UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS
ECOLOGÍA

RESILIENCIA Y SUCESIÓN ECOLÓGICA DE UN ARRECIFE DE CORAL AFECTADO POR UN ENCALLAMIENTO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS BIOLÓGICAS

PRESENTA:

ISAEL VICTORIA SALAZAR

TUTOR PRINCIPAL DE TESIS: DR. HÉCTOR HERNÁNDEZ ARANA
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CIUDAD DE MÉXICO AGOSTO, 2018

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CIUDAD DE MÉXICO **AGOSTO, 2018**

UNAM POSGRADO
Ciencias Biológicas

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UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
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OFICIO FCIE/DAIP/561/2018

ASUNTO: Oficio de Jurado

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **23 de abril de 2018**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **VICTORIA SALAZAR ISAEL** con número de cuenta **98041185** con la tesis titulada: **"Resiliencia y sucesión ecológica de un arrecife de coral afectado por un encallamiento"**, realizada bajo la dirección del (la) **DR. HÉCTOR ABUID HERNÁNDEZ ARANA** y la co-dirección del **DR. JORGE ARTURO MEAVE DEL CASTILLO:**

Presidente: **DR. JUAN JACOBO SCHMITTER SOTO**
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Suplente: **DR. MIGUEL ÁNGEL RUÍZ ZÁRATE**

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 7 de junio de 2018

COORDINACIÓN

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

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DEDICATORIA

A Mariana y Quetzal,
por su amor y compañía durante estos años

A Toña e Isaac.

A MAN IS MADE

A man is made
Of flesh and blood
Of eyes and bones and water.
The very same things make his son
As those that make
His daughter.

A tree is made
Of leaf and sap,
Of bark and fruit and berries.
It keeps a bird’s nest
In its boughs
And blackbirds eat the cherries.

A table’s made
Of naked wood
Planed as smooth as milk. I wonder
If tables ever dream of sun,
Of wind, and rain, and thunder?

And when man takes
His axes and strikes
And sets the sawdust flying
Is it a table being born?
Or just a tree that’s dying?

ÍNDICE

Resumen

La resiliencia es un atributo complejo de las comunidades biológicas fundamental porque determina la recuperación después de un disturbio. La resiliencia de un comunidad biológica está compuesta por dos elementos: la resistencia a los disturbios y la sucesión ecológica. Entender la sucesión ecológica representa una herramienta en el camino para evitar que estos sistemas transiten hacia estados estables alternativos de manera permanente. En esta investigación se identifica si el proceso de sucesión ecológica que ocurre en un parche arrecifal afectado por un encallamiento, dentro de un área natural protegida, permite la recuperación del estado estable típico, en el cual los corales hermatípicos dominan.

Debido a que el encallamiento antecede a esta investigación por más de una década fue necesario identificar cuál era el estado estable previo al disturbio. Además, se reconstruyó la trayectoria sucesional seguida a partir de éste, en los sectores afectado y no afectado. Finalmente, se analizan las particularidades del proceso sucesional que ocurren en la comunidad. En el capítulo dos, el análisis basado en una perspectiva de escalas describe que antes del encallamiento el parche arrecifal Cuevones ya mostraba indicios de la pérdida de resiliencia del arrecife, y que transitaba hacia un estado estable alternativo, dominado por macroalgas carnosas, baja cobertura de coral, ausencia de reclutas de corales hermatípicos y bajas abundancias de erizos *Diadema antillarum*. Las particularidades del proceso sucesional, detalladas en el capítulo tres con la ayuda de modelación estadística, mostraron que sin importar la condición del sector analizado la cobertura de coral se redujo sin importar su contribución al desarrollo arrecifal. Las macroalgas carnosas incrementaron su cobertura, mientras las algas costrosas incrustantes mostraron una reducción. Además, la baja resiliencia de la comunidad de

Cuevones es una combinación entre una tasa mayor de reclutamiento de los corales con estrategias oportunistas, como *Porites astreoides* y virtual ausencia de los reclutas de los corales hermatípicos. Por otra parte, la contribución de *D. antillarum* en el control de la cobertura de las macroalgas carnosas se encuentra en un umbral subóptimo.

Se concluye que los resultados de esta investigación permitieron identificar qué componentes de la estructura de la comunidad y de la trayectoria sucesional brindan una mejor imagen sobre la complejidad de la resiliencia. Por otra parte, se identificó que el encallamiento actuó como un catalizador ya que las trayectorias sucesionales en los dos tipos de sectores, con y sin encallamiento, convergen sin que esto represente evidencia de recuperación sino de una transición hacia un estado estable alternativo.

Abstract

Resilience is a complex attribute of biological communities that is fundamental for community recovery. Resilience has two main features, resistance to disturbances and ecological succession. Understanding ecological succession represents a powerful tool to deter that these systems transit to alternative stable states. Hence, this research determines whether the ecological succession process of a coral patch reef affected by a ship grounding, within a marine protected area, allows the recovery of the previous stable state, in which reef building corals dominate.

Due to the ship grounding occurred more than a decade before this research, identifying the previous state was a necessary. The post-disturbance successional trajectory was revealed using historical information in both impacted and non-impacted sectors; also the current details of the ecological succession were analyzed. In chapter two, a multiscale-based analysis details that before the ship grounding the site already showed evidence of an ongoing transition towards an alternative stable state, in which fleshy algae dominated the reef surface, a low coral cover and virtual absence of recruits from reef-building coral species, together with an abundance of the sea urchin *Diadema antillarum* below the threshold of effective algal consumption. Details of the ongoing ecological succession, which are described in chapter three with the aid of statistical modeling, showed that regardless of the sector condition there was a reduction in coral cover. Fleshy algae increased their cover while crustose calcareous algae reduced it. It was inferred that the low resilience displayed by the Cuevones patch reef is a combination of a higher recruitment rate of opportunistic corals, as *Porites astreoides* than the rate of reef building corals, which were virtually absent.

Finally, it is concluded that the results of these research allowed identifying how community structure and ecological succession shape the complexity of resilience, and our results showed that the ship grounding catalyzed the transition towards an alternative stable state in the impacted sector, which converged with the trajectory of the non-impacted sector.

Introducción General

Presentación del estudio

Los arrecifes de coral son los ecosistemas marinos más productivos y albergan aproximadamente a 30 phyla (Birkeland, 2015). Cuentan con una extensión menor al 1% de la superficie del planeta y pueden generar hasta USD$352 000 ha^{-1} año^{-1} (Costanza et al., 2014). Sin embargo, la situación actual de los arrecifes de coral es preocupante. En la década de 1960 la diversidad biológica de estos ecosistemas comenzó a reducirse como consecuencia de un creciente número de actividades humanas asociadas (Jackson, Donovan, Cramer, & Lam, 2014), ocasionando cambios drásticos en la manera que funcionan. Esto permitió el reemplazo de los corales hermatípicos, elementos clave para la continua acreción arrecifal, por corales con menor capacidad de construcción arrecifal o por macroalgas carnosas, principales competidoras por espacio. Este cambio en la dominancia de especies ha desencadenado la transición generalizada de los arrecifes de coral hacia estados estables alternativos, situación que pone en riesgo su continuidad.

