Fig. 5. (A) Frequency of coral spat with distance from the distal edge on the underside of settlement plates. *Porites* recruits significantly closer to the outer edge ($p < 0.01$; see text). (B) Average size per mm size class (±SE) (i.e. spat size rounded to nearest mm size class) of newly settled corals with distance to outer under-side edge

ment plates (Fig. 5A). The mean distance to the edge was 5.6 and 9.0 mm for *Porites* and *Agaricia*, respectively (Student's $t = 3.58$, $p = 0.0005$, $df = 125$). The distance-frequency for *Porites* settlement was strongly skewed to the left (mode of 0 mm from the edge of the settlement plate) as reflected in its higher degree of skewness and kurtosis relative to *Agaricia* (Fig. 5A). In our other studies of coral spat on terra-cotta plates at 10 m that were monitored every 2 to 4 mo from March 2004 through August 2005, we found *Porites* settlement was greatest in early summer (i.e. over 70% of *Porites* spat were observed during the month of June), and spat settled within the underside area from the edge to about 1.5 cm from the edge (average distance from the edge: >5 mm) (S. Arnold unpubl. data). The pattern of no preferential settlement near the edge of the plate did not change during periodic observations over the year. The spat that did settle early but away from the edge of the plate appeared not to have grown much over the course of the year. Thus we interpret the differences in coral size with respect to the edge as relating to differences in coral growth rates.

The largest and thus most rapidly growing newly settled *Porites* were near the distal edge on the underside of settlement plates (Fig. 5B). *Agaricia* sizes and growth rates were relatively unchanged with distance from the plate edge (with a possible maximum 10 mm from plate's edge). The size of recently settled corals on settlement plates reflects both the timing of settlement and their subsequent rates of growth. We assumed that for any given settlement event there was no systematic temporal difference in habitat selection so intraspecific differences in size reflect differences in growth rates.

Coral recruitment densities declined with algal abundance surrounding settlement plates (Fig. 6). We pooled all treatments and observed that *Porites* declined more precipitously than *Agaricia* as a function of local macroalgal abundance.

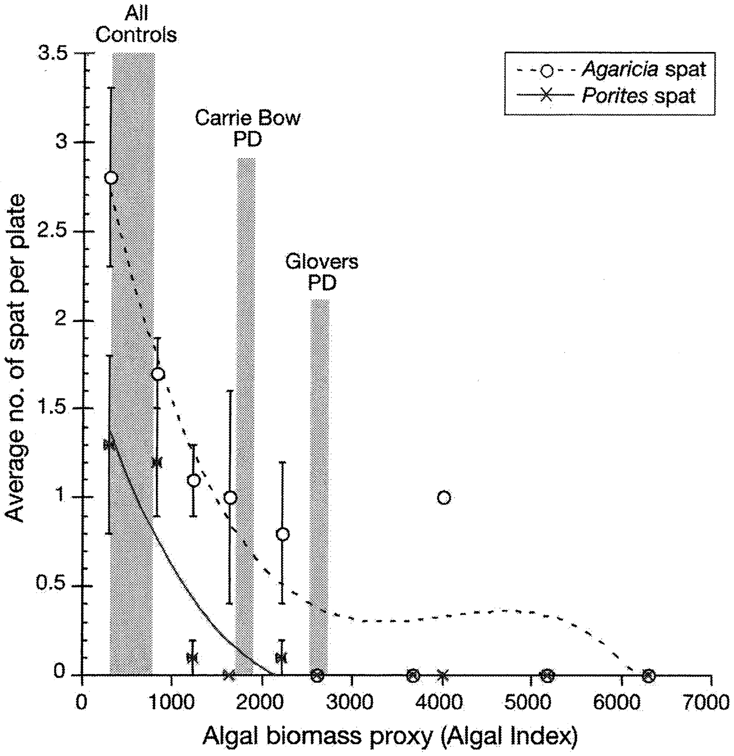


Fig. 6. Population density of newly recruited corals (±SE) as a function of algal biomass surrounding the settlement plates at Carrie Bow and Glovers. All treatments and sites are pooled but algal abundance recorded for parrotfish deterrents (PD) treatment and controls are represented by vertical gray bars. None of the macroalgae was physically in contact with coral spat growing on the underside of settlement plates. Best fit curves were 3rd order polynomial for both taxa; R^2 = 0.53, 0.40 for *Porites astreoides* and *Agaricia*, respectively

Scaling up parrotfish deterrent manipulation to ecosystem stability

When the bite rates upon PDs were scaled to a community-wide impact on total parrotfish grazing (Eq. 1), the total grazing intensity was predicted to fall by 52% from 1.14 to 0.55% h^{-1}. Converting this to a proportion of reef grazed, the PD manipulation was equivalent to a decline in grazing from 0.3 to ~0.15 (Eq. 2). Given a coral cover at the study sites of ~15% (mean ranging between 12 and 17%), the change in reef state was superimposed upon a plot of reef equilibria (Fig. 7A). It can be seen that a 52% fall in grazing at a coral cover of 15% is predicted to shift the system from one basin of community attraction to another. At the higher level of grazing, coral population dynamics tend towards the upper stable equilibrium and would therefore tend to exhibit a trajectory of recovery, with recruitment and growth exceeding mortality. In contrast, the reduction in grazing crosses an unstable equilibrium (threshold), resulting in the system becoming driven towards a coral-depleted state, rich in macroalgae.

The proposed mechanism for development of a coral-depleted system state is a bottleneck in recruitment. The model can be used to illustrate this mechanism. A simulation of coral trajectories under the experimental PD manipulation versus full grazing reveals divergent pathways as expected from the location of reefs on either side of the unstable equilibrium (Fig. 7B). Censusing the size distribution of corals as they approach equilibrium (Fig. 7C) reveals that the low grazing system does not possess enough juvenile corals (sizes 14 to 60 cm^2) to sustain larger size classes. Under high grazing, cohorts move through size classes resulting in an accumulation of large adult corals (Fig. 7C). Note that higher settlement was found in the low grazing model because (1) the system was modeled conservatively as completely open and (2) because space occupied by macroalgae is more dynamic than that of adult corals (which dominate the high grazing treatment) and therefore allows for greater coral recruitment, albeit with high post-settlement mortality. Note also that the model differs slightly from the experiment in that it does not attempt to model pre-recruitment processes; corals enter the population at a diameter of 1 cm. However, despite this ontogenetic offset between the model and experiment, both found an algal-driven bottleneck in the population dynamics of corals associated with early ontogeny.

DISCUSSION

By locally and modestly impeding the grazing rates of large parrotfish (Fig. 2A,B), PDs created microphase shifts of elevated algal abundance (Figs. 1C & 3). These phase shifts depressed coral recruitment nonlinearly within the algal dominated footprint (Fig. 6). Algal domination was greatest inside the parrotfish deterrent crowns so herbivory was the most likely driver of algal abundance. All of this suggests that processes controlling algal abundance indirectly control the recruitment potential of coral reef ecosystems (sensu Steneck & Dethier 1994) for settling corals and create the reinforcing feedbacks necessary for alternative attractors.

Since coral mortality initiates reef phase-shifts from coral dominance to some other dominant(s), the struc-

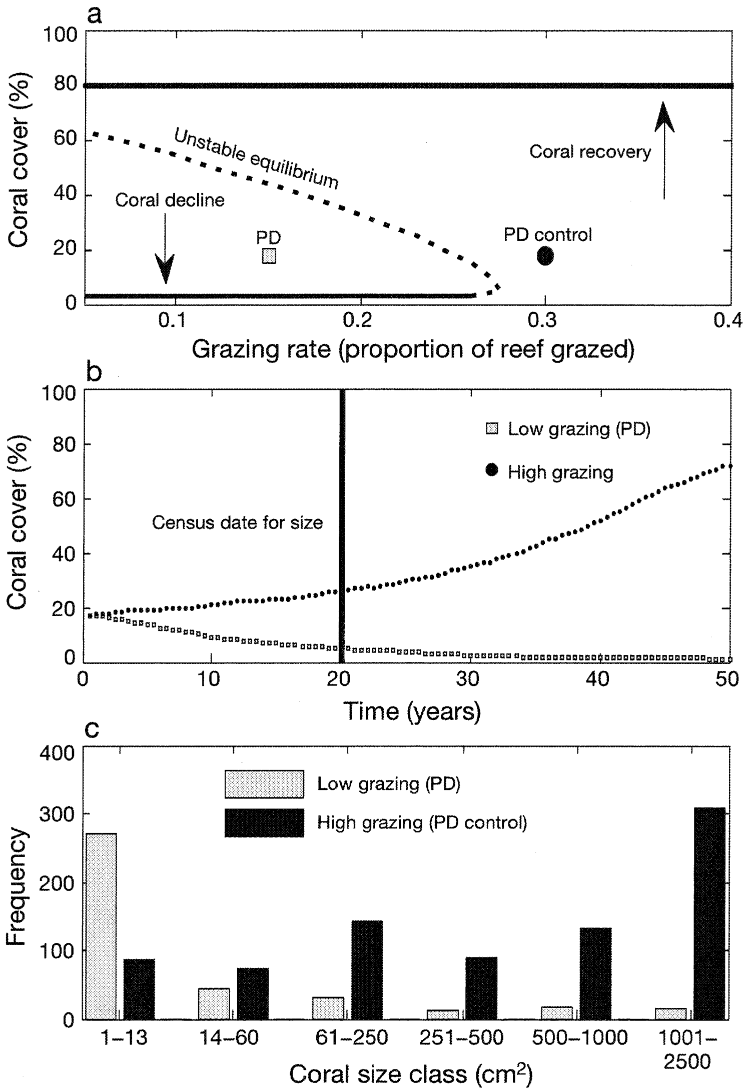


Fig. 7. Projected ecosystem effects of the experimental manipulation of grazing. (A) The system's stable (solid lines) and unstable equilibria (dotted line) in the absence of perturbation. (B) Projected long-term trajectories of coral assemblages under experimental grazing in the absence of external perturbation. (C) Predicted size distributions of corals under experimental grazing levels censused after 20 yr. PD: parrotfish deterrent

turing processes in place at that time will likely canalize succession in ways that can affect coral recruitment and the likelihood of coral reef ecosystems returning to coral dominance. Succession can result in myriad alternative states for coral reefs such as soft corals, other colonial cnidarians and sponges (Norström et al. 2009). However, despite those end results, virtually all coral reefs at first become colonized by algae following disturbances simply because they are ubiquitous and can respond most rapidly. Of all possible phase shifts, those to algal dominance are most common (Hughes 1994, McManus & Polsenberg 2004). However, depending upon herbivory, productivity, and succession, algal community structure may stabilize at different end point functional groups ranging from encrusting coralline algae that can facilitate coral recruitment (Arnold et al. 2010), to diminutive to modest-canopy height filamentous algal turfs, and finally to taller-canopy macroalgae that can inhibit coral recruitment in their nursery microhabitats (Birkeland 1977, reviewed in Steneck 1988). In essence, as algal biomass and canopy height increase, coral reefs become more hostile to recruiting corals.

Of the 2 corals commonly recruiting in our experiment, *Porites astreoides* is a reef builder (Pandolfi & Jackson 2006), and it may be most susceptible to light effects from macroalgal phase shifts. As with most reef-building corals, it has small feeding polyps, may be more autotrophic (Porter 1976), and thus requires higher light for growth and survival. In contrast, the larger polyped *Agaricia* may be more heterotrophic, allowing it to occupy more habitats as an opportunistic or fugitive species. The requirement for microhabitats having a higher productivity potential may also explain the proclivity of *Porites* to settle and grow most rapidly in high light nursery microhabitats on the distal underside edge of settlement tiles (Fig. 5A,B). Subcryptic nursery habitats for newly settled corals are important for keeping this vulnerable stage relatively safe from predators and competitors so that with modest growth they will be under full sunlight. Other studies found that when *P. astreoides* larvae contact *Dictyota* spp. macroalgae, the larvae die or fail to recruit (Paul et al. 2011). Taken together, our results and those of other studies (Arnold et al. 2010) suggest that algal abundance regulates the process of coral recruitment by reducing or eliminating coral nursery microhabitats, and thus is the proximate 'driver' of recovery in Caribbean coral reef ecosystems (Fig. 8).

Ecological cascades can be of several forms. Best known are trophic cascades (e.g. Paine 1980), but there are others including those involving ecosystem engineers (Jones et al. 1997). All require a functional — and often sequential — nexus with strong interactors and their associated processes. These create reinforcing feedbacks in the physical–biological system that self-organizes towards different alternative states (Rietkerk et al. 2004). Such ecological cascades and feedbacks transmitted from herbivory to algal development and finally to coral recruitment have

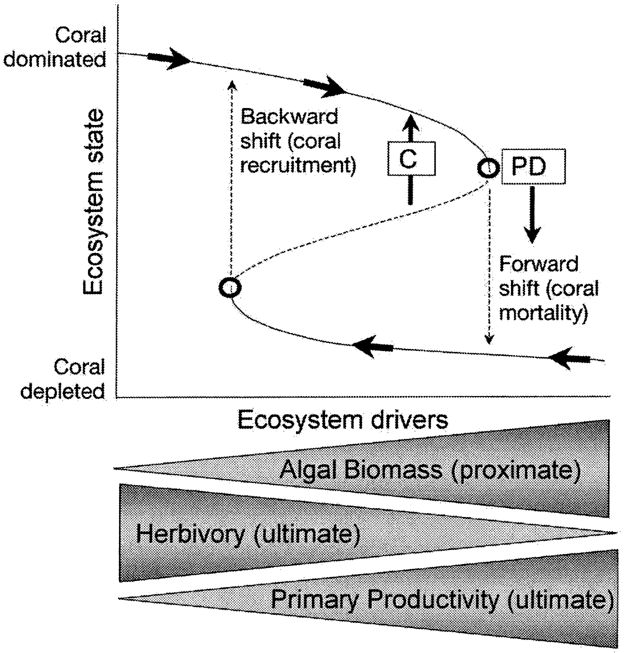


Fig. 8. Alternative attractors as traditionally illustrated (e.g. Scheffer & Carpenter 2003) with ecosystem state varying as a function of environmental conditions or parameters ('ecosystem drivers'). The strength of the driver is indicated by the width of the wedge. Circles represent bifurcation points. The right bifurcation forward shifts to a coral depleted state (down arrows). To the right of this point, coral recruitment and ecosystem recovery may be impossible. Left of this point towards the backward shift bifurcation (up arrows) reflects the hysteresis lag for recovery to a coral dominated state. Left of the backward shift bifurcation indicates ecosystem drivers without hysteresis for recovery. Solid curved lines denote stable states to the bifurcation points that have basins of attraction that will move the ecosystem towards those coral dominated (upper) or coral depleted (lower) states. Dotted curved line denotes an unstable state that will shift backwards to coral dominated if above, or forward to a coral depleted state if below that line. Solid upward arrow indicates perturbations that will move the ecosystem state towards recovery to the previous state; and solid downward arrow indicates perturbations that will move the system to the coral depleted state with little chance of rapid recovery. Note the relatively small difference between control (C) and parrotfish deterrent (PD) experiments resulting in a large difference in the capacity of the ecosystem to recover from perturbations

also been proposed for coral reefs (Mumby & Steneck 2008), but, as far as we know, never tested with experiments for only the role of large herbivores (but see Jayewardene 2009 for experiments demonstrating the proportionately greater reduction in algal abundance by large parrotfish).

Locally elevated algal abundance developed around PDs at both study regions. However, subtle differences in algal abundance between the regions could be important. Both reefs were qualitatively similar and PD treatment effects excluded the reef building coral *Porites* at both. However, *Agaricia* recruitment declined significantly only at Glovers. The simplest explanation for this result is that the magnitude of the PD effect on algal biomass (i.e. cover, canopy height and hence the algal index) was greater at Glovers, both in absolute terms (algal index in the PD treatment was 1.6 times greater at Glovers than Carrie Bow) and in relative terms, with PDs causing a 4.3 fold rise in algal index at Glovers compared to only a 2.2 fold rise at Carrie Bow (Fig. 6). This regional difference may have only a modest effect on *Agaricia*, a low, light-tolerant (perhaps more heterotrophic) coral more suited to persisting under moderate algal growth at Carrie Bow than the larger algal bloom at Glovers (Figs. 4 & 6). Understanding what drives such subtle but potentially important geographic differences in algal abundance may help explain differences in rates of recovery following perturbations in these ecosystems.

The ecological processes of primary productivity and herbivory drive algal abundance, which causes declines in coral recruitment (Steneck & Dethier 1994; Fig. 8). Parrotfish deterrent results illustrate the importance of herbivory from large parrotfishes. Note that the Carrie Bow site had overall higher bite rates from parrotfishes, but they were primarily small fish (Fig. 2A). Thus the high frequency of low intensity herbivore-induced disturbance and relatively few large parrotfish maintained an overall lower algal abundance in PD treatments at Carrie Bow compared to Glovers reef (Figs. 2 & 3). This may be due to higher algal growth rates and productivity at Glovers. Elevated productivity potential of the environment could result from Glover's higher wave exposure and water flow that increases nutrient delivery and gas exchange due to its relatively long fetch and incident wave exposure (Mumby et al. 2014). Glovers' fetch is functionally unlimited (>100 km, see Ekebom et al. 2003) whereas Carrie Bow is in the lee of Glovers 20 km up wind (Fig. 1A; see arrows indicating wind direction). Future studies will examine the impact of the PDs under a wider range of bottom-up and top-down forcing functions. Indeed, the position of thresholds (at or near bifurcation points) would be expected to change with shifts in the driving processes of productivity, herbivory or both (Fig. 8 bottom).

At some low level of algal biomass resulting from high rates of herbivory, low rates of productivity or both, the reef ecosystem will be unaffected by the negative effects of algae (left of the backward shift bifurcation point; Fig. 8). At that point, reefs recover without hysteresis lags. This condition has been described in concept as 'surplus herbivory' (Mumby & Steneck 2008). It represents the conditions where even massive coral mortality does not result in a persistent phase shift to macroalgae. Under those conditions we would not expect to see micro-phase shifts resulting from parrotfish deterrents. We intend to test this prediction in future studies to compare results with what we found in Belize.

To scale up to an entire reef the consequences of the 52% reduction in parrotfish grazing resulting from PDs, we developed a field-tested ecosystem stability model for the Belize reef ecosystem. The model predicted that a shift in grazing of this magnitude would cause the ecosystem to flip from a coral-dominated basin of attraction to an alternative, algal-dominated basin. This switch in attractor occurs in the model because a rise in algal cover reduces the rate of coral recruitment until it can no longer sustain the population (Mumby et al. 2013c). Here, by experimentally manipulating herbivory, we show that the model behavior is borne out empirically; the micro phase shift of algae drastically reduces coral recruitment. The pivotal role of macroalgae on coral recruitment also helps interpret the hysteresis predicted by models of the ecosystem (Figs. 7 & 8). The unstable equilibria that distinguish alternative basins of attraction (diagonal curve in Fig. 7) reflect the interaction of coral cover (*y*-axis) and grazing rate (*x*-axis) on the intensity of grazing upon macroalgae, assuming no differences in rates of primary productivity. When coral cover is low, a high grazing rate (number of herbivores) is needed to exert sufficient constraints upon macroalgae that a bottleneck in coral recruitment is avoided (Fig. 7). However, increases in coral cover reduce the foraging area available to grazers and therefore intensify grazing. This increase in grazing intensity with rising coral cover has been demonstrated experimentally (Williams et al. 2001). When coral cover is high, fewer grazers are needed to generate sufficiently intense grazing that coral recruitment is maintained. Thus, unstable equilibria represent an isocline of grazing intensity from high-coral/low-grazing rate to low-coral/high-grazing rate. We also note that increases in macroalgae might exacerbate negative reinforcing feedbacks by further reducing grazing, poisoning or reducing reproductive output of corals (Hoey & Bellwood 2011, Rasher & Hay 2010, Foster et al. 2008, respectively).

We focused on the importance of cascading processes on system stability, beginning with how modest changes in the process of herbivory (i.e. reduction of disturbance intensity from large parrotfish) affect algal biomass. This in turn affected and even halted the process of coral recruitment for *Porites* species now known to dominate contemporary coral reef frameworks in the Caribbean (Pandolfi & Jackson 2006). While coral recruitment is essential for the recovery of this ecosystem following a perturbation, the overall effect of cascading processes involving herbivory, algal productivity, and coral recruitment complicates and makes less predictable how this ecosystem behaves.

We are not arguing that our experiments prove the existence of alternative states. Rather, we provide mechanistic evidence from our experiment that a modest reduction in grazing is sufficient to shut down coral recruitment. We provided empirical support for the theoretical mechanisms and feedbacks that drive alternative attractors (sensu Scheffer & Carpenter 2003), which could lead to alternative stable states on coral reefs. While little mystery remains why coral dominance declines on reefs (i.e. from bleaching events or disease), few experimental studies have focused on what prevents them from recovering. Our experiments showed that modest reductions only in herbivory from large parrotfish allow macroalgae to bloom, which creates a bottleneck in the process of coral recruitment, thereby driving conditions at our 2 study regions towards a 'catastrophic bifurcation' (sensu Scheffer & Carpenter 2003; Fig. 8) from which recovery is stopped (e.g. for *Porites*) or greatly slowed. Our empirical study, together with mechanistic models, strongly support the supposition that Caribbean reefs exhibit nonlinear dynamics resulting in persistent algal-dominated states.

Acknowledgements. This research was funded by the National Fish and Wildlife Foundation, the Connectivity Working Group of the Global Environmental Fund Targeted Coral Reef Research and Capacity Building Project, The Wildlife Conservation Society (for research at Glovers Reef), and the Smithsonian Institution (for research at Carrie Bow Cay). Additional support came from NERC and European Union 7th Framework programme (P7/2007-2013) under grant agreement No. 244161. Parrotfish deterrents and controls were welded by Mid-Coast Machine Fabrication & Repair. S. Prendergast helped with manuscript preparation. To all we are grateful. This is contribution number 953 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution.

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Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA

Submitted: December 2, 2013; Accepted: February 11, 2014
Proofs received from author(s): May 24, 2014

Subject: RIN 0648-XD325; Scoping Comments, Comprehensive Amendment to the U.S. Caribbean FMPs: Annual Catch Limit Control Rule -- Msg. 2

From: Andrea Treece (atreece@earthjustice.org)

To: graciela_cfmc@yahoo.com; roy.crabtree@noaa.gov;

Date: Friday, July 25, 2014 3:37 PM

Attachments to EJ-CBD-CORALations comment letter:

Arnold et al 2010

Edwards et al 2013

Hay & Rasher 2010

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Vol. 414: 91–105, 2010
doi: 10.3354/meps08724

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 13

Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment

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ABSTRACT: Mortality of corals is increasing due to bleaching, disease and algal overgrowth. In the Caribbean, low rates of coral recruitment contribute to the slow or undetectable rates of recovery in reef ecosystems. Although algae have long been suspected to interfere with coral recruitment, the mechanisms of that interaction remain unclear. We experimentally tested the effects of turf algal abundance on 3 sequential factors important to recruitment of corals: the biophysical delivery of planktonic coral larvae, their propensity to settle, and the availability of microhabitats where they survive. We deployed coral settlement plates inside and outside damselfish *Stegastes* spp. gardens and cages. Damselfish aggression reduced herbivory from fishes, and cages became fouled with turf algae, both locally increasing algal biomass surrounding the plates. This reduced flushing rates in nursery microhabitats on the plate underside, limiting larvae available for settlement. Coral spat settled preferentially on an early successional crustose coralline alga *Titanoderma prototypum* but also on or near other coralline algae, biofilms, and calcareous polychaete worm tubes. Post-settlement survival was highest in the fully grazed, lowest algal biomass treatment, and after 27 mo 'spat' densities were 73% higher in this treatment. The 'gauntlet' refers to the sequence of ecological processes through which corals must survive to recruit. The highest proportion of coral spat successfully running the gauntlet did so under conditions of low algal biomass resulting from increased herbivory. If coral recruitment is heavily controlled at very local scales by this gauntlet, then coral reef managers could improve a reef's recruitment potential by managing for reduced algal biomass.

KEY WORDS: Coral reef · Algal biomass · Herbivory · Parrotfish · Recruitment limitation · Caribbean · Demographic bottleneck · Bonaire

INTRODUCTION

Coral reefs worldwide suffer from large-scale and relatively sudden disturbances due to coral bleaching, disease, and other insults (e.g. Knowlton 2001, Hughes et al. 2003). Unfortunately, we know much more about what causes coral reefs to collapse than we do about what contributes to their recovery (Vermeij 2006). In the Caribbean, this was most evident in recent decades when many coral-dominated reefs phase-shifted to algal-dominated reefs (e.g. Hughes 1994, Gardner et al. 2003). Further, most Caribbean reefs have shown little or no recovery from disturbances (Connell et al. 1997, Hughes et al. 2005), and, while they decline, the debate regarding what drives coral recruitment and how to best manage for reef recovery persists.

Coral recruitment is central to the recovery of coral reefs. Logically, this involves 3 sequential steps: (1) the availability of competent larvae ready to settle to the benthos — dependent on connectivity, (2) the propensity to settle — often aided by chemical cues that induce settlement and metamorphosis, and (3) the availability of nursery habitats where post-settlement mortality of newly settled corals is low.

It is widely thought that most larvae contributing to coral recruitment originate relatively locally (Sammarco & Andrews 1989, Hughes et al. 2000, Shanks et al. 2003). This is because corals have relatively short

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larval durations (days to weeks; Ritson-Williams et al. 2009) compared to other reef organisms such as reef fish (months) or reef lobsters (up to a year) (Steneck et al. 2009). Within this local domain, settlement occurs only after certain conditions bring competent larvae to specific depths, light (meter scale), and biogenic substrata (e.g. coralline algae) that induce metamorphosis and settlement (millimeter scale; Raimondi & Morse 2000). Thus, for coral settlement, larval availability and the propensity to settle involve complex organismal and environmental factors that operate at multiple scales. Larval behavior at the smallest scale controls movement, metamorphosis, and settlement. Larger local-scale environmental conditions enable advection of larvae. Post-settlement survival is also strongly influenced by the local biological environment. For example, post-settlement survival for Indo-Pacific corals was enhanced at millimeter scales by particular species of coralline algae (Harrington et al. 2004). Conversely, areas of high algal biomass are known to be poor nursery habitats for settling corals (Birkeland 1977, Harriott 1983). Thus, it is possible that phase shifts to high algal biomass could reduce post-settlement survival and thereby suppress coral recruitment (Hughes & Tanner 2000).

In the Caribbean, coral recruitment rates have declined sharply over the past few decades (Hughes & Tanner 2000, Vermeij 2006). Hughes & Tanner (2000) argued that loss of live coral in Jamaica reduced the number of available larvae and caused recruitment failure. However, Vermeij (2006), comparing recent coral recruitment studies with identical studies 20 yr ago from the same location in Curacao, Netherlands Antilles, concluded that macroalgal growth had caused the reef to become hostile to settling corals, resulting in a 5-fold decline in coral recruitment there between 1979 and 1998. Thus, there is no consensus on whether the decline in coral recruitment results from a supply-side limitation in larval availability, a change in the receptivity of the reef itself, or both.

To address these questions and better manage for reef recovery, it is important to understand the causes of recruitment failure. We seek to determine what improves the chances for a coral larva to run the gauntlet of processes leading to coral recruitment. Specifically, are there demographic bottlenecks involving pre-settlement, settlement, or post-settlement processes such as the availability of larvae, their propensity to settle, or their post-settlement survivorship, respectively?

To determine the scale and rate at which recruitment operates and to develop a process-level understanding of critical steps to recruitment, we conducted experiments measuring the effects of algal abundance on recruitment in Bonaire, Netherlands Antilles. We chose Bonaire's coral reefs because the abundance of algae there is the lowest in the Caribbean (Kramer 2003) making experiments examining the effects of elevated algal abundance relatively easy to pursue. Further, by conducting the experiment on reefs with abundant corals, supply-side limitations should be relatively low (Steneck et al. 2009).

Although macroalgal abundances are low, territorial damselfish *Stegastes* spp. create small patches of elevated biomass in their filamentous turf 'gardens' (Brawley & Adey 1977) by reducing herbivory in their territories (Sammarco & Williams 1982, reviewed by Ceccarelli et al. 2001). We used the gardens from the 2 dominant territorial damselfish species on Bonaire, the three-spot *S. planifrons* and the longfin damselfish *S. diencaeaus*, to determine whether these localized differences in algal biomass affect the settlement and subsequent recruitment of corals.

We sought to determine whether potential demographically relevant limitations occur at the level of local supply of available larvae, their propensity to settle, and/or the availability of nursery habitats. We examined coral recruitment by using damselfish-induced algal turf gardens and wire cages for natural and manipulated locally elevated algal patches. We also determined the microhabitat on or near which corals settle and, with millimeter-scale spatially explicit monitoring, established the per capita survivorship and growth of newly settled corals in our experimental treatments and controls.

MATERIALS AND METHODS

Study sites. The study was conducted on the island of Bonaire, Netherlands Antilles, in the southern Caribbean (12° 15′ N, 68° 28′ W). Our 6 replicate sites, all >1 km apart, were along the major fringing reef track on the western (lee) side of Bonaire. Site names, from north to south, are Karpata, Barcadera, Reef Scientifico, Forest (on Klein Bonaire), Eighteenth Palm, and Windsock. The sites were chosen to characterize coral recruitment on the lee reefs of Bonaire. None of the sites were seriously damaged by Hurricane Lenny, which impacted several sites on Bonaire in November 1999.

Quantifying patterns in algae and juvenile corals. At each site, 4 replicate, 10 × 2 m permanent belt transects were established parallel to the shore at 10 m depth. Within each belt, damselfish territories were determined through observations of both three-spot *Stegastes planifrons* and longfin *S. diencaeaus* damselfish over 3 min intervals, and algal community structure and density of juvenile corals were quantified. Approximately 237 quadrats of 25 × 25 cm were placed inside and outside of damselfish territories within the belt transects on hard substrate, where algae or corals could recruit. Substrates with sediment or live invertebrates such as sponges, gorgonians, and adult coral were avoided.

In each quadrat, visual estimates of percent cover of turf algae, macroalgae, crustose coralline algae, non-coralline algal crusts (primarily peyssonnelid red algae), articulated algae (primarily *Halimeda opuntia*, although rare on Bonaire), and any adult coral or gorgonians and sponges were recorded. Algal turfs, or the epilithic algal community (sensu Hatcher 1983), include a multispecies group of primarily filamentous algae with canopy heights of <10 mm (i.e. *Ceramium* spp., *Polysiphonia* spp., *Herposiphonia* spp., *Centroceras* spp., *Taenioma* spp., and *Ectocarpus* spp.; Steneck 1988). Macroalgae on Bonaire are rare (Kramer 2003) and primarily included diminutive (means ± SE: 4.97 ± 0.22 mm) forms of both *Dictyota* spp. and *Lobophora variegata*. Crustose coralline algae refer to nongeniculate encrusting calcified red algae in the order Corallinales. The non-coralline encrusting algae are primarily peyssonnelid algae that differ from crustose coralline algae by being variably calcified with aragonite or not calcified at all and possessing tetrasporangial sori rather than conceptacles. We measured average canopy heights of foliose algae to the nearest millimeter. We calculated an algal index as a proxy for algal biomass by multiplying per group (e.g. turf) canopy height with its percent cover (Kramer 2003).

Densities of juvenile corals having recruited to the reef were determined by recording all juveniles, identified to the highest taxonomic resolution possible (i.e. genus or species level), in each quadrat. Juvenile corals included those with a maximum diameter of 40 mm or less (Bak & Engel 1979, Edmunds & Carpenter 2001), omitting those with characteristics of asexual fragmentation and those species that are characteristically small as adults (of which there are relatively few) (Richmond & Hunter 1990). The 237 quadrats were scored, and numbers were extrapolated to square meter densities.

Settlement plates to mimic microhabitat for newly settling corals. In March 2004, 40 terra-cotta coral settlement plates of 10 × 10 × 1 cm were deployed at each site (methods of Mundy 2000; Fig. 1A). Ten plates were affixed per belt transect, half inside and half outside of damselfish territories. Thus, there were 20 plates outside damselfish territories and 20 plates inside damselfish territories per site. Multiple plates were not placed in a single damselfish territory. Holes of 0.79 cm diameter were drilled into dead substrate with a pneumatic drill, and stainless steel lag screws (6.35 cm in length) were threaded through the plate's 0.8 cm center hole and screwed into 3.81 cm nylon wall anchors inserted into the drill holes.

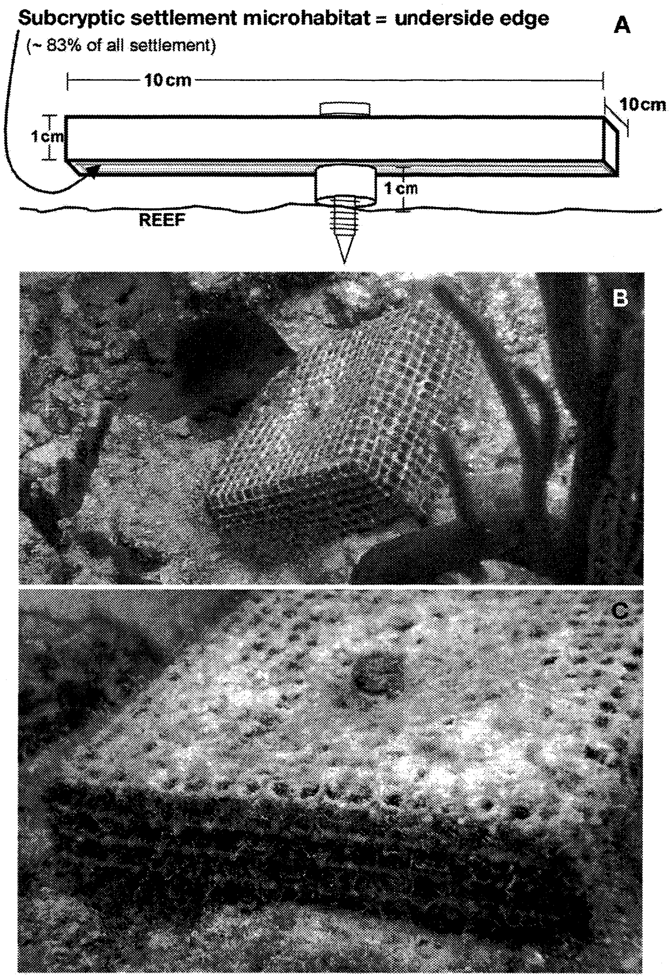

Fig. 1. Settlement plate design and algal fouled cages inside and outside of damselfish *Stegastes* spp. territories. (A) Sketch of 10 × 10 × 1 cm terra-cotta coral settlement plate. The subcryptic settlement microhabitat, where 83% of all spat settled, is the outside 1.5 cm perimeter of the plate underside hidden from grazers but in close proximity to the photic zone. (B) An inside territory/caged plate–non-fully grazed treatment. (C) A cage fouled with turf algae 8 mo after cage deployment

Bare surfaces are rare on a coral reef; however, these can occur following a catastrophic disturbance, or an event damaging or killing an individual or colony. Using plates allowed not only for tracking rates of coral recruitment but also for the opportunity to track succession of colonizing organisms. Plates also homogenized topographic variance at the millimeter scale due to the simplified architecture provided by the smooth-fired terra-cotta and the 1 cm spacer separating the plate from the reef. Since we could not standardize the topography of the substratum, we placed plates to the greatest extent possible on even, horizontal, dead coral, to reduce the irregularity in the gap between the reef and the plate as well as the variability of the plate orientation. At 10 m depth, studies have shown that spat are most frequently found on the undersides of surfaces (Carleton & Sammarco 1987, Maida et al. 1994). Specifically in Bonaire, Raimondi & Morse (2000) reported that, given the choice, larvae of *Agaricia humilis* settle on underside surfaces.