Para hacer frente a este problema, el conocimiento sobre la resiliencia de los arrecifes de coral brinda una oportunidad para desarrollar estrategias que desaceleren o detengan la transición hacia estados estables alternativos. En esta investigación se analiza la capacidad de resiliencia de un parche arrecifal a través de la sucesión ecológica, porque de la forma en que ésta ocurre depende que un arrecife recupere su estado estable típico, dominado por los corales hermatípicos o que, por el contrario se desarrolle uno alternativo. Para indagar sobre las particularidades del proceso de sucesión, esta investigación se desarrolló en un parche arrecifal afectado parcialmente por un encallamiento, el encallamiento sólo provoco daños físicos, es decir no hubo contaminación por combustible o carga derramados. Debido a que éste ocurrió hace más de 15 años esta investigación se divide en dos partes. En la primera, se determinan las características del estado previo al encallamiento y de la trayectoria sucesional de las porciones afectadas y no afectadas por el disturbio, así como sus diferencias y similitudes actuales. En la segunda parte de la investigación, se muestran los detalles del mecanismo sucesional que mantienen a la comunidad en un estado dominado por especies oportunistas de coral y por macroalgas carnosas.

Sucesión ecológica

El concepto de sucesión ecológica se utiliza para referirse a los cambios en la estructura y dinámica de una comunidad después de que se ha abierto un espacio lo suficientemente grande que permita un proceso de recolonización (Clements, 1916). El proceso sucesional, en términos de las condiciones iniciales, puede distinguirse en dos tipos: sucesión primaria, que ocurre en ambientes totalmente desprovistos de vida; y sucesión secundaria, que tiene lugar cuando la comunidad ha sido desprovista de algunos elementos, generalmente los dominantes (Begon, Townsend, & Harper, 2006). En este último proceso, la comunidad se recupera a partir del crecimiento de los individuos que sobreviven a la remoción y de la colonización de las zonas vecinas al sitio abierto. El proceso sucesional puede ocurrir a través de tres mecanismos (Connell & Slatyer, 1977). El primero se conoce como facilitación y consiste en que las especies que se establecen consecutivamente en el sitio van modificando el ambiente de manera constante, favoreciendo que otras especies puedan ingresar y reemplazarlas, ya que las que han modificado el ambiente no son capaces de sobrevivir en las condiciones de vida que crean. Cuando las especies en turno ya no facilitan la entrada de otras especies el mecanismo deja de actuar (e.g., Gallagher, Jumars, & Trueblood, 1983). La segunda forma en la que puede operar la sucesión, denominada tolerancia, establece que las especies que llegan primero no facilitan ni perjudican el establecimiento de otras y pueden coexistir con las especies de etapas tardías, a diferencia de lo que ocurre con el mecanismo de facilitación, aunque deben ser capaces de crecer con niveles más bajos de recursos. El tercer mecanismo sucesional, denominado inhibición, en realidad puede considerarse el mecanismo antisucesional, ya que establece que algunas especies pioneras acaparan el sitio, impidiendo que las especies posteriores puedan desarrollarse, lo cual resulta además en un cambio mucho más lento en las comunidades. Las especies tardías se caracterizan por ser más longevas y acumularse gradualmente al ir sustituyendo a los individuos de las especies pioneras que son removidos.

Los procesos sucesionales están determinados por tres condiciones generales (disponibilidad de espacio, disponibilidad de especies y el desempeño de las especies) las cuales, a su vez, responden a factores que actúan en diferentes escalas espacio-temporales (Pickett, Collins, & Armesto, 1987; Sheley, Mangold, & Anderson, 2006; Sousa, 1984). Entre los factores que actúan sobre estas tres condiciones están los cambios en el ambiente, para los cuales se pueden distinguir dos extremos (Sousa, 1984). Uno de ellos corresponde a los cambios que ocurren con mucha frecuencia y cuya intensidad no produce grandes modificaciones en la comunidad. El otro extremo corresponde a los cambios que ocurren más o menos de manera esporádica, pero cuya intensidad es tan grande que modifica la dinámica de las comunidades, y que cuando sobrepasan la capacidad de resistencia de la comunidad representan catástrofes para éstas (Fig. 1). En los cambios que constituyen catástrofes para la comunidad se pueden identificar dos componentes. Por un lado está el disturbio, fenómeno que ha sido definido como un evento que genera cambios sustanciales en la comunidad, favoreciendo la apertura de espacios para colonizar, y que normalmente es caracterizado por su tipo, por su frecuencia, por el área sobre la que se percibe su efecto y por su intensidad (Rykiel, 1985; Sousa, 1984; White & Pickett, 1985). Por otro lado, el componente conocido como perturbación se refiere a la magnitud y la dirección de los cambios que tienen lugar en la comunidad como consecuencia de un disturbio (Connell, 1978; Connell & Keough, 1985; Connell & Slatyer, 1977; Rykiel, 1985; White & Pickett, 1985).

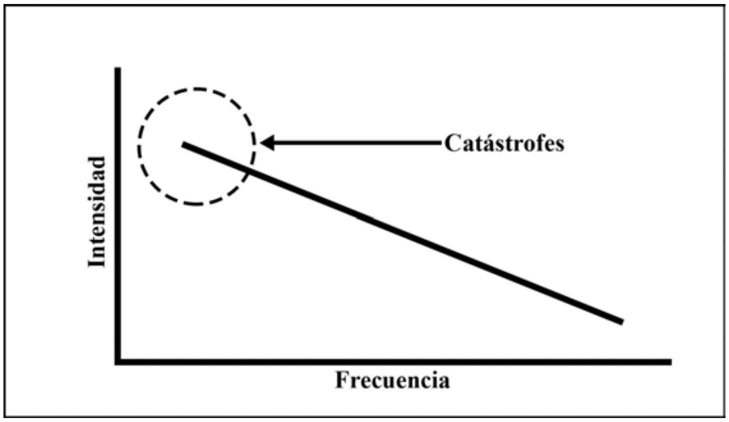

Figura 1. Relación entre los frecuencia y la intensidad de los cambios ambientales que actúan sobre una comunidad.

La forma en que ocurre el proceso de sucesión después de un disturbio ha sido tema de discusión por mucho tiempo. En el primer cuarto del siglo XX dos propuestas buscaron dar claridad a cuestiones tales como el origen, función y mantenimiento de las comunidades bióticas. La primera de ellas, conocida como la hipótesis superorganísmica (Clements, 1916), establece que en las comunidades existe una interdependencia muy fuerte entre las especies que la componen, lo cual hace que la forma en que aquella se estructura una cierta comunidad sea predecible. En contraste, la hipótesis individualista (Gleason, 1926) sostiene que las asociaciones de especies son el resultado de que éstas tengan comportamientos ecológicos diferenciados. Además, otorga mayor importancia al azar, reconociendo que las comunidades no tienen límites definidos y que su composición no es predecible. A un siglo del surgimiento de estas contrastantes visiones, las diversas interpretaciones de esas propuestas originales han dado lugar a una notable diversificación en el campo de la ecología de comunidades de las ideas relacionadas con su naturaleza (Stiling, 2002; Wilson, Ullmann, & Bannister, 1996). Entre esta diversidad de ideas, destaca una que es particularmente relevante para este estudio, la de los estados estables alternativos (Holling, 1973; Lewontin, 1969; May, 1977).

Estado estables alternativos

La hipótesis de los estados alternativos surge a partir del reconocimiento de que el contexto ambiental en el que se desarrollan las comunidades es dinámico y, con frecuencia, impredecible. De esta consideración se desprenden preguntas sobre la capacidad de las comunidades de persistir en el tiempo y de ocupar el espacio, de transformarse en unas comunidades nuevas, de modificarse para hacer frente a las condiciones que no se habían presentado antes, y sobre las circunstancias en las que ocurren tales modificaciones o transformaciones de las comunidades (Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Tokeshi, 1998). Inicialmente, el estado estable de una comunidad se definió como un dominio de atracción hacia el que se dirige una comunidad durante su desarrollo (Lewontin, 1969), y la existencia de estados estables alternativos depende de si todas las trayectorias posibles de una comunidad la conducen a un solo punto de atracción o si las condiciones iniciales determinan el punto al que al que la comunidad sería atraída (Dudgeon, Aronson, Bruno, & Precht, 2010; Holling, 1973; May, 1977). Las formas en que una comunidad se desplaza hacia un estado estable alternativo se pueden agrupar en dos perspectivas (Beisner, Haydon, & Cuddington, 2003). La perspectiva comunitaria reconoce que las variables de estado son las especies que componen a la comunidad y que la modificación directa de sus poblaciones conduce a la comunidad hacia un estado estable alternativo (Beisner et al., 2003; Holling, 1973). En esta perspectiva la transición de un estado a otro es causada por disturbios puntuales, razón principal de que haya múltiples puntos de atracción bien definidos de manera simultánea en función de un mismo conjunto de condiciones ambientales (Beisner et al., 2003; Dudgeon et al., 2010; Fung, Seymour, & Johnson, 2011; Holling, 1973; Lewontin, 1969). Desde esta perspectiva, cuando la magnitud del disturbio que afecta a una comunidad produce un rompimiento de las relaciones entre las especies, se ejerce un forzamiento sobre la comunidad, favoreciendo el reinicio del proceso sucesional. Si el proceso sucesional culmina con la recomposición de las relaciones entre las especies y los procesos originales, y además ocurre de manera independiente del tipo de disturbio, se considera que la comunidad sólo posee un estado estable (Fung et al., 2011; Holling, 1973; Knowlton, 1992; Lewontin, 1969; Scheffer et al., 2001). Un ejemplo de la existencia de estados alternativos acorde con la perspectiva comunitaria lo ofrecen los mecanismos de sucesión propuestos por Connell y Slatyer (1977). En contraste, en la perspectiva conocida como perspectiva ecosistémica (Scheffer *et al*., 2001; Scheffer & Carpenter, 2003), los cambios de estado son consecuencia de las modificaciones en los parámetros que determinan la abundancia de las poblaciones en una comunidad; por ejemplo, las tasas a las que las larvas de coral se establecen. Al ser los parámetros los que se modifican, los puntos de atracción no existen de manera simultánea, sino que existen una vez que los parámetros se modifican (Scheffer et al., 2001). En este caso, la comunidad potencialmente posee tantos estados como disturbios ocurran, si es que éstos modifican las condiciones en las que se desarrollan las comunidades.

Aunque el significado del concepto de estabilidad en Ecología de Comunidades dista de ser fijo, es posible reconocer en los sistemas un cierto grado de continuidad espacial y temporal (Tokeshi, 1998). La estabilidad de los estados que alcance una determinada comunidad depende tanto del contexto ambiental en el que se desarrolla como de la trayectoria previa de ésta, lo que determina los patrones espaciales y temporales de las especies que la componen y alrededor de un dominio de atracción (Lewontin, 1969). En el caso de la capacidad de desarrollar múltiples estados estables, éstos pueden presentarse bajo el mismo régimen ambiental. La capacidad que tienen las comunidad de recuperar el estado estable previo a un fenómeno de disturbio se denomina resiliencia (Ives & Carpenter, 2007; Ives, Dennis, Cottingham, & Carpenter, 2003; Nyström, Graham, Lokrantz, & Norström, 2008).

La resiliencia como una medida de estabilidad de las comunidades

El estrés ambiental que se genera después de un disturbio actúa como un filtro para las especies que alcanzan el sitio (Sousa, 1984). La importancia que las interacciones tengan en la forma en que la comunidad funciona determinarían su resiliencia y su estabilidad. Si una comunidad se desplaza de un estado a otro, y permanece en este último, su resiliencia es menor que la de una comunidad que es capaz de regresar al estado previo al disturbio (Ives & Carpenter, 2007; Ives et al., 2003). Después de un disturbio, la resiliencia de una comunidad depende de: (1) de la identidad específica de las poblaciones que logran permanecer en el sitio después del disturbio, (2) del tipo, intensidad e importancia de las interacciones que entre éstas se (re)establezcan (Freckleton & Watkinson, 2001), y (3) de la conectividad que la comunidad afectada mantenga con otras (Mumby & Hastings, 2008). La resiliencia de la comunidad y la velocidad de recuperación a un estado pre-disturbio son utilizadas como medidas de la estabilidad del sistema. Una comunidad posee una estabilidad alta cuando después de un disturbio la dinámica adquirida le permite invariablemente recuperar la estructura que caracterizaba previamente dicha comunidad. En contraste, una comunidad es poco estable cuando el disturbio propicia que la dinámica del sistema derive hacia un estado alternativo. Mientras más estados potencialmente pueda adquirir una comunidad, menos resiliente y estable será (Ives & Carpenter, 2007; Ives et al., 2003), y menor será la probabilidad de recuperarse después de un disturbio.

Características generales de los arrecifes de coral

Los arrecifes de coral son estructuras biogénicas producto de la acumulación, durante largos periodos de tiempo, de los esqueletos calcáreos de las especies de corales hermatípicos (Schuhmacher & Zibrowius, 1985; Veron, 2000). Estos arrecifes se desarrollan preferentemente en zonas someras del litoral tropical en donde las aguas son transparentes y carecen de grandes variaciones en la temperatura, poseen una tasa de resuspensión baja y son pobres en términos de los nutrientes, ya que esto es un requisito para que sean las colonias de coral las que crezcan (Knowlton, 2001; Moberg & Folke, 1999). En los arrecifes de coral se han reconocido tres grupos que funcionan como los principales estructuradores de la comunidad. El primero de ellos corresponde a los grupos algales, además de ser los productores primarios, juegan un papel fundamental en la dinámica de la comunidad, ya que son capaces de favorecer o impedir el establecimiento de las especies de coral (Belliveau & Paul, 2002; Diaz-Pulido, Harii, McCook, & Hoegh-Guldberg, 2010; Morse, Hooker, Morse, & Jensen, 1988; Mumby, Foster, & Fahy, 2005). El segundo componente que posee un papel importante en el proceso de estructuración de una comunidad son los consumidores primarios. Los principales herbívoros de las comunidades arrecifales son los peces (Acanthuridae y Scaridae). En su conjunto una comunidad sana de peces herbívoros tiene la capacidad de mantener la cobertura de macroalgas carnosas bajo límites en los cuales la cobertura de coral se pueda incrementar (Mumby et al., 2006) permitiendo conservar la resiliencia de los arrecifes de coral. Con el incremento en la intensidad de pesca y la consecuente reducción gradual de la biomasa de peces se generaron las condiciones óptimas tanto para el incremento de la cobertura de coral como para el incremento en importancia del erizo de mar *Diadema antillarum* como consumidor de la algas (Carpenter, 1981; Carpenter & Edmunds, 2006; Jackson et al., 2001). Esta reducción en la abundancia de la comunidad de peces favoreció que los erizos de mar, especialmente *D. antillarum*, incrementaran su importancia como consumidores de la biomasa algal (Carpenter, 1981; Carpenter & Edmunds, 2006). La persistencia de los efectos de la sobrepesca junto con la mortalidad masiva de *D. antillarum* en los años 1983-1984 permitió identificar a esta especie como el principal herbívoro en las comunidades de Caribe (Carpenter, 1990; Edmunds & Carpenter, 2001). Después de la mortalidad masiva, el proceso de recuperación del erizo de mar tuvo un efecto negativo sobre la cobertura de algas y uno positivo sobre la densidad de reclutas, lo que sustenta el reconocimiento del erizo de mar como especie clave en la dinámica de las comunidades arrecifales (Hay, 1984; Myhre & Acevedo-Gutierrez, 2007; Tuya, Boyra, Sanchez-Jerez, Barbera, & Haroun, 2004). Por último, las especies de corales hermatípicos son las constructoras de la matriz de carbonato de calcio sobre la cual se establecen todas las especies asociadas a las comunidades arrecifales (Schuhmacher & Zibrowius, 1985; Veron, 2000). La importancia de estas especies de coral en la acreción de la matriz arrecifal depende de las formas de crecimiento que éstas tengan; las que tienen un crecimiento ramificado tienen un mayor aporte al desarrollo de la complejidad física del arrecife y la generación de sitios de refugio, en comparación con las que tienen un crecimiento masivo (Knudby & LeDrew, 2007).