The damselfish acclimated almost immediately to this new sessile object within their territories, and the changes in territory location were negligible according to high-resolution maps created every 3 mo within the first year.

Manipulating recruitment microhabitats — damselfish territories/cages. In June 2004, 3 mo after the deployment of all the plates, we affixed 6 plates at each site with galvanized fine wire mesh (6.35 mm) cages to mimic the inhibitory effects of algal overgrowth on subcryptic coral recruitment microhabitats. All plate undersides were thus allowed to undergo succession free of the cages for the first 3 mo of the study. The cages, with the wire mesh nearly adhering to the plate itself, were not typical exclusion cage treatments, but rather designed to become fouled with algae (Fig. 1B,C). This treatment was deemed necessary because Bonaire has low abundances of macroalgae (Kramer 2003) compared to most Caribbean reefs that have phase-shifted to macroalgae as a result of the overfishing of grazers (Hughes 1994). Grazers, such as large denuding and scraping (sensu Steneck 1988) herbivorous fish including parrotfish (Scaridae) and surgeonfish (Acanthuridae), are effective at cropping algae on reefs and are still relatively abundant on Bonaire (Bruggemann et al. 1994, Choat et al. 2003). Thus, given our large sample size of plates, we wanted to ensure a subset would become sufficiently algal fouled without potentially confounding effects of damselfish, such as urine or mucous, on coral recruitment.

The study then consisted of settlement plates in 4 treatments. The first treatment, uncaged plates outside of damselfish territories (n = 102; 17 site^{-1}), was the only fully grazed treatment, expected to have the lowest algal biomass and the highest coral recruitment. The other 3 treatments, caged plates outside damselfish territories (n = 18; 3 site^{-1}), uncaged plates inside damselfish territories (n = 102; 17 site^{-1}), and caged plates inside damselfish territories (n = 18; 3 site^{-1}) were all designed to increase algal biomass. These treatments test the hypothesis that anything that increases algal abundance, decreases coral recruitment.

Measuring larval availability. Algal biomass can reduce epibenthic water flow and thus possibly limit larval availability and settlement densities. Considering that flowmeters do not lend themselves to miniaturization to be able to measure flow in the 1 cm gap between the benthos and the plate underside, and that any sort of flow probe would encounter problems with the 'viewing' geometry of the experiment, to integrate flow over time, we used plaster clod cards under plates in all treatments. However, the clod cards were an appreciable fraction of the gap between the benthos and the plate in size, thereby affecting what they are designed to measure. Thus, to most realistically measure flow, we used fluorescene dye to determine flushing rates in the subcryptic microhabitat between the benthos and the underside of the plates. For this, 1 mm^3 of dye was ejected from a syringe through a 1 mm hole drilled through the center of the plates. The duration of time from ejection to when the dye became visible at the plate edge was recorded as the treatment's flushing time.

Quantifying recruitment, substrate selectivity, and early survivorship. The plates were monitored 6 times during a 27 mo deployment period (June 2004, August 2004, November 2004, March 2005, July 2005, and June 2006). Half of the plates from each site, including all caged plates, were analyzed under the microscope each of the 6 times for newly settled corals and their subsequent survival relative to the successional community states that may positively or negatively impact recruitment. The plates censused microscopically were transported in seawater, analyzed while immersed in seawater, and returned to the reef within 6 h. The other half of the plates remained in the water until the July 2005 monitoring period, in order to be able to detect any negative impacts of handling on the regularly sampled plates, none of which were observed. Newly settled corals are coral larvae that have recently attached themselves to the substratum and metamorphosed, defined by Morse et al. (1988) as a developmental event following attachment consisting of the differentiation and calcification of the septal ridges. For the purposes of the present paper, 'recruitment' is used in an operational sense, referring to those newly settled corals (called 'recruits' or 'spat') that have survived metamorphosis and have recognizable skeletons, dead or alive, at the time of the retrieval of the plates.

Each spat on the plate underside was identified to genus, measured, determined to be dead or alive based on the presence or absence of coral tissue and responsive polyps, and mapped for its location on the plate as well as its settlement substrate. The location of *Titanoderma prototypum*, an early successional coralline alga thought to be an inducer of coral settlement (Harrington et al. 2004, Ritson-Williams et al. 2010), was also mapped on the plate underside. *T. prototypum* is also unique in that it is relatively easy to identify early on without destructive sampling (i.e. cross section). The specific locations of spat and *T. pro-*

totypum were recorded for the purposes of tracking survivorship and dispersion patterns over time. All 240 plate tops and undersides were photographed underwater to monitor for succession of fouling species. Percent coverage of encrusting biota on plate undersides (crustose coralline algae, non-coralline algal crusts, articulated algae, macroalgae, turf algae, sponges, bryozoans, and polychaete worm tubes) was determined from these digital pictures. Thus, we recorded and analyzed time series data on recruitment, growth, and mortality in reference to the succession of fouling organisms.

Analyses. ***Effects of damselfish territories on turf algae, juvenile corals, and spat density:*** Since abundance data for turf algae, juvenile corals, and spat were taken from 6 sites, for each of the 3 variables (turf algal index, juvenile coral density, and spat density), we used linear mixed effects models to examine site and treatment effects. In these tests, treatment (outside damselfish territory or inside damselfish territory) was the fixed factor and site was the random factor.

Effects of all non-fully grazed treatments on spat density and survivorship: Spat densities were generally low, and we anticipated the need to pool data in order to have sufficient power to test certain effects of the study, particularly that damselfish and cage treatments should be similar but differ from the uncaged treatment outside of a damselfish territory. In principle, we could have pooled data across the 6 sites or across the 3 cage and damselfish treatments that were expected to deliver a similar response. However, given that uneven spatial patterns of larval supply could occur among sites, we focused on the latter. To test whether pooling data from the 3 treatments was justified, we first calculated the mean recruit density per site and treatment. For each of the 6 sites, we then determined which of the 3 treatments had the highest observed spat density (note that this excluded the fourth treatment, uncaged outside damselfish territories, because this was expected to differ from the other 3 treatments). We found that each of the 3 treatments had the greatest recruit density at 2 of the 6 sites. Thus, the probability that all 3 treatments had equal likelihood of having the greatest recruit density across 6 independent sites, which would justify pooling the data from these treatments, is 0.98, providing strong justification for pooling the treatments. This gave us 2 new treatments, 'non-fully grazed' (involving damselfishes and/or cages) and 'fully grazed'. We used these pooled data for 2 of our analyses. First, to test for a significant effect of algal fouling on spat number in 2005, we ran a mixed effects general linear model (Pinheiro & Bates 2000), explicitly specifying site as a random effect, fouling ('non-fully grazed or 'fully grazed') as a fixed effect, and using quasi-Poisson errors. Second, we pooled the non-fully grazed treatments to examine survivorship of the August 2004 cohort because of low recruit numbers.

Multivariate analysis: Changes in the substrate composition of the undersides of the tiles were examined using non-metric multidimensional scaling ordination (MDS). Data were double square-root transformed to allow minor components of the community to influence the analysis. The relative importance of immersion time (2004 or 2005) and treatment on community composition was evaluated using 2-way ANOSIM based on the Bray-Curtis similarity coefficient with double square-root-transformed data (Clarke 1993).

RESULTS

Small-scale abundance patterns in turf algae, juvenile corals, and spat density

The calculated turf algal index surrounding the settlement plates was significantly greater (Fig. 2A; positive coefficient for 'inside damselfish territories' at 148.49, $p < 0.0001$, with reference level 'outside damselfish territories'), and juvenile coral density on natural substrate was significantly lower inside damselfish territories than outside damselfish territories (Fig. 2C; negative coefficient for 'inside damselfish territories' at –0.53, $p < 0.01$). Turf algae comprised most of the algal biomass since macroalgae were rare or absent at all study sites (Kramer & Bishof 2003). Turf algal canopy heights were also significantly greater (unpaired *t*-test 2-tailed $p < 0.0001$) on the upper surfaces of the plates inside damselfish territories (mean ± SE: 4.14 ± 0.16 mm) versus outside damselfish territories (2.14 ± 0.12 mm). Cumulative newly settled coral spat densities on the undersides of the settlement tiles were also significantly lower inside damselfish territories (Fig. 2E; rank-transformed spat density data, negative coefficient for 'inside damselfish territories' at –13.35, $p < 0.01$, with reference level 'outside damselfish territories'). Linear mixed effects models revealed for the 3 variables (turf algal index, juvenile coral density, and spat density) that site level differences did not mask the treatment patterns. Fig. 2B, D and F emphasize the variability among sites, but still show treatment effects.

Population densities of newly settled corals on plates corresponded with population densities of juvenile coral (≤40 mm) growing on natural reef substrata (Fig. 2C,E). Most spat were of the genera *Agaricia* (88.8%) and *Porites* (8.3%), with the remaining 2.9% unidentifiable. At this early stage, spat are only visibly discernible with a dissecting microscope to the family

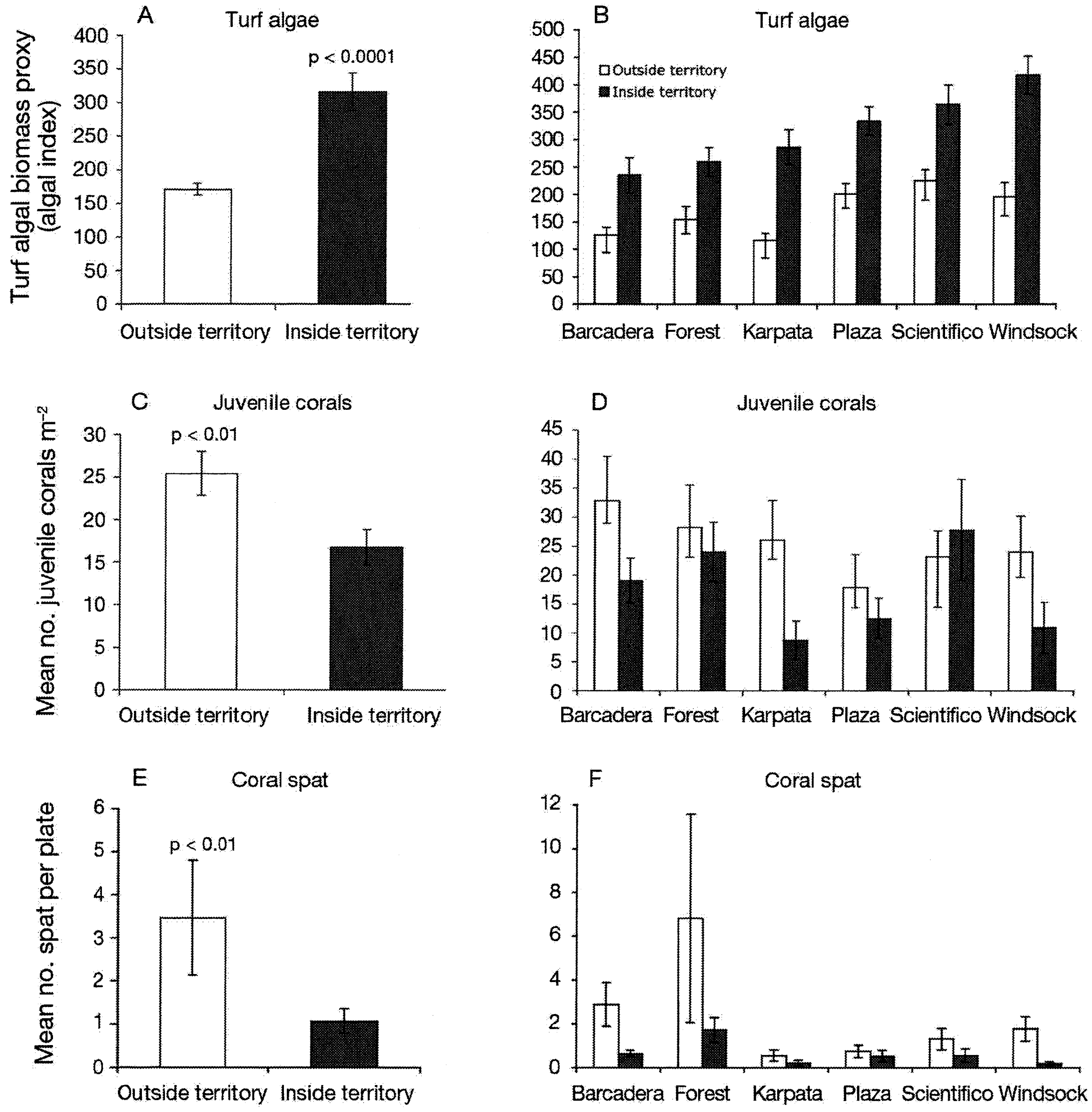

Fig. 2. Turf algal biomass proxy, juvenile coral densities, and spat densities on settlement plates outside and inside of damselfish (*Stegastes planifrons*, three-spot; *S. diencaeaus*, longfin) territories. Turf algal abundance surrounding the settlement plates ('algal index') is a dimensionless proxy for turf algal biomass. (A, B) Mean turf algal index (A) outside and inside damselfish territories (n = 109 for outside territory, n = 127 for inside territories, including 74 three-spot territories and 53 longfin territories) and (B) outside and inside territories across the 6 sites. (C, D) Mean population density of juvenile corals (C) outside and inside damselfish territories and (D) outside and inside territories across the 6 sites. (E, F) Mean number of spat per terra-cotta plate (underside surface only) (E) outside and inside damselfish territories after 809 d, pooled across sites, and (F) outside and inside territories across the 6 sites. Note that damselfish and other fish were unable to access these spat located on the underside of the plate, elevated 1 cm from the reef substrate. Error bars are ±1 SE

or genus level (Hughes et al. 1999, Baird & Hughes 2000). Based on juvenile abundance in the area, the species were probably *Agaricia humilis*, *A. agaricites*, and *Porites astreoides*, all of which are simultaneous hermaphroditic brooders, with brooding seasons ranging from year round for *A. humilis*, spring and summer for *A. agaricites* (Van Moorsel 1983), and January to September for *P. astreoides* (Szmant 1986).

To determine if there was a negative effect from removing plates for microscopy, we left a subset of the plates (60 uncaged plates outside damselfish *Stegastes* spp. territories and 60 uncaged plates inside damselfish territories) untouched until July 2005. Rates of recruitment were greater than or equal to those recorded on plates left untouched for the first 16 mo of the study. This indicates there were no negative effects due to periodic handling and observation of the plates. Of the 303 spat recorded on 240 plates, 230, or 76%, of them were found on the 120 plates that were regularly collected and examined microscopically. This high percentage included the 36 plates surrounded with wire mesh, on which there were 38 settlers. Of the 303 total spat recorded, 83% settled within 1.5 cm of the outer edge of the plate's underside. This 'subcryptic settlement microhabitat' (see Fig. 1A) cannot be accessed by grazers but is close to fully illuminated regions at that depth.

Recruitment microhabitat manipulations—damselfish and cage effects

Cages surrounding the coral settlement plates, like damselfish territories, were expected to increase algal biomass around the plates. The cages were deployed inside and outside damselfish territories in June 2004, and became noticeably algal-fouled by August 2004. By July 2005, rates of recruitment were highest on uncaged plates outside of damselfish territories compared to all other treatments (Fig. 3A). The 3 non-fully grazed treatments were pooled because after calculating the mean recruit density per site per treatment these 3 treatments were found to systematically lead to the same result. Once pooled into 'fully grazed' and 'non-fully grazed', we used a generalized linear mixed effects model with quasi-Poisson errors. Here, we allowed for site effects by specifying site as a random effect. Site was found to have no significant influence and treatment effect ('fully grazed' vs. 'non-fully grazed') had a significant impact on recruit density. The coefficient for grazing was positive (1.07), and, therefore, shifting from the 'non-fully grazed' treatment to 'fully grazed' led to an increase in recruitment. The *t*-value was 3.12, which was highly significant ($p < 0.01$).

Larval availability

The increase in algal biomass surrounding the plate (i.e. not on the plate underside) reduced the rates of water flushing (Fig. 3B) in all subcryptic settlement microhabitats. The dispersal rates of dye from the gap between the plate and the reef were significantly slower among caged plates inside and outside of damselfish territories than among uncaged plates outside of damselfish territories (Tukey's honest significance multiple comparison test). Dye retention was also greater in uncaged plates inside damselfish territories than it was in uncaged plates outside of damselfish territories (Fig. 3B).

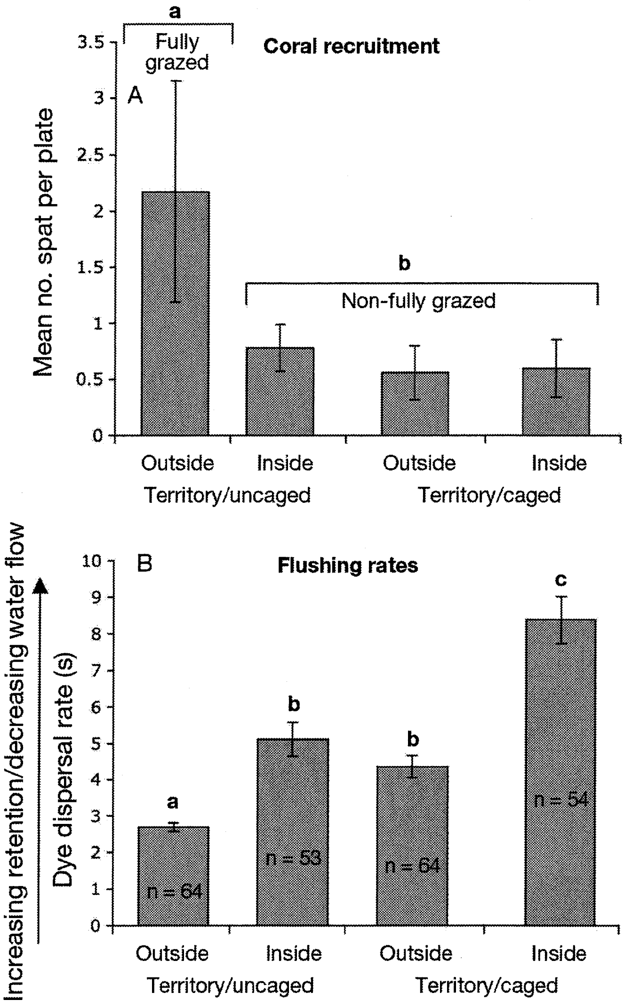

Fig. 3. Coral recruitment in the 4 treatments with corresponding flushing rates. (A) Coral spat densities on caged and uncaged plates inside and outside of damselfish *Stegastes* spp. territories from August 2004 through July 2005. Different letters above bars mean significant differences in mean number of recruits. (B) Dispersal rates of fluorescene dye from the plate underside for simulated treatments. Different letters above bars mean significant differences in dye dispersal rates. Error bars are ±1 SE

Substrate selectivity

Coral spat preferentially recruited to specific substrates and avoided others relative to their abundance (Fig. 4A). Over half of all spat in the outer 1.5 cm perimeter of the plate undersides recruited to crustose coralline algae (CCA), with 33.8% on *Titanoderma prototypum* and 21.8% on all other species of CCA (Fig. 4A). Whereas spat recruiting in proportion to substrate abundance showed no selectivity, those recruiting to specific substrates at proportionately higher frequency than their abundance preferred the substrate and/or early post-settlement mortality on it was low. In either case, the substrate facilitated the process of recruitment. *T. prototypum* and other CCA were thus recruitment 'facilitators' based on this analysis (Fig. 4A). This was irrespective of coral species, since spat settling on *T. prototypum* were 94.6% *Agaricia* spp. and the overall makeup of spat on all substrates was 88.8% *Agaricia* spp. Conversely, turf algae and encrusting invertebrates had few or no recruits relative to their abundance and were thus recruitment 'inhibitors'. Recruitment on polychaete worm tubes could be desirable due to their micro-spatial heterogeneity, since many marine invertebrate larvae prefer to settle on irregular biogenic substrata (Knight-Jones 1951, Carleton & Sammarco 1987). Once a biofilm developed on terra-cotta plates, the otherwise bare substrate also became suitable for settling corals.

Substrate-specific coral recruitment densities in subcryptic settlement habitats were greatest on polychaete worm tubes, followed by *Titanoderma prototypum* and other species of CCA. Spat densities were lowest or absent from invertebrate crusts, turf, and macroalgae (Fig. 4B). While polychaete tubes had high spat density, they were relatively unimportant for settling corals because they comprised such little surface area (Fig. 4A). Thus, coral spat recruited preferentially to early successional species. Coralline algal species are thin and recruit early (Adey & Vassar 1975) to the underside of the settlement plates. We observed *T. prototypum* rapidly recruit and reach peak abundance (12% cover of the entire plate underside) within 5 mo of the deployment of settlement plates. Other CCA reached peak abundance within 8 mo. In contrast, encrusting invertebrates (i.e. tunicates and sponges) and turf algae increased steadily over the 2 yr of the study, reaching 70% cover by the end of 2 yr. As these recruitment inhibitors increased, the recruitment facilitators declined to less than half their maximum abundance due to competitive overgrowth. Thus, the 'window' for successful coral recruitment was short-lived, as succession in subcryptic microhabitats became increasingly hostile to settling corals.

To test for reductions in recruitment within this 'window' due to reduced larval availability resulting from cages and/or algal fouling, we compared the annual density of spat on coralline (facilitator) substrates in each of the 4 treatments before and after algal fouling

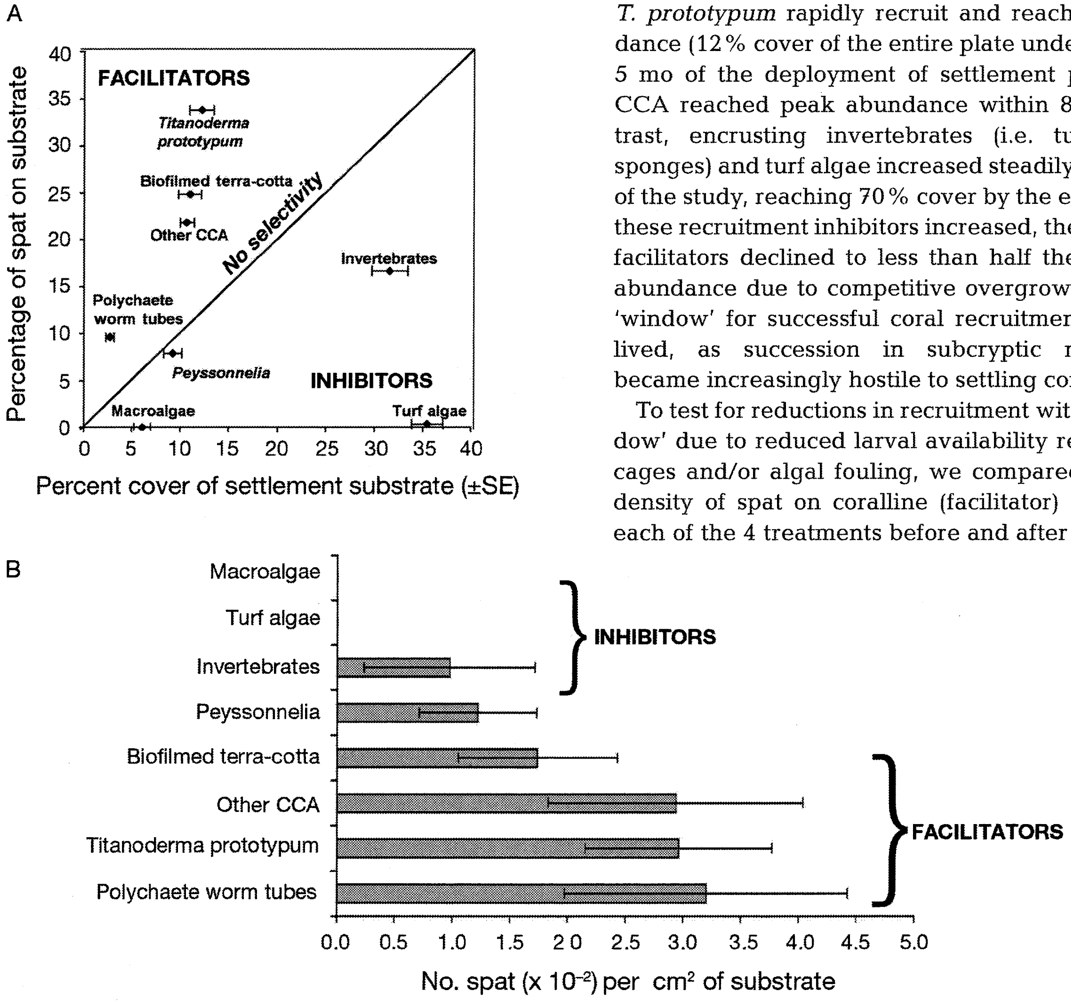

Fig. 4. Spat selectivity and density by substrate. (A) Selectivity of recruits shown by the percent cover of settlement substrates growing on the 1.5 cm perimeter of plate undersides, with corresponding recruitment and a diagonal line of no selectivity. Selectivity data were based on 251 newly settled spat in the subcryptic settlement microhabitat. Separate analyses were done for each substrate, including only the subset of plates on which the substrate was present. The *y*-axis represents the number of spat on each substrate as a percentage of the total number of recruits on that subset of plates. The percent cover of fouling organisms on the plate underside was recorded at the time of first observation of the newly settled spat. (B) Spat densities (spat per cm^2 of substrate) on the outside 1.5 cm perimeter of the undersides of uncaged settlement plates. Error bars are ±1 SE

of cages in 2004 and 2005, respectively. Minimal algal-fouling was evident 2 mo following the June 2004 cage installation. However, cages were fully turf-fouled by November 2004, resulting in a decline in coral recruitment similar to what we had recorded inside of damselfish territories. Assuming all competent larvae encountering a facilitating substrate would settle on or near it, the difference in rates of recruitment on crustose coralline algae indicates differences in larval availability (Fig. 5A). By the summer of 2005, only fully grazed treatments (uncaged settlement plates outside of damselfish territories) had increased recruitment rates on these facilitators (*t*-test, $p = 0.035$). Recruitment on plates inside territories remained low or declined slightly, and recruitment outside of territories (initially well-grazed) that were caged in June 2004 declined significantly ($p = 0.048$).

To determine whether the treatment was influencing the community composition of the plate undersides, we compared the relative effects of treatment type and year on the substrate cover of the plates using 2-way ANOSIM. We found that year had a moderate influence ($R = 0.23$, $p < 0.001$), whereas treatment had a very weak influence ($R = 0.098$, $p < 0.001$) (Fig. 5B, year not shown). Similarity percentage (SIMPER) analysis (Clarke 1993) revealed that the abundance of *Titanoderma prototypum* was the strongest discriminating factor between the community structure of high- and low-grazing treatments (e.g. *T. prototypum* was ranked first for discrimination between the community structure of caged plates inside damselfish territories and uncaged plates outside territories, accounting for 18% of the mean dissimilarity in community structure between groups). Further, the fully grazed treatment was found to have a significantly greater cover of *T. prototypum* on the plate undersides (Fig. 5C, mixed effects linear model of arcsine-transformed cover using site, plate, and sampling time as random effects and treatment as a fixed effect gave a positive coefficient for uncaged/outside territory at 4.89, $p < 0.0001$, with the reference level caged/outside territory).

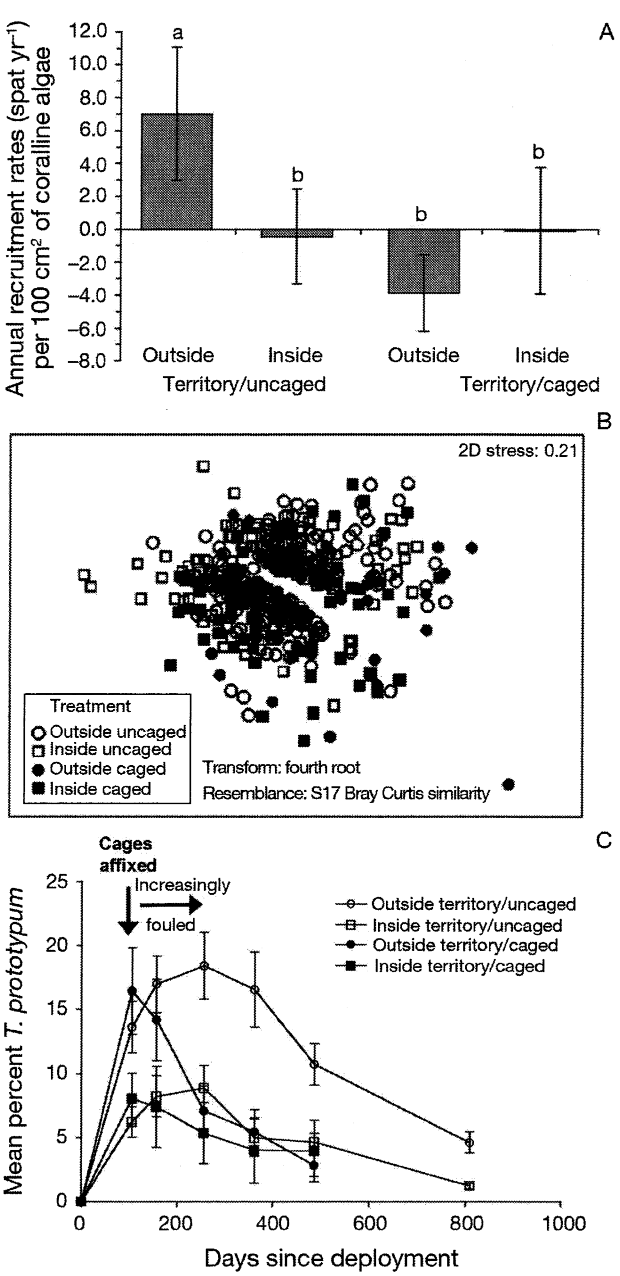

Fig. 5. Changes in rates of coral recruitment on crustose coralline algae, and a comparison of community composition resulting from elevated turf algal abundance surrounding but not on the settlement microhabitats (inside damselfish *Stegastes* spp. territories and inside algal fouled cages, but not on undersides of plates). (A) Deviation from initial annual recruitment (2004, prior to algal colonization of cages) for the treatment 'outside territory/uncaged' was significantly greater than for all other treatments (no overlap of 95% CI). (B) Effect of treatment type on the community composition of the plate undersides. (C) *Titanoderma prototypum* made up the greatest amount of difference in community composition. *T. prototypum* percent cover in the outside 1.5 cm perimeter of plate undersides. Data from caged plates were not included beyond July 2005, when the cages were no longer all fully intact. All error bars are ±1 SE

Early survivorship

Average cohort survivorship was 18% after 365 d, and, despite slightly different trajectories, mortality converged to a value >90% for those cohorts by the end of 2 yr (Fig. 6A). A closer look at post-settlement survival of the August 2004 cohort (the cohort with observations closest to a 12 mo time frame) revealed that only recruits in the fully grazed treatment (uncaged plates outside of a damselfish territories) had significantly greater survivorship (Fig. 6B). Again, we

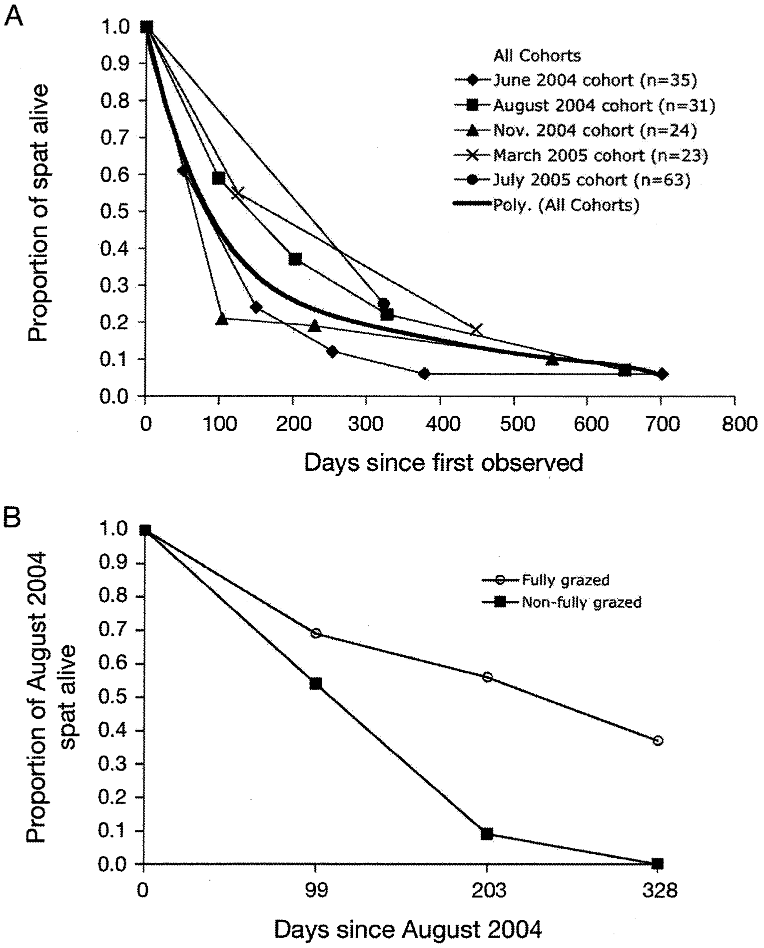

Fig. 6. Proportion of spat alive by cohort and treatment. (A) Survivorship curves for each cohort (including all treatments) from each subsequent monitoring period. A fifth-order polynomial (poly.) trendline curve fits all cohorts (in bold), highlighting an average survivorship of 18% after 365 d and overall mortality converging to >90% by the end of the study. (B) Proportion of August 2004 cohort (n = 27) surviving during the first year of life

pooled the non-fully grazed treatments because of low sample size (only 31 total spat were in this cohort, with 27 found alive—16 on the outside/uncaged treatment, 4 on the inside/uncaged treatment, 4 on the outside/caged, and 3 on the inside/caged treatment). This cohort consisted of 87.0% *Agaricia* spp., 6.5% *Porites* sp., and 6.5% unidentified species. To investigate the effects of treatment on survivorship, we used the nonparametric Cox proportional hazards. The fit of the Cox model showed a significant difference in survivorship between the fully grazed treatment and the non-fully grazed treatment ($p = 0.016$).

Of the spat that recruited from March 2004 through June 2006, very few survived to large size, but the highest percentage of the survivors were found under fully grazed conditions. The mean (±SE) yearly growth rate of surviving *Agaricia* spp. spat monitored over the course of the study period was 3.46 ± 0.47 mm. In fully grazed conditions (uncaged plates outside of territories), 51.2% of the spat observed survived past 3.5 mm in diameter. Pooling the other 3 higher algal biomass treatments, only 32.3% of spat survived beyond 3.5 mm. Considering only the surviving *Agaricia* spp. spat from the August 2004 cohort (n = 25), those in the fully grazed treatment (n = 13) had greater survivorship over time, with >50% surviving over 200 d. Pooling the 3 other treatments (n = 12) resulted in only 1 spat surviving beyond 200 d and 0 spat surviving until the final monitoring in June 2006.

DISCUSSION

Our study suggests that elevated turf algal abundance within centimeters of possible settlement habitats decreases the recruitment potential of reefs by impeding larval access to those habitats, steering succession away from facilitator substrates, and increasing post-settlement mortality. Specifically, we suggest that 3 sequential steps—(1) the availability of competent larvae, (2) their propensity to settle, and (3) available nursery habitats (i.e. microhabitats where post-settlement mortality is low)—represent a 'gauntlet' through which coral must pass to recruit (Fig. 7). Chronic failure at any step creates a demographic bottleneck. We found that the highest proportion of surviving coral spat to successfully run the gauntlet occurred under conditions of relatively low turf algal biomass.