Los encallamientos como disturbios

Como consecuencia del número y la intensidad de disturbios humanos que afectan a las estructuras arrecifales (e.g., pesca, desarrollo industrial y turístico; Belliveau & Paul, 2002), estos sistemas enfrentan una situación de cambio de estado estable (e.g., las algas carnosas; Box & Mumby, 2007; Jompa & McCook, 2002a, 2002b, 2003a, 2003b; McCook, Jompa, & Diaz-Pulido, 2001; Mumby et al., 2005; Quan-Young & Espinoza-Avalos, 2006; Titlyanov & Titlyanova, 2008, 2009), ya que de ser arrecifes cuya cobertura estaba dominada por las colonias de coral, se convierten en sitios dominados por algas y coberturas de coral bajas (Edmunds & Carpenter, 2001). Las algas crecen sobre el sitio ocupándolo casi por completo, y al impedir a través de diferentes mecanismos como la competencia el establecimiento de las larvas de coral, retardan la recuperación de las comunidades arrecifales.

Los encallamientos ocurren cuando, por accidente o negligencia, una embarcación ha golpeado y queda varada por encima de algún componente de la línea costera o el litoral marino. Los encallamientos en arrecifes de coral afectan a las estructuras calcáreas que se acumulan como producto de la actividad metabólica de los pólipos que viven sobre ellas. En realidad, más que ser un tipo de disturbio, los encallamientos son eventos complejos que pueden provocar diferentes disturbios en cadena (Jaap, 2000). Por un lado, los encallamientos desprenden y fracturan las colonias de coral al ser golpeadas. Esto trae por consecuencia que algunas especies desaparezcan de la zona. Posteriormente, el movimiento del agua hace que las embarcaciones que encallan se muevan y sigan ocasionando daños a las colonias y a los fragmentos sueltos. El encallamiento, además, favorece la incorporación de sedimentos en el arrecife, dificultando la fijación de los fragmentos desprendidos y el establecimiento posterior de las larvas de coral. Además, por si esto fuera insuficiente, durante el rescate se corre el riesgo de que el sustrato resulte con mayor daño, haciendo que el problema al que se enfrenta la comunidad se agrave.

Objetivo

El objetivo de esta tesis es investigar si el proceso de sucesión secundaria que tiene lugar en una comunidad arrecifal afectada por un encallamiento permite que los procesos clave en la continuidad de las comunidades arrecifales se recuperen, o si, por el contrario, el proceso sucesional que se desarrolla más bien favorece la transición hacia un estado estable alternativo. La hipótesis general que subyace esta investigación es que la comunidad es resiliente; la predicción que se hizo a partir de esta hipótesis es que la dinámica del proceso sucesional del sitio conducirá a la dominancia de las principales especies constructoras del arrecife.

Estructura de la tesis

El lapso entre el encallamiento y el presente estudio requirió que se identificara cuál era la condición previa al impacto del encallamiento y su trayectoria posterior a éste. En el Capítulo 2 se presenta un análisis de la información histórica del sitio contenida en los reportes no publicados de diversas fuentes. Del análisis resultó que antes del encallamiento la comunidad del parche arrecifal Cuevones se encontraba en un proceso de cambio de estado estable. La comunidad de corales pasó de estar dominada por corales hermatípicos, como las especies de *Acropora*, a un estado dominado por especies submasivas como *Porites astreoides*. Además, las especies de coral perdieron cobertura para ceder el espacio a los grupos de algas, especialmente las macroalgas carnosas. También se encontró que en términos de la comunidad de corales, el sector de impacto no se distingue de la comunidad de corales en los sectores de referencia, lo que se interpretó como una convergencia de los procesos sucesionales hacia un estado estable alternativo.

En el capítulo 3, se estudió, en un lapso de dos años, algunas de las particularidades del proceso de sucesión en los sectores de impacto y no impacto del parche arrecifal Cuevones. Se determinó que los corales hermatípicos tienen una cobertura baja y ésta se redujo durante el tiempo que duró el estudio, mientras que los corales no hermatípicos (e.g., *Porites astreoides*) dominaron la comunidad de corales. En cuanto a la comunidad de reclutas, la contribución de los corales hermatípicos fue prácticamente nula, ya que sus abundancias y coberturas son virtualmente cero. En contraste, los reclutas del género *Porites* son los que dominaron la comunidad de reclutas y se registraron con mayor frecuencia durante el periodo de estudio. Por otra parte, las algas incrustantes calcáreas, importantes por su capacidad de favorecer el establecimiento y metamorfosis de las larvas de coral, mostraron en el lapso de estudio un decremento en la proporción del sustrato ocupada.

Finalmente, en el capítulo 4 se integran y se discuten los resultados vinculando la trayectoria histórica de los sectores de impacto y no impacto, analizada en el capítulo 2, con las particularidades del proceso sucesional encontradas en el capítulo 3. Adicionalmente, se presentan algunos puntos en los cuales el conocimiento generado en esta investigación pueden ser usados para buscar modificar los procesos de sucesión ecológica actuales del parche arrecifal Cuevones.

Did the community structure of a coral reef patch affected by a ship grounding recover after 15 years? Merging historical and recent data sets

Isael Victoria-Salazar, Héctor A. Hernández-Arana, Jorge A. Meave, Miguel A. Ruiz-Zárate, Alejandro Vega-Zepeda, Juan P. Carricart-Ganivet and Haydée López-Adame.

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Did the community structure of a coral reef patch affected by a ship grounding recover after 15 years? Merging historical and recent data sets

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Shifts in dominance from coral to other benthic groups in coral reefs have raised concerns about the persistence of coral reefs and their ability to provide ecosystem services. Acute disturbances such as ship groundings offer the opportunity to examine the dynamics of successional processes in coral reefs, since understanding them is a prerequisite for their proper management. In this study, we investigated whether a ship grounding area in a reef located in a marine protected area in Cancún, Mexico, showed signs of recovery 15 years after the incident. We evaluated the reef's composition and structure by taking samples at three different scales (reef scale, 1 m^2, and 0.01 m^2). In these samples, we analysed coral density and recruitment, the abundance of five functional algal groups, and the abundance of the grazer sea urchin *Diadema antillarum*. If recovery had already occurred, we expected the impacted sector to have a community composition and structure similar to that of a contiguous, non-impacted sector. Using historical information, we found indications of a long-term phase shift, with *Porites astreoides* being the dominant coral species some time ago and at all scales of analysis; this species also showed intense recruitment. In agreement with previous studies of Caribbean reefs, architectural complexity was low. The algal cover was similar in impacted and non-impacted sectors though the density of sea urchins differed between them. Fifteen years after the ship grounding and despite the enforcement of the prohibition of tourism and fishing activities at the site, the impacted sector does not show signs of recovery. On the contrary, like other reefs in the Caribbean Sea, the non-impacted sector is becoming degraded due to the loss of reef builder key species and the increase of the algae-covered area, mirroring the path observed in the impacted sector.

1. Introduction

Around the globe, many coral reefs have lost their typical community structure and turned into a degraded condition. In the Caribbean, this situation has triggered the implementation of a number of strategies aimed at recovering the communities' original status (e.g., Jaap, 2000; Young et al., 2012). Common strategies include the establishment of marine protected areas (MPA), conceived as buffers against stressing factors and facilitators of coral recovery through the reestablishment of trophic cascade feedbacks (Mumby et al., 2006, 2007; but see Kramer and Heck,

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2007; Huntington et al., 2011). The populating of areas with sexual or asexual fragments (Johnson et al., 2011; Lindahl, 1998; Lirman, 2000; Young et al., 2012) is also a frequent strategy, and to a lesser degree, the implementation of land-based activities such as residual water treatment (Jackson et al., 2014) has been the selected tool. Among the factors contributing to coral reef deterioration, physical impacts, such as ship-groundings, are the most destructive of both the biological community and the reef framework (Gittings et al., 1990; Riegl, 2001).

Ship groundings are complex, acute disturbances that often reset coral reef communities almost to zero (Precht et al., 2001). The degree of damage caused by these disturbances depends on reef features (i.e., the reef zone that was affected), the environmental conditions at the time of the impact (tidal level, wave conditions), and ship-related features (vessel speed, load condition, ship heading angle) (Jaap, 2000; Nguyen et al., 2011). When a ship strikes a coral reef, it immediately removes the live cover, opening space for colonisation (Schroeder et al., 2008). The coral reef framework can be broken and crushed because of the ship's weight and impact strength, thus flattening the reef surface (Precht et al., 2001). Also, the site may be polluted if the hull brakes and fuel or cargo spill into the sea (Lirman et al., 2010; Precht et al., 2001). Rescue activities may increase the extent of damage. Ships towing off the grounded vessel may cause a new grounding or, in the worst case, the use of explosives may be needed (Smith, 1985).

Records of the effects of ship groundings on coral reefs around the world reveal contrasting community responses to these disturbances. After five years of the *Wellwood* grounding in Florida, the coral community showed increases in abundance from 0% to ca. 80% due to an intense recruitment process in the affected site, and an average recovery of ca. 20% cover was observed for hard corals dominated by *Favia fragum*, *Porites* sp. and *Agaricia agaricites* (Gittings et al., 1990). In contrast, no signs of recovery were observed in the *Evening Star* grounding four years after the impact (Lirman et al., 2010). In the Red Sea, several reefs affected by ship groundings showed a positive linear relationship between coral cover and time elapsed since the impact (Riegl, 2001). A common trend is that, after groundings, opportunistic species start preempting the space. For example, in Bermuda *Favia fragum* and *Porites astreoides* started to recolonise the site affected by the *Mari Boeing* in 1977 (Smith, 1985). The functional traits of *P. astreoides* (i.e., brooding species with several reproductive events in a year) enable it to rapidly colonise habitats subjected to physical damage that cause hard coral mortality (Alvarez-Filip et al., 2013; Green et al., 2008; Knowlton, 2001).

Ship groundings, when limited to physical impact, represent an opportunity to explore and understand community resilience and stability. Community resilience [i.e., the capacity to absorb changes on state variables while relationships among them persist (Holling, 1973)] depends on the biological legacies of the pre-disturbance elements (i.e., coral fragments), the nature and intensity of the relationships among them after disturbance (Carpenter, 1990; Fung et al., 2011), and the connectivity with other communities or ecosystems (Mumby and Hastings, 2008). In terms of stability, an ecological system is more stable when its post-disturbance dynamics induces the development of a community structure that is similar to that existing previously (Holling, 1973). In Caribbean coral reefs, resilience relies mainly on three biotic drivers of coral reef succession: (1) hard coral species (reef builders), which confer physical complexity and thus create, for many species, habitat and refuges from predators or harsh environmental conditions (Precht et al., 2001; Idjadi and Edmunds, 2006; Precht and Robbart, 2006); (2) algal groups, which either facilitate or deter coral recruitment, depending on their identity and environmental conditions (Birrell et al., 2008; Box and Mumby, 2007; Kuffner et al., 2006; Ritson-Williams et al., 2009); and (3) grazers such as herbivorous fish and sea urchins, among which *Diadema antillarum* is a prime example, which reduce algal cover, freeing space for potential coral recruitment (Edmunds and Carpenter, 2001; Idjadi et al., 2010; Myhre and Acevedo-Gutierrez, 2007). Herbivore impact depends largely on spatial feeding patterns; for example, fish can move between reefs and are less likely to feed at the same place, whereas *Diadema antillarum*, due to its limited migrating ability between-reefs, feeds more frequently at the same location; thus its ability to free space locally is greater than that of fish (Carpenter, 1986; Kellner et al., 2010). Once space is free and coral larvae establish, the fate of the potential coral community is determined mostly by the identity of the established colonies rather than by competition between algae and corals (Sandin and McNamara, 2012).

In this work, the benthic structure of a Mexican Caribbean reef affected 15 years earlier by a ship grounding is examined. The study aimed to determine whether the sector affected by the ship grounding was similar, based on reef community structure, to that observed in the adjacent non-impacted sector one decade and a half after the grounding damage. Recognising that the distribution of any species is patchy across a range of scales (Levin, 1992) and that coral communities can respond to disturbance by changing its structure in terms of dominance (Holling, 1973), a multi-scale spatial approach was applied to contrast community structure patterns between impacted and non-impacted sectors. We hypothesised that the ship-grounding could potentially facilitate a change of state. If this was the case, we anticipated that the structurally-complex hard coral species should be absent, or if present, that their abundances or cover would have lower values compared to the non-affected sector.

2. Materials and methods

2.1. Study site

This study was carried out from October 2012 to January 2013 in Cuevones within the Costa Occidental de Isla Mujeres, Punta Cancún y Punta Nizuc National Park, hereinafter Cancún National Park (CNP). Cuevones is an elongated patch reef located ca. 2.5 km north of Punta Cancún (UTM 526909, 2340046, WGS84 16N). The patch reef is approximately 180 m long, 25 m wide and 4–7 m deep (Fig. 1), and has an overall NW–SE orientation. Across the patch reef, there is an apparent change in coral type dominance from hard coral species on the windward side to soft coral species on the leeward side (Fig. 1). Throughout the hard coral (windward) section, architectural complexity appears to decrease from SE to NW. Within the soft coral (leeward) section, architectural complexity does not show an equivalent strong variation, except for the impact that occurred at the SE end. Based on this apparent variation in coral type dominance and physical complexity, the patch reef was divided into four sectors, one impacted (Imp) and three reference non-impacted sectors (R1-R3) (Fig. 1). The impacted sector runs, on the leeward side, from the south-eastern edge of the reef through the soft coral-dominated sector. The second sector included the more architecturally complex hard coral-dominated sector (R1) on the windward side, contiguous to the impacted area. The third sector was located on the leeward side and corresponds to the area dominated by soft corals (R2), where architectural complexity is minimal due to the shape of the holdfast of soft coral colonies. The fourth sector (R3), located on the windward side, was the least complex hard coral-dominated area.