The species composition of coral settling on our experimental plates roughly matched those naturally recruiting to the reef. For example, *Agaricia* spp. comprised >88%, and *Porites astreoides* was the second most abundant settler in our study comprising 8.3% of all spat. Similar proportions were observed among juvenile corals recruiting to natural substrates on the shallow reefs of Bonaire. Thirty years earlier in nearby Curacao, Bak & Engel (1979) also reported densities of *Agaricia* spp. and *P. astreoides* to be 80 and 7.6%, respectively.

Advection of coral larvae to subcryptic settlement microhabitats is the first step in coral settlement and ultimately recruitment to the benthos. Estimating coral larval availability is difficult because larval set-

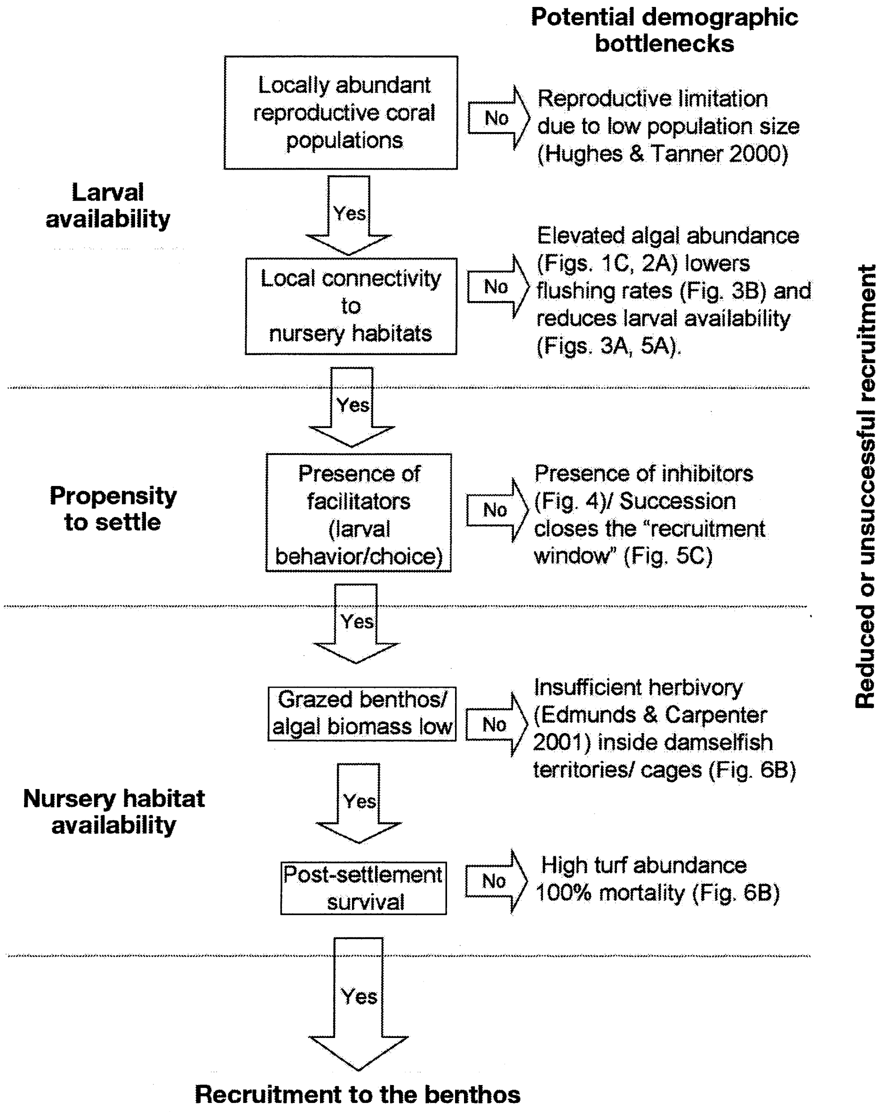

Fig. 7. Conceptual model of sequential processes leading to coral recruitment to the benthos (i.e. 'the gauntlet'). Arrows to the right represent possible recruitment limitation due to demographically significant bottlenecks. Arrows down indicate a coral larva's successful progression through the sequential steps to recruitment

tlement traps do not work for corals. Thus, we used the density of coral spat on settlement-facilitating substrates (i.e. crustose coralline algae) to estimate larval availability among treatments (Fig. 5A). We reasoned that at this microhabitat scale, spat will readily settle on inducing substrata when present (Raimondi & Morse 2000, Harrington et al. 2004), so the spat densities on these substrates should reflect the abundance of competent larvae. Over the first 158 d of the experiment, the recruitment density on coralline substrates did not vary among treatments. However, over the next year, as cages became increasingly fouled by turf algae, only the fully grazed uncaged plates had elevated rates of settlement (Fig. 5A). These results, together with significantly higher rates of flushing (Fig. 3B), suggest more larvae were available to settle under the fully grazed treatment. Furthermore, in terms of algal abundance, we demonstrated that the treatments only influenced the upper surfaces of the plates rather than the turf algal abundance on the undersides of the plates (Fig. 5B), ruling out the possibility that the decline in recruitment was due to anoxic conditions associated with the non-fully grazed treatments. Thus, fouled cages, damselfish *Stegastes* spp. gardens (Ceccarelli et al. 2001), or macroalgal-dominated reefs may reduce coral recruitment by starving subcryptic nursery habitats of larvae.

The behavior of coral larvae regulates their propensity to settle (Ritson-Williams et al.2009, 2010). Settlement requires that pelagic larvae undergo a sequence of behavioral changes that brings them to specific depths, seeking specific light intensities that get them to or close to subcryptic settlement habitats in relatively shallow zones of the reef (Bak & Engel 1979, Raimondi & Morse 2000). Once coral larvae contact the benthos, chemical cues from organisms such as encrusting coralline algae trigger their metamorphosis and settlement (Morse et al. 1988, Heyward & Negri 1999). Preferential settlement varies among coral taxa and regions. Several coral species were induced to metamorphose and settle on a variety of encrusting and articulated calcareous algae (Heyward & Negri 1999). Subsequent studies found several coral taxa strongly prefer to settle on the coralline alga *Titanoderma prototypum* (Harrington et al. 2004) on which coral spat survival is also higher. To date, the strongest species-specific coral settlement responses in the Caribbean are reported for the coralline alga *Hydrolithon boergesenii*, which induced settlement of the corals *Agaricia humilis* (Morse et al. 1988), *Acropora cervicornis*, and *Acropora palmata* (Ritson-Williams et al. 2010), as well as the CCA *T. prototypum*, which also induced settlement of *A. cervicornis* and *A. palmata*. Ritson-Williams et al. (2010) also reported that, in the field, post-settlement survival of *A. palmata* was facilitated by *H. boergesenii* and *T. prototypum*, whereas *A. cervicornis* survived only on *T. prototypum*. We found that 2 species of Caribbean coral, *Porites* spp. and *Agaricia* spp., settle preferentially on *T. prototypum* despite its low abundance (Fig. 3A). *T. prototypum* was found in greatest abundance on plate undersides in fully grazed treatments. However, unlike the strong facilitation of the Indo-Pacific *T. prototypum*, the Caribbean *T. prototypum* was only a slightly better settlement substrate than all other subcryptic corallines (Fig. 3). Although the Indo-Pacific and Caribbean *T. prototypum* are indistinguishable anatomically and morphologically, it is very possible they are sibling or convergent species (e.g. Steneck 1986) and may differ biochemically.

The effectiveness of 'nursery habitats' for settling corals relates to the habitat's architecture and its colonizing organisms. Shallow water corals usually settle in small crevices close to outer exposed reef habitats (Carleton & Sammarco 1987, Maida et al. 1994, Raimondi & Morse 2000). The proximate explanation for this pattern is light-seeking behaviors (Maida et al. 1994), but the ultimate explanation is likely that intense ecological pressures such as parrotfish grazing and overgrowth competition (Vermeij 2005) make outer exposed surfaces in shallow reefs hostile to microscopic settling corals. Thus, there are survivorship advantages to finding subcryptic habitats from which little growth brings them to full light and subsequent rapid growth. We used terra-cotta plates to create small subcryptic microhabitats and to simplify the geometry of habitat architecture. This standardized method is used internationally (Mundy 2000). The smooth featureless settlement plate surface lacks the micro-spatial heterogeneity found on coral substrates soon after they die. Commonly, the micro-spatial heterogeneity created by the corallites of reef corals facilitates turf colonization, since their rhizoids easily attach to such spaces. Usually, grazing by excavating herbivores (Steneck 1988) and colonization by coralline algae effectively smoothes dead coral surfaces. Terra-cotta tiles effectively shorten the succession time to dominance by coralline crusts (Adey & Vassar 1975).

Succession changes the receptivity of subcryptic habitats to coral recruitment. During the course of our experiment, the underside perimeter of plates became increasingly fouled with turf algae and heterotrophic species inimical to settlement and survival, such as invertebrate crusts. Recruitment facilitators, *Titanoderma prototypum* and other CCA species increased in abundance rapidly within the first half a year, but, by Day 257, their abundances peaked and then steadily declined through the duration of the study. Since thinner crusts are easily overgrown by thicker crusts (Steneck et al. 1991), the extremely thin (40 µm thick) thallus of *T. prototypum* will be readily overgrown. In an intensely competitive environment like the underside of a branched or platy coral (or settlement plate), the growth of one organism comes at the expense of another (Jackson & Hughes 1985). The net effect in subcryptic habitats is a gradual increase of recruitment inhibitors such as turf algae and the even more detrimental invertebrate crusts. Invertebrate crusts were absent at the start of the experiment, but they steadily increased over the duration of the experiment and accounted for approximately 50% of the substrate by the last monitoring period. The regular handling of 120 of the plates during the first 16 mo of the experiment may have caused desiccation of the sponges on the underside of the plates, explaining the higher rates of settlement on the subset of plates left untouched for the first 16 mo of the experiment. It is possible that, immediately following a disturbance that bares primary substrate, a 'recruitment window' opens as early succession-facilitating species such as *T. prototypum* (see Adey & Vassar 1975, then called *Tenarea prototypum*) become established, before being overgrown by recruitment inhibitors. While this window is open, coral spat are more likely to successfully 'run the gauntlet' to recruitment.

As with most marine organisms, post-settlement mortality is greatest during the first year when, on average, 80% of all coral spat died (Fig. 5A). In Year 2, only an additional 10% of the spat died. However, in following 1 cohort (August 2004), during our caging experiment, only coral spat from fully grazed treatments survived the first year (Fig. 5B). In fact, over the entire study, the greatest proportion of agaricid spat to reach the largest size classes were in the fully grazed treatments.

Spat survival is not merely a function of the attributes of the settlement substrate, but of their ability to resist overgrowth by algae and encrusting invertebrates (Richmond 1997). As recruits grow, their mortality rates usually decline and they are less likely to be overgrown by competitors (Hughes & Jackson 1985). However, the slow growth rates of newly settled corals keep them at risk of losing this battle. A critical but largely unstudied dynamic may be how, as surrounding algal biomass increases, subcryptic habitat colonizers shift from slow growing, recruitment facilitating autotrophs (e.g. *Titanoderma prototypum*) to faster growing, recruitment inhibiting heterotrophs (e.g. encrusting invertebrates). During the timescale of the present study, the community structure of the plate undersides actually varied little between treatments (Fig. 5B), with the percent cover of the facilitator *T. prototypum* (Fig. 5C) making up the majority of the difference. It is possible that a macroalgal-dominated reef, more typical of other Caribbean reefs, would have led to a more rapid decline of facilitator species and rise of heterotrophs, thereby decreasing settlement and survivorship.

As the decline of Caribbean reefs continues (Gardner et al. 2003), so too does the dichotomy in thinking as to why they fail to recover. Is the lack of recovery due to the loss of reproductive populations and the resulting decreased larval pool (Hughes & Tanner 2000), or is it more the result of local declines in the recruitment potential of the benthos (Hughes & Tanner 2000, Bellwood et al. 2004)?

Our study suggests that local herbivory-induced low algal biomass increases the receptivity of the reef and may be critical for recruiting corals and the recovery of the reef ecosystem. In Jamaica live coral cover was remarkably low following the mass mortality of the herbivorous sea urchin *Diadema antillarum* (e.g. Hughes 1994); as this urchin increased in abundance, so too did juvenile corals (Edmunds & Carpenter 2001) and eventually adult corals (Idjadi et al. 2006).

We suggest that herbivory, or whatever controls algal abundance, has a strong effect on coral recruitment. Thus, that which effects herbivory, even at local scales measured in centimeters, explains a considerable portion of the variance associated with coral recruitment. The management implications of this are obvious. First, managing for low algal biomass is both a laudable and attainable goal. Herbivory from abundant, deep-grazing sea urchins and/or parrotfishes may be necessary for reef recovery due to the positive indirect effects they have on the recruitment potential of reefs. Second, if large predators control damselfish abundance (Hixon & Beets 1993) and damselfish reduce local herbivory (Ceccarelli et al. 2001), then predator abundance may also indirectly control herbivory and thus the recruitment potential of the reef.

Finally, we suggest that a sequence of local processes control coral recruitment at small spatial scales. This, together with studies finding limited larval dispersal among corals (Sammarco & Andrews 1988, Hughes et al. 1999), suggests we should not rely on 'recruitment effects' or large-scale, supply-side spillover from healthier upstream reefs, but focus management efforts locally (Steneck 2006). While massive coral die-offs often result from pulse events operating at landscape scales, recovery is usually highly variable and spatially limited (Idjadi et al. 2006, Golbuu et al. 2007). Thus, the recovery of coral reef ecosystems depends on the few survivors that successfully run the gauntlet to recruitment through the sequence of local multiscale processes.

Acknowledgements. This research was only possible due to the support received on Bonaire, particularly by the Bonaire National Marine Park (STINAPA). Specifically, support was received from Elsmarie Beukenboom, Ramon de Leon, Fernando Simal, Din Domacasse, Kalli de Mayer and all the STINAPA rangers, staff, and volunteers who contributed their time and helped with logistics. Jeanne Brown, Curt Brown, Susan Porter, and Thew Suskiewicz helped us in the field. Early drafts of the manuscript were critiqued by Susan Brawley and Dan Brumbaugh. Funding was from the Pew Fellows for Marine Conservation, the Kendall Foundation, the Connectivity Working Group of the Global Environmental Fund Research and Capacity Building Project, National Fish and Wildlife Foundation, NERC, and STINAPA Bonaire. To all we are grateful.

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Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA

Submitted: March 17, 2010; Accepted: July 4, 2010
Proofs received from author(s): August 27, 2010

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Proc. R. Soc. B 2014 **281**, 20131835, published 20 November 2013

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Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects

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Research

Cite this article: Edwards CB *et al.* 2014 Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B* **281**: 20131835.
http://dx.doi.org/10.1098/rspb.2013.1835

Received: 23 July 2013
Accepted: 4 October 2013

Subject Areas:
ecology, systems biology, environmental science

Keywords:
fishing, reef-fish, phase shift, resilience, herbivory, macroalgae and turf algae

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On coral reefs, herbivorous fishes consume benthic primary producers and regulate competition between fleshy algae and reef-building corals. Many of these species are also important fishery targets, yet little is known about their global status. Using a large-scale synthesis of peer-reviewed and unpublished data, we examine variability in abundance and biomass of herbivorous reef fishes and explore evidence for fishing impacts globally and within regions. We show that biomass is more than twice as high in locations not accessible to fisheries relative to fisheries-accessible locations. Although there are large biogeographic differences in total biomass, the effects of fishing are consistent in nearly all regions. We also show that exposure to fishing alters the structure of the herbivore community by disproportionately reducing biomass of large-bodied functional groups (scraper/excavators, browsers, grazer/detritivores), while increasing biomass and abundance of territorial algal-farming damselfishes (Pomacentridae). The browser functional group that consumes macroalgae and can help to prevent coral–macroalgal phase shifts appears to be most susceptible to fishing. This fishing down the herbivore guild probably alters the effectiveness of these fishes in regulating algal abundance on reefs. Finally, data from remote and unfished locations provide important baselines for setting management and conservation targets for this important group of fishes.

1. Introduction

Understanding the causes and consequences of phase shifts from coral to algal dominance on tropical reefs has been a central theme in reef research for several decades [1–3]. Coral reef degradation generally results in a reduction in or loss of key ecosystem services including fisheries productivity, coastal protection and economic revenue associated with tourism. Primary drivers of system-wide shifts include anthropogenic disturbances occurring on both global and local scales [1,4,5]. Globally, anthropogenic carbon emissions have led to ocean warming and acidification that can profoundly reduce the growth and fitness of stony corals and other calcifiers [6]. Locally, and at the scale most relevant to resource managers, overfishing of herbivores, disease and declines in water quality can alter benthic competitive dynamics to favour fleshy algae over corals and other reef-building organisms [3,7–11]. However, we still lack comprehensive and necessary first-order knowledge of the magnitude and patterning of individual

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2013.1835 or via http://rspb.royalsocietypublishing.org.

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disturbances around the tropics. Here, we conduct a global synthesis of the status of coral reef herbivorous fish populations, and investigate the potential impacts of fishing on the abundance, biomass and community composition of these fishes.

As consumers of benthic algae, coral reef herbivores directly affect the structure and composition of benthic communities. Numerous experimental studies have shown that herbivore exclusion quickly and consistently leads to dominance by fleshy turf or macroalgae across many marine ecosystems [10]. Similarly, observational studies in the Caribbean and the Pacific have found negative correlations between herbivorous fish biomass and macroalgal cover, suggesting that herbivores can exert top-down control on macroalgal abundance [12,13], but the magnitude of these effects may vary by system [14]. Other studies have shown that coral recruitment and the abundance of crustose coralline algae (CCA) are positively associated with grazing intensity [15] or the presence of grazers [7,8], suggesting that herbivores directly facilitate reef-building taxa. Further, some herbivores may regulate coral–algal competition by consuming seaweeds that produce allelopathic chemicals that cause coral mortality [16]. But because not all herbivores consume the same types of algae, at the same rates or in the same way, functional diversity within the guild should be considered and has been shown to increase resilience following bleaching events [17] and crown-of-thorns (*Acanthaster planci*) outbreaks [18]. Although herbivorous fishes are clearly important for regulating reef community structure and function, critical information is lacking about the status of this group of fishes globally.

Accurately characterizing the distribution and ecological roles of herbivorous fishes at broad spatial scales is challenging due to species-specific variability in feeding mode and biogeographic limits on species ranges [19]. Pooling species into higher taxonomic groups, such as major families or subfamilies, is a common solution. However, because feeding behaviour can vary among species, even within families, examining how individual species feed may be more informative. Distinct herbivore feeding sub-guilds have been identified that are largely decoupled from taxonomy and instead defined by the feeding mechanism and behaviour of a given species [20,21]. However, dietary flexibility within some species is expected and precise functional designations of all species can be difficult without context-specific data [16,21–23]. Despite these limitations, functional group designations are useful for describing community-level feeding patterns, allow for broad biogeographic comparisons and provide an important characterization of how the herbivore guild as a whole may influence the reef benthos [23,24].

Coral reef fish assemblage structure has been examined over large spatial scales and across gradients of human population density (as a proxy for fishing intensity), latitude and across reserve boundaries [25–28]. These large-scale studies show clear declines in fish biomass and more equivocal patterns in numerical abundance with fishing pressure (although see [29]). Discrepancies between these biomass and abundance metrics probably arise from the fact that fishing disproportionately removes larger-bodied species and individuals, leaving many smaller individuals in heavily fished locations (high abundance, low biomass [25,30,31]). Several regional studies have shown negative effects of human populations on higher trophic-level reef fishes or fish assemblages as a whole, but much less is known about the impacts on the abundance, biomass or composition of herbivorous fishes. Recently, Bellwood *et al.* [11] documented strong evidence of fishing effects on functional roles of parrotfishes (Scaridae) in the Pacific and Indian Oceans (e.g. corallivory, bioerosion), suggesting that fishing can systematically affect at least some functional characteristics of the herbivore community.

To more accurately characterize the role of herbivores in structuring coral reef benthic environments, comprehensive baseline knowledge of the abundance, biomass and composition of herbivorous fish assemblages across the tropics is needed. Further, before effective conservation strategies can be designed, there is a need to determine the direction and magnitude of the effects of fishing on this important group of coral reef fishes. Here, using a broad geographical approach, we collate and synthesize data from peer-reviewed publications and from rigorous monitoring programmes to establish comprehensive 'current-condition' levels of herbivorous fishes around the world and to assess the extent to which fishing alters their abundance, biomass and the structure of the assemblage.

2. Material and methods

(a) Database

We used ISI (now Thomson Reuters) Web of Knowledge to identify peer-reviewed studies that reported coral reef herbivorous fish abundance and biomass using the following search strings: coral reef and herb*; graz*; biomass; abundance; density; fish*. We only used studies that included metadata on reef zone/habitat (e.g. fore- versus back-reef), depth, year, description of sampling methods and survey effort (e.g. number of survey stations). We also used original data collected using underwater visual census (UVC) methods from 1989 to 2009. To enhance comparability between areas, only data from fore-reef sites between 5 and 20 m were included as this habitat type is available in most reef areas, it supports a high diversity and abundance of herbivorous reef fishes [32–34] and encompasses a depth range that includes the home ranges of many of the species of interest.

We limited our analyses to data collected using either of two standardized UVC methods—stationary point count (SPC) or belt transect (BLT) [35,36]. Although the relative efficacy of these methods is debated [37], they each sample roughly the same area (150–175 m^2) and several studies have demonstrated that for most mobile non-cryptic mid-sized fishes there is little effect of method on estimates of density [28]. However, in order to ensure comparability between methods here, we conducted analyses explicitly testing the effects of sampling method on herbivore biomass. Given that we found little evidence of differences between methods (see electronic supplementary material, table S1), we pooled data collected using both methods for our regional and global analyses. Owing to the nature of our dataset (spanning across multiple years), we were unable to examine the effects of a variety of physical (exposure, temperature), chemical (nutrient availability) or biological (predator abundance, food availability) factors on herbivore populations and instead focused specifically on the probable effects of fishing on this important group of fishes.

(b) Accessibility by fisheries

All sites were classified as either 'not fisheries accessible' (NFA) or 'fisheries accessible' (FA) based upon human habitation, isolation and level of protection. Sites were classified as NFA if they were located on remote and uninhabited islands where fishing is formally banned or severely limited by remoteness (e.g. *de facto* marine reserves *sensu* Williams *et al.* [28]) or inside protected areas on inhabited islands or coastlines. Because the efficacy of protected areas is a function of compliance, enforcement and reserve age [38,39], we identified sites within protected areas as NFA only if they had been protected from fishing for a minimum of six years, received institutional enforcement and lacked evidence of non-compliance. FA sites were the remainder of locations, which due to accessibility and regulations are likely to experience fishing.

Data varied in level of resolution, especially in terms of sampling design and taxonomic detail. While the majority of studies reported estimates of biomass and abundance (per unit area), approximately 31% of studies only reported abundance. Additionally in some regions only data from NFA locations, or alternatively FA locations, were available. Sample sizes of analyses reflect the availability of data specific to the question addressed (see below).

(c) Statistical analyses

(i) Total herbivore assemblage

Global assessment

The global mean for herbivore biomass and abundance across NFA and FA locations was calculated using all data compiled. The basic sampling unit was the 'site', the position where surveys were conducted. Site estimates were pooled to calculate 'location'-specific means. Locations were defined as continuous continental or bank areas, or islands and atolls; in some cases provinces or groups of many small islands (e.g. the Solomon Islands) were considered a location. To maintain sufficient statistical power, only locations with more than four sites were included in the analysis. Some of the data were reported only at the location level. When multiple estimates were available for a single location (e.g. separate studies or years), we calculated a single mean for that location. When comparing estimates of mean biomass and abundance worldwide, we pooled location estimates to compute global NFA and FA means. A two-sample *t*-test was used to determine whether significant differences existed in the abundance and biomass of herbivorous fishes between all NFA and FA locations.

Regional assessments

Where raw site-level data were available (see electronic supplementary material, table S2), we explored regional differences in herbivore biomass and abundance between NFA and FA locations. Here, regions were designated as a group of locations and usually represented individual archipelagos (e.g. the Hawaiian Islands); in some cases, due to a lack of adequate data, we pooled locations at higher levels based on natural geographical breaks (e.g. the Caribbean basin).

For some regions, data were non-normal, even after transformations, making use of parametric statistics inappropriate. Because comparisons of back-transformed values are often uninterpretable and data were not evenly available across study regions, a non-parametric bootstrapping procedure was used to calculate regional differences between NFA and FA locations. A repeated random resampling of site means with replacement was used to generate new location-level estimates [40]. These bootstrapped estimates of mean biomass and abundance from NFA and FA locations were then used to calculate regional means. By repeating this process 10 000 times, we estimated the distribution of probable differences between the means for NFA and FA locations within regions. We consider differences between NFA and FA means to be statistically significant if the 95% quantile range (QR) of bootstrapped differences does not overlap zero [28].

(ii) Functional groups

Using studies with full species lists and site-level data, we subdivided herbivorous fish assemblages into functional groups based broadly on the studies of Steneck [41] and Green & Bellwood [20] and analysed the effects of fisheries accessibility on each group separately. Four herbivore functional groups were considered: (i) scraper/excavators, (ii) grazer/detritivores, (iii) browsers and (iv) territorial damselfishes (see electronic supplementary material, figure S1; electronic supplementary material, table S3 for designations). Deviations in previous designations were adopted because we were unable to separate the large versus small scraper/excavators groups due to lack of size data from published studies and lack of fine-resolution feeding behaviour for some non Indo-Pacific species. Additionally, we designated *Ctenochaetus* spp. as grazer/detritivores as they have been shown to consume significant amounts of turf algae [42]. Finally, we included territorial damselfishes as they are herbivores and we were interested in examining the entire herbivorous fish assemblage.

Scraper/excavators graze primarily on turf algae but often remove portions of the underlying carbonate substratum as they feed. Grazer/detritivores intensely graze turf algae but rarely alter the underlying substratum; some species also obtain portions of their diets by feeding on organic material in sediments. Browsers feed almost exclusively on macroalgae and associated epiphytic material, removing only the algae without directly affecting the underlying substratum. Finally, territorial damselfishes comprise the only group whose unique behaviour is linked by taxonomy; they employ a grazer/detritivore feeding method but also aggressively repel competitors and selectively cultivate algal farms that can differ markedly from outside territories [43,44]. When available, species were categorized based on previously published designations; the remainder were categorized based on the best available dietary and behavioural information.

To test whether fisheries accessibility altered the structure of the herbivorous fish guild globally, a non-parametric bootstrapping procedure was used. However, instead of calculating mean differences, we generated a distribution of scale-independent ratios between the biomass means for NFA and FA locations for each of the four functional groups. Statistically significant differences were reported if the 95% QR of the biomass ratio did not overlap 1.

Analyses were performed using the program R version 2.9.2 (http://www.r-project.org).

3. Results

(a) Effects of fishing on total herbivore assemblage

We collected 2706 site-level estimates of biomass and abundance from 145 locations across the globe (figure 1). Biomass values varied among regions and across locations, ranging from 2.5 g m^{-2} at the FA sites of Santa Rosa, Mariana Islands, to 175.1 g m^{-2} at NFA sites in the Seychelles (figure 2). The grand mean biomass of herbivores in NFA locations was 56.4 g m^{-2} (±7.9 s.e.) which was significantly greater than at FA locations with only 20.5 g m^{-2} (±1.6 s.e.; $T = 9.5$, $p < 0.001$). There was no significant difference in numerical abundance of herbivores across levels of fisheries accessibility ($T = 0.4$, $p > 0.10$; electronic supplementary material, table S4 and figure S2), with an average of 0.48 individuals (ind.) m^{-2} (±0.13 s.e.) at NFA locations and 0.55 ind. m^{-2} (±0.54 s.e.) at FA locations.

Biomass varied considerably within and among regions (figure 2) but overall NFA locations tended to support higher biomass values than FA locations (see electronic supplementary material, table S4). For all regions where raw site-level data were available, the estimated difference in biomass between NFA and FA locations ranged

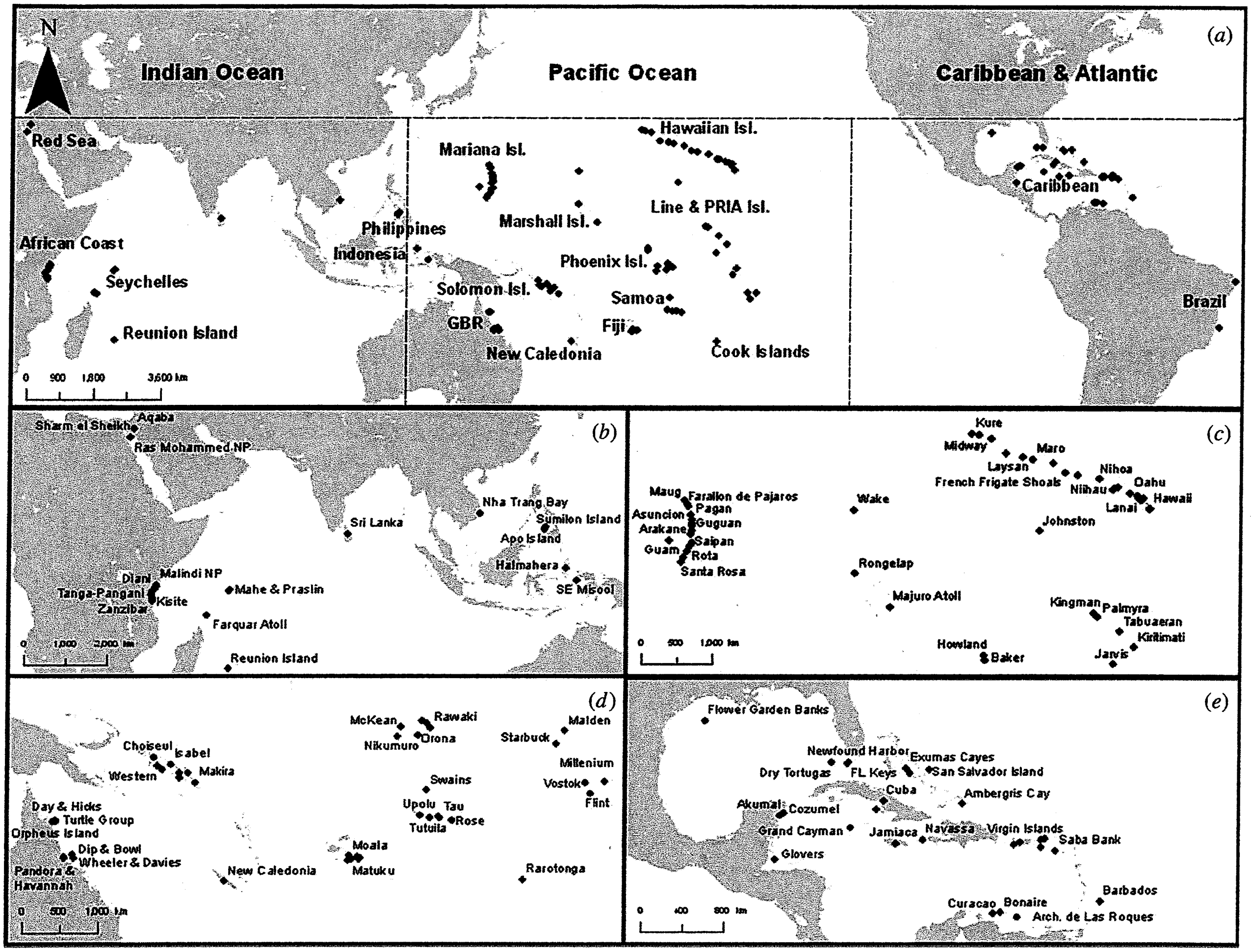

Figure 1. (*a*) Distribution of locations included in the database. Dotted lines delineate ocean basins and inset maps (*b–e*) are provided for detail. The number of survey sites ($n > 4$) and the types of data (abundance versus biomass) for each sampling location are variable (see electronic supplementary material, table S2). Some location names have been excluded from inset maps for ease of display. Identification of locations as FA or NFA is shown in electronic supplementary material, table S2.

between 6.6 and 25.4 g m^{-2} (95% QR) with a median of 15.6 (figure 3*a*), indicating moderate-to-strong declines in biomass in fisheries-accessible locations. By contrast, the 95% QR of the mean difference in abundance between NFA and FA locations included zero, with some regions having higher abundance and others having lower abundance or demonstrating no difference (figure 3*b*; electronic supplementary material, figure S3 and tables S3 and S4).

(b) Effects of fishing on herbivore functional groups

We analysed the effects of fisheries accessibility on herbivore functional groups for 109 locations around the globe. None of the functional group response ratios (between the NFA and FA locations) overlapped 1, indicating significant differences for all groups (figure 4). Specifically, three functional groups (scraper/excavators, browsers and grazer/detritivores) showed significantly lower biomass at locations accessible to fishing. However, these three groups showed no difference in abundance between NFA and FA locations. By contrast, both biomass and abundance for territorial damselfish were greater at FA locations.

Biomass of scraper/excavators was 14.4 g m^{-2} (±1.0 s.e.) and 9.5 g m^{-2} (±0.4 s.e.) at NFA and FA locations, respectively, or 33% (95% QR: 8–57) lower biomass at FA locations. Browser biomass was 21.9 (±11.1 s.e.) and 2.0 g m^{-2} (±0.4 s.e.) at NFA and FA locations, respectively, or more than 80% lower biomass at FA locations (95% QR: 70–88). Biomass of the grazer/detritivores was 17.5 (±1.6 s.e.) and 8.4 g m^{-2} (±1.1 s.e.) at NFA and FA locations, respectively, amounting to more than 50% (95% QR: 48–61) lower biomass at FA locations. Territorial damselfish made the smallest contribution to total biomass with 1.0 (±1.7 s.e.) and 1.3 (±1.7 s.e.) g m^{-2} or 2 and 6% of total herbivore biomass at NFA and FA locations, respectively. Territorial damselfishes were the only group with higher biomass at FA locations (45% higher; 95% QR: 4–85) and were the only group that showed a significant difference in numerical abundance, with 0.9 (±0.2 s.e.) and 1.2 (±0.1 s.e.) ind. m^{-2} at NFA and FA locations, respectively ($T = -2.5$, $p = 0.05$).