2.1.1. The ship-grounding

In December 1997 the Norwegian Cruiser *Leeward* hit Cuevones

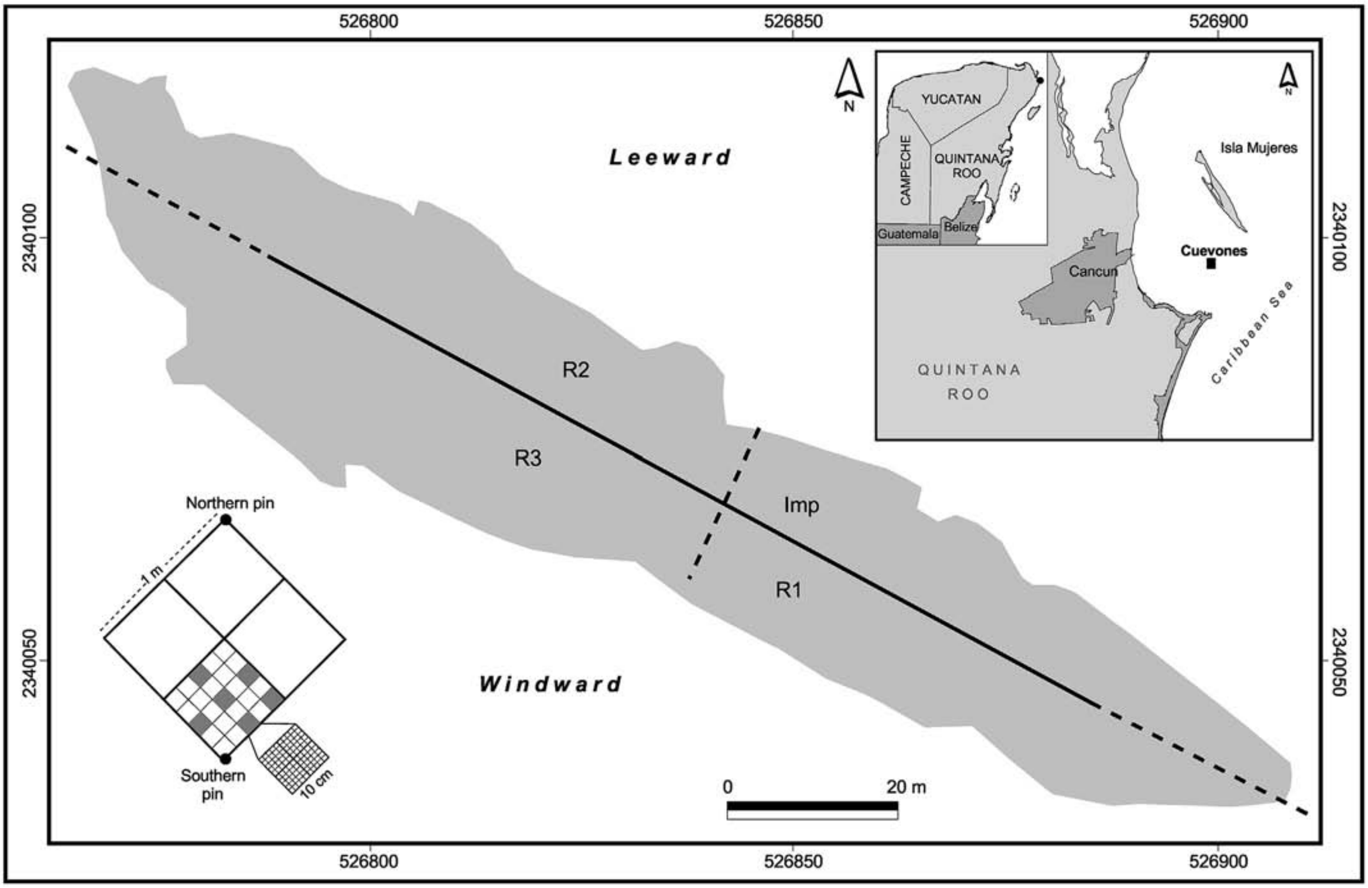

Fig. 1. The Cuevones patch reef within Cancún National Park, Quintana Roo, Mexico. The patch reef was subdivided into four sectors: impacted (Imp) and three non-impacted sectors (R1-R3). Coordinates are UTM (zone 16N). Lower inset details a sample quadrat where 10 × 10 cm units were randomly selected.

on its north-eastern side, damaging an approx. 75-m long and 6-m wide fringe (10.5% of total area of the patch reef), and creating a 15-m long and 2.3-m wide fracture of the reef framework. The largest survivor fragments were moved to sites outside the Cuevones patch reef. However, several colonies were killed after the impact due to the sediment produced by the incident (Reefkeeper International, 1999a). Long-term effects of pollution inside and outside the affected area can be assumed to be absent since the ship kept sailing without spilling cargo or oil in the water. After the impact, the borders of the impacted areas were marked with steel pins, thus the affected area could always be spatially identified.

To gain a deeper understanding of sustained changes in the benthic community, historical information available on the cover and presence of benthic components from the site was gathered from a set of reports prepared by Reef Keepers (1997, 1999a, b, 2000), Vega-Zepeda et al. (2005, 2006, 2007) and Carriquiry (2010). The reports revealed that the patch reef was sampled using the point intercept transect (PIT) and line intercept transect (LIT) methods (Table A5), three times within a year before, as well as two months after, the ship-grounding incident. Then, in 2001 and from 2005 to 2007 the patch was sampled again using LIT, without distinction of the disturbance condition. Finally, in November 2006 and May 2007 additional samplings based on PITs were conducted without considering different conditions.

2.2. Recent sampling design

2.2.1. Patch reef scale

2.2.1.1. Spatial relief. To determine the architectural complexity of the four sectors through the Rugosity Index (RI) (Risk, 1972), four to five 10-m long tapes were laid down along the reef bottom within each sector; tapes were placed 10 m apart from each other, across each sector and starting from the reef's mid-line. To accurately assess the complex details of reef surface and branched coral colonies a PVC non-floating chain, with 4.5-cm long links, was placed carefully under the tape (Aronson et al., 1994). RI was calculated as the ratio between the total length of the plastic chain used and the reference tape (10 m). For the flattest surfaces, the index scores a value of 1 (Risk, 1972).

2.2.1.2. Community structure. With the same 10-m long tapes used for assessing RI as a reference, coral community structure in all four sectors was estimated based on composition and abundance of coral colonies. Every colony intercepted by the tape was identified and recorded. For hard coral colonies the live linear cover, the longest diameter (LD) and perpendicular diameter (PD) were measured; these were used to calculate cover area by assuming an elliptic shape. Also, the percent mortality of every hard coral colony, as well as the percent area for other groups, were recorded. For soft coral colonies whose holdfast was under the tape the height was recorded to the nearest cm, since size class structure offers insights on population dynamics. The area where mortality was observed as well as the area occupied by other groups were subtracted from colony estimated area to obtain an estimated live tissue (ELT).

Relative algal cover and coral recruits were assessed using 19 to 25 PVC frames (25 × 25 cm) by sector. The PVC frames were placed every 2 m along the linear transects, without overlapping. Within each frame, the relative covers of five algal functional groups were estimated visually. Algal functional groups were: (1) fleshy macroalgae (i.e., erect green and brown algae) (FA), (2) branched coralline algae (BCA), (3) turf algae (i.e., dense or sparse filamentous algae of <2 cm height) (TA), (4) crustose coralline algae (CCA), and (5) crustose non-coralline algae (i.e., horizontally growing talli) (CnCA). Any individual colony with maximum diameter $\leq$4 cm was considered a recruit (Bak and Engel, 1979). For soft coral species, only colonies with a height $\leq$10 cm were considered recruits (Brazeau and Lasker, 1990). Densities of *D. antillarum* were estimated by recording every adult and young sea urchin occurring within 1 × 10 m belt transects centred along the linear transects described above.

2.2.2. The 1-m^2 scale

At this scale, both the coral community structure and *D. antillarum* densities were evaluated. Forty 1-m^2 permanent sampling units were established on the impacted sector and 40 on the more complex sector by using 316-stainless steel labelled pins (Jokiel et al., 2001). The square units were N–S diagonally oriented, and a pair of pins was used to securely place every unit (Fig. 1). Pins were fixed in place using a pneumatic drill (Jokiel et al., 2001); drilling through live coral colonies was avoided. To assess coral community structure, all colonies of hard and soft coral species within the sampling units were tallied. Additionally, LD, PD, as well as old and new percent mortality area were recorded to calculate ELT for hard corals, as described above. Within these sampling units, we also recorded all adult and young individuals of *D. antillarum*. Young sea urchins were recognised by the presence of a ringed pattern on their spines (Hendler et al., 1995).

2.2.3. The 0.01-m^2 scale

To determine whether recruitment occurred differentially under the impacted and non-impacted conditions, a 50 × 50-cm PVC frame, divided into 25 (10 × 10 cm) units, was attached to the southern pin of the frame using the stainless steel pins as a reference (Fig. 1). Nine 10 × 10-cm units were randomly selected, and hard and soft coral recruits were searched for and identified to genus level. The sampling unit was a 10 × 10-cm acrylic frame with a 1-cm grid, which was placed lying on the substrate, and the recording of every grid square was systematic and following a zigzag path. The data for this scale were gathered in October 2012 and December 2012 for the impacted sector, and in December 2012 for the non-impacted sector, as these were the first two sampling rounds for a long-term study of recruitment patterns.

2.3. Statistical analysis

2.3.1. Historical comparison

Due to differences in sampling techniques, design and available information, the comparison of historical data (point intercept method) with the present study (line intercept method) was based on a multivariate approach performed on presence/absence data of hard coral species community composition. This approach allowed comparing changes in stony coral species composition from 1996 to 2013, based on the assumption that the stony coral community had undergone a change both from the ship grounding impact and from a previous degradation process (see results). We constructed a square presence/absence matrix using the reported composition in each sampling period. The square matrix was converted into a similarity matrix based on Jaccard similarity index. Finally, a NMDS ordination plot was computed using PRIMER V6 (Clarke and Gorley, 2006). The ordination plot helped follow the temporal pattern of change, as sampling periods with similar composition are placed near each other on the ordination map.

2.3.2. Patch reef scale

2.3.2.1. Rugosity index analysis. With the rugosity values for each sector, a one-way ANOVA was performed to compare architectural complexity among the four sectors (three non-impacted and one affected); pairwise comparisons were done with a Tukey HSD test (Zar, 2009).

2.3.2.2. Current condition analysis

To compare the coral community structure among sectors, a multivariate approach was used based on square matrices of coral species with colony abundance, colony height, hard coral linear cover and estimated live tissue (ELT) as response variables. Squared root transformation was used for abundances, whereas a logarithmic transformation was chosen for ELT and soft coral heights before computing the Bray-Curtis similarity index (Clarke and Gorley, 2006). To determine whether community structure varied among sectors, independent one-way PERMANOVAs for coral abundances, ELT and soft coral heights using PRIMER V6 (Anderson et al., 2008; Clarke and Gorley, 2006) were computed. For coral species with abundance >20 colonies, size class distribution was determined using Sturges' rule. Skewness (Zar, 2009) was computed to determine if size class distribution was skewed to the right, which would imply a high incidence of young colonies, thus denoting a successful post-settlement survivorship (Crabbe, 2009). Assessing differences in algal cover groups among sectors was achieved with a one-way PERMANOVA test (Anderson et al., 2008), while for sea urchin densities a one-way ANOVA was performed. The relation between Rugosity Index and *D. antillarum* densities was examined through a Pearson product-moment correlation.

2.3.3. The 1-m^2 scale

A one-way PERMANOVA test was used to compare coral abundance between the impacted and non-impacted conditions. Additionally, size class distribution (colony area or colony height) based on Sturges' rule was analysed for those species with abundances > 20 colonies for each condition (impacted and non-impacted), and skewness was computed (Zar, 2009).

2.3.4. The 0.01-m^{-2} scale

Relative recruit survivorship by genus was calculated using the recruits recorded in October 2012 that were still present in December 2012 in the impacted sector. For the algal cover, the comparison between October and December 2012 values in the impacted sector was performed with a one-way PERMANOVA. The same test was used to compare the impacted and non-impacted sectors using the December data set, as the sampling season was unfinished due to adverse weather conditions in October. When differences between sampling dates or condition were detected, a Similarity Percentage (SIMPER) analysis was used to identify the algal group or recruit genus that most contributed to the differences.

3. Results

3.1. Historical information

3.1.1. Before, after, affected and non-affected conditions

According to the historical information, the patch reef was dominated by *Acropora palmata*, *Millepora complanata* and *Porites astreoides* before the time of impact (Reefkeeper International, 1999a). From October 1996 to August 1997, before the incident, at the patch scale, percent cover ranges for hard corals, algae and abiotic substrate were 22–36%, 39–66% and 5–14%, respectively (Fig. 2). Two months after the impact, in February 1998, the coral cover was reduced to 4.5% in the impacted sector (Fig. 2). In December 1998, the coral cover in the non-impacted sector ranged from 11.6% to 29.1% (Fig. 2). Based on percent cover, from October 1996 to January 2013, the historical information allowed identifying the following tendencies of change for this patch reef. First, hard coral cover dropped from October 1996 to March 1997, before the ship grounding, and continued decreasing until January 2013. Second, algae were the only group whose cover increased throughout the observation period, regardless of the sector (i.e., impacted or not). Algal cover rose from October 1996 to March 1997 and remained above 50%, with the highest cover in August 2001 (Fig. 2). Particularly, in the impacted sector the algal cover had reached 68% in April 1999, with its highest cover (83.5%) recorded in September 1999. In turn, in the non-impacted sector algal cover peaked in May 2000 (71.5%).

The grouping of sampling times before the impact indicates that hard coral species across the patch was similar (Fig. 3). Noteworthy, in February 1998, two months after the ship-grounding impact, hard coral composition drifted away from the composition recorded in 1996 and 1997, before the ship grounding. This change was mediated by the absence of *Orbicella annularis* in the impacted sector in February 1998 (Table A6). Also noticeable in the ordination