4. Discussion

The locations included in this analysis span a range of environmental and oceanographic parameters (e.g. temperature, productivity, exposure, depth) known to influence the structure of local fish stocks. Despite such variability, our results show that globally, herbivorous fish assemblages at locations not accessible to fisheries supported on average more than twice the total biomass, relative to those accessible to fisheries. Although other studies have noted similar trends

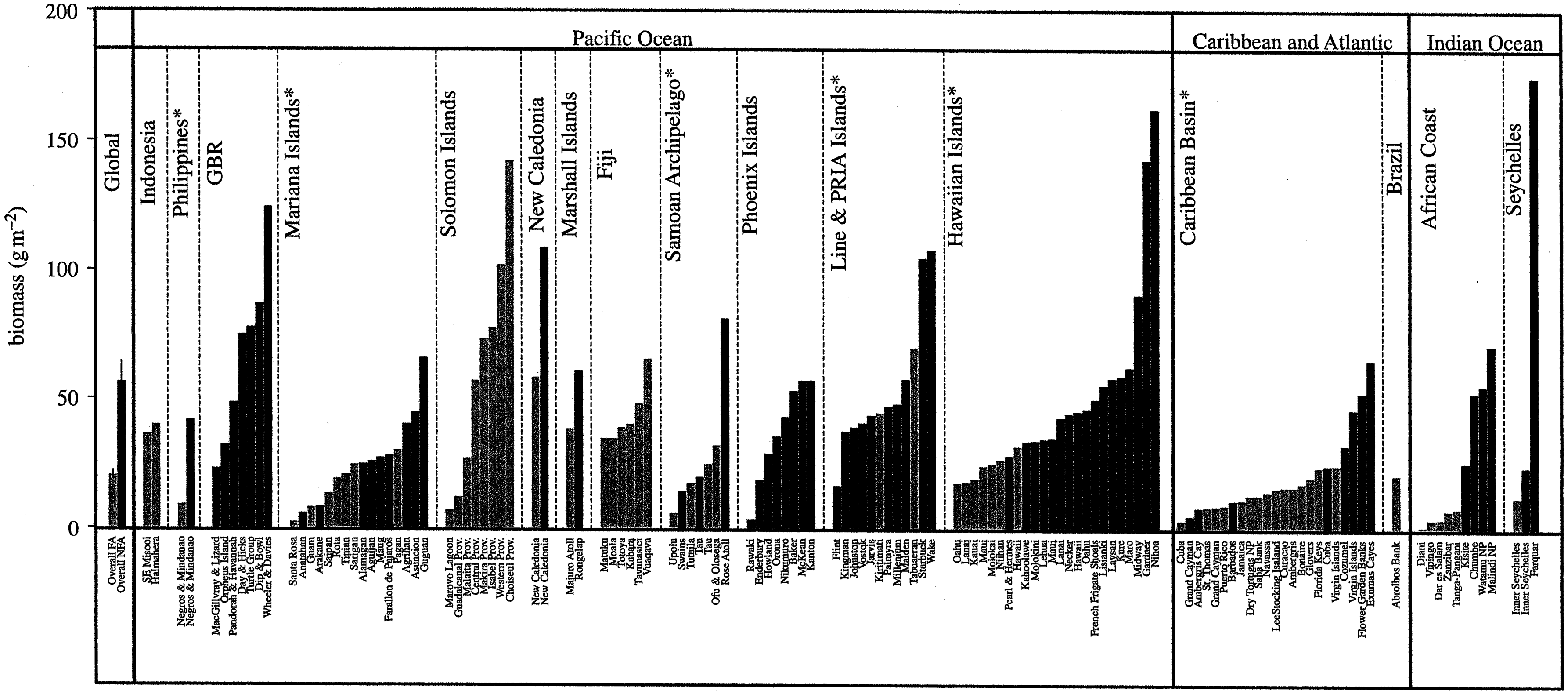

Figure 2. Mean herbivore biomass (g m^{-2}) for NFA (black bars; $n = 86$) and FA (grey bars; $n = 74$) across the globe ($n > 4$ sites per location) organized by ocean basin and geographical region (dashed lines). Regions are arranged longitudinally. The grand mean (±1 s.e.) of herbivore biomass at NFA and FA locations is shown on the far left. Asterisks indicate regions where raw site-level data were available to conduct more detailed regional comparisons (figure 3). GBR, Great Barrier Reef; PRIA, Pacific Remote Island Areas.

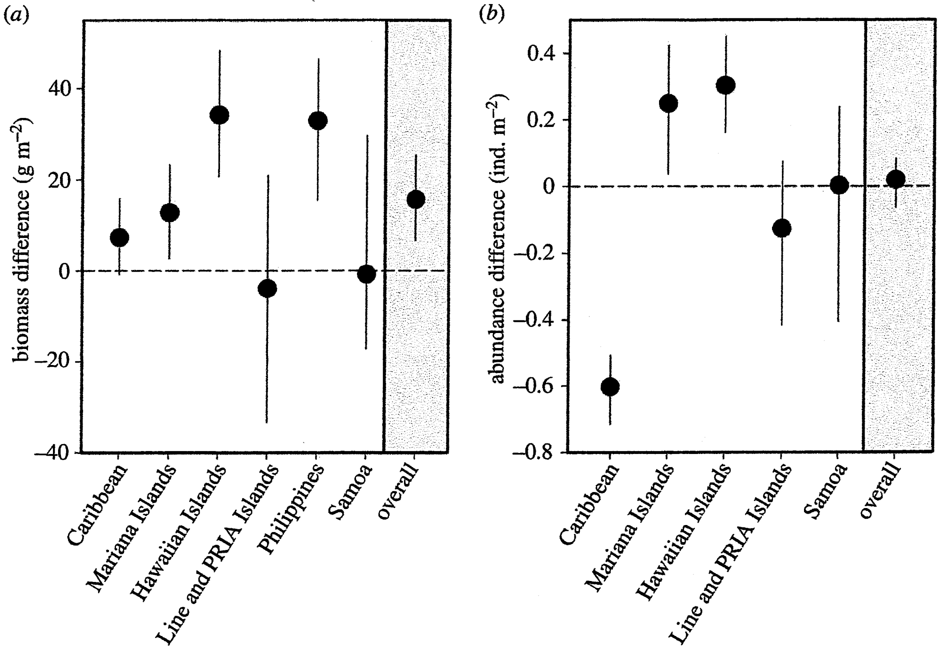

Figure 3. Distribution of mean bootstrapped differences between NFA and FA locations among regions around the world (see asterisks in figure 2) for: (*a*) herbivorous fish biomass (g m^{-2}) and (*b*) abundance (ind. m^{-2}). Circles are median differences within regions; vertical lines are 95% quantile ranges of differences. Dashed lines represent mean differences of 0 indicating no significant difference between FA and NFA locations within regions.

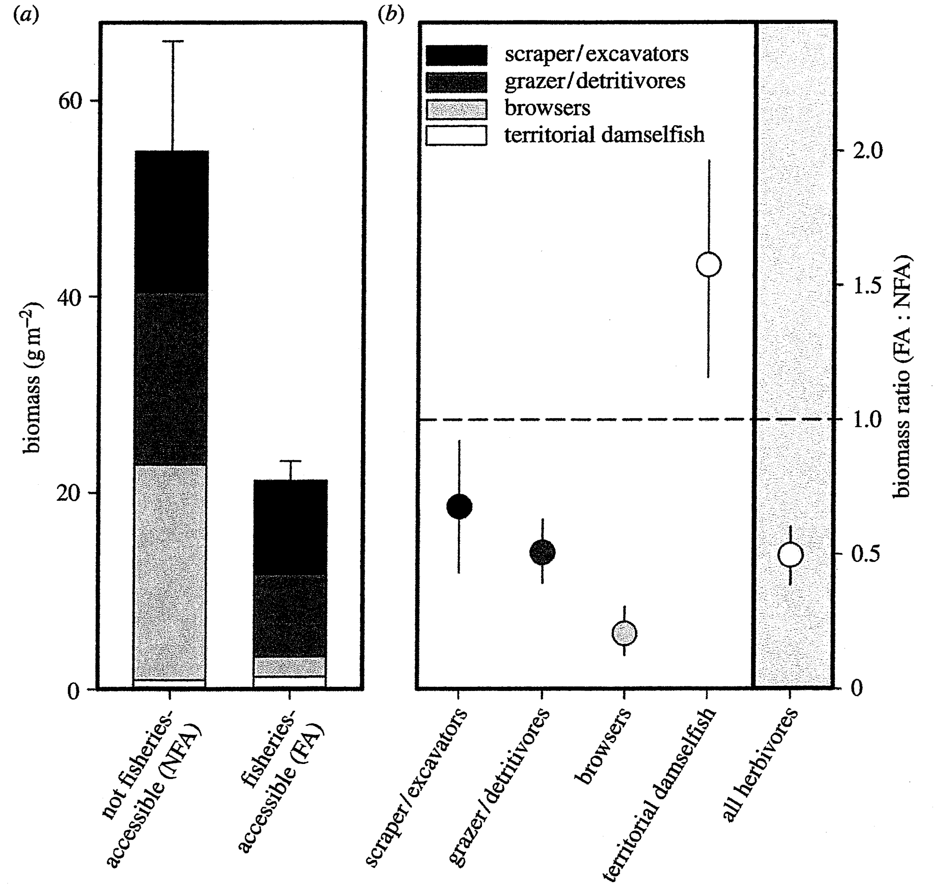

Figure 4. Bootstrapped functional group biomass at NFA and FA locations around the world. (*a*) The bar on the left is the mean of NFA locations ($n = 57$) and the bar on the right is the mean of FA locations ($n = 52$). Vertical lines are +1 s.e. for the entire herbivore assemblage and data are broken down into the respective feeding guilds. (*b*) Bootstrapped biomass ratios of overall herbivore and functional group biomass (g m^{-2}) between NFA and FA locations around the world; circles are medians and vertical lines are 95% quantile ranges of ratios. The dashed line indicates a ratio of 1 (no significant difference in biomass between FA and NFA locations).

in herbivore biomass across regional gradients in fishing pressure [11,28,45], this is the first study to demonstrate this pattern globally.

Despite strong evidence of fishing impacts on herbivorous fish biomass, there was no clear pattern in numerical abundance between NFA and FA locations. These contrasting patterns between biomass and abundance suggest an alteration in the size structure of the herbivorous fish assemblage, as has been observed in other regional studies investigating fishing effects on all reef fishes [25,46]. In our study, the more than twofold decline in herbivore biomass, but no difference in abundance, indicate that FA locations are dominated by a relatively higher number of smaller-bodied fish. Shifts in the overall size structure can result from within-species reductions in size or among-species shifts in relative abundance favouring smaller-bodied species [46]. Both have important consequences for the emergent foraging capacity of the herbivore guild, as there are size-dependent effects, within and among species and functional groups, on algal consumption and feeding impacts. Larger individuals generally consume more algae and expose larger areas of substratum [22,47]. A shift to smaller-bodied fishes may also result in a loss of key ecological functions provided by the largest species, such as bioerosion and coral predation by scraper/excavators [11] and the targeted removal of macroalgae, including many allelopathic taxa, by browsers [16]. Thus, reductions in total herbivore biomass and a shift to smaller-bodied fishes may lead to multiplicative declines in herbivory potential—less herbivore biomass with lower foraging capacity per unit biomass with less breadth of potential algal prey.

Our most striking finding was the extreme range of herbivore biomass values observed across study locations, in particular the high values reported from some remote, protected NFA locations. Several NFA locations across the Pacific (Nihoa and Gardner: Northwestern Hawaiian Islands, Wake: central Pacific, Starbuck: Line Islands and Wheeler and Davies Reefs: Great Barrier Reef) and the Indian Ocean (Farquar: Seychelles) have herbivore biomass values exceeding 100 $\mathrm{g\,m^{-2}}$ (figure 2). These trends still hold even after removing the largest-bodied species (e.g. *Bolbometopon muricatum* and *Chlorurus* spp.) from the analysis. The biomass potential of the herbivore assemblage is highlighted when comparing these values to *total* fish biomass from some FA locations. Our global mean herbivore biomass from NFA locations was 56.4 $\mathrm{g\,m^{-2}}$, while a recent study estimated the *total* reef fish biomass from inhabited islands in Hawaii, the Marianas and American Samoa to be 33.2 $\mathrm{g\,m^{-2}}$ [28]. Herbivores clearly play an important trophic role on coral reefs, and our findings show that their contribution to total fish biomass and fisheries potential should not be undervalued.

There are notable differences in the biomass of the herbivorous fish guild across the globe, with the Caribbean having particularly low values (see electronic supplementary material, table S2). The highest values reported from the Caribbean were from a protected area in the Bahamas with approximately 65 $\mathrm{g\,m^{-2}}$; however, many locations have much lower values (figure 2). These low biomass values may be due to reduced regional species richness or complete absence of many of the largest-bodied herbivore taxa, including large parrotfishes and many browsers (e.g. *Naso* spp.). Alternatively, lower herbivore biomass may be the result of a longer history and greater impact of fishing in the Caribbean, including poaching in NFA locations; thus, our results may not reflect the true biomass potential in this region. Large differences in herbivore biomass between Pacific and Caribbean reefs have been previously noted (Pacific: 29.0 and Caribbean: 9.25 $\mathrm{g\,m^{-2}}$) and may possibly explain why the Caribbean seems more susceptible to macroalgal blooms than the Pacific [14]. However, with a larger dataset, we show a wider range of values across basins and, importantly, demonstrate a much higher biomass potential for both the Pacific and the Caribbean (mean herbivore biomass in NFA sites: 59.9 ($\pm$2.2) and 29.2 ($\pm$6.2) $\mathrm{g\,m^{-2}}$, respectively). If management strategies are to be effective at increasing the feeding capacity of the herbivore guild, restoration targets should not be based on limited data from highly exploited areas. Rather, they should consider the maximum potential biomass of locations not accessible to fishing within and among regions.

The binary evaluation of sites as NFA/FA allows for a straightforward examination of the effects of fishing on fish populations. Because this approach does not quantify levels of fishing our results are probably conservative, underestimating the true differences in herbivore biomass between the most remote locations and the most heavily fished ones [28]. For example, unprotected sites in Jamaica with a human population density of 23 people per square kilometre were classified as FA and had a mean biomass of 16 $\mathrm{g\,m^{-2}}$. However, the Western Province of the Solomon Islands, with only 5.2 people per square kilometre but also classified as FA, supports some of the highest biomass values observed (102.1 $\mathrm{g\,m^{-2}}$). Similarly, NFA locations include areas near large population centres such as protected areas on densely populated islands (e.g. Oahu, Hawaii), where active or inadvertent reductions of herbivores are probable, as well as isolated locations, such as in the Line and Northwestern Hawaiian Islands, hundreds of kilometres away from any direct human disturbance. Without standardized measures of fishing intensity, it is difficult to move beyond simple designations of fisheries accessibility. However, despite the crudeness of our designations, mean herbivore biomass values in NFA locations were still more than double those in FA locations.

Alterations of consumer communities due to anthropogenic activities have been linked to myriad dramatic shifts in structure and functioning of ecosystems worldwide [48]. Although many of these shifts are caused by reductions in the abundance (or biomass) of key consumers, it is also important to consider functional transitions within trophic groups. For example, disproportionate reductions of large-bodied herbivores due to exploitation by Late Pleistocene humans of the Beringia tundra have been implicated in broad-scale transitions of the biome from domination by grasses to mosses [49]. Herbivorous megafauna on land maintained more open and heterogeneous vegetative assemblages due to their physical impacts on plants. With the extinction of many of these large herbivores, there is consistent evidence of the emergence of more dense and homogeneous vegetative landscapes [50]. Because of the ecosystem services conferred disproportionately by large-bodied herbivores, some scientists and conservationists have proposed the so-called 'Pleistocene re-wilding' of landscapes to restore the critical ecosystem services provided by large animals.

A parallel pattern of anthropogenic downsizing of herbivores is evident in our study where there is significantly lower biomass of all feeding guilds of herbivorous fishes, aside from the smallest-bodied taxa, in areas accessible to larger than they ever were naturally, in order to effectively control algal abundance on degraded reefs. Moreover, because of the complementarity among herbivore functional groups, it is important to ensure that members of each group are represented if the full suite of ecological services they provide is to be preserved. Even within a given functional group, diversity, complementarity and redundancy of different taxa will probably help to ensure the stability and resilience of reefs to disturbance events. Most management strategies today focus on restoring overall fish populations to levels comparable to unfished reefs, without specific focus on herbivore assemblages. Given that this is impractical in many locations, we believe that more effort should be directed towards managing both the biomass and composition of key groups of fishes, such as the herbivores. Finally, our results from unfished locations provide important templates that can be used for setting management priorities for herbivorous fish populations, both regionally and around the globe.

Acknowledgements. We thank the National Ocean and Atmospheric Administration (NOAA), the Australian Institute of Marine Sciences, the Department of Marine and Wildlife Resources in American Samoa and The Nature Conservancy Indonesia Marine Program for contributing to this extensive dataset. We would like to thank N. Price, L. Lewis, J. Harris, E. Kelly and R. Morrison for comments on earlier drafts of the manuscript, and L. Sagustume, who helped with database development.

Funding statement. Funding for this work was provided by The National Science Foundation and NOAA through the collaborative program Comparative Analysis of Marine Ecosystem Organization (CAMEO) award number NSF OCE10417212 to J.E.S. and S.A.S. Additional funding for research cruises was provided by the National Geographic Society to E.S.

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BIOLOGY REPORTS

Published: 23 September 2010

Coral reefs in crisis: reversing the biotic death spiral

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F1000 Biology Reports 2010, **2**:71 (doi:10.3410/B2-71)

Abstract

Coral reefs are disappearing due to global warming, overfishing, ocean acidification, pollution, and interactions of these and other stresses. Ecologically informed management of fishes that facilitate corals by suppressing seaweeds may be our best bet for bringing reefs back from the brink of extinction.

Introduction and context

Coral reefs are declining dramatically due to cascades of interacting stresses ranging from global warming, overfishing, pollution, and ocean acidification to catastrophic events like the oil spill in the Gulf of Mexico. One of the world's most productive, species-rich, and visually spectacular ecosystems is in unprecedented global decline [1-8], mandating immediate and informed action. Accidents like the oil spill in the Gulf of Mexico capture public attention and bring needed focus to declining marine ecosystems. But the insidious, day-to-day insults from overfishing, elevated CO_2, and nutrient pollution may be just as devastating because they are chronic and omnipresent. Reef ecologists are rapidly gaining new insights into the mechanisms driving reef decline and by doing so are discovering additional options for protecting and restoring coral reef ecosystems. Strategic management of fish stock across broader spatial scales may be our best bet for bringing reefs back from the brink of ecological extinction in the near term. Long-term, we will also need to address drivers of climate change and ocean acidification [1,9].

Over the last 30-40 years, coral cover in the Caribbean has declined by 80% [6] and in the Indo-Pacific by 50% [4,7]. In the early 1980s, the Caribbean had such huge stands of elkhorn and staghorn corals (*Acropora palmate* and *A. cervicornis*, respectively) that entire reef zones were named after these species and patches the size of city blocks were common. Today, both species are scarce and a patch the size of a desk merits gathering graduate students for a viewing. In the early 1980s, these were the two most abundant corals in the Caribbean. In 2006, both species were listed as vulnerable under the US endangered species act and in 2009 both were elevated to threatened status. At present, 30% of the world's corals are at elevated risk of extinction [8]. This is an unprecedented decline; it would be the ecological equivalent of losing pine trees from the southeastern United States, hardwood trees from New England, or aspens from the Rocky Mountains - all in little more than a decade. Coral decline affects not only coral reefs; the US Commission on Ocean Policy estimates that coral reefs provide a staggering $375 billion per year in goods and services.

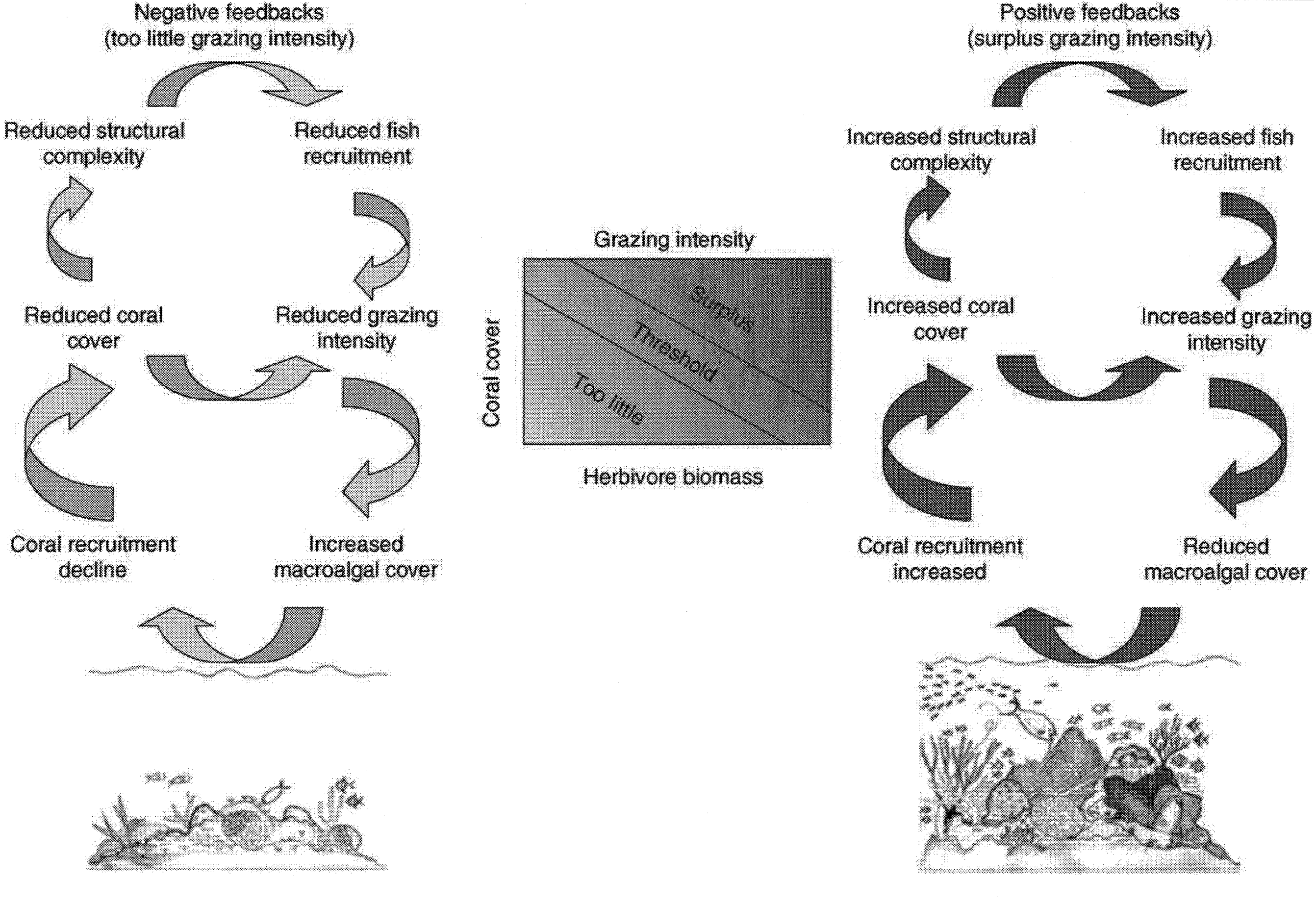
Some reasons for coral loss are better documented than others [2,5,9-11], but it is clear that a host of both global and local phenomena play a part. This mix of local-scale stresses (which can be altered by local management efforts) and global-scale stresses (which local managers cannot control) makes it challenging to prevent, and especially to reverse, coral decline. However, if we don't act both quickly and wisely, coral reefs will be gone. The frequency and scale of climate-induced bleaching of coral reefs in recent decades has affected hundreds of reefs and at times whole ocean basins [1,9]. But bleaching is just one part of the problem. Coral diseases have also increased dramatically, often in association with increased temperatures and coral bleaching [2].

Additionally, corals decline and seaweeds proliferate following any of a host of disturbances such as coral bleaching, epidemics of coral disease, or overfishing of reef herbivores [2-5,10,11]. Once reefs become dominated by seaweeds, negative feedback reinforces seaweed-dominance and produces a coral 'death spiral' from which recovery is difficult (see Figure 1). Once seaweed growth outpaces the ability of reef herbivores to control seaweed biomass, seaweeds bloom and reef degradation can be quick and difficult to reverse because seaweeds directly damage corals [5,12,13] and also suppress colonization of their larvae [14-16], thus preventing coral recovery. Corals are foundation species that provide the physical structure and habitat complexity upon which fishes and other reef species depend. Therefore, the decline in corals leads to a decline in herbivorous fishes [5,17,18], which leads to even more seaweeds, which leads to further decline in corals as seaweeds shade, abrade, and chemically poison remaining corals as well as suppressing their ability to reproduce and prevent the recruitment and survival of their larvae [10,11,13-15]. Many researchers have documented this coral reef death spiral, when herbivorous fish were experimentally removed on a small scale [10,11,13], as well as over large scales in the Caribbean following overfishing or herbivore disease [1,3-5]. There is considerable concern that similar losses are now beginning world-wide, with global climate change and ocean acidification driven by increased CO_2 production presenting even larger challenges to conservation and recovery.

Major recent advances

Marine protected areas are necessary but not sufficient to save coral reefs. Conservation and restoration of coral reefs is currently focused on establishing marine

Figure 1. Feedbacks producing the biotic death spiral versus the resilience of a healthy coral reef



Schematic of the biotic interactions producing positive or negative feedbacks that drive a reef toward either an unhealthy state of seaweed dominance, with declining corals, fishes, and structural complexity (left side of image), or toward a resilient healthy state of coral dominance, with few seaweeds, many fishes, and a high structural complexity formed by coral growth (right side of image). Rate of herbivory is the critical interaction determining whether the feedback is positive or negative. Reprinted from [5], © 2008, with permission from Elsevier.

protected areas where local stresses such as fishing and pollution are reduced or eliminated. However, these boundaries affecting human's use of the area don't afford reefs with protection from stresses such as pathogens, storms, ocean-acidification, and elevated sea-surface temperatures that do not stop at political or regulatory borders. This being the case, the effectiveness of marine protected areas in lessening global-scale stresses can be questioned [17,20]. However, recent analyses demonstrate that marine protected areas are useful despite global-scale stresses, and also suggest possible improvements in management options for conserving healthy reefs and reviving damaged ones [21,22].

Marine protected areas are assumed to serve two critical functions for coral reefs: first, to protect the community in the marine protected area from further damage, and second, to allow the corals and other reef organisms in the marine protected area to reproduce and provide larvae that can facilitate recovery of adjacent communities. The first function recently has been demonstrated; the second is more debatable.

Recent studies show that marine protected areas indeed help increase reef resistance to, and recovery from, global-scale stresses, at least within the protected areas [21,22]. Elizabeth Selig and John Bruno from the University of North Carolina at Chapel Hill recently completed a world-wide comparison of coral cover inside 310 marine protected areas versus similar unprotected reefs [21]. They found that average coral cover remained constant over recent years in marine protected areas while cover on unprotected reefs declined. Additionally, coral cover in older marine protected areas tended to be higher than in newer ones. This analysis covered 1969-2006 so it includes the severe global bleaching event of 1998. Bleaching occurs both inside and outside marine protected areas but coral recovery was quicker inside marine protected areas due to the greater abundance of herbivorous fishes, which initiated a feeding cascade that reduced seaweeds and prevented their suppression of corals [5,10,11,23-25].

Maintaining an intact food web (a complex of interrelated food chains) of diverse fishes can even diminish coral disease. Laurie Raymundo [26] and her colleagues at the University of Guam observed a higher frequency of coral diseases on more heavily fished reefs. In particular, they found that overfishing removed predators that in turn were controlling a group of coral-feeding fishes. The coral-feeding fishes, which became more abundant with their predators removed, vectored coral diseases as they fed.

Advances in understanding how the damage is done

Another recent advance highlights the way multiple man-made stresses exacerbate damage to coral reefs. Although bleaching is a response to high sea surface temperatures associated with global-scale stresses, local man-made stresses also have an effect, so even local-scale management can affect coral response to global-scale disturbance. In a recent overview of coral bleaching and climate data, a group of collaborating marine scientists lead by Jessica Carilli from Scripps Institution of Oceanography in San Diego noticed that the first large scale bleaching in the Caribbean occurred in 1998 despite the fact that both 1937 and 1958 were warmer years [27]. This suggested that temperature was not the sole driver of bleaching. Further analysis indicated that bleaching was better explained by temperature together with nearby human population density than by temperature alone, suggesting that chronic local stresses were depressing heat tolerance and increasing the risk of coral bleaching. Local man-made stresses also slowed coral recovery following a bleaching event. After the Caribbean bleaching of 1998, growth rates of the important reef-building coral *Montastraea faveolata* took 8 years or more to recover in areas with more man-made disturbance, but only 2-3 years in areas experiencing less man-made stress. A study along the Great Barrier Reef [22] found a similar relationship; a synergism between heat stress and nutrient flux appeared to be a major causative mechanism for the geographic pattern of coral bleaching.

While it is well established that stresses such as bleaching, disease, overfishing, and pollution tend to suppress corals and enhance seaweeds, the mechanisms involved have been clarified only recently. Meta-analysis of experiments manipulating herbivorous fishes and nutrients show that the former are critical for suppressing seaweeds on reefs and that the latter play a much lesser role [28]. Different types of investigations emphasize this same point. Field experiments in which herbivorous reef fishes were experimentally excluded from 4-25 m^2 caged areas on natural reefs (to represent the effects of overfishing) demonstrated a dramatic increase in seaweeds and a significant decline in coral fitness within the cages via changes in herbivorous fishes alone [10,11]. When we manipulated the quantity and species of herbivorous fish in large enclosures on deeper (17 m) natural reefs in the Florida Keys, we saw that a mix of herbivores with complementary diets were especially efficient at preventing seaweed growth and aiding corals [10]. Corals in enclosures with the mix of herbivore species grew 22% in 10 months and experienced no mortality. In contrast, corals in enclosures without herbivores shrank in size by more than 20% and experienced more than 20% mortality in the same period [10]. Working on shallower reef flats in Australia, Terence Hughes and his collaborators at James Cook University demonstrated similar impacts of fish grazing; herbivorous fishes were critical for suppressing seaweeds and preventing them from suppressing corals [11].

These studies have shown a clear association between seaweed abundance and coral decline, but until recently the mechanisms producing such declines were unclear. It was well known that seaweeds suppressed the recruitment and survival of juvenile corals [11,14-16] but how seaweeds damaged established corals was unclear [5]. In recent field manipulations in both the Caribbean and tropical Pacific, we placed seaweeds in contact with corals and demonstrated that numerous common seaweeds caused coral bleaching and sometimes death via transfer of toxic compounds from seaweed surfaces [13]. Other studies demonstrated that some seaweeds also transmit coral disease in the field or, under laboratory conditions, exude metabolites that stimulate coral-damaging microbes [29,30]. Thus, seaweeds not only suppress recruitment of coral larvae, but also can damage older corals.

The general consensus emerging from many studies on many different types of coral reefs is that reefs need to be managed for resiliency to a host of anthropogenic and natural stresses and that a critical aspect of this is preserving natural densities and diversities of herbivorous fishes that will keep seaweeds in check and promote coral recruitment [4,5,10,11,23-26].

Advances in understanding reef resiliency

The second purpose of marine protected areas, to help adjacent areas recover their natural community composition and function, is inadequately demonstrated and can be questioned [17,20]. Marine protected areas can provide 'spill-over' of fish to adjacent areas, helping replenish fish stocks. However, that spill-over is often too rapidly harvested [31] to suppress seaweed and subsequently enhance coral growth in unprotected areas. Thus, marine protected areas may fail to help adjacent reefs recover unless stocks of critical herbivorous fishes are elevated enough to make these areas receptive to recruiting coral larvae [5,32].

Enhancing fish stocks is critical for preventing or reversing coral loss, but some fishes are more critical than others in this process. Experimental removal and reintroduction of herbivorous fishes alone can induce regime shifts from corals to seaweeds or from seaweeds back toward corals [10,11,19], but recent research also indicates that herbivorous fish diversity [10], identity [33], and size [34] can all be critical for controlling seaweeds and facilitating corals. In our field enclosures we found that a mix of herbivores with complementary diets facilitated both the survival and growth of corals, while enclosures with equal densities and masses of single herbivore species did not [10]. Fish size within a species can also be critical. Large fish are disproportionately better grazers than small fish – for some parrotfish, it takes 75 fish of 15 cm length to graze as much as one fish of 35 cm length [34]. It follows that fishing methods targeting larger individuals will disproportionately suppresses grazing. This suggests that reefs may need long-term protection from fishing before grazers achieve a size at which they are most effective [23,31,34]. To be healthy, coral reefs must have a mix of bioeroding fishes that scrape away dead coral and expose hard surfaces, scraping fishes that limit filamentous algae and sediments on these hard surfaces, and grazers that remove macroalgae [4].

Recent studies make another point relevant for management: it seems that the fish that prevent seaweed taking over reefs in the first place may not be the same fish that can reverse the shift once it occurs. When we manipulated the diversity and identity of herbivorous fishes in enclosures on a Caribbean reef and determined their effects on both the established reef community and on uncolonized substrates newly placed on the reef, herbivore diversity was critical for suppressing seaweeds on the established community but less so for the newly colonizing community [10,35]. Additionally, the herbivore species that most strongly suppressed larger seaweeds in the mature community had the least impact on larger seaweeds colonizing the new substrate. Even more dramatic was work by David Bellwood and colleagues of James Cook University in Australia. When they caged large herbivorous fishes out of reef areas for long periods, an algal forest developed and harmed corals; however, when they removed the cages, this algal forest was consumed primarily by a species of reef fish that had not previously been recognized as herbivorous [33].

Future directions

Reefs need to be managed for resilience to a host of interacting local and global stresses; the rapid losses, slow recoveries, and host of accelerating stresses make it urgent that we develop efficient strategies for intervention, based on an understanding of the ecology of coral reefs. While marine protected areas are critical to success, they alone are unlikely to allow reef survival because most are too isolated, too small, and cannot adequately leverage recovery of adjacent areas. We need to find effective ways to make damaged reefs more receptive to larval corals and thus better able to stop the death spiral that is occurring on today's reefs (Figure 1); this will involve limiting the harvest of a critical mix of reef herbivores that prevent seaweeds from blooming on coral reefs. Because almost all major stresses shift reefs from corals to seaweeds, a better understanding of the processes and mechanisms underlying this shift, and its reversal, will be critical for preventing and reversing losses of coral reefs. To optimize our management efforts, we need information on the mechanisms involved in seaweed-coral interactions at all stages of the life cycle, the seaweeds that are most damaging to corals, and the mix of herbivorous fishes that consume the most damaging seaweeds. In short, we need proactive management that goes beyond establishing marine protected areas and hoping for the best.

Competing interests

The authors declare that they have no competing interests.

Acknowledgments

This work was supported by the US National Science Foundation (OCE 0929119), the National Institutes of Health (U01 TW007401-01), and the Teasley Endowment to the Georgia Institute of Technology.

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Subject:	RIN 0648-XD325; Scoping Comments, Comprehensive Amendment to the U.S. Caribbean FMPs: Annual Catch Limit Control Rule -- Msg. 3 (final)
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Attachments to EJ-CBD-CORALations comment letter:

Mumby & Harborne 2010

Mumby 2014

Williams et al 2001

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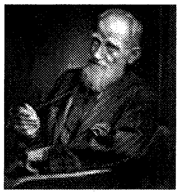

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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that ‘fish’ could be spelt ‘ghoti’. That is: ‘gh’ as in ‘rough’, ‘o’ as in ‘women’ and ‘ti’ as in palatial.

Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs

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Abstract

The problem of ecosystem overfishing has mostly focused on the function of forage fish as prey for apex predators. Here, I consider another ecosystem function, herbivory, that affects habitat quality. Parrotfish are an important fishery in many parts of the Caribbean and the dominant herbivorous fish on its coral reefs. Herbivory helps to control macroalgae which compete with coral and can impede reef resilience if allowed to bloom. Thus, long-term maintenance of reef habitat quality, which underpins fisheries, requires sufficient parrotfish stock. Ecosystem models predict that reductions in parrotfish grazing could have deleterious impacts on reef habitat yet the determination of ecologically sustainable levels of parrotfish harvest remains elusive. An initial solution to this dilemma is proposed for areas where an outright ban on herbivore exploitation is considered infeasible. Fisheries management has tended to consider coral reefs as a single habitat such that regulations apply evenly throughout exploitable areas. But reef habitats are not equally susceptible to ecosystem overfishing and some do not appear to have a strong requirement for parrotfish grazing. One habitat, *Orbicella* reef, has a high dependence on herbivory, whereas the state of another dominant habitat – gorgonian plain – appears to be driven by environmental factors (e.g. wave exposure). Ecosystem-based fisheries management

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Received 25 Jan 2014
Accepted 26 Jan 2014

DOI: 10.1111/faf.12078

could be improved by restricting parrotfish harvest on *Orbicella* reefs yet allowing exploitation on gorgonian plain. Management could then focus on achieving a sustainable yield on gorgonian plains without the added complexity of estimating catch levels that avoid ecosystem overfishing.

Keywords ecosystem-based management, parrotfish

Introduction

The advent of ecosystem-based approaches to fisheries management (EBFM) requires consideration of the impact of the fishery on the wider ecosystem (Francis *et al.* 2007). In general, two types of fishery impacts have been studied. First, are the detrimental impacts of fishing gear on the ecosystem, such as the effects of bottom trawls on habitat structure (George *et al.* 2007; Gjerde 2007; Morgan *et al.* 2007), the impacts of blast fishing on habitat (Ainsworth *et al.* 2008) and means of reducing bycatch (Richards *et al.* 2012). Second, are the ecosystem functions of the target fisheries species themselves. Perhaps the best known (and studied) examples are the importance of forage fish to seabird populations (Furness 2007; Okes *et al.* 2009) and large mammals (Hill *et al.* 2006). Some forage fish fisheries include closed areas or seasons to reduce impacts on predators (Sainsbury *et al.* 2000; Greenstreet *et al.* 2006) and the setting of ecologically safe target stock biomass is being explored through the use of whole-ecosystem models (Constable 2011; Smith *et al.* 2011; Kaplan *et al.* 2014). However, the role of fisheries species as a prey item is only one ecosystem function; there are several others that have not been considered.

Fisheries species can take on particularly important functions if they interact with the ecosystem engineers of biogenic habitats, such as kelp forests and coral reefs. Here, an interaction between the fisheries species and ecosystem engineer (Hastings *et al.* 2007) can have profound impacts on the wider ecosystem and affect habitat integrity, biodiversity and fisheries productivity. For example, by controlling densities of herbivorous sea urchins, large lobster can help maintain a structurally complex kelp-dominated ecosystem (Ling *et al.* 2009; Ling and Johnson 2012). Here, lobster is the fishery species and kelp the ecosystem engineer.

The actions of some fisheries species on ecosystem engineers can even go so far as to create reinforcing feedbacks to the fishery itself. Fisheries for coral reef parrrotfish provide a useful example that will be developed throughout this paper. In the Caribbean, grazing by parrotfish plays an important role in controlling the abundance of macroalgae, which are small seaweeds (Williams and Polunin 2000; Kramer *et al.* 2003b; Mumby *et al.* 2006; Newman *et al.* 2006). This function of grazing provides indirect support to the fishery through two mechanisms. First, because macroalgae are competitors of coral, grazing can facilitate coral recovery (Mumby and Harborne 2010), coral growth (Lirman 2001; Nugues and Bak 2006; Ferrari *et al.* 2012), and coral fecundity (Foster *et al.* 2008). It follows that resilient coral populations, which deposit a limestone skeleton as they grow, can assist the bioconstruction of reef structures when grazing levels are adequate (Bozec *et al.* 2013; Kennedy *et al.* 2013). Bioconstruction provides a structurally complex habitat that supports high densities and diversities of fishes (Luckhurst and Luckhurst 1978; Gratwicke and Speight 2005) and, presumably, elevated fisheries productivity (Pratchett *et al.* 2011). Second, by promoting the abundance of cropped algal turfs rather than unpalatable fleshy macroalgae (Steneck and Dethier 1994), parrotfish help maintain the flow of primary production into fish-based consumption rather than the detrital pathways associated with decomposition of macroalgae (Carpenter 1990).

Where fisheries species like parrotfish play an important ecosystem function, particularly one that reinforces the fishery, an EBFM policy should ideally consider the ecosystem requirement for grazing rather than simply focus on the short-term sustainability of harvest (Appeldoorn 2008). There has been limited progress in this regard. Three countries – Belize, Bonaire and the Turks and Caicos Islands – have undertaken blanket bans on the exploitation of herbivorous fish (Montero 2009; Government of Bonaire 2010), Bermuda has long-protected parrotfish by banning fish traps

(Luckhurst 1999), and the US Caribbean has banned the exploitation of three large and rare parrotfishes, modified fish traps, reduced net use, and imposed catch limits based on historical catch (SEDAR 2011). Elsewhere, however, the vast majority of parrotfish management is limited to no-take marine reserves. This is inadequate because it leaves the majority of the seascape open to unregulated exploitation, thereby placing ecosystem function and future habitat quality at risk. Pikitch *et al.* (2004) described this general phenomenon as 'ecosystem overfishing'.

Here, I consider the problem of incorporating the ecosystem need for herbivory within a fisheries management plan. I begin by outlining the complexity and urgency of the problem and then develop an interim solution that stratifies fisheries activities by habitat type. Although the case study focuses on the Caribbean region, the general principle of stratifying management by the ecological needs of each habitat can be applied in many contexts and might actually provide novel solutions to the challenges we face in achieving EBFM.

A challenge for EBFM of coral reefs

As stated, some countries have undertaken a ban on the exploitation of herbivorous reef fishes. However, a blanket ban is not always possible, particularly where there exists a high dependence on parrotfish fisheries, often as a consequence of over-exploiting more desirable carnivorous species. If fisheries are to continue, an ideal management strategy would first quantify the ecosystem needs for parrotfish and then regulate effort to achieve the target stock size, assuming that the target stock size was greater than that needed simply to maintain yield. The first task has received some analysis by generating simulation models of the ecosystem and quantifying the resilience of corals (Mumby *et al.* 2007b) and the ability of forereefs to continue undergoing bioconstruction when parrotfish populations are reduced (Kennedy *et al.* 2013). Results suggest that even a minor reduction in parrotfish could have strong deleterious impacts because reefs are predicted to lose their resilience if parrotfish grazing is reduced at a time when coral cover is low (Mumby *et al.* 2013), as is frequently the case today (Gardner *et al.* 2003). This prediction is consistent with empirical studies of coral recruitment; coral replenishment requires moderate to high levels of herbivory (Edmunds and Carpenter 2001; Arnold *et al.* 2010; Mumby and Harborne 2010).

The second task, the regulation of parrotfish fisheries to maintain sufficient grazing that ecosystem overfishing is avoided, has not yet been undertaken. Existing regulations, where present, are focused on maintaining a sustainable fishery rather than considering the ecosystem requirements of parrotfish *per se*. This is not a criticism of the fishery's management; the science is not yet available to set catch limits with EBFM in mind. For example, there have been few attempts (if any) to create a demographic model of parrotfish populations that link harvesting and function (Van Rooij *et al.* 1998). Thus, what can be done now to help achieve EBFM for parrotfish fisheries on Caribbean reefs? This is a contentious issue as the US government was recently sued for not going far enough to control parrotfish fisheries within its jurisdiction. Earth Justice, representatives of the plaintiffs, the Center for Biological Diversity, argue that greater restrictions are required to help protect corals that were listed under the Endangered Species Act (Earth Justice case number 2318).

I describe a potential solution to the challenge of implementing EBFM of Caribbean reefs in the continued absence of fisheries models. The solution stratifies fishing according to the ecological needs of different habitats.

Seeking EBFM of coral reefs through habitat stratification

Reef habitats and their stratification for management

Coral reef habitats can be defined and categorized over a hierarchical range of scales (Holthus and Maragos 1995). Major divisions might distinguish coral reef from seagrass beds and sand flats, whereas the finest divisions might recognize different ecological communities within a single geomorphological zone (Mumby and Harborne 1999). The coarsest divisions can be mapped easily with remote sensing (Mumby *et al.* 1997) and the resulting habitat maps are often used as a framework for management planning, such as setting the boundaries to management zones (Green *et al.* 1996). Fine levels of habitat discrimination can be much harder to operationalize for reef management. In some cases, habitats cannot be discriminated reliably using remote sensing because they are spectrally similar and much of the light available for discrimination is attenuated by the overlying water column (Hedley *et al.* 2012). Moreover, even when habitats can be mapped in detail, there has been little attempt to consider their respective ecological functions and management needs (Harborne *et al.* 2006b). Usually, the most sophisticated use of habitat maps is to achieve habitat representation as part of the design of marine protected areas (Roberts *et al.* 2003; Fernandes *et al.* 2005). As far as the author is aware, most fisheries regulations have treated coral reefs as a single habitat class, or, at best, stratified on the basis of simple geomorphology such as 'patch reef' versus forereef. Yet, reef habitats have strikingly different ecological needs.

Two fundamentally different habitats on coral reefs

Much of the functionally important, accreting reef habitat lies on the 'forereef', which is found seaward of the reef crest (if a crest exists). The forereef can be divided into two principal types of habitat in the Caribbean. First, the structurally complex habitats that are currently dominated by massive corals, many of which stand more than a metre high (Fig. 1a). This habitat is often referred to as 'annularis zone' or '*Montastraea* reef' after one of the coral genera that build it (Goreau 1959; Geister 1977), though several members of this genus have recently been renamed *Orbicella*. Even where corals have died, *Orbicella* reefs still tend to retain significant structural complexity because the rates of erosion tend to be low (Perry *et al.* 2013). The second major habitat is a relatively featureless flat pavement that typically possesses very low relief and is dominated by octocorals, including gorgonians (Fig. 1b). This habitat has been named 'hardbottom' or 'gorgonian plain' (Mumby and Harborne 1999).

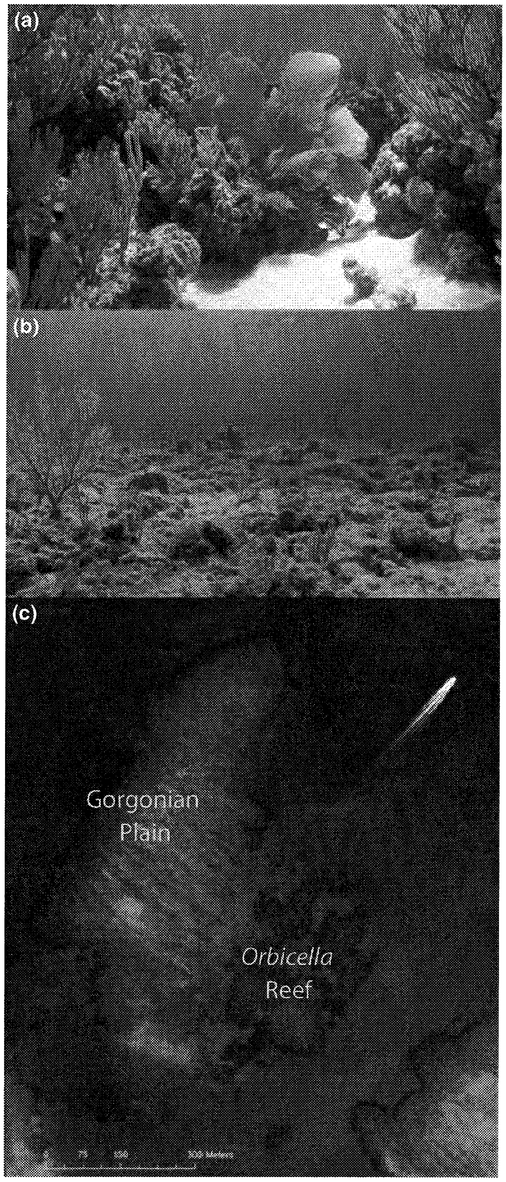

Figure 1 Contrasting Caribbean coral reef habitats; complex *Orbicella* reef (a) versus relatively flat Gorgonian plain (b). Both habitats can be discriminated on high-resolution satellite imagery (c).

Both habitats are described from many parts of the Caribbean including Belize (Burke 1982), Bonaire (van Rooij *et al.* 1996a), the Bahamas (Harborne *et al.* 2008), Dominican Republic (Torres *et al.* 2001), Florida Keys (Chiappone and Sullivan 1996), Puerto Rico (Pittman *et al.* 2007), Turks and Caicos Islands (Sullivan *et al.* 1994), and US Virgin Islands (Wolff *et al.* 1999; Harborne *et al.* 2006a). Gorgonian plains tend to be found in areas with higher wave exposure (Burke 1982; Torres *et al.* 2001), although the differences do not have to be sufficiently great that boat access to gorgonian plains becomes impeded by rough seas. In Belize, for example, the distribution of *Orbicella* reef versus gorgonian plain can reflect minor, albeit important, changes in the aspect of the reef with respect to the prevailing wind direction (Chollett and Mumby 2012). Indeed, gorgonian plains are often fished extensively (Wolff *et al.* 1999).

Using data from a large marine reserve in Belize, we see that gorgonian plains have a strikingly different community structure to *Orbicella* reefs. First, the benthic community structure contrasts dramatically with an Anosim, R, of 0.93 (Fig. 2a, $P = 0.001$). To put this result in perspective, $R = 1$, when a pair of samples (habitats) have no species/substrates in common. *Orbicella* reef has a greater cover of coral and fleshy macroalgae whereas the gorgonian plain has low levels of coral and algae but high levels of fine mobile sediment (Fig. 2b). Indeed, the major discriminating feature of the benthic community structure between habitats was the relatively high level of sand and sediment-laden turf in the gorgonian habitat (combined contribution to average dissimilarity between habitats, SIMPER, was 45%). The location of gorgonian plains in areas with slightly higher wave exposure appears to cause chronic resuspension of naturally occurring carbonate sediments that overlay the substratum (Torres *et al.* 2001). It is likely that this continual resuspension of sediment inhibits the settlement and growth of many sessile taxa. Typically, corals are scarce and macroalgae are often confined to rocky outcrops that sit above the substratum.

The overall fish assemblage also differs greatly and significantly ($R = 0.68$, $P = 0.001$, Fig. 3a). If we look specifically at differences in the parrotfish assemblage, it is clear that the *Orbicella* reef has a much higher biomass of all species except *Sparisoma chrysopterum* which is found commonly in both habitats (Fig. 3b). These results agree with differences found between these habitats in the Bahamas (Harborne *et al.* 2008).

Importantly, not only is there less macroalgae on the gorgonian habitat (mean 12% vs 30% for *Orbicella* reef, *t*-Test $P < 0.0001$), but there appears to be no relationship between parrotfish biomass and the cover of macroalgae (Fig. 4a, $r = 0.4$, $P = 0.15$). A similar analysis from the opposite side of the Caribbean, in the Exuma Cays (Central Bahamas), also shows no significant relationship between the biomass of parrotfish and macroalgal cover on the gorgonian habitat (Fig. 4b, $r = -0.34$, $P = 0.10$). This non-significant relationship was highly sensitive to a single point of relatively high algal cover and low herbivore biomass and if removed the relationship weakened further to $r = -0.25$ ($P = 0.25$). In contrast, a linear negative relationship has been found repeatedly between the cover of macroalgae and parrotfish biomass on *Orbicella* reefs (Williams and Polunin 2000; Kramer *et al.* 2003a; Mumby *et al.* 2006; Newman *et al.* 2006; Burkepile *et al.* 2013). The relationship for *Orbicella* reefs in the Exuma Cays (Central Bahamas) was strong and negative ($r = -0.63$, $P = 0.047$) (Mumby *et al.* 2007a).

To summarize, much of the exploited reef area can be separated into two habitats. One, the *Orbicella* Reef, appears to have a strong dependence on

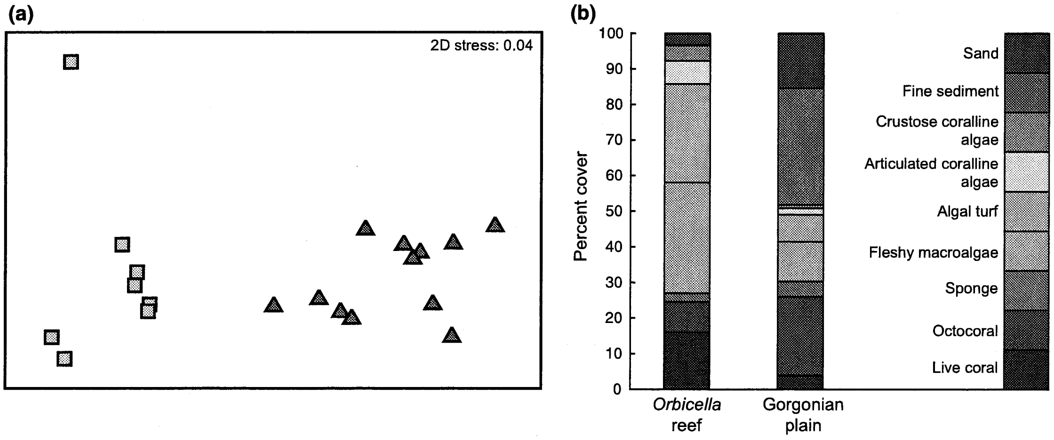

Figure 2 Benthic composition of *Orbicella* reefs and gorgonian plains from Glovers Reef Marine Reserve, Belize. Non-metric multidimensional scaling ordination of community structure (a) with *Orbicella* reef as green squares and gorgonian plain as red triangles. Detailed breakdown of major functional categories (b). Benthos was sampled using 18 one metre quadrats per site (8 *Orbicella* sites and 12 gorgonian plains).

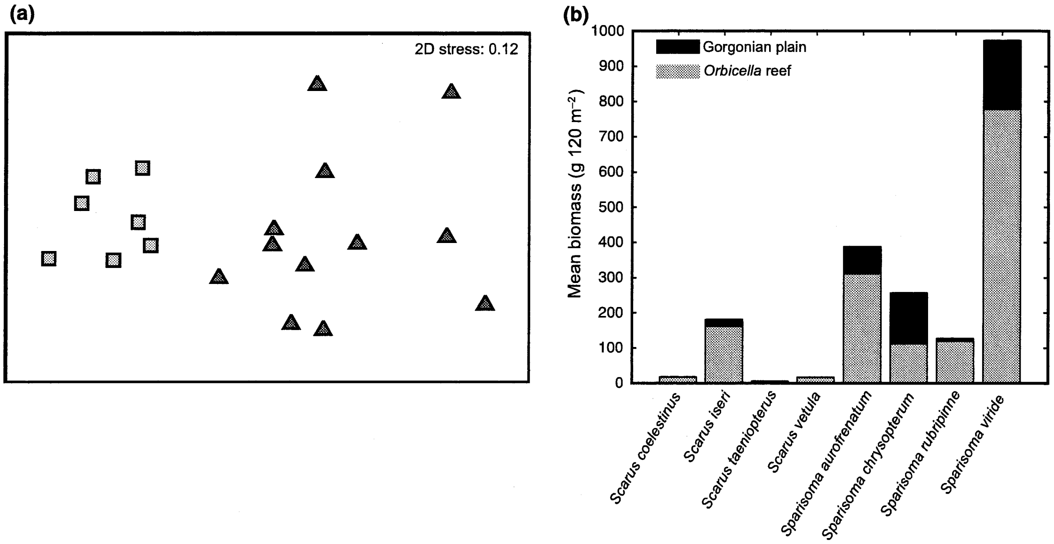

Figure 3 Interhabitat differences in the composition of reef fish between *Orbicella* reefs and gorgonian plains from Glovers Reef Marine Reserve, Belize. Non-metric multidimensional scaling ordination of the full fish assemblage (a) with *Orbicella* reef as green squares and gorgonian plain as red triangles. Subset of the assemblage, contrasting the mean biomass of each parrotfish species in each habitat (b). Small reef-attached species, which typically have high densities, such as damselfish and small labrids, were sampled using two 30 × 2 m belt transects per site. All other reef fish species (except except cryptic species) were sampled using 10 replicate 30 × 4 m belt transects per site. Size estimated visually to the nearest centimetre and converted to biomass using the allometric relationships of Bohnsack and Harper (1988). For further details of fish sampling methods, see Bejarano *et al.* (2011).

parrotfish to consume algae and mediate coral reef resilience. The other, gorgonian plain, appears to be influenced more strongly by chronic physical processes, and there is no compelling evidence to date that parrotfish play an important role here. Furthermore, coral cover appears to have been persistently and naturally low in this habitat (Burke 1982), and reef consolidation appears to be low (Gischler and Hudson 2004). The question is, can these differences be used to operationalize EBFM?

Operationalizing EBFM from habitat maps

Fisheries regulations have tended to apply ubiquitously across coral reefs, making no distinction among habitats. Yet, the requirement of parrotfish for EBFM seems to apply to one forereef habitat much more than the other. In principle, EBFM could be achieved by zoning reef habitats and adjusting the harvesting rules based on the needs of each habitat. Parrotfish exploitation might be heavily constrained, or prohibited, on *Orbicella* reefs but allowed on gorgonian plains. Fisheries regulations could then focus on sustaining the fishery on gorgonian plains rather than tackle the more challenging question of avoiding ecosystem overfishing of *Orbicella* reef.

The first step of operationalizing this concept is straightforward: *Orbicella* reefs and gorgonian plains can be mapped using a variety of complementary approaches including the mapping of wave exposure (Chollett and Mumby 2012), use of high-resolution airborne images (Harborne *et al.* 2006a), or boat-based acoustic surveys of seabed roughness (Bejarano *et al.* 2010). Both habitats are often segregated by wave exposure, either by aspect or distance offshore (Fig. 5). The relatively predictable separation of these forereef habitats should mean that fisheries zoning is feasible (Fig. 5). For example, trap use and parrotfish spearing might be prohibited in sheltered areas with *Orbicella* reef (a 'habitat protection zone', HPZ) but permitted in more exposed areas.

Several options for enforcement are possible and their feasibility will depend on the spatial scale of the fisheries zoning plan, the technical capacity of the fishery, fishing methods employed and available resources. At one extreme, a ban on herbivore exploitation within the 'habitat protection

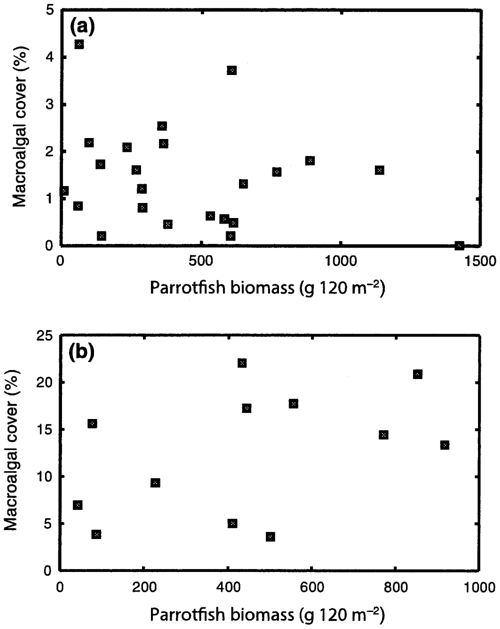

Figure 4 Lack of relationship between parrotfish biomass and macroalgal cover in the gorgonian plain habitat of Belize (a) and The Bahamas (b). For Belize survey methods, see Figs 2and 3. Reefs in the Bahamas were sampled throughout the Exuma Cays at a depth of 8–12 m. Benthos was sampled using 40 one metre quadrats per site. Parrotfish were sampled using the same methods (and observer) as Belize.

zone' could be policed by patrol boats. This might be feasible (i) where the extent of reefs is relatively small; (ii) where there are only a limited number of HPZs; and (iii) where enforcement is routinely carried out *in situ*. However, patrols are often prohibitively expensive and enforcement is often centred on monitoring the catch at landing sites. Here, the greatest challenge is detecting whether landed parrotfish were caught in the prohibited areas or not. Unfortunately, this problem is more complex than knowing whether fishing occurs inside full no-take marine reserves. Automated identification systems (AIS), a high-resolution vessel monitoring system, can be used to detect whether fishing boats spend time in no-take marine reserves and any incursion is clearly illegal (Castrejon and Charles 2013; Jones 2013). However, a boat could legally enter and fish inside an HPZ providing that herbivores were not caught. For example, fishers could legally take parrotfish from general fishing grounds and then enter an HPZ for snapper. The AIS record would reveal that the fisher entered the HPZ but could not resolve whether the parrotfish were caught legally outside the zone or not. A possible solution to this problem would be to stipulate (i) mandatory use of AIS; and (ii) that parrotfish cannot be caught on fishing trips that include an HPZ. That way, if parrotfish were landed, the AIS could be used to verify unambiguously that they could not have been collected in the HPZ. If parrotfish were not landed there would be no need to consult the AIS. In practice, this would influence fisher behaviour on a daily basis. For example, a fisher might designate some days for parrotfish capture, in which case, fishing would focus outside HPZs. Similarly, if fishing was conducted outside the HPZ and no parrotfish were caught then it would be possible for the fisher to then enter the HPZ for non-herbivorous species. Enforcement might be easier if the parrotfish are primarily caught in traps. Here, it would be appropriate to ban trap usage in HPZs yet allow alternative methods for carnivorous species like hook and line.

An obvious question is whether gorgonian habitats provide a suitable environment for sustainable fisheries? Studies from the US Virgin Islands provide some context here. Historically, reef fisheries targeted *Orbicella* reefs, but there has been an increasing shift towards gorgonian habitats as the abundance of reef fish in *Orbicella* reefs declined (Wolff *et al.* 1999). One advantage of gorgonian habitats is their lack of complexity which reduces the problem of fishing gear becoming snagged on coral. The lack of habitat complexity also increases the catchability of many reef fish. For example, Wolff *et al.* (1999) compared the catchability of reef fish between *Orbicella* reefs and gorgonian plains in St. John, US Virgin Islands. Using a combination of visual fish census and deployment of fish traps (the local fishing gear), they quantified the vulnerability of fish to traps in each habitat. The absolute catch per fish trap was usually greater in gorgonian plain than *Orbicella* reef, though this might reflect the intense history of exploitation in the latter habitat. More importantly, most fish groups, including parrotfish, were far more vulnerable to traps in the gorgonian habitat. A likely explanation for this increase in catchability is that the trap provides a relatively complex structure and apparent refuge for fish in an otherwise flat gorgonian habitat. In contrast, the refuge offered by a trap in a complex *Orbicella* reef is relatively weak.

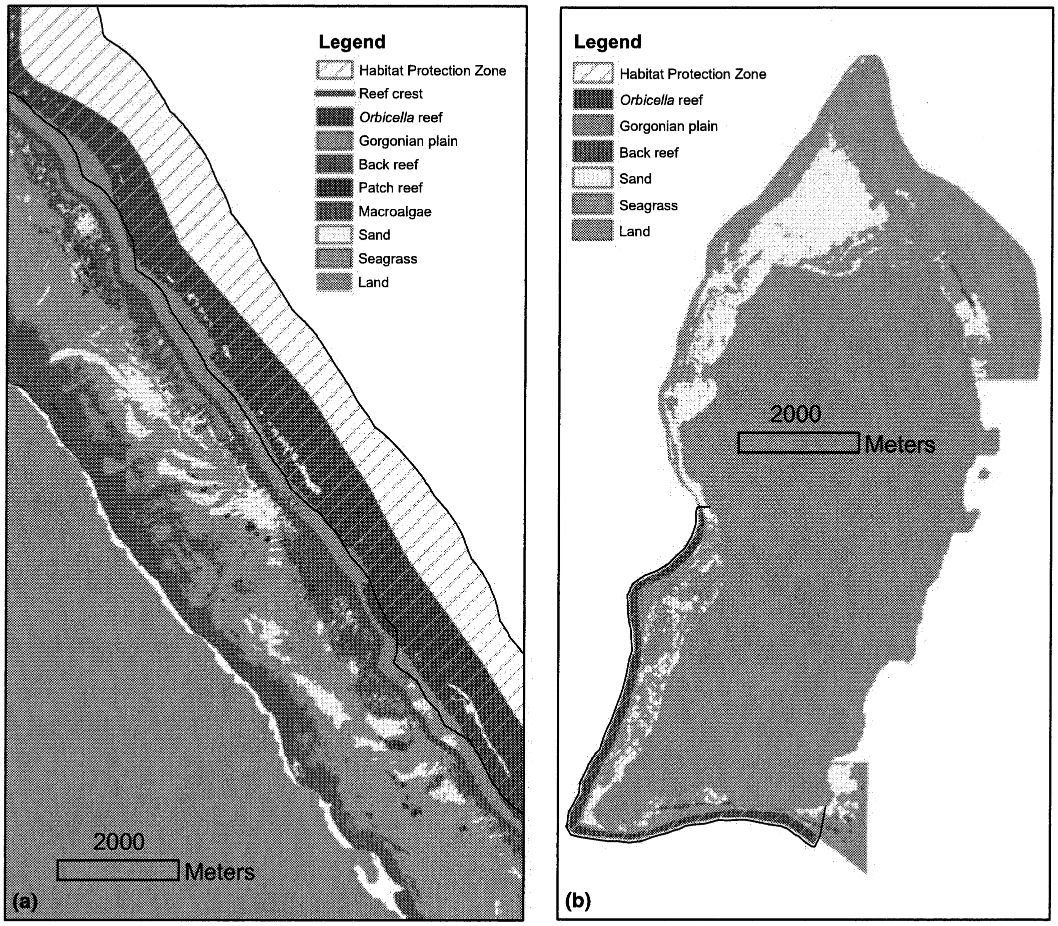

Figure 5 Illustration of the creation of Habitat Protection Zones for two contrasting seascapes in the Bahamas: Andros Island (a) and San Salvador (b). Andros is a linear and relatively sheltered system with little variation in wave exposure and a continuous *Orbicella* reef. San Salvador comprises a great range of exposure with prevailing winds emanating from the north-east. *Orbicella* reefs are located in the sheltered south-western parts of San Salvador. Gap on the eastern side of San Salvador because high-resolution Quickbird imagery was not available (though such reefs are mostly gorgonian plain).

Gorgonian plains are, therefore, an important fisheries habitat. Moreover, the areal coverage of this habitat can exceed that of *Orbicella* reefs by an order of magnitude (Harborne *et al.* 2006a), and therefore, the overall stock of parrotfish might be greater in this habitat despite lower average fish density.

Discussion and caveats

Stratifying fishing effort by the ecological needs of dominant habitats is likely to be feasible and has the potential to help attain EBFM while minimizing disruption to a herbivore fishery. There are, however, some important caveats and research requirements that ought to be considered if the ideas outlined here were implemented.

While there is no evidence to date that herbivorous fish facilitate coral recruitment and growth on gorgonian habitats, this question has not been studied in detail. It would, therefore, be useful to study algal patch dynamics and quantify the role of herbivory versus abiotic factors such as sediment scour and dislodgement under high water flow. Although herbivory tends to be relatively low in this habitat (van Rooij *et al.* 1996a; Mumby and Wabnitz 2002), it is possible that a large reduction in herbivory could have surprising and adverse effects on the octocorals that dominate the habitat. Another consideration is that the shallowest margins of a gorgonian habitat can grade into another habitat; the high relief spur and groove zone, just windward of the reef crest (Jordan-Dahlgren and Martin 1987). Before the advent of white band disease, this shallow habitat was often dominated by corals of the genus *Acropora*. Grazing tends to be intense in this shallow habitat (Hay 1981), although other herbivores, such as acanthurids also tend to be more abundant in this environment (Mumby 2006). Whether a fishery on a gorgonian plain would have an adverse effect on this shallow habitat is unclear, though the habitat rarely seems to develop high levels of macroalgae (pers. obs.). Indeed, the principle raised here – that the role of fisheries species as drivers of the health of individual reef habitats – should be extended to consider other habitats like reef crests, and shallow patch reefs.

Although the two principal forereef habitats described here tend to occur in different physical environments, any practical zoning plan would be imperfect such that fishable zones would include some coral-rich areas that benefit from high levels of herbivory. In fact, a trade-off is likely to occur between the simplicity of the zoning plan (where simple plans tend to be easier to implement) and the degree of habitat mixing within zones. The extent of such trade-offs will vary geographically depending on seascape configuration and is therefore difficult to generalize here. However, an insight can be gained by contrasting two seascape configurations in the Bahamas where herbivore exploitation is allowed (i.e. the regions of San Salvador and Andros; Fig. 5). San Salvador has a large gradient of wave exposure and it would be relatively simple to demarcate forereefs where herbivore exploitation might be permitted, that is, the southwest and southern coasts (Fig. 5b). However, *Orbicella* reefs are found throughout Andros because the reefs are somewhat sheltered and tend to have relatively little variability in exposure. Under these circumstances, the habitats exhibit a general zonation such that gorgonian plains are found just windward of the reef crest and *Orbicella* reefs are found deeper and a little further offshore than the gorgonian plain (Fig. 5a). One practical means of implementing a HPZ would be to demarcate an inner boundary a fixed distance from the conspicuous reef crest (Fig. 5a). However, if the boundary is set too close to the reef crest, it will encompass a considerable amount of the gorgonian plain and constrain fishing grounds unnecessarily. In contrast, setting the inner boundary too far from the reef crest will fail to protect some of the *Orbicella* habitat. Looking at this trade-off quantitatively, we find an optimal distance of 300–400 m from the reef crest such that it is possible to protect >85% of the *Orbicella* habitat at a cost of excluding less than 8% of potential fishing grounds (Fig. 6).

Density-dependent migration of some reef fishes has been reported from marine reserves (high density) to neighbouring fished areas where densities are lower (Abesamis and Russ 2005). It seems reasonable to ask, therefore, whether a fishery targeted on one habitat could eventually reduce the density of fish in protected habitats, thereby undermining the policy of protecting a habitat from fishing. However, there is little reason to believe that this would happen for most parrotfish. With the possible exception of one species, *Sparisoma chrysopterum*, most parrotfish appear to prefer structurally complex habitats to a gorgonian plain (Mumby and Wabnitz 2002). Moreover, because parrotfishes are highly territorial on *Orbicella* reefs (van Rooij *et al.* 1996b; Mumby and Wabnitz 2002) and prefer to spawn in this habitat (van Rooij *et al.* 1996b), it appears unlikely that migration from a desirable to less desirable habitat would occur (note that this contrasts with cases of spillover from marine reserves where density-dependent processes operated within a single habi-

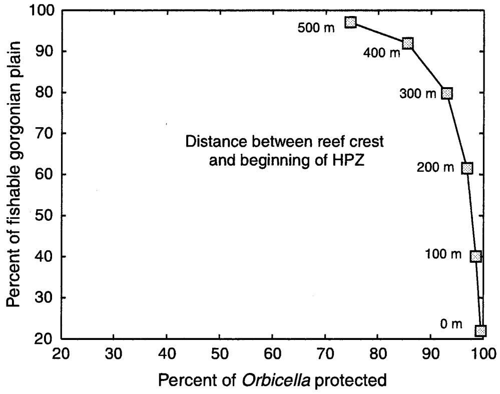

Figure 6 Trade-off incurred between habitat protection and fishery access when setting the boundary of a Habitat Protection Zone at various distances from a reef crest. Data analysed for a central section of Andros Island (Bahamas – see Fig. 5a) which represents a relatively challenging seascape for segregating fishing activities between *Orbicella* reef and gorgonian plain.

tat type). An important caveat is the assumption that parrotfish spawn within or close to their territories on the *Orbicella* reef. Relatively, few studies have quantified parrotfish spawning behaviour in the Caribbean and of these, most were carried out on *Orbicella* reefs that lie within hundreds of metres of deep water (van Rooij *et al.* 1996b; Mumby and Wabnitz 2002). In some seascapes, it appears that some parrotfish (e.g. *Sparisoma rubripinne*) undertake spawning migrations to reach deeper reefs (R.S. Nemeth, pers. comm.). The extent of such migrations should be studied and their implications considered for developing practical and efficaceous zoning plans. It would also be prudent to monitor parrotfish populations on *Orbicella* reefs if the ideas presented here were implemented.

The most effective means of avoiding ecosystem overfishing of coral reefs is to undertake a blanket ban on herbivore fisheries. Doing so avoids some of the uncertainties of parrotfish function by habitat and allows all habitat patches to experience the highest levels of herbivory possible. Thus, the recommendations presented here are not an endorsement that harvesting herbivores is a desirable outcome. Yet, if a fishery must exist then taking into account the needs of individual habitats appears to be a prudent option and one that might help to achieve EBFM. Marine spatial planning is an appropriate framework for implementation because the proposed zoning of forereef habitats for fisheries is consistent with other management considerations in the coastal zone, including biodiversity conservation and the maintenance of ecosystem services. Habitats differ in their conservation, ecological and social importance (Harborne 2009). Of eleven tropical coastal habitats, *Orbicella* reefs contain approximately 70% of Caribbean reef biodiversity and 66% of benthic species were only found in this habitat (Mumby *et al.* 2008). *Orbicella* reefs are also the most valuable habitat for a host of ecosystem services, including diving tourism, pharmaceutical products, generation of sand and species used in the curio-trade (Mumby *et al.* 2008).

Avoiding ecosystem overfishing is an important challenge for EBFM (Pikitch *et al.* 2004). To date, most attention has been placed on incorporating the role of forage fish as a prey item for apex predators. Modelling such trophic relationships is challenging but is relatively straightforward because it usually involves only one or two trophic links (Hill *et al.* 2006). However, many other ecosystem functions are considerably more complex. Here, for example, there are at least four links: parrotfish consume macroalgae, macrolgae compete with coral, corals contribute to habitat complexity, habitat complexity affects fish density by mediating predator–prey interactions, food availability, nursery and reproductive sites. It is, perhaps, not surprising that the setting of ecologically sustainable levels of parrotfish catch remains enigmatic. Moreover, even if such targets could be estimated they would generate a trade-off between fishery yield and incremental losses of ecosystem function, which itself is difficult to reconcile objectively. In short, practical measures, such as stratifying the fishery by the ecological needs of different habitats, provide a potential interim solution to a complex problem.

Acknowledgements

This research was funded by a Pew Fellowship in Marine Conservation and the European Union 7th Framework programme (P7/2007-2013) under grant agreement No. 244161. I thank Al Harborne, Nick Wolff and two referees for helpful discussions on the paper. The author apologises for the self-citation!

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Marine Reserves Enhance the Recovery of Corals on Caribbean Reefs

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Abstract

The fisheries and biodiversity benefits of marine reserves are widely recognised but there is mounting interest in exploiting the importance of herbivorous fishes as a tool to help ecosystems recover from climate change impacts. This approach might be particularly suitable for coral reefs, which are acutely threatened by climate change, yet the trophic cascades generated by reserves are strong enough that they might theoretically enhance the rate of coral recovery after disturbance. However, evidence for reserves facilitating coral recovery has been lacking. Here we investigate whether reductions in macroalgal cover, caused by recovery of herbivorous parrotfishes within a reserve, have resulted in a faster rate of coral recovery than in areas subject to fishing. Surveys of ten sites inside and outside a Bahamian marine reserve over a 2.5-year period demonstrated that increases in coral cover, including adjustments for the initial size-distribution of corals, were significantly higher at reserve sites than those in non-reserve sites. Furthermore, macroalgal cover was significantly negatively correlated with the change in total coral cover over time. Recovery rates of individual species were generally consistent with small-scale manipulations on coral-macroalgal interactions, but also revealed differences that demonstrate the difficulties of translating experiments across spatial scales. Size-frequency data indicated that species which were particularly affected by high abundances of macroalgae outside the reserve had a population bottleneck restricting the supply of smaller corals to larger size classes. Importantly, because coral cover increased from a heavily degraded state, and recovery from such states has not previously been described, similar or better outcomes should be expected for many reefs in the region. Reducing herbivore exploitation as part of an ecosystem-based management strategy for coral reefs appears to be justified.

Citation: Mumby PJ, Harborne AR (2010) Marine Reserves Enhance the Recovery of Corals on Caribbean Reefs. PLoS ONE 5(1): e8657. doi:10.1371/journal.pone.0008657

Editor: Brian Gratwicke, Smithsonian's National Zoological Park, United States of America

Received October 23, 2009; **Accepted** December 15, 2009; **Published** January 11, 2010

Funding: Funding for this study was provided by the Khalid bin Sultan Living Oceans Foundation (http://www.livingoceansfoundation.org/); the National Science Foundation (NSF - http://www.nsf.gov/); the Environmental Protection Agency (EPA - http://www.epa.gov/); the Natural Environment Research Council (NERC - http://www.nerc.ac.uk/); the Undersea Research Program of the National Oceanic and Atmospheric Administration (NURP - http://www.nurp.noaa.gov/). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

With increasing rates of global change, the need to conserve key ecosystem services, largely through conservation measures, is greater than ever [1]. In many cases, the implementation of conservation measures for dealing with global change involves a short-term economic cost to local stakeholders and adoption of conservation practices is most likely to be successful when the impacts of the conservation tool are demonstrably beneficial [2]. Frequently, however, the efficacy of conservation tools, such as reserves, is incompletely understood or controversial. This problem is amply demonstrated on coral reefs, where no-take marine reserves are the most widely-used conservation tool [3,4]. While the efficacy of reserves in promoting biodiversity and fish biomass by reducing local-scale stressors has been widely documented [5–7], there is an increasing desire to establish whether reserves can also build coral resilience and offset the effects of global climate change that elevate coral mortality and constrain coral calcification [8,9].

In Caribbean systems, protecting large herbivorous fishes from fishing can generate a trophic cascade that reduces the cover of macroalgae [10], which is a major competitor of corals [11,12]. In principle, such a shift in benthic community structure should facilitate the recovery of coral populations after bleaching events, or indeed other disturbance events such as hurricanes, that cause sudden and extensive coral mortality [13,14]. Thus, reserves in Caribbean systems have the potential to increase the resilience of coral to climate change [15], and thereby enhance the long-term services provided by these systems, such as coastal defence, tourism, and fisheries [16]. However, reserves have not yet been demonstrated to enhance coral recovery [17].

There are several explanations for the lack of data demonstrating the effects of entire reserves on coral recovery. Small-scale experimental manipulations have demonstrated that drastic reductions in fish grazing can cause harmful macroalgal blooms and reduce recovery of corals following bleaching-induced mortality [18]. While these results imply that the conservation of herbivores inside marine reserves should benefit coral recovery, extrapolating small-scale experiments to the spatial scale at which management occurs can be problematic. For example, experimental manipulations that use cages to exclude most fish do not necessarily represent conservation interventions, where relatively modest changes in fish communities are expected. Demonstrating larger-scale, *in situ* reserve impacts are also challenging because disturbances and variations in initial benthic community compositions complicate the attribution of cause and effect on individual reef trajectories.

We studied coral population dynamics at 10 sites throughout the Exuma Cays (Bahamas; Supporting Information Figure S1) over a 2.5 year period (2004–2007) in order to contrast the trajectories of coral populations both inside and outside reserves. Four sites were located in the Exuma Cays Land and Sea Park (ECLSP), a large reserve (456 km^2) that was designated in 1958 and enforced by wardens since 1986. Importantly, because the reserve location was not biased by the quality of reefs contained [19] and natural processes of larval supply do not appear to differ significantly between reserve and neighbouring reefs [20], the reserve serves as a large-scale experimental study of fishing impacts on ecosystem processes [10,20–22]. Previous studies in the ECLSP have shown that a doubling of parrotfish biomass in the reserve has reduced the cover of their macroalgal prey fourfold and that this reduction in macroalgae has led to an increase in the density of juvenile corals [10,20]. Indeed, the cover of macroalgae is strongly, linearly, and negatively related to the extent of parrotfish grazing across reefs in this region of the Bahamas (Supporting Information Figure S2, $r^2 = 0.68$, $P = 0.004$). A 2.5 year period was considered long enough to detect changes in coral cover yet short enough that differences in the trajectories among sites were not heavily influenced by multiple stochastic disturbance events.

Results and Discussion

Because the Bahamas was severely disturbed by the 1998 coral bleaching event [23], and later by hurricane Frances in the summer of 2004, coral cover was low at the beginning of the study, averaging only 7% at reserve and non-reserve sites (Supporting Information Table S1). The proportional increase in coral cover after 2.5 years was fairly high at reserve sites (mean of 19% per site) and significantly greater (one-tailed t-test $P = 0.004$) than that in non-reserve sites which, on average, exhibited no net recovery. A mechanistic insight into the change in coral cover was sought using regression onto the cover of macroalgae at the start of the study (Figure 1). Macroalgal cover explained 43% of the variance in the change in total coral cover over time ($P = 0.041$). Coral cover increased at sites with relatively low macroalgal cover but declined at sites with higher cover. The change in cover was mostly driven by two diminutive brooding species of coral (*Porites astreoides* and *Agaricia agaricites*) and one framework-building species, *Montastraea annularis*. In each of these species, the overall pattern of recovery contrasted across park boundaries, showing net recovery (increase in percentage cover) inside the park but net mortality outside (one-tailed Mann-Whitney U-test, $P<0.05$ for the brooders though only marginally significant for *M. annularis* at $P = 0.068$). The change in cover of *Agaricia* and *Porites* was moderately-strongly and negatively related to macroalgal cover ($r^2 = 0.46$, $P<0.03$ in both species) but a relationship with macroalgal cover was not evident for the trajectory of *M. annularis*.

Although trajectories of coral cover were positive inside reserves and generally negative outside reserves, our results were potentially biased by differences in the initial size-distribution of corals which varied significantly among sites in several species, including *A. agaricites* and *M. annularis* (Kolmogorov-Smirnoff test, $P<0.05$). Bias is possible because coral populations of equivalent cover but different size distributions have strikingly different scope for recovery. Imagine a series of reefs, each with identical coral cover, but some comprise a few large corals whereas others comprise many small corals. As encrusting corals grow in a linear, radial fashion [24] the final coral cover after, say, 1 year of growth is substantially greater in the community dominated by many small colonies (e.g., if the initial cover comprised 20 small colonies then the absolute increase of cover would be six times greater than a community of identical initial cover that comprised a single large colony). To address this problem we developed an abstract alternative measure using Monte Carlo simulation that took the initial size distribution of each species at each site and found the radial growth rate that most closely accounted for the difference in total cover between sampling intervals. The process was repeated at each site giving an overall 'size-adjusted rate of change of cover' (SARCC) for each coral species based on the size distribution and observed change in coral cover at that site. Although SARCC is calculated as a linear extension rate of coral it does not directly represent a radial growth rate because it is a population-level property that subsumes coral colonisation, growth, shrinkage and mortality. However, basing its calculation on the radial growth of individual corals has the desirable property of explicitly incorporating the initial size distribution of corals. It is not intended to offer any demographic insight other than if the value is positive then recruitment and growth outweigh mortality and *vice versa* (the properties of SARCC are discussed further in the Materials and Methods).

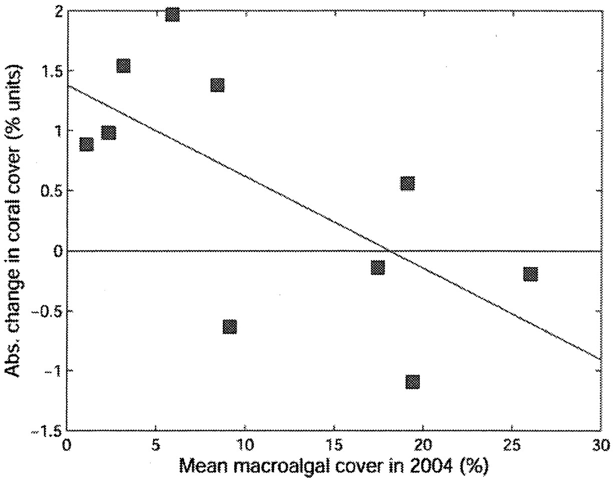

Figure 1. Effect of macroalgal cover on the absolute change in total coral cover at survey sites. Changes were between 2004 and 2007 for 10 sites in the Exuma Cays, Bahamas. The four sites in the Exuma Cays Land and Sea Park had the lowest macroalgal cover.
doi:10.1371/journal.pone.0008657.g001

Repeating our analyses with SARCC instead of absolute or proportional change in coral cover did not alter our conclusions (Figures 2 and 3). However, the difference in SARCC between reserve and non-reserve sites for *M. annularis* moved from marginal ($P = 0.068$) to clear significance ($P = 0.018$), and macroalgal cover explained a greater proportion of the variance in SARCC of *A. agaricites* ($r^2 = 0.59$, $P = 0.009$).

We also subjected our analysis to one further refinement in light of the coral bleaching event of 2005 [14]. Although coral bleaching was not severe in the Bahamas [14] (also confirmed by *in situ* observations at the study sites, Mumby pers. obs.), we calculated the accumulated thermal stress in 2005 above that of the climatological maximum monthly mean [25]. We then asked whether differences in thermal stress constituted a plausible alternative explanation of our results to that of macroalgal cover.

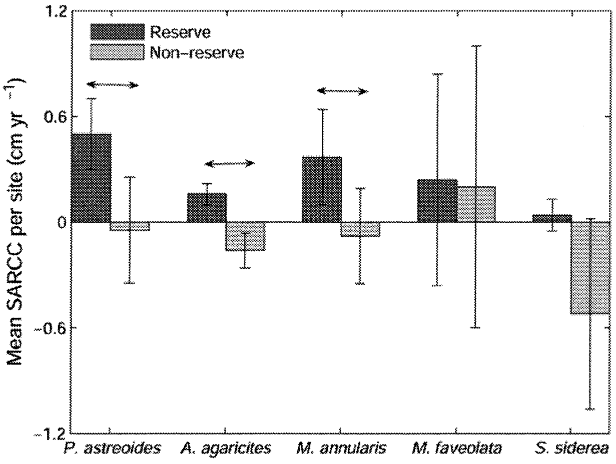

Figure 2. Size-adjusted rate of change of cover (SARCC) of dominant coral species at survey sites. Sites were inside and outside of the Exuma Cays Land and Sea Park, Bahamas. Error bars denote s.e.m. Horizontal arrow denotes significant differences (one-tailed t-test $P<0.05$).

doi:10.1371/journal.pone.0008657.g002

Adding accumulated thermal stress in a linear model against either absolute change in coral cover, proportional change in cover or SARCC did not result in a significant coefficient. In fact, the most severe thermal stress was encountered at one site in the ECLSP and no significant differences were found between the stress experienced at reserve and non-reserve sites.

Some of the most abundant macroalgae on Caribbean reefs, such as *Lobophora variegata* and *Dictyota pulchella*, compete with corals through a variety of mechanisms including direct overgrowth [12,26], pre-emption of settlement space and reduced colony growth rate [27]. Our data do not allow us to disentangle the detailed way in which macroalgae influence coral recruitment, growth and mortality because there are many ways in which demographic processes can generate the observed size distributions [28] and additional data on demographic rates would be required. However, our results do provide some insight into macroalgal impacts at population scales. Comparing the size structure of coral populations from 2004 to 2007 reveals a striking difference between reserve and non-reserve sites (Figure 4), that complements the analyses of coral cover trajectories (Figures 1–3). Coral populations exhibited a healthy demographic flux inside reserves with colonies growing from smaller size classes to larger classes (Figure 4). In the case of *Porites* and *Agaricia*, the increase in smaller size classes in 2007 was partly due to continued recruitment between census dates but successful somatic growth of established colonies also took place because new recruits could not have grown large enough to reach the fifth and fourth size classes (for *Porites* and *Agaricia* respectively) in the time elapsed between census dates. In contrast, coral populations outside the reserve lacked the demographic succession among size classes that was observed inside the reserve, implying that populations were, on average, not recovering (Figure 4). Relatively little recruitment was observed in *Porites* outside reserves and the density of colonies in larger size classes either remained stable or declined over time (Figure 4), strongly implying that a macroalgal-induced population bottleneck restricts the supply of smaller corals to larger size classes. The degree to which this bottleneck is caused by macroalgal impacts on colony somatic growth or mortality cannot be determined definitively from our data though the identification of a population bottleneck is consistent with small-scale field experiments [27] and predictions from ecological models [29]. The bottleneck appeared to be even more extreme in *Agaricia* where there was no sign of net recruitment or growth outside the reserve, a pattern in stark contrast to that observed within the reserve (Figure 4).

The mechanisms driving change in the recovery of *M. annularis* are more difficult to identify. Recruitment occurs rarely in this species and the increased densities found in the smaller size classes outside the reserve were almost entirely attributable to fission of established colonies rather than recruitment. Colony somatic growth appears to have occurred across a range of size classes inside the reserve but not so outside its boundaries; indeed a significant decline occurred in the largest size class (Figure 4). The role of macroalgae in arresting recovery outside the reserve is unclear given the lack of a simple linear relationship. Contact with macroalgae certainly has energetic costs for *M. annularis* [30] but if algae are a cause of diminished recovery, the relationship may either be complex or simply difficult to measure, possibly because

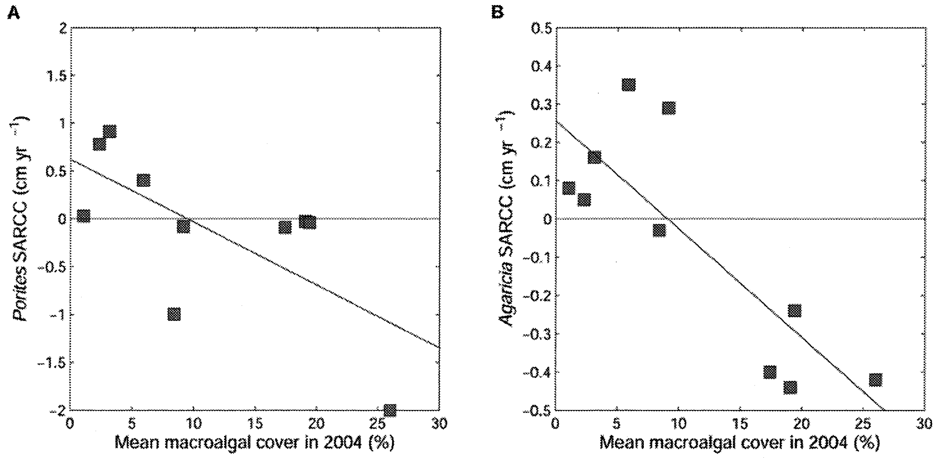

Figure 3. Effect of macroalgal cover on the size-adjusted rate of change of cover (SARCC). Panels show relationships for SARCC of *Porites astreoides* (A) and *Agaricia agaricites* (B) between 2004 and 2007 for 10 sites in the Exumas Cays, Bahamas. The four reserve sites had the lowest macroalgal cover.

doi:10.1371/journal.pone.0008657.g003

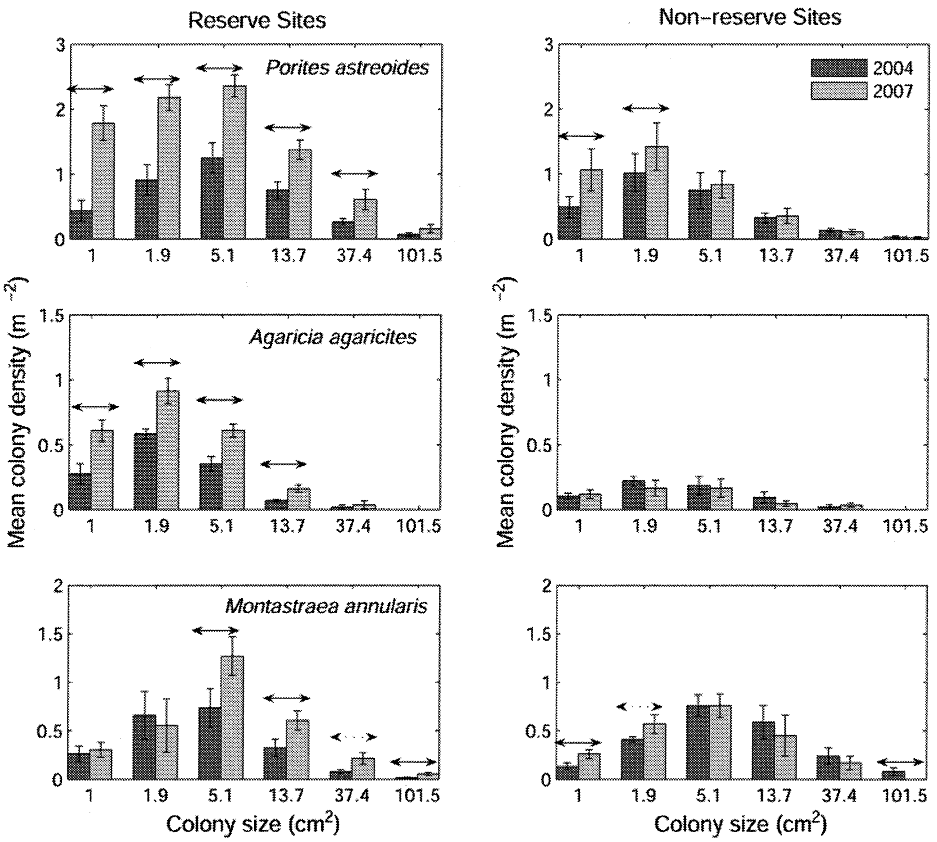

Figure 4. Size distributions of coral density in three coral species. Size distributions highlight changes over time (2004 to 2007) and differences between reserve and non-reserve sites. Error bars denote s.e.m. from site-averaged data. Horizontal arrows denote significant differences (one-tailed t-test, solid arrows for $P<0.05$, dashed arrows for $0.05<P<0.1$).
doi:10.1371/journal.pone.0008657.g004

of the high susceptibility of *M. annularis* to disease [31] which may obscure the effects of processes like algal competition.

Most studies of macroalgal impacts on coral have taken place in small experimental plots and our results provide new insight into the scalability of such studies from individual to population scales. Experimental manipulations have found that *A. agaricites* is highly susceptible to macroalgal overgrowth [32], and our study suggests that this conclusion is borne out at ecosystem scales. Experimental studies of macroalgal impacts on *P. astreoides* led us to expect a weaker impact than that found for *A. agaricites* because *P. astreoides* has been found to be relatively resistant to *Lobophora* encroachment [32] and contact with *Dictyota* has reduced coral growth rate but not led to mortality [26]. Again, this *a priori* expectation was generally supported because, despite some inter-site variation (Figure 3), mean *Porites* SARCC outside the reserve appeared to be in near-stasis (Figure 2) whereas *Agaricia* exhibited a sharp contraction (negative SARCC; Figure 2). Further, comparing the relative magnitudes of contraction outside the reserve and expansion inside the reserve (Figure 2) shows that the proportional level of contraction is tenfold weaker in *Porites* than *Agaricia* (contraction/expansion 0.05/0.5 vs. 0.16/0.16 respectively, Figure 2).

The response of large spawning corals to a gradient of macroalgal cover exhibited a variable fit to experimental predictions. Previous studies have found *Siderastrea siderea* to be unaffected by *Dictyota* contact [26] which is consistent with the absence of a significant effect in our study (Figure 2). In contrast, *Montastraea faveolata* has been found to be highly susceptible to algal overgrowth [26] whereas we found no effect (Figure 2) despite *Lobophora* and *Dictyota* being common in our study area [22]. Our finding of mixed levels of scalability from experimental outcomes to ecosystem-level effects in the Bahamas in no way implies criticism of the original experiments. However, it does reinforce the need to repeat experiments in different biophysical environments and test their scalability under a variety of conditions; a process that is rarely attempted.

Marine reserves cannot protect corals from direct climate-induced disturbance [17], but they can increase the post-disturbance recovery rate of some corals providing that macroalgae have been depleted by more abundant communities of grazers that benefit from reduced fishing pressure. Such trophic cascades are most likely in the Caribbean because of the depauperate herbivore community and increased functional importance of parrotfishes following a disease-induced mortality event that significantly reduced densities of a major herbivore taxon, the urchin *Diadema antillarum* [33]. The only other study that has attempted to quantify trajectories of coral populations inside and outside of reserves was conducted in the Indian Ocean, and found insignificant differences in coral cover growth rates [34]. The higher diversity of herbivores compared to Caribbean reefs, and therefore smaller differences in trophic cascades between fished and unfished reefs, is likely to have been an important factor limiting the effect of the reserves on coral recovery rates.

While the absolute rate of coral recovery in the ECLSP was low, it must be borne in mind that these reefs had little coral to start with and that recovery trajectories would normally accelerate as corals recover [35]. The degree to which reserve-driven rates of recovery will buffer the anticipated rise in rate of coral bleaching, disease, and severe hurricanes is currently unclear and will undoubtedly vary regionally [29]. Indeed, coral cover does not appear to be increasing in some Caribbean reserves [36] and the causation might include overwhelming coral mortality, a lack of reserve impacts on fish, or a lack of herbivore impacts on the benthos if other processes, such as nutrification or sedimentation, were to dominate the response of algae. Nonetheless, it is perhaps significant that the first documentation of net recovery from a heavily-depleted Caribbean coral community (<10% cover) stems from one of the region's most successful marine reserves. The need to take local action to reduce anthropogenic stress on reefs is both warranted and urgent.

Materials and Methods

Study Sites

Surveys were conducted at the same sites in and around the Exuma Cays Land and Sea Park (ECLSP) in October 2004 and May 2007. The location of the ECLSP was the result of a general desire for conservation in The Bahamas, and the availability of Crown Land in the Exuma Cays relatively close to the tourism centre of Nassau [19]. There is no evidence of the reserve containing especially healthy or diverse reefs before its establishment, and the entire Exuma Cays remain an area of relatively low population density and limited land-based pollution. A ban on fishing has been enforced by warden patrols since 1986. Poaching inside the ECLSP has been assessed as low [3]. Of the large commercial fishing vessels registered as fish traps in the Bahamas, 40% have sufficient size (>10 m) and are in close enough proximity (Nassau to Exuma Cays) to fish around the reserve [10]. In addition, 30 fish traps are deployed locally to the south of the reserve. Although such traps are used to target grouper species, they result in bycatch of parrotfishes [37]. The reduction in fishing inside the reserve has led to higher densities of fish and invertebrates than found outside the reserve [10,21,22]. All surveys were conducted within the forereef habitat '*Montastraea* reef' (coral-rich areas visually dominated by *Montastraea* spp.), which has the greatest diversity and density of all fish and invertebrates in the Bahamas [38]. This habitat was sampled at four sites (≈150 m×≈150 m) near the centre of the ECLSP, three sites between 5.8 and 18.1 km north of the park, and three sites around Lee Stocking Island ≈70 km south of the park (Figure S1). The same sites were used during both survey periods and identified by GPS co-ordinates, and are on a continuous stretch of forereef. The depth at each site varied from 8–17 m.

Benthic Surveys and Derivation of Coral Cover and Size-Frequency Data

At each survey site between 28 and 99 (mean 42.9) randomly-placed 1 m^2 quadrats were used to quantify coral and macroalgal cover. Content of quadrats was filmed in 20 cm swathes, using a high-resolution digital video camera. After the swathes were filmed, a second pass of the camera was made close to the substrate surface to reveal cryptic substrata on the sides of structure or under macroalgae. Coral and macroalgal covers were assessed at each site using the Vidana software [freely available from www.ex.ac.uk/msel]. Individual corals were identified to species level and their cover (size) was measured using Vidana within five randomly sub-sampled 0.04 m^2 quadrats in every 1 m^2 quadrat. The smallest corals censused by using this technique had a diameter of ≈1 cm. Corals that extended beyond quadrat boundaries were noted and removed from analyses of size distributions. More than 9,000 individual corals (>6000 for 2004, >3000 for 2007) were sampled. Although it was most appropriate to regress coral recovery onto macroalgal cover at the start of the study (i.e., 2004 which represented the level of algal cover from which corals had to recover), we also verified that the pattern of macroalgal cover persisted throughout the study. Thus, the regression of change in coral cover against macroalgal cover in 2007 was also significant, linear and negative ($r^2 = 0.63$, $P = 0.006$) as it was using 2004 data.

Calculation and Properties of SARCC for Individual Coral Species

A Monte Carlo method was used to determine SARCC. For each species and site the algorithm generated a probability distribution of finding corals in each of 10 size classes in 2004. The ten equally spaced categories of size were allowed to vary among species as appropriate. The size distribution was converted into a probability distribution by calculating the number of colonies in size class i as a proportion of the total number of colonies, n. The probability distribution was then used to generate a virtual sample of corals with the same areal cover as that species at that site. Each colony within the virtual sample was then allowed to grow for 30 months, using a fixed putative SARCC varying from -3 (contraction) to $+3$ cm yr^{-1} (expansion), in 0.05 increments. SARCC was applied as a linear radial extension rate, in a manner consistent with growth studies in corals [39]. For each possible SARCC, the total predicted cover of the species at the end of 30 months was compared to that observed in our 2007 surveys. The SARCC that resulted in the closest match between predicted and observed cover was recorded. As an example of the algorithm, if an annual growth rate of 8 mm yr^{-1} was applied to the individual colonies of *P. astreoides* observed in 2004 at site 2 of the ECLSP, then the predicted total cover of these colonies when we returned to resurvey in 2007 would match that observed. In this case, the rate of 8 mm yr^{-1} was found heuristically by trying many possible growth rates. The entire process was then repeated for a minimum of 100 virtual coral samples. Finally, the mean of the most accurate results for SARCC was calculated. The disparity in predicted and observed coral covers associated with the selected SARCC were within 0.05 of 1%.

SARCC is an abstract concept that reflects the net expansion or contraction of the entire coral population, weighted appropriately for the initial size distribution of corals. Here we summarise its desirable properties and limitations. SARCC is not a tool for demographic analysis because it subsumes processes of recruitment, growth and mortality. However, it is important to appreciate the impact of different demographic processes on SARCC.

Desirable properties of SARCC for comparisons among sites:

1) If all sites have *identical rates of recruitment, growth, and mortality and similar initial size distribution* (but perhaps different initial abundance) then they will have identical SARCC.
2) If all sites have identical demographic rates but differ in their *initial size distribution*, then SARCC is a direct measure of potential recovery rate and differs among sites appropriately
3) If all sites are identical with the exception of having *different levels of recruitment* then SARCC will be positively correlated with recruitment rate. This is appropriate because SARCC will have to 'grow faster' to account for the higher-than-expected coral cover at sites with greater rates of recruitment. After all, coral cover will have increased at a faster rate as these sites.

4) If all sites are identical with the exception of having *different levels of mortality rate* then SARCC will be negatively correlated to the pattern of mortality rate. This is appropriate because SARCC will have to select low radial growth rates (possibly negative rates) in order to match the lower-than-expected coral cover. Negative values of SARCC are possible and imply a contraction of coral colonies.
5) If all sites are identical with the exception of having *different levels of coral growth rate* then SARCC will reflect this directly and SARCC can be interpreted as a rate of colony somatic growth under these circumstances.

Limitations of SARCC:

1) SARCC should not be interpreted as a measure of somatic coral colony growth unless other demographic processes are identical among populations (which is unlikely).
2) Alone, SARCC does not quantify the relative importance of demographic processes other than if the SARCC is positive then recruitment and growth outweighs mortality and colony shrinkage (and the opposite applies if SARCC is negative).
3) In principle, two sites could have the same SARCC but very different underlying demographic processes; however, the absolute change in coral cover would also be identical so this simply underscores the inability of SARCC to reveal the *relative* rates of recruitment, growth and mortality.

Size-Distribution of Corals

To examine changes in the size distribution of coral colonies, corals were binned into six categories following a log scale (<1, 1.01–2.72, 2.73–7.39, 7.40–20.09, 20.10–54.60, 54.61–148.41 cm^2). Note that larger colonies existed in *Montastraea annularis* in 2004 but their frequency was so low that they were omitted from plots. To determine whether an increase in the density of colonies within a size category could be due to recruitment alone, we determined the maximum expected size of corals if they had recruited at some point after the first survey in 2004. Growth rates were extracted from van Moorsel's detailed observations of growth of *Porites* and *Agaricia* in this size range (1.9 mm mo.$^{-1}$ and from 0.05 mm mo.$^{-1}$ to 1 mm mo.$^{-1}$ respectively) [39]. For *Porites astreoides*, the mean growth rate implied that no coral could have reached size class 6 (54.60–148.41) and only a small fraction could have reached size class 5 (20.10–54.60) as this would require 27 months growth. Even allowing for the fastest published growth rate for *Agaricia agaricites*, corals would not have reached size class 4 if recruiting between October 2004 and May 2007.

Supporting Information

Figure S1 Location of survey sites in and around the Exuma Cays Land and Sea Park.
Found at: doi:10.1371/journal.pone.0008657.s001 (0.68 MB TIF)

Figure S2 Relationship between parrotfish grazing intensity and macroalgal cover at 10 sites in the Exumas.
Found at: doi:10.1371/journal.pone.0008657.s003 (0.58 MB TIF)

Table S1 Absolute and proportional change in coral cover, plus macroalgal cover, at each site surveyed.
Found at: doi:10.1371/journal.pone.0008657.s002 (0.04 MB DOC)

Acknowledgments

Dan Brumbaugh, Craig Dahlgren, Fio Micheli, Carrie Kappel, Kate Holmes, Kevin Buch, Renata Ferrari, Glenn Page, and Annelise Hagen helped collect data. J. Williams extracted coral size-frequency data for the 2004 surveys. Bruce Purdy of Blackbeard's cruises facilitated three field surveys.

Author Contributions

Conceived and designed the experiments: PM AH. Performed the experiments: PM AH. Analyzed the data: PM AH. Contributed reagents/materials/analysis tools: PM. Wrote the paper: PM AH.

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Vol. 222: 187–196, 2001 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published November 5

Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize

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ABSTRACT: Widespread rises in the abundance of fleshy macroalgae on Caribbean reefs within the last 20 yr have variously been attributed to eutrophication, overfishing, or the 1983–4 mass mortality of the grazing sea urchin *Diadema antillarum*. However, none of those factors can satisfactorily explain why macroalgae are abundant today even on lightly fished mid-depth reefs in sparsely populated areas. Here we explore another explanation for rises in macroalgal cover on such reefs, namely that they are a side effect of declines in coral cover. We suggest that grazing by herbivorous fishes can exclude macroalgae from mid-depth reefs with high cover of hard corals, but that on low-cover reefs, the amount of space occupied by algae overwhelms the ability of grazing fishes to crop it down. We simulated the effect of 10% and 25% rises in coral cover by attaching 'pseudo-corals' (PVC tiles covered in a non-toxic anti-fouling coating) to reef substratum in 5 × 5 m plots (3 groups: control, 10%T and 25%T) on a 12 m deep forereef site in front of Ambergris Caye, Belize. Within 3 mo of attaching tiles, macroalgae had declined by approximately 10% in 10%T plots and 25% in 25%T plots compared with control plots, and these new states persisted for the duration of the experiment (macro-algae averaging 38.0% in control plots, 28.7% in 10%T plots, and 13.6% in 25%T plots). Dramatic reductions in macroalgae may have made the 25%T plots more attractive to herbivorous fishes, as, in the later stages of the experiment, herbivorous fish biomass and acanthurid feeding rate were higher in those plots than in 10%T and control plots.

KEY WORDS: Coral reef · Grazing thresholds · Macroalgal dominance · Herbivorous fish · Caribbean

INTRODUCTION

Within the last 20 yr many Caribbean coral reefs have experienced dramatic shifts from coral-dominated to macroalgae-dominated states (Hughes 1994, Shulman & Robertson 1996, Connell 1997, Rogers et al. 1997, McClanahan & Muthiga 1998). Rises in macroalgal cover and the inability of reefs to return to their former states have been attributed to eutrophication (Lapointe 1997) or reduced grazing intensity as a consequence of overfishing of herbivorous fishes and the Caribbean-wide mass mortality of the grazing sea-urchin *Diadema antillarum* in 1983–4 (Lessios 1988, Hughes 1994, 1996, Rogers et al. 1997).

However, while there is ample evidence linking reduced herbivory and nutrient enrichment to local alterations in benthic community structure (Liddel & Ohlhorst 1986, Levitan 1988, Morrison 1988, Carpenter 1990, Lapointe et al. 1992, Hughes 1994, Aronson & Precht 2000a), there is a growing awareness that not all rises in macroalgal cover on Caribbean reefs are explicable in terms of those factors alone (McClanahan et al. 1999a, Aronson & Precht 2000b). A clear example is the rise in macroalgal cover from <5% to >60% on forereefs at Carrie Bow Caye in Belize between 1980 and 1992 (Littler et al. 1987, Aronson et al. 1994). The remoteness of those reefs, the low fishing pressure in the locality (McClanahan et al. 1999a), and the fact that *Diadema antillarum* were scarce there even in 1980 (Hay 1981) implies that the macroalgal bloom

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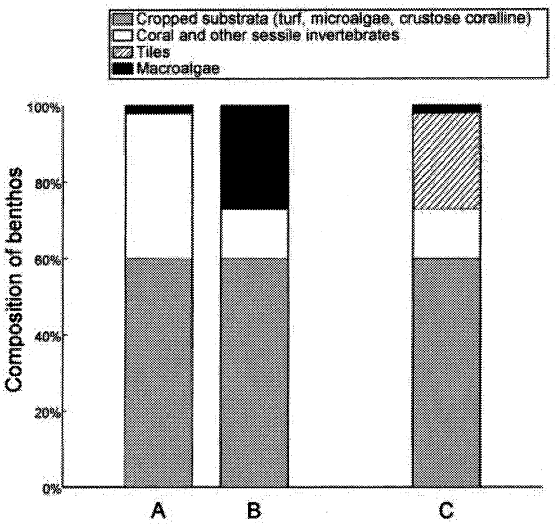

Fig. 1. Conceptual model of 'space-availability' explanation for macroalgal overgrowth of mid-depth reefs in the Caribbean: Column A represents reefs with high coral cover; Column B represents low coral-cover reefs; Column C represents the expected outcome of using 'pseudo-corals' (PVC tiles coated with non-toxic anti-fouling resin) to simulate the effect of a rise in coral cover on a low coral-cover reef

was driven by some factor other than nutrient enrichment, overfishing, or the *D. antillarum* mass mortality.

In a large-scale study of 12 to 15 m deep Caribbean reefs (Williams & Polunin 2001), we suggested a possible alternative explanation, namely that the widespread abundance of macroalgae on surveyed reefs might have been, at least in part, a side-effect of recent declines in cover of hard corals, apparently caused by bleaching events and disease epidemics on an unprecedented scale (Williams & Bunkley-Williams 1990, Shulman & Robertson 1996, Aronson & Precht 1997, McClanahan & Muthiga 1998). The basis for our 'space-availability' model (Fig. 1) was that, although biomass of herbivorous fishes was positively correlated with cover of 'cropped substrata' (i.e., turf, microalgae, or crustose corallines), herbivorous fish populations were never large enough to 'crop down' more than about 50 to 65% of substratum, even though several surveyed reefs were within effectively managed marine reserves far from any obvious source of nutrient pollution (Williams & Polunin 2001). We speculated that some combination of recruitment (Doherty & Williams 1988), territoriality (van Rooij et al. 1996), availability of hiding places (Risk 1973, Roberts & Ormond 1987), and predation (Hixon 1991) may generally limit herbivorous fish populations on mid-depth reefs to levels too low to prevent macroalgae from developing when very large amounts of substratum are colonised by algae. According to our model, on reefs with substantial cover of hard corals and other sessile invertebrates (approaching 40% or more), grazing by resident fishes, concentrated within a manageably small proportion of substratum, is sufficient to maintain benthic algal communities in cropped states and thus macroalgae are virtually excluded from such reefs (Column A in Fig. 1). However, hard coral cover is now frequently 20% or less on mid-depth Caribbean reefs (Aronson et al. 1994, Williams & Polunin 2001), and therefore, in many locations, the amount of substratum occupied by algae apparently exceeds the amount that can be kept in check by grazing fishes alone, with the result that substantial stands of macroalgae have developed and persisted (Column B in Fig. 1).

The corollary of the space-availability model is that, at sites where there is now substantial macroalgal cover, resident fish populations would be able to exclude macroalgae were coral cover to increase. To test that model, we simulated the effect of rises in coral cover by attaching pseudo-corals (PVC tiles covered in a non-toxic anti-fouling coating) to reef substratum within experimental plots. Tiles attached to the substratum covered both cropped substrata and macroalgae, and so the immediate effect of tiling would be to reduce coverage of both those algal groups in tiled plots compared with control plots. According to our model, coverage of cropped substrata is a function of local herbivorous fish biomass, and coverage of macroalgae is effectively the amount by which the proportion of substratum occupied by algae exceeds the local cropping threshold (Fig. 1). Therefore, our expectations were that (1) cover of cropped substrata within tiled plots would return to levels similar to that found in control plots, but that (2) macroalgal cover in tiled plots would decline relative to control plots by amounts approximately equivalent to the amount of space occupied by the pseudo-corals (Column C in Fig. 1). Alternative explanations for any alterations in algal community structure might be that placing tiles within plots either attracted or repelled herbivorous fishes, or altered their feeding behaviour; we therefore also monitored biomass and grazing of herbivorous fishes to establish whether there were any such differences between control and treatment plots.

METHODS

Study location. This study was conducted at a 12 m deep forereef site in front of Ambergris Caye, Belize (17° 54.9' N, 87° 56.8' W). The site appeared typical of the forereef at this depth for a distance of at least 10 km north and south of the selected study area, consisting of gently sloping low-relief spur and groove formations with hard coral cover of around 10% or less, and with abundant macroalgae, particularly *Dictyota*, *Stypopodium* and *Lobophora species* (Williams & Polunin, unpubl. data). Fishing pressure in the vicinity of the site appeared to be extremely light, as at no time during the course of an 8 mo study did we observe any fishing activity or traps on the forereef within more than 1 km of the site. *Diadema* appeared to be effectively absent from mid-depth reefs around the study area, as we saw no *Diadema* at all in the course of nearly 300 dives there. The study site was within 1 of the larger areas which we had surveyed in 1997–8, and was selected as being representative of the several lightly fished reefs on which, we speculated, high macroalgal cover might be a side-effect of low coral cover (Williams & Polunin 2001). Approximately 7 to 9 mo before the initiation of this experiment (between August and October 1998), the Belize Barrier Reef experienced 2 substantial disturbances: a major warming event (Aronson et al. 2000) and the near-miss of Hurricane Mitch. The immediate effects were dramatic in both cases: widespread coral bleaching and the near total removal of the visible portions of macroalgae from reef substratum (I. D. Williams pers. obs.). However, by the time we returned to the site in April 1999 to initiate this experiment, the 12 m deep forereef appeared to have returned to a state very similar to its pre-disturbance condition: coral cover was marginally lower in April 1999 than in April 1998 (8% compared with 10%), but macroalgal cover was almost identical (23% in April 1998, 22% in April 1999) (Williams & Polunin unpubl. data).

Experimental design. Pseudo-corals (henceforth 'tiles') were made from 1 cm thick PVC sheets cut into 15 × 15 cm squares and coated with Ceram-Kote CuBR (Freecom Inc., Big Spring, TX), a US Environmental Protection Agency-approved non-toxic and non-sloughing anti-fouling resin coating that is embedded with copper flakes. Marine growth does not attach to copper and therefore algae were prevented from colonising substratum covered by these tiles.

In late April 1999, nine 5 × 5 m experimental plots were established haphazardly along the 12 m depth contour on flat portions of solid substrate separated from each other by at least 25 m. The corners of each plot were marked with stainless steel nails that were made more visible by attachment of small strips of pink nylon tape. The 9 plots were then randomly allocated into 3 treatment groups of 3: control (no treatment), 10%T (10% of plot substratum = 2.5 m^2, to be covered in tiles), and 25%T (25% of plot substratum = 6.25 m^2, to be covered in tiles). Before the tiles were placed in the plots, benthos, herbivorous fish, and substrate rugosity were surveyed in each plot. Between 10 and 31 May 1999 approximately 1600 tiles in all were attached to the reef in the 6 treatment plots (3 × 10%T, 3 × 25%T). Tiles were attached directly onto the reef surface using stainless steel nails and were placed on areas of substrate previously occupied by algae (i.e., cropped substrata or macroalgae). Sediment was wiped off tiles at approximately monthly intervals to prevent it from building up sufficiently for algal colonisation. Tiles were initially copper coloured but within days of submersion, they changed to a light green.

Survey methodology. Benthos within plots was video surveyed 7 times: first as part of the preliminary surveys; then immediately after the tiles were fixed in experimental plots; and subsequently at 1 mo intervals for the duration of the experiment (5 mo ending in late October 1999). To reduce the impact of edge effects, only the central 3 × 3 m portion of each plot was surveyed. Preceding the preliminary surveys, each of these 3 × 3 m areas was divided into 12 permanent belt transects (each 3 × 0.25 m) using 2.5 cm stainless steel nails to fix the corners of each transect (i.e., 13 nails each 25 cm apart fixed along 2 opposite sides of the survey area). For each video survey, nylon line looped round the marking nails was used to temporarily demarcate these fixed transects. A diver swam slowly along the transects holding the camera perpendicular to the reef and using the lines bounding each transect as a visual reference to maintain the desired belt width and direction. In each survey, the entire 3 × 3 m area was video surveyed by this method. Percentage cover of benthic organisms was recorded by replaying the video tape on a television with a clear plastic sheet containing 3 randomly located 1.5 cm circles placed over the screen. Analysis began with the first frame of each transect, after which the tape was advanced to the next non-overlapping position, at which point the tape was paused and that frame analysed, and so on. Data from the 12 transects were then pooled into a total for the plot. Around 20 frames were analysed per 3 m belt and, therefore, approximately 720 points were sampled per survey per plot (12 transects × 20 frames × 3 points). A high quality digital video camera was used and hence very good resolution of single frames was obtained. Benthic organisms were recorded in the following functional categories: 'bare' substratum (i.e., no algae or other organism discernible from photograph but presumably colonised by microalgae), sand, hard coral (scleractinians), sponge, gorgonian, other invertebrates, crustose-coralline algae, turf (mixed species assemblages of diminutive algae), fleshy macroalgae (upright and anatomically complex algae with frond extension >1 cm), blue-green algae, and tile. Macroalgae were identified to genus.

Herbivorous fish (scarids, acanthurids, and pomacentrids) were censused at 4 time periods: before the tiles were attached, then 1, 3, and 5 mo after the tiles were placed. From 9 to 11 survey dives were conducted in each period, all of the plots being censused once during each survey dive. First, all scarids and acanthurids observed in or passing through a plot during a 3 min period were recorded by an observer remaining as immobile as possible approximately 3 m above the substrate at 1 corner of the plot. Species, length (estimated to nearest centimetre), and whether the fish took a bite within the plot were recorded for each fish. At the end of the 3 min period, an instantaneous count of pomacentrids was made by swimming slowly through the plot. For each fish censused, biomass was estimated using previously published mass-length relations for Caribbean fishes (Bohnsack & Harper 1988). All survey dives were carried out between 09:30 and 15:30 h (approximately 3 h after sunrise and before sunset, respectively) and by the same observer. Accuracy of length estimates was achieved by initially practising with precut lengths of electrical cable of known length and then maintained by regularly checking estimates of length of benthic objects with a scale on the side of the recording slate. Before the start of this study, accuracy of length estimation was assessed using the methods of Polunin & Roberts (1993). The mean error of estimates (30 lengths ranging from 5 to 38 cm) was <0.5 cm (Williams & Polunin unpubl. data).

As part of the preliminary surveys, substrate rugosity of each plot was estimated by 6 to 14 randomly located transects in each plot, in each of which a 3m long chain was carefully draped over the reef substratum and the straight line distance between the 2 ends measured. Rugosity was calculated by dividing the distance following bottom relief by the straight line distance between the 2 end points.

In the final month of the experiment (Month 5: October 1999), grazing rate (bites min^{-1} fish^{-1}) and pressure (bites min^{-1} plot^{-1}) of acanthurids and scarids were estimated by means of 9 to 11 replicate 20 min surveys plot^{-1}. Each of these grazing surveys had 2 components: an instantaneous estimate of abundance of acanthurids and scarids of length 5 cm and above inside the plot, followed by a 20 min period of observation in which bite rates of individual fishes were recorded by direct observation (a total of 180 to 220 min plot^{-1}). Fishes were selected haphazardly and then observed for a period up to 1 min fish^{-1}. Species, length (estimated to the nearest centimetre), total number of bites, and length of time of observation were recorded for each fish. If the fish being observed moved out of the plot in less than 20 s then the bite-count for that fish was abandoned and the data were not used in the final analysis. Grazing pressure for each species was calculated separately for each plot by multiplying estimated mean abundance (number plot^{-1}) by mean bite rate (bites min^{-1}) giving a figure for each species in terms of bites min^{-1} plot^{-1}.

Statistical analysis. To look for broad differences in benthic algal communities among the 3 treatments, algae were pooled into 2 functional categories: (1) macroalgae; and (2) the sum of the turf, bare, and crustose-coralline categories (hereafter 'cropped substrata'). Biomass of herbivorous fishes was pooled into 2 categories: (1) scarids; and (2) acanthurids. In preliminary testing of our methods we noted that although the majority of scarids and acanthurids in surveys appeared to be actively engaged in feeding, there were 2 groups of fishes that evidently covered much larger areas and fed considerably less frequently: terminal phase parrotfishes engaged in territorial defence; and small purposefully swimming groups apparently migrating up or down the reef. As our survey method involved counting all fishes in or passing through a plot during a 3 min period, we were concerned that these highly mobile fishes would be over-represented. Therefore, to strengthen the association between the derived estimates of herbivore biomass and their likely grazing impact within plots, we excluded fishes that had not been observed to feed within the plot during the 3 min survey period. Pomacentrids made up less than 5% by biomass of all herbivorous fishes censused, and we therefore considered that their greatest impact on plot benthos would probably be in territorial defence. For this family, therefore, we pooled abundance data rather than biomass data.

There were sufficient grazing data for only 3 species (*Acanthurus bahianus*, *Scarus isertii*, *Sparisoma aurofrenatum*) for us to make meaningful comparison of bite rate or local abundance of individual species among experimental groups. To enable higher level comparisons, however, data on grazing pressure (bites min^{-1} plot^{-1}) were also pooled into totals by family and for both families combined.

Differences among the 3 experimental groups (control, 10%T, 25%T) in benthic cover in each survey period, coral cover and rugosity before tiles were placed, and grazing rate in Month 5 were compared using 1-way ANOVAs (3 experimental groups, 3 replicate plots group^{-1}). We used nested ANOVAs (as there were multiple replicate fish counts for each plot in each survey) to test for differences among groups in herbivorous fish biomass or abundance at each survey period (3 experimental groups, 3 plots group^{-1}, 9 to 11 replicate counts plot^{-1} survey period^{-1}). Where ANOVA indicated significant differences among groups for any variable, Tukey's test was used to identify significant pairwise differences between groups. Differences among groups in cover of benthic algae over the last 3 mo of the experiment (i.e., Months 3 to 5, August to October 1999) were tested using repeated measures ANOVAs (3 experimental groups, each consisting of 3 replicate plots sampled at 3 survey periods). Before

ANOVA all data sets were tested for homogeneity of variance using Levene's test and normality using the Ryan-Joiner test. Where necessary (in 1 case only, pomacentrid abundance in Month 5) a square root transformation was applied to correct heterogeneity.

RESULTS

Benthos

Before the tiles were attached, there were no significant differences among experimental groups in rugosity, coral cover, macroalgal cover, or cover of cropped substrata (Table 1). All plots had low cover of hard corals (group means between 7.0 and 8.1 %), conspicuous macroalgae (group means between 21.5 and 27.0 %, consisting predominantly of *Dictyota*, *Stypopodium*, and *Lobophora* species), and substantial cover of cropped substrata (63.3 to 68.1 %).

The effect of placing tiles in treatment plots was that substratum previously occupied by algae was covered over with tiles and, therefore, immediately after the tiles were placed, mean cover of both macroalgae and cropped substrata was lower in tiled than in control plots (Fig. 2). Within 3 mo of placing the tiles, the difference in mean cover of cropped substratum between the control and tiled plots had declined to close to zero, and it remained negligible for the remaining 2 mo of the experiment (Fig. 2D). In contrast, differences between tiled and control plots in mean cover of macroalgae tended to increase until apparently reaching new equilibria after about 3 mo (Fig. 2B).

Over the final 3 mo of the experiment mean cover of cropped substrata was similar in the 3 experimental groups, namely (mean ± SD) 51.7 ± 5.7 % in control plots, 50.8 ± 4.8 % in 10 %T plots, and 51.8 ± 4.7 % in 25 %T plots. Mean macroalgal cover over the same time period differed substantially among groups (repeated measures ANOVA, $p < 0.001$), being highest in control plots (mean 38.0 ± 6.1 %), approximately 10 % lower in 10 %T plots (28.7 ± 4.3 %), and almost 25 % lower in 25 %T plots (13.6 ± 3.6 %) (Fig. 3).

Herbivorous fish

Before attachment of the tiles, there were no significant differences among the 3 treatment groups in terms of biomass of scarids or acanthurids (Table 1, Fig. 4). Pomacentrid abundance did, however, differ slightly between plots intended for 25 % tile cover and plots intended for 10 % tile cover (Tukey's $p < 0.05$, Table 1, Fig. 5). The absolute level of difference was, however, small (mean densities of 3.2 and 2.4 per 25 m^2 plot, respectively) and neither group differed from the control group.

Scarid biomass was the largest portion of total herbivore biomass for all treatment groups at all time periods. Among the 3 treatments (control, 10 %T, 25 %T) and 4 survey periods (before and 1, 3, and 5 mo after tiling), biomass of scarids was 65.4 ± 5.4 % of total herbivore biomass, acanthurids constituted 30.1 ± 5.2 %, and pomacentrids 4.5 ± 2.6 %.

There appeared to be little short-term effect of the experimental manipulation on the larger herbivores, as 1 mo after tiles were placed, there were no significant differences among treatments in scarid biomass or acanthurid biomass (Fig. 4). However, there were significant differences among treatments in the later stages of the experiment: in Month 3, mean scarid biomass was higher in 25 %T plots than in control plots (Tukey's $p < 0.05$, Fig. 4) and in Month 5 acanthurid biomass was higher in 25 %T plots than in control plots (Tukey's $p < 0.005$, Fig. 4).

Table 1. Mean ± SD benthic cover rugosity, fish density, and biomass of the 3 plots in each experimental group (control: no treatment; 10 %T: 10 % of plot substratum to be covered in tiles; 25 %T: 25 % of plot substratum to be covered in tiles) before attachment of tiles (data were pooled into averages per plot before calculation of mean and SD and therefore n = 3 in each case). p indicates results of 1-way ANOVA. *Significant difference at $p < 0.05$

Experimental group	Control	10 %T	25 %T	p
Benthos				
Macroalgae (%)	21.5 ± 6.4	27.3 ± 4.6	27.0 ± 6.9	0.291
Cropped substrata (%)	68.1 ± 5.7	63.8 ± 4.6	63.3 ± 2.8	0.415
Coral cover (%)	8.1 ± 2.3	7.2 ± 1.1	7.0 ± 1.5	0.714
Rugosity	1.2 ± 0.1	1.2 ± <0.1	1.2 ± <0.1	0.585
Herbivorous fish (mean per 25 m^2 plot)				
Scarids (g 25m^{-2})	279.7 ± 164.4	220.2 ± 83.9	311.2 ± 142.4	0.575
Acanthurids (g 25m^{-2})	159.4 ± 34.8	125.2 ± 20.4	109.3 ± 59.6	0.166
Pomacentrids (ind. 25m^{-2})	2.9 ± 2.9	2.4 ± 0.2	3.2 ± 1.4	0.034*

More than 95 % of all pomacentrids censused were of 1 species, *Stegastes partitus*, and no other species of pomacentrid was recorded in any plot at any time period at a density >0.03 m^{-2} (<1 plot^{-1}). Placing tiles had a clear and immediate effect on the abundance of these small pomacentrids (Fig. 5). From Month 1 onwards there were significant differences among treatments (1-way ANOVA, $p < 0.005$) and mean abundance per 25 m^2 plot increased in 10 %T plots over the course of the experiment from 2.4 to 15.6, and in 25 %T plots from 3.2 to 23.0, compared with a small increase in control plots (2.9 to 5.8 plot^{-1}) (Fig. 5).

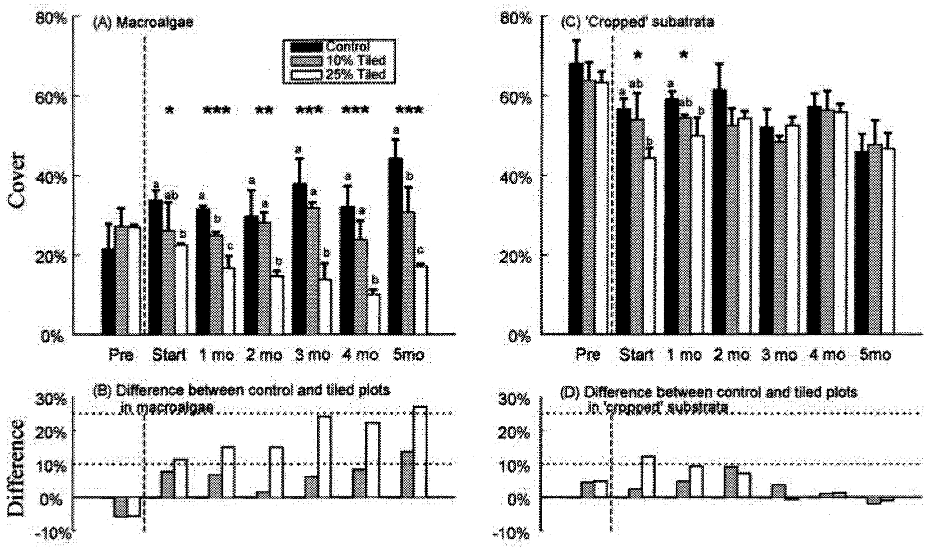

Fig. 2. Mean percentage cover of (A) macroalgae and (C) 'cropped substrata' in treatments at each survey period. Broken vertical line indicates the period in which experimental manipulation (i.e., fixing of tiles) occurred. 'Pre' indicates surveys before tiles were fixed, 'start' immediately after placing tiles, and '1 mo' to '5 mo' monthly surveys 1 to 5 mo after placing of tiles. Error bars indicate ±1 SD (n = 3 in each case). $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.005$ significant differences among groups at any survey period. Letters attached to bars indicate groups that did not differ significantly at each time period (Tukey's pairwise comparisons). The differences between control and tiled groups within survey periods (mean of control group – mean of tiled group) are shown in (B) for cover of macroalgae and (D) for cover of cropped substrata

Grazing

There was no evidence that scarid grazing rates (bites min^{-1} fish^{-1}) or grazing pressure (bites min^{-1} plot^{-1}) varied among treatments at the time that we surveyed them (Month 5, Table 2). That was true not only for pooled family data, but also for the 2 species, *Sparisoma aurofrenatum* and *Scarus isertii*, for which there were sufficient data for meaningful species-level comparison. In contrast, acanthurid grazing pressure was significantly higher in 25%T plots than in 10%T and control plots (Tukey's $p < 0.05$, Table 2). Bites by *Acanthurus bahianus* made up the great majority of acanthurid grazing (e.g., 70.5 out of a total of 77.4 bites min^{-1} in 25%T plots), and the higher grazing pressure of this species in 25%T plots than in 10%T and control plots (Tukey's $p < 0.05$, Table 2) seems to have been driven by a combination of greater mean density and higher feeding rates (Table 2).

DISCUSSION

The effects of placing tiles to simulate rises in coral cover matched the predictions of our model almost exactly (compare Fig. 3 with Fig 1). Within 2 to 3 mo of tile attachment, there were no differences in cover of cropped substrata between control and tiled plots (Fig. 2C,D), but, over the same time period, macroalgal cover in 10%T and 25%T plots had declined relative to control plots by amounts approximately equivalent to the 10% and 25%, respectively, of substratum occupied by tiles in those groups (Fig. 2A,B). Those new states then persisted for the remainder of the experiment. These results strongly support the idea of a local grazing threshold for herbivorous fishes, and, by extension, that herbivorous fishes may be able to exclude macroalgae from high coral-cover reefs but not from low coral-cover reefs, at least at the specific depth and location of this study.

An alternative explanation for declines in macroalgal cover in tiled plots is that fixing tiles in manipulated plots somehow made those areas more attractive to grazing fishes resident in the vicinity of the tiled plots and therefore artificially increased grazing pressure within those plots compared with control plots. We cannot completely rule out the possibility that our results were to some extent confounded in that way, particularly as biomass of her-

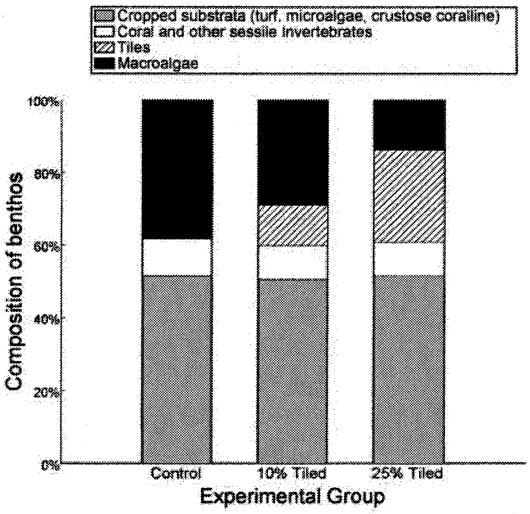

Fig. 3. Mean proportion of substratum occupied by macroalgae, 'cropped substrata', sessile invertebrates, and tiles in experimental groups during the last 3 mo of the experiment (August to October 1999)

Table 2. Mean ± SD abundance, bite rate and grazing pressure of fishes > 5 cm in experimental groups in October 1999 (Month 5). n = 3 in each cases as data were pooled into means per plot before analysis. p indicates results of 1-way ANOVAs. When ANOVA indicated significant difference among groups, Tukey's test was used to determine significant pairwise differences (at $p < 0.05$). *: significance at $p < 0.05$. C: control group

Experimental group	Control	10 %T	25 %T	p
Sparisoma aurofrenatum				
Abundance (25 m^{-2})	1.0 ± 0.3	1.0 ± 0.1	1.0 ± 0.2	0.963
Bite rate (bites min^{-1} $fish^{-1}$)	16.3 ± 3.3	13.0 ± 1.9	10.9 ± 1.6	0.083
Total bites(bites min^{-1} $plot^{-1}$)	15.8 ± 5.3	13.6 ± 10.9	10.9 ± 1.6	0.319
Scarus isertii				
Abundance (25 m^{-2})	1.9 ± 0.5	1.3 ± 0.8	2.0 ± 0.8	0.485
Bite rate (bites min^{-1} $fish^{-1}$)	34.9 ± 5.8	40.6 ± 2.5	38.7 ± 0.7	0.224
Total bites (bites min^{-1} $plot^{-1}$)	65.7 ± 21.5	53.7 ± 30.7	77.8 ± 30.0	0.596
Acanthurus bahianus				
Abundance (25 m^{-2})	0.6 ± 0.5	0.9 ± 0.2	1.3 ± 0.3	0.123
Bite rate (bites min^{-1} $fish^{-1}$)	30.0 ± 8.6	47.5 ± 5.2	54.4 ± 13.7	0.054
Total bites (bites min^{-1} $plot^{-1}$)	15.6 ± 10.9	40.7 ± 7.2	70.5 ± 33.1	0.046 *25 %T > C
Acanthurid total				
Abundance (25 m^{-2})	0.9 ± 0.6	1.1 ± 0.3	1.6 ± 0.1	0.185
Total bites (bites min^{-1} $plot^{-1}$)	24.7 ± 16.5	47.5 ± 6.3	77.4 ± 28.8	0.044 *25 %T > C
Scarid total				
Abundance (25 m^{-2})	3.0 ± 0.8	2.8 ± 0.8	3.3 ± 1.2	0.804
Total bites (bites min^{-1} $plot^{-1}$)	83.2 ± 22.5	69.8 ± 34.2	92.4 ± 33.9	0.680
Acanthurid and scarid				
Total bites (bites min^{-1} $plot^{-1}$)	107.9 ± 35.2	117.3 ± 27.9	169.8 ± 58.9	0.241

bivorous fish was greater in 25 %T plots than in control plots in the later stages of the experiment (specifically of scarids in Month 3 and acanthurids in Month 5, Fig. 4). Our subjective impression, however, was that grazing fishes were initially scarcer in tiled plots than in control plots, and it was only after substantial alterations to benthic algal communities were well under way in 25 %T plots that those areas became more attractive to grazing fishes. Evidence of fish censuses tends to support that view as (1) it was not until the 2nd census, 3 mo after tiles were placed, that there were any significant differences between 25 %T and control plots in terms of biomass of scarids or acanthurids (Fig. 4); and (2) there was no evidence that herbivore biomass was greater in 10 %T plots than in control plots at any time during the experiment (Fig. 4), in spite of which mean macroalgal cover was

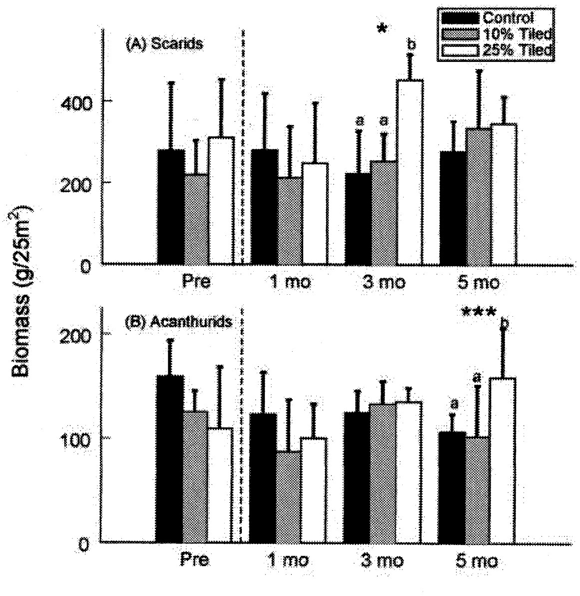

Fig. 4. Mean biomass of (A) scarids and (B) acanthurids in treatments at each survey period. Broken vertical line and *x*-axis labels as for Fig. 2. Error bars indicate ±1 SD (data were pooled into averages per plot before calculation of mean and SD and therefore n = 3 in each case). $^*p < 0.05$; $^{***}p < 0.005$ significant differences among groups at any survey period. Letters attached to bars indicate groups that did not differ significantly (Tukey's pairwise comparisons)

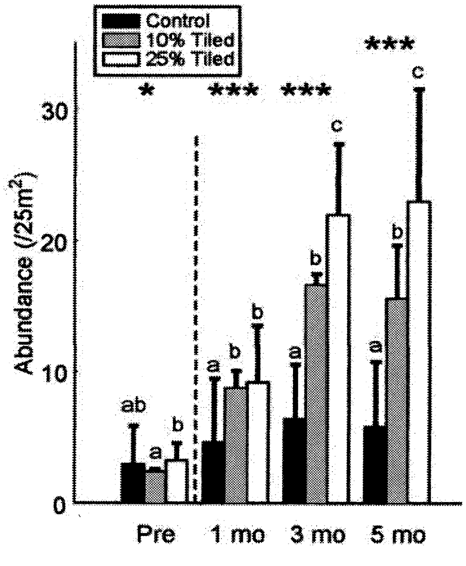

Fig. 5. Mean abundance of pomacentrids in experimental groups. Broken vertical line and column labels as for Fig. 2. Error bars indicate ±1 SD (data were pooled into averages per plot before calculation of mean and SD and therefore n = 3 in each case). $^*p < 0.05$; $^{***}p < 0.005$, significant differences among groups at any survey period. Letters attached to bars indicate groups that did not differ significantly within survey periods (Tukey's pairwise comparisons)

significantly lower in 10%T plots (28.7%) than in control plots (38.0%) over the last 3 mo of the experiment (Fig. 3). Grazing surveys were conducted in Month 5 (October 1999) by which time differences among groups in the functional composition of benthic algal communities were well established. In spite of those differences, scarid feeding rate (bites min^{-1} fish^{-1}) and total grazing pressure in plots (bites min^{-1} plot^{-1}) did not differ among experimental groups (Table 2), suggesting that placing tiles within plots had little impact on the grazing behaviour of scarids. In contrast, feeding rate and grazing pressure of the dominant acanthurid, the ocean surgeonfish *Acanthurus bahianus*, were significantly higher in 25%T than in control plots (Table 2). We assume that this was a response to improved grazing conditions in plots with comparatively low macroalgal cover (McClanahan et al. 1999b) rather than being a significant cause of macroalgal declines in the first place.

Placing tiles within plots led to a 3- to 4-fold increase in density of the pomacentrid *Stegastes partitus* (Fig. 5). This was probably a response to the large number of small hiding places under tiles that were not completely flush with the reef substrate. De Ruyter van Steveninck (1984) found no difference in terms of biomass or diversity between algal communities inside and outside of *S. partitus* territories, and similarly we think it unlikely that they had a large impact on benthic algae in plots. The impact of grazing by *S. partitus* was probably negligible as, even after local increases in density, they comprised a very small proportion of total herbivore biomass (<5%) and in any case they appeared to feed predominantly on pelagic rather than benthic algae (I. D. Williams pers. obs., Emery 1973, Nemeth 1998). If anything, the effect of increases in pomacentrid density would be to reduce grazing intensity within tiled plots as territorial defence might deter grazing by other herbivorous fishes. However, we believe that the effects of territorial defence were probably not substantial as *S. partitus* is a small pomacentrid and only appeared to defend territories against juvenile scarids and acanthurids. Even then, actual charges or attacks were rare and, generally, attacked fishes moved only a short distance away and rapidly resumed feeding (I. D. Williams pers. obs.).

For practical reasons, the spatial and temporal scale of the experiment were rather small (i.e., 5 × 5 m plots monitored for 5 mo at 1 location) and the experiment took no account of any of the longer-term changes that might follow alterations in coral and algal community structure. In particular, it is not clear from this experiment what the likely longer-term effects on herbivorous fish populations and therefore grazing potential would be. The likelihood though is that rising coral cover would be accompanied by increased 3-dimensional complexity of reef structure, which in turn would probably increase the reef's capacity to support large and diverse herbivorous fish population (Risk 1973, Roberts & Ormond 1987, Szmant 1997). Therefore, a degree of caution should be applied when extrapolating the results of this study to the wider problem of macroalgal overgrowth of Caribbean reefs. Nevertheless, these results do provide support for the concept of an upper threshold of substratum that can be cropped down by herbivorous fishes on reefs at this depth and are consistent with our large-scale correlative work (Williams & Polunin 2001).

Clearly, the concept of an upper threshold to grazing by herbivorous fishes that is implied by the model (Fig. 1) is a simplistic one. It is not our intention to imply that there are rigidly fixed or precisely predictable limits to grazing by herbivorous fishes on Caribbean reefs at this depth. In fact, the considerable short-term variability in the functional composition of benthic algal communities even in unmanipulated plots clearly argues against the idea of a fixed threshold (e.g., mean cover of cropped substrata in control plots varied between 46 and 68% over the 6 mo of the experiment, Fig. 2). We attribute that short-term variability to seasonal differences in algal growth rates, grazing rates, and the amount of scouring or other inhibition of algae during stormy weather (Aronson et al. 1994, Rogers et al. 1997). Among widely separated reefs and over extended time periods, there would inevitably be large differences in other factors affecting algal growth and succession such as sediment regime (McClanahan 1997) and nutrient supply (Cronin & Hay 1996), and in the carrying capacity and population structure of herbivorous fishes, driven by variability in factors such as microhabitat availability (Tolimieri 1998) and reef structural complexity (Risk 1973, Roberts & Ormond 1987). However, a reasonable broad generalisation is that the amount of substratum occupied by algae on high coral-cover reefs is within the range that can be cropped down by existing populations of herbivorous fishes, but, as coral cover is lost and replaced by algae on degrading reefs, and in the continuing absence of *Diadema*, then at some point the amount of substratum occupied by algae will probably overwhelm the ability of resident herbivorous fishes to crop it down. In such circumstances, stands of macroalgae can be expected to develop and tend to persist, perhaps further reinforcing the shift towards macroalgal domination by overgrowing corals and substratum and thereby adversely affecting growth, fecundity, and recruitment of corals (Tanner 1995, Hughes 1996).

The inability of herbivorous fishes to crop down the large amount of substratum occupied by algae on low-cover reefs raises the question of how important the loss of *Diadema* has generally been on reefs at this depth. Even before the *Diadema* die-off, urchin densities were ordinarily rather low on mid-depth and deeper reefs, certainly much lower than in shallow water (Lewis & Wainwright 1985, de Ruyter van Steveninck & Breeman 1987, Morrison 1988, Jackson 1991). Nevertheless, urchin grazing apparently played an important role in preventing establishment of macroalgae on mid-depth reefs in at least some locations. For example, Liddel & Ohlhorst (1992) reported *Diadema* density in August 1982 of 6.4 m^{-2} on a 15 m deep forereef site in Discovery Bay, Jamaica. Two years later (after the die-off) urchins were absent at this depth, and mean macroalgal cover had increased from 20.5% to 56.9%. *Diadema* were evidently also present even on some lightly fished deeper reefs; for example, de Ruyter van Steveninck & Breeman (1987) reported that before the mass mortality event *Diadema* were 'abundant' at 12 m deep and 'present' down to 30 m on 1 of their study reefs in Curaçao. After the loss of *Diadema* grazing from these deeper reefs, the abundance of the macroalga *Lobophora* increased from 'present' to 'patchy'. Conceivably, therefore, urchins might generally have been important grazers on mid-depth reefs with low coral cover.

It should also be noted that the results of this study, from a 12 m deep site, and our large-scale correlative work, based on a number of 12 to 15 m deep reefs (Williams & Polunin 2001), are not directly generalisable to reefs at other depths. On Caribbean reefs, grazer densities tend to be greatest in shallow water and decline with depth (Hay 1981, Hay et al. 1983, de Ruyter van Steveninck & Breeman 1987, Morrison 1988), and, therefore, although that may be offset to some extent by greater algal productivity in shallow water (Hay et al. 1983), the likelihood is that herbivore populations in shallower water would generally be able to crop down larger amounts of substratum. Certainly, in some circumstances, grazing by herbivorous fish alone can be sufficient to virtually exclude macroalgae from shallow reefs with very low coral cover (Lewis 1986, Bruggemann et al. 1994).

The few published studies of mid-depth Caribbean reefs from the early 1980s and before generally report coral cover to be 30 to 60% (Dustan & Halas 1987, Liddel & Ohlhorst 1992, Porter & Meier 1992). More recent reports indicate that coral cover is now typically 20% or less on Caribbean reefs at this depth (Aronson et al. 1994, Rogers et al. 1997, Williams & Polunin 2001). It is therefore at least plausible that declining coral cover has widely contributed to rises in macroalgal domination, at least on mid-depth reefs, and similarly that any future increases in coral cover would tend to reverse such rises in macroalgal cover.

Acknowledgements. Logistic support and permission to undertake the work were provided by Miguel Alamilla (Hol Chan Marine Reserve, Belize) and James Azueta (Department of Fisheries, Belize). James Guest, Ineke Wesseling, Mark Reynolds, and Kim Last assisted substantially with field work. We are particularly grateful for the assistance of the owners and staff of Amigos Del Mar dive shop in San Pedro, Belize.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: August 8, 2000; Accepted: February 1, 2001
Proofs received from author(s): October 16, 2001

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comentario vista publica Mayaguez

2 messages

Centro Interdisciplinario Estudios del Litoral <ciel.uprm@gmail.com> Sat, Jul 26, 2014 at 6:13 PM
To: Graciela.Garcia-Moliner@noaa.gov, graciela_cfmc@yahoo.com, Miguel.A.Rolon@noaa.gov, miguel_rolon_cfmc@yahoo.com

Consejo de Pesca del Caribe

Hato Rey, Puerto Rico

25 de Julio de 2014

Estimados Señores:

Luego de 45 años en la pesca comercial, 25 en el buceo y 15 en la pesca de los pargos de profundidad mayormente, someto a consideración mi opinión en el importante asunto que nos compete.

1- La pesca de corrida en las tres áreas (Abrir la Sierra, Bajo de Sico y Tourmaline) debe permitirse todo el ano.

2- El anclaje y cualquier arte de fondo que impacte el hábitat debe ser prohibido en todas las tres áreas.

3- Tourmaline y Abrir la Sierra deben permanecer con la temporada de veda de tres meses, como están actualmente.

4- En el área del Bajo de Sico se debe cambiar la época de veda a 12 meses.

5- En el Bajo de Sico se debe prohibir la pesca de langosta y el uso del arpón (Acción 6, Alternativa 3).

El daño provocado a nuestros recursos marinos debe y tiene que ser detenido sobre cualquier otra consideración. El hombre que actúa en contra de su conciencia será un esclavo de ella.

Edwin Font (Pauco)

Rincón, Puerto Rico

Caribbean Fishery Management Council

Hato Rey, Puerto Rico

July 25, 2014

Dear Sirs:

After 45 years as a commercial fisher, 25 of them SCUBA diving and 15 fishing mainly for deep water snappers, I would like to provide my opinion on this important matter for your consideration.

1. Surface trolling gears should be allowed in all three areas (Abrir la Sierra, Bajo de Sico y Tourmaline) during all 12 months of the year.
2. Anchoring as well as any bottom tended gear should be prohibited year-round in all three sites.
3. Tourmaline and Abrir la Sierra should remain with the currently established closed season of three months.
4. The closed season at Bajo de Sico should be changed to twelve months of the year.
5. At Bajo de Sico there should be a prohibition of lobster fishing as well as the use of spears (Action 6, Alternative 3).

The damages caused to our marine resources should be stopped over any other consideration. The man who acts against his conscience will become its slave.

Edwin Font (Pauco)

Rincón, Puerto Rico

Graciela Garcia-Moliner - NOAA Affiliate <graciela.garcia-moliner@noaa.gov> Tue, Jul 29, 2014 at 4:14 PM
To: Iris_oliveras_cfmc@yahoo.com

Comments ABT
[Quoted text hidden]

Subject:	FW: comentario vista publica Mayaguez
From:	Graciela Garcia-Moliner (graciela_cfmc@yahoo.com)
To:	Britni.LaVine@noaa.gov; Bill.Arnold@noaa.gov; Miguel.Lugo@noaa.gov; Maria.Lopez@noaa.gov; iris_oliveras_cfmc@yahoo.com;
Date:	Saturday, July 26, 2014 9:05 PM

Hola - more comments ABT!

Sent from Yahoo Mail for iPhone

From: Centro Interdisciplinario Estudios del Litoral <ciel.uprm@gmail.com>;
To: <Graciela.Garcia-Moliner@noaa.gov>; <graciela_cfmc@yahoo.com>; <Miguel.A.Rolon@noaa.gov>; <miguel_rolon_cfmc@yahoo.com>;
Subject: comentario vista publica Mayaguez
Sent: Sat, Jul 26, 2014 10:13:41 PM

Consejo de Pesca del Caribe

Hato Rey, Puerto Rico

25 de Julio de 2014

Estimados Señores:

Luego de 45 años en la pesca comercial, 25 en el buceo y 15 en la pesca de los pargos de profundidad mayormente, someto a consideración mi opinión en el importante asunto que nos compete.

1- La pesca de corrida en las tres áreas (Abrir la Sierra, Bajo de Sico y Tourmaline) debe permitirse todo el ano.

2- El anclaje y cualquier arte de fondo que impacte el hábitat debe ser prohibido en todas las tres áreas.

3- Tourmaline y Abrir la Sierra deben permanecer con la temporada de veda de tres meses, como están actualmente.

4- En el área del Bajo de Sico se debe cambiar la época de veda a 12 meses.

5- En el Bajo de Sico se debe prohibir la pesca de langosta y el uso del arpón (Acción 6, Alternativa 3).

El daño provocado a nuestros recursos marinos debe y tiene que ser detenido sobre cualquier otra consideración. El hombre que actúa en contra de su conciencia será un esclavo de ella.

Edwin Font (Pauco)

Rincón, Puerto Rico

Caribbean Fishery Management Council

Hato Rey, Puerto Rico

July 25, 2014

Dear Sirs:

After 45 years as a commercial fisher, 25 of them SCUBA diving and 15 fishing mainly for deep water snappers, I would like to provide my opinion on this important matter for your consideration.

1. Surface trolling gears should be allowed in all three areas (Abrir la Sierra, Bajo de Sico y Tourmaline) during all 12 months of the year.

2. Anchoring as well as any bottom tended gear should be prohibited year-round in all three sites.

3. Tourmaline and Abrir la Sierra should remain with the currently established closed season of three months.

4. The closed season at Bajo de Sico should be changed to twelve months of the year.

5. At Bajo de Sico there should be a prohibition of lobster fishing as well as the use of spears (Action 6, Alternative 3).

The damages caused to our marine resources should be stopped over any other consideration. The man who acts against his conscience will become its slave.

Edwin Font (Pauco)

Rincón, Puerto Rico

Subject:	FW: Protect grouper and snapper populations at ABT -- Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank
From:	Graciela Garcia-Moliner (graciela_cfmc@yahoo.com)
To:	miguel_rolon_cfmc@yahoo.com; Britni.LaVine@noaa.gov; Miguel.Lugo@noaa.gov; Bill.Arnold@noaa.gov; Maria.Lopez@noaa.gov;
Cc:	iris_oliveras_cfmc@yahoo.com;
Date:	Monday, July 28, 2014 12:02 PM

Comments for the record

Sent from Yahoo Mail for iPhone

From: Chris Lish <lishchris@yahoo.com>;
To: graciela_cfmc@yahoo.com <graciela_cfmc@yahoo.com>;
Subject: Protect grouper and snapper populations at ABT -- Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank
Sent: Mon, Jul 28, 2014 2:43:02 PM

Monday, July 28, 2014

Mr. Miguel A. Rolón, Executive Director
Caribbean Fishery Management Council
270 Muñoz Rivera Avenue, Suite 401
San Juan, Puerto Rico, 00918-1903

Subject: Protect grouper and snapper populations at ABT -- Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank

Dear Executive Director Rolón and the U.S. Caribbean Fishery Management Council,

I am writing to urge you to protect coral reef habitats and fish spawning aggregations in special ocean areas off western Puerto Rico. These resources are critical to ensure the health of marine ecosystems and coastal economies that depend on them. It is well known that fishing in areas that host annual fish spawning events threatens successful reproduction. Populations of ecologically and economically important grouper and snapper, and the fishing communities that depend on them, could suffer without these aggregations. The Council has an opportunity right now to improve protections for these important fish.

> *"As we peer into society's future, we—you and I, and our government—must avoid the impulse to live only for today, plundering for our own ease and convenience the precious resources of tomorrow. We cannot mortgage the material assets of our grandchildren without risking the loss also of their political and spiritual heritage. We want democracy to survive for all generations to come, not to become the insolvent phantom of tomorrow."*
> *-- Dwight D. Eisenhower*

Specifically, I support restricting all fishing in spawning aggregation areas at three sites off western Puerto Rico (Abrir la Sierra, Bajo de Sico, and Tourmaline) every year from December 1 through May 31. The science shows that several species of grouper and snapper spawn only during this time of year, including the Nassau grouper at Bajo de Sico, which is threatened with extinction according to the International Union for the Conservation of Nature. In addition, anchoring boats in these areas should be prohibited year-round to protect fragile coral reefs.

> *"Every man who appreciates the majesty and beauty of the wilderness and of wild life, should strike hands with the farsighted men who wish to preserve our material resources, in the effort to keep our forests and our game beasts, game-birds, and game-fish—indeed, all the living creatures of prairie and woodland and seashore—from wanton destruction. Above all, we should realize that the effort toward this end is essentially a democratic movement."*
> *-- Theodore Roosevelt*

Puerto Rico's unique natural heritage, our national passion for ocean recreation, and our brethren fishermen depend on healthy fisheries and thriving coral reefs. The Council has recognized the importance of protecting grouper and snapper spawning grounds in taking steps toward ecosystem-based fisheries management. Yet better protection is necessary to ensure a healthy future for our fish and the next generation of fishermen.

> *"A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise."*
> *-- Aldo Leopold*

Thank you for your consideration of my comments. Please do NOT add my name to your mailing list. I will learn about future developments on this issue from other sources.

Sincerely,
Christopher Lish
Olema, CA

Subject: Personal Public Comments on the Proposed Actions for Closed Seasons

From: Joe Kimmel (joe.kimmel@tampabay.rr.com)

To: graciela_cfmc@yahoo.com;

Cc: joe.kimmel@tampabay.rr.com;

Date: Wednesday, July 30, 2014 11:42 AM

Hi Graciela - Hope all is well with you. Please find attached my comments on the subject actions to be considered by the CFMC at their next meeting

Personal Public Comments on the Proposed Actions for Closed Seasons in Each of the Abrir la Sierra, Bajo de Sico and Tourmaline Banks Closed Areas. By Joe Kimmel (joe.kimmel@tampabay.rr.com 727-480-1595)

In the 1990's the Caribbean Fishery Management Council moved to establish protective measures for three areas West of Puerto Rico where fishes were known to spawn - Tourmaline Bank, Abrir La Sierra Bank, and Bajo de Sico. This management action was considered and implemented as a result of recommendations from local fishers. The implemented closed season has been and continues to be one of the most effective management measures the Council has ever promulgated. The rationale is to protect several species, originally red hind, which were being caught at reduced size and in lower numbers than in the recent past and fishers wanted to see measures taken so the red hind and associated stocks could rebound. The EEZ portions of the three areas were eventually closed to all fishing between December 1 and the end of February of each year. The number and size of individuals at the 3 sites has increased since implementation and these areas represent some of the most successful management the Council has ever supported.

Recent data collected from some of these areas (García-Sais 2007; 2010; 2013) suggests that the closures were helping the recovery of not only red hind (i.e., red hind catches had very gradually increased in size and number) but in the area of Bajo de Sico more large individuals of other groupers, snappers, lobsters, and other marine resources (corals, sponges, etc.) were seen to be in higher relative abundance and in good health. The spawning season closures seems to have been a good move by the Council and supported by fishers and the local Puerto Rican Government. One reason spawning season closures in these areas have been successful is that the general fishing public understands the needed protection of spawning resources and has accepted this form of management (i.e., it makes good common sense) and the areas are quite small – less than 3 miles square each so there are adjacent and alternative fishing areas close-by that can be fished. Thus, not only are the spawning species protected but nearby fishing for pelagic species (dolphin, wahoo, mackerel, etc.) and Highly Migratory Species such as tuna is available.

I support the Council's efforts to develop compatible regulations with those established in Federal waters. But the approach taken for the proposed actions is contrary to the protection of the fishable resources available to the people of Puerto Rico and the associated fishers. For example, by changing from a no fishing policy to allowing trolling in the closed season, the spawning groupers or snappers might be caught or the aggregations could possibly be disrupted. When groupers come together or aggregate to spawn many ripe individuals of both species gather near the bottom but eventually rise together in the water column for spawning (often 10s of meters coming very close to the water's surface). As they rise from the bottom the water pressure on their swim bladders is decreased and the bladders expand forcing eggs and sperm into the water column where the two mix so the eggs can be fertilized. Any disruption of this spawning effort (like trolling through an aggregation, reeling in a fish of any species through the aggregation, or chasing, swimming, or spearing a fish in or close by an aggregation) could jeopardize the success of the spawning event resulting in a less successful fertilization of eggs (i.e., lower percentage of fertilized eggs) or possibly a complete disruption of the spawning effort, thus limiting recruitment to these or other areas and limiting the value of having fishery management protection measures for these areas.

García-Sais, J. R, S. M. Williams, R. F. Esteves, J. Sabater, M. A. Carlo. 2013. Characterization of mesophotic benthic habitats and associated reef communities at Tourmaline Reef, Puerto Rico. Final Report submitted to the Caribbean Fishery Management Council, 94 pp.

García-Sais, J. R., R. Castro-Gomez, J. Sabater-Clavell, R. Esteves, S. Williams, and M. Carlo. 2010. Mesophotic benthic habitats and associated marine communities at Abrir La Sierra, Puerto Rico. Final Report submitted to the Caribbean Fishery Management Council for Grant FNA07NMF4410117, 122 pp.

García-Sais, J.R., R. Castro, J. Sabater-Clavell, M. Carlo, and R. Esteves. 2007. Characterization of benthic habitats and associated reef communities at Bajo de Sico Seamount, Mona Passage, Puerto Rico. Final Report submitted to the Caribbean Fishery Management Council for Grant Number NA04NMS4410345, 98 pp.

I appeal to the Council to reconsider some of their preferred actions and consider those recommended below. My suggested alternatives or revisions of Council alternatives are in red letters and highlighted in yellow. The Council alternatives with which I agree are in black letters and highlighted in blue.

Action 1: Modify the Length of the Closed Fishing Season

Alternative 1: No Action: Retain the existing length of the closed season in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Modify the Bajo de Sico closed season to be December 1– February 28.

Alternative 3: Modify the closed season to be October 1–March 31 (Preferred).

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Tourmaline Bank (Preferred).

Add a Sub-Alternative c: Bajo de Sico (Preferred). Rationale - Council needs to include all areas to develop rules as compatible.

Alternative 4: Modify the closed season to be December 1–May 31.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Alternative 5: Modify the closed season to be year round.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Action 2: Modify Reef Fish Fishing Activities

Alternative 1: No Action: Retain the existing reef fish harvest regulations in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Prohibit fishing for Council-managed reef fish in Bajo de Sico during the seasonal closure established in Action 1.

Alternative 3: Prohibit all fishing ~~for and possession of Council-managed reef fish~~ during the seasonal closure established in Action 1 (Preferred). Rationale – Any fishing in the closed areas during the spawning season may disrupt the spawning event such that recruitment protection is jeopardized .

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Tourmaline Bank (Preferred).

Suggested Sub-Alternative c: Bajo de Sico(Preferred). Need to include all areas to be compatible among areas

Action 3: Modify Spiny Lobster Fishing Activities

Alternative 1: No Action: Retain the existing spiny lobster regulations in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Prohibit fishing for spiny lobster in Bajo de Sico during the seasonal closure established in Action 1.

Alternative 3: Prohibit fishing for and possession of spiny lobster during the seasonal closure established in Action 1. (Preferred) Rationale - Scuba divers fishing for spiny lobster can disrupt spawning success of groupers and snappers by swimming through aggregations which may result in failed recruitment of fishes to this or other areas in the future.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Alternative 4: Prohibit fishing for spiny lobster year round. (Preferred).

Sub-Alternative a: Abrir La Sierra Bank. (Preferred)

Sub-Alternative b: Bajo de Sico. (Preferred)

Sub-Alternative c: Tourmaline Bank. (Preferred)

Alternative 5: Prohibit fishing for and possession of spiny lobster year round.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Alternative 6: Allow fishing for spiny lobster year round (Preferred).

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Bajo de Sico (Preferred).

Sub-Alternative c: Tourmaline Bank (Preferred).

Action 4: Prohibit Anchoring

Alternative 1: No Action: Retain the existing anchoring prohibitions in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Prohibit anchoring during the seasonal closure established in Action 1.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Alternative 3: Prohibit anchoring year round (Preferred).

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Tourmaline Bank (Preferred).

Action 5: Modify Highly Migratory Species Fishing Activities

Alternative 1: No Action: Retain the current Highly Migratory Species (HMS) fishing regulations in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Upon request of the Council, prohibit bottom longline fishing for HMS year-round in Bajo de Sico (Preferred).

Alternative 3: Upon request of the Council, prohibit fishing for, and possession of, HMS in some or all of the three areas during the seasonal closure established in Action 1.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Revised Alternative 4: Upon request of the Council, prohibit fishing for HMS ~~in some or all of the three areas during the seasonal closure established in Action 1, with an exception that would allow only surface trolling, as defined at §635.21(a)(4)(iv), for all HMS~~ in all of the three areas during the seasonal closure established in Action 1 (Preferred). Rationale – Trolling, spearing, or other human activity in the closed area could disrupt spawning success and could jeopardize recruitment to this and other areas.

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Bajo de Sico (Preferred).

Sub-Alternative c: Tourmaline Bank (Preferred).

Alternative 5: Upon request of the Council, allow fishing for bigeye, albacore, yellowfin and skipjack (BAYS) tunas with speargun fishing gear in some or all of the three areas during the seasonal closure established in Action 1.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Action 6: Modify Spearfishing Activities

Alternative 1: No Action: Retain the existing spearfishing regulations in each of the Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank closed areas.

Alternative 2: Prohibit spearfishing for Council-managed reef fish during the seasonal closure established in Action 1.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Alternative 3: Prohibit spearfishing ~~for all non-HMS-managed species~~ during the seasonal closure established in Action 1 (Preferred).

Sub-Alternative a: Abrir La Sierra Bank (Preferred).

Sub-Alternative b: Bajo de Sico (Preferred).

Sub-Alternative c: Tourmaline Bank(Preferred).

Alternative 4: Prohibit spearfishing for all non-HMS-managed species year-round.

Sub-Alternative a: Abrir La Sierra Bank.

Sub-Alternative b: Bajo de Sico.

Sub-Alternative c: Tourmaline Bank.

Written comments can be sent to the Council not later than July 31st, 2014, by regular mail to the address below, or via email to graciela_cfmc@yahoo.com. These comment were emailed aound 12:00 noon on July 30, 2014.

Subject: Pew comments on ABT

From: Leda Dunmire (LDunmire@pewtrusts.org)

To: carlosfarchette@gmail.com; gpsfish@yahoo.com;

Cc: miguel_rolon_cfmc@yahoo.com; graciela_cfmc@yahoo.com;

Date: Wednesday, July 30, 2014 1:59 PM

Good afternoon,

Attached please find our comments on the CFMC public hearing draft for developing consistent regulations for 3 seasonally closed areas off Puerto Rico. Please circulate among Council members and other interested parties. We look forward to working with the Council on this and other efforts to advance sustainable fisheries management in the region. Thank you,

Leda

Leda Dunmire
Manager, U.S. Oceans, Southeast

The Pew Charitable Trusts
p: 305.393.0934 | *e:* LDunmire@pewtrusts.org

www.pewenvironment.org

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THE PEW CHARITABLE TRUSTS

July 30, 2014

Mr. Carlos Farchette, Chairman
Caribbean Fishery Management Council
268 Munoz Rivera Ave., Suite 1108
San Juan, Puerto Rico 00918

RE: Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank

Dear Mr. Farchette,

On behalf of The Pew Charitable Trusts, please accept these comments for consideration by the Caribbean Fishery Management Council (CFMC). Right now, the CFMC has the opportunity to provide more comprehensive protection of ecologically and economically important fish spawning aggregations under its jurisdiction at three seasonal marine protected areas (MPAs) off the west coast of Puerto Rico via the amendment for consistent regulations at Abrir la Sierra, Bajo de Sico, and Tourmaline Bank (ABT). We urge the CFMC to take action at its August meeting to prevent overfishing of vulnerable and depleted grouper and snapper populations when they gather to reproduce and to protect fragile coral reef habitat. Specifically, we urge you to confirm current preferred management alternatives and adopt new ones as follows:

Action 1:

- **Change the current preferred alternative** to increase the length of the closed fishing season from October 1 through March 31 (Alternatives 3a and 3b) **to December 1 through May 31 of each year (Alternatives 4a, 4b, and 4c)** to best protect important snapper and grouper species known to spawn at these locations throughout this six-month time period.

Action 2:

- **Confirm preferred alternatives 3a and 3b** that prohibit fishing for and possession of Council-managed reef fish during the seasonal closure established in Action 1 to fully protect spawning fish, including the endangered Nassau grouper.

Action 3:

- **Change the current preferred alternative** to modify spiny lobster fishing activities at ABT from allowing fishing for spiny lobster year-round (Alternatives 6a, 6b, and 6c) **to prohibiting fishing for and possession of spiny lobster during the seasonal closure established in Action 1 (Alternatives 3a, 3b, and 3c)** to minimize impacts to critical coral reef habitat and facilitate enforcement efforts.

Action 4:

- **Confirm preferred alternatives 3a and 3b** that prohibit anchoring within ABT during the entire year to avoid impacts to critical coral reef habitat.

Action 5:

- **Confirm preferred alternative 2** that prohibits bottom long-line fishing for highly migratory species (HMS) at Bajo de Sico year round.
- **Change the current additional preferred alternative** that prohibits fishing for HMS within ABT during the seasonal closure established in Action 1 with the exception of surface trolling (Alternatives 4a, 4b, and 4c) **to prohibit fishing for HMS within ABT during the seasonal closure established in Action 1 with no exceptions (Alternatives 3a, 3b, and 3c)** to protect coral habitat and avoid incidental bycatch of vulnerable resident reef fish during the HMS fishery.

Action 6:

- **Confirm preferred alternatives 3a, 3b, and 3c** that prohibit spearfishing for all non-HMS managed species during the seasonal closure established in Action 1 to avoid bycatch and facilitate enforcement efforts.

The CFMC has proposed adopting consistent regulations at the ABT MPAs to provide more effective protection of spawning aggregations of reef fish and the benthic habitat supporting those aggregations.[1] Protections for spawning sites can help the recovery of depleted species and further boost healthy populations. A wealth of experience and research in the Caribbean region, highlighted below, underscores the need for protecting these critical reproductive events because spawning aggregations are highly susceptible to overfishing.

Fishing at spawning sites can exponentially reduce fish populations because breeding success is linked to the number of spawning fish. The best breeders may be the easiest to catch because they are large, focused on reproduction, and therefore vulnerable to capture. Grouper and snapper typically amass to spawn from a wide radius, so the losses can affect a large area. There is ample evidence documenting the rapid reduction or complete disappearance of spawning

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[1] CFMC Public Hearing Draft, Developing Consistent Regulations for Three Seasonally Closed Areas off Puerto Rico: Abrir La Sierra Bank, Bajo de Sico, and Tourmaline Bank, July 2014, p. 1.

aggregations and the resulting decline in fish populations due to heavy fishing pressure.[2,3,4,5] Commercial fishers have also provided information that indicates that these sites harbor multi-species spawning aggregations, some of which have since disappeared.[6]

However, the very behavior that makes these fish so vulnerable can also aid in their recovery. Identifying and then safeguarding spawning aggregation areas is a proven way to increase abundance. In spawning areas where fishing has stopped, fish have grown larger and more numerous, and their populations have expanded over a wider area, replenishing nearby fishing grounds.[7] In such instances, they can also produce greater numbers of eggs more likely to survive and hatch. Additional species can be attracted to this abundance, so food webs grow more robust.

Recognizing this, the CFMC helped form a regional working group on spawning aggregations through the United Nations Food and Agriculture Organization's Western Central Atlantic Fishery Commission (WECAFC). Importantly, the WECAFC Working Group expressed concerns regarding the continued decline in grouper and snapper populations that reproduce in spawning aggregations, and recommended the implementation of management measures that protect fish during their spawning season as a top priority.[8]

The CFMC has shown additional leadership in this area by implementing some seasonal fishing closures aimed at protecting known aggregation sites. The ABT MPAs were originally selected as seasonally closed areas to prevent fishing at known red hind spawning aggregation sites during their reproductive period. Protecting a red hind spawning aggregation at Hind Bank Marine Conservation District in St. Thomas, U.S. Virgin Islands, has yielded benefits for the fishery and the species, showing that adequate protection is a win-win situation.[9]

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[2] D.A. Olsen and J.A. LaPlace (1978), A study of a Virgin Islands grouper fishery based on a breeding aggregation, *Proceedings Gulf & Caribbean Fisheries Institute* 31:130-144.

[3] A. Aguilar-Perera (2006), Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast, *Marine Ecology Progress Series* 327:289-296.

[4] Y. Sadovy (1999), The case of the disappearing grouper: *Epinephelus striatus* the Nassau grouper in the Caribbean and Western Atlantic, *Proceedings Gulf & Caribbean Fisheries Institute* 45: 5–22.

[5] E. Sala, E. Ballesteros and R.M. Starr (2001), Rapid Decline of Nassau Grouper Spawning Aggregations in Belize: Fishery Management and Conservation Needs, *Fisheries* 26:23–30.

[6] Ojeda-Serrano *et al.* (2007), Reef Fish Spawning Aggregations of the Puerto Rican Shelf, *Proceedings of the Gulf and Caribbean Fisheries Institute Proceedings* 2: 401–408.

[7] C.F.G. Jeffrey, V.R. Leeworthy, M.E. Monaco, G. Piniak, and M. Fonseca (eds). 2012. *An Integrated Biogeographic Assessment of Reef Fish Populations and Fisheries in Dry Tortugas: Effects of No-Take Reserves.* NOAA Technical Memorandum NOS NCCOS 111. Prepared by the NCCOS Center for Coastal Monitoring and Assessment Biogeography Branch. Silver Spring, MD. 147 pp.

[8] FAO Western Central Atlantic Fishery Commission (2014), Report of the first meeting of the CFMC/WECAF/OSPESCA/CRFM Working Group on Spawning Aggregations, Miami, United States of America, FAO Fisheries and Aquaculture Report No. 1059, 29 pp.

[9] R.S. Nemeth (2005), Population Characteristics of a Recovering US Virgin Islands Red Hind Spawning Aggregation Following Protection, *Marine Ecology Progress Series* 286: 81–97.

New research, some of it supported by the CFMC, demonstrates that increased protections are needed to recover depleted snapper and grouper populations and maintain a healthy fishery for the future. This research has identified the existence of spawning aggregations within the ABT MPAs for red hind, Nassau, black, yellowfin and tiger grouper; as well as dog and cubera snapper from December through the end of May each year.[10,11,12,13,14,15] These recently discovered spawning aggregations of snappers and other groupers, as well as nearly pristine deep-water (*i.e.,* mesophotic) coral reef formations, at ABT are not afforded complete protection by the existing system of seasonal MPAs.[16]

Currently, the seasonal fishing closure at Bajo de Sico is six months (October 1 through March 31), but only three months at Tourmaline Bank and Abrir La Sierra Bank (December 1 through February 28). The Council's current suite of preferred alternatives would allow fishing to continue during the months when Nassau, tiger, black and yellowfin grouper; cubera, mutton, and dog snapper aggregate to spawn. To stem the decline and foster the recovery of these economically and ecologically important populations of grouper and snapper, seasonal closures for all types of fishing are needed. The timing of the closure should be aligned for all three MPAs and encompass the entire six-month period from December 1 through May 31 to fully protect all spawning aggregations at these sites.

At the April 2014 CFMC meeting in St. Croix, Science and Statistical Committee (SSC) Chairman and spawning aggregation expert Dr. Richard Appeldoorn suggested that a six-month fishing closure period from December 1-May 31 for all three areas would provide the greatest benefit in terms of protecting spawning aggregations of managed snapper and grouper species. He also requested that the CFMC not finalize any action on this amendment until the SSC had the opportunity to officially provide guidance, which we anticipate will take place during the SSC meeting scheduled for August 5-7, 2014.

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[10] J.R. García-Sais, R. Castro, J. Sabater and M. Carlo (2007), Characterization of benthic habitats and associated reef communities at Bajo de Sico Seamount, Mona Passage, Puerto Rico, Final Report submitted to Caribbean Fishery Management Council (CFMC/NOAA), 91 pp.

[11] J.R. García-Sais *et al.* (2012), Fishery independent surveys of commercially exploited fish and shellfish populations from mesophotic reefs within the Puertorrican EEZ, Final Report submitted to the Caribbean Fishery Management Council (CFMC/NOAA), 86 pp.

[12] J.R. García-Sais, S. Williams. R. Estéves, J. Sabater and M. Carlo (2013), Characterization of mesophotic benthic habitats and associated reef communities at Tourmaline Reef, Puerto Rico, Final Report submitted to the Caribbean Fishery Management Council (CFMC/NOAA), 94 pp.

[13] M. Schärer, R. Nemeth, E. Tuohy, K. Clouse, M. Nemeth and R. Appeldoorn (2014), Nassau grouper *Epinephelus striatus* Fish Spawning Aggregations in the US Caribbean, *Proceedings of the Gulf and Caribbean Fisheries Institute* 66 (in press).

[14] M.T. Schärer *et al.* (2013), Sound production associated with reproductive behavior of Nassau grouper *Epinephelus striatus* at spawning aggregations, *Endangered Species Research* 19: 29–38.

[15] M.T. Schärer *et al.* (2014), Sounds associated with the reproductive behavior of the black grouper (*Mycteroperca bonaci*), *Marine Biology* 161: 141-147.

[16] See notes 1-6 above.

Also at that meeting, NOAA General Counsel indicated that the CFMC should defer to its SSC's scientific recommendation. The CFMC is required to establish and maintain its SSC to provide scientific advice and information to support Council actions and each SSC is required to provide ongoing scientific advice for fishery management decisions.[17] Therefore, we urge the Council to seek the SSC's guidance *before* finalizing a preferred fishing closure period for ABT in Action 1 of this amendment, in order to base this decision on the best scientific information available.

Actions 2, 3, 5, and 6 should seek to minimize bycatch mortality and maximize enforcement efforts by prohibiting all fishing for and possession of reef fish, lobster, and HMS at ABT during the closed season. This should include fishing with spear and bottom long-line to protect coral habitat and avoid incidental bycatch of vulnerable resident reef fish during the HMS fishery.

Finally, in Action 4, the CFMC has rightly prioritized fragile deep-water coral reef habitat protections by selecting a prohibition on vessel anchoring within all three ABT sites during the entire year as its preferred alternative. Currently, anchoring is prohibited year-round in both the federal and state waters of Bajo de Sico only. We strongly support extending the year-round anchoring prohibition to Abrir La Sierra Bank and Tourmaline Bank to protect sensitive habitats and to provide consistency, which will simplify and enhance enforcement.

Taken together, these measures have the potential to provide much needed protection for known spawning aggregations of grouper and snapper as well as protect valuable coral reef habitat on which the fish and the fisheries depend. Consistent regulations for all three areas will also make it easier for fishers to comply and for the law enforcement agencies to implement the regulations. Thank you for considering these comments. We look forward to working with you to better protect grouper and snapper spawning aggregations as part of a strategy to ensure sustainable fish populations to support fisheries in the U.S. Virgin Islands and Puerto Rico.

Sincerely,

Leda A. Dunmire
Manager, U.S. Oceans, Southeast
The Pew Charitable Trusts

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[17] MSA § 302(g)(1)(A-B), 16 U.S.C. § 1852(g)(1)(A-B).