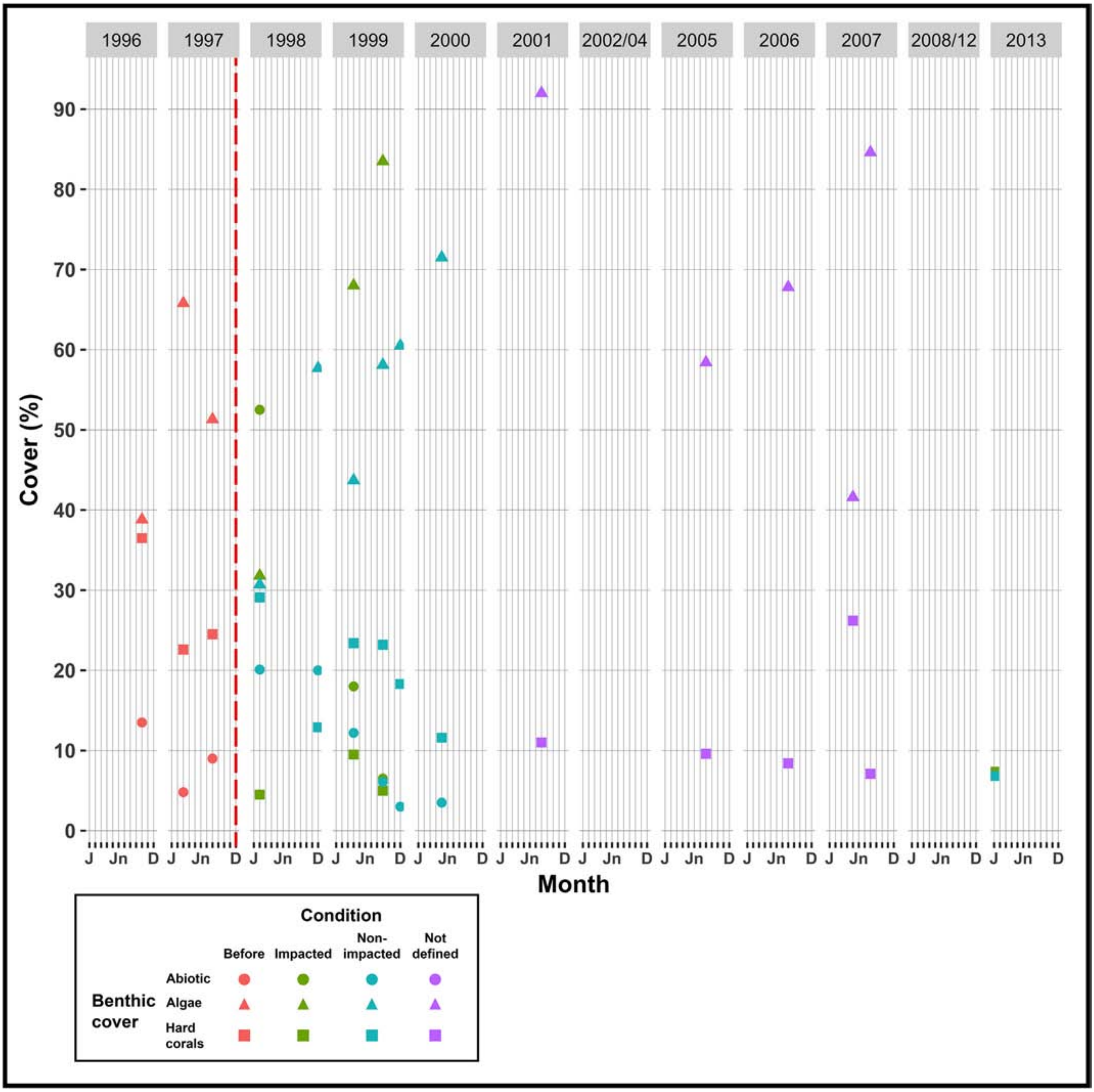

Fig. 2. Percent cover of different benthic components before and after the impact, both for the impacted and non-impacted sectors. Data from Reefkeeper International (1997, 1999a, b, 2000), Vega-Zepeda et al. (2005, 2006, 2007) and Carriquiry (2010). Dashed red line in December 1997 represent the time of ship grounding. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

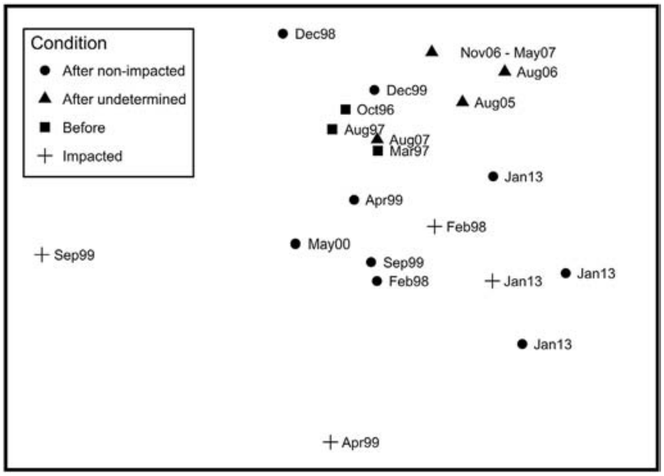

Fig. 3. NMDS ordination plot of temporal changes in hard coral species composition within Cuevones patch reef in 15-year period. Data from Reefkeeper International (Reefkeeper International, 1997, 1999a, b, 2000), Carriquiry et al. (Carriquiry, 2010), and this study.

plot is that at the patch scale and after the impact, there is a pattern of increasing variability (dispersion) in the 1998, 1999, and 2000 data, compared to data from 1996 to 1997. Data from the impacted area in 2013 showed a clear change in composition, mediated by the presence of *Siderastrea siderea*, *Porites furcata* and the absence of *O. annularis*, when compared with the condition before, and immediately after the impact. Also, hard coral composition of the non-impacted sectors was different from that recorded during 1996–2000.

3.2. *Patch reef (10 m) scale*

3.2.1. *Rugosity index analysis*

The ANOVA revealed statistical differences among sectors ($F = 6.15$, d.f. $= 3$, $P < 0.01$). The pairwise comparisons indicated no statistical differences between the impacted sector and R1, due to large variation (Fig. 4). The only significant difference was between sector R1, which had the highest value, and R3, which had the lowest. The pooled Rugosity Index for the whole patch was 1.3.

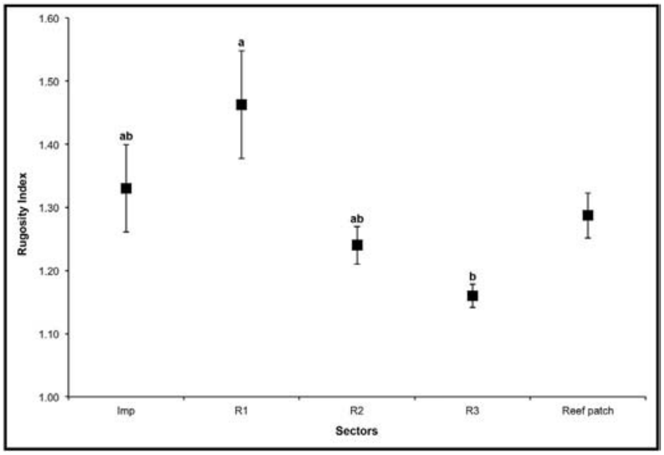

Fig. 4. Mean (±1 S.E.) Rugosity Index at the four sectors [impacted (Imp) and non-impacted (R1, R2, and R3)], and for the whole patch reef. Different letters indicate significant differences (Tukey HSD test).

3.2.2. *Coral community structure*

Twelve species of scleractinian and milleporian corals, with 136 colonies, and 14 octocorallian species, with 248 colonies, were recorded at the patch scale (Tables A1 and A2). The richest sector was R2 with 21 species (8 hard and 13 soft coral species), whilst the poorest was the impacted sector with 13 species (7 hard and 6 soft coral species). Five hard coral and three soft coral species were common to all four sectors, and *Porites astreoides* and *Eunicea mammosa* were the most abundant coral species. *Porites astreoides* had the highest abundance of colonies in all sectors and its mean linear cover dominated in the impacted, R1 and R3 sectors (Table A1). With respect to ELT, the dominating species were *P. astreoides* in Imp (0.128 m^2), *Acropora palmata* (0.264 m^2) in R1, *Orbicella faveolata* (0.321 m^2) in R2, and *Millepora complanata* (0.850 m^2) in R3 (Table A1). The PERMANOVA did not reveal any significant differences among sectors in the number of colonies, hard coral linear cover, ELT and soft coral heights (Table 1). The size class distribution of *Eunicea mammosa* was similar across sectors, with the 15–25 cm height class being the most frequent; only R1 and R3 had colonies in the size classes ≥35 cm height, but with lower relative frequency (2–8%) (Fig. 5).

3.2.3. *Coral recruits and algal functional groups*

Thirty-two coral recruits from four genera were recorded (Table 2). Hard coral recruits occurred in low numbers (9 colonies) compared with the genus *Eunicea* (23 colonies), the only soft coral taxon with recruits in all sectors. The genus *Eunicea* had the largest number of recruits in R3, and *Porites astreoides* dominated in the impacted sector (Table 2). Fleshy algae was the group with the largest mean relative cover in all sectors but R2, where branching calcareous algae had the highest cover; the PERMANOVA for algal community cover showed significant differences among sectors and pairwise tests showed that R2 differed from all other sectors (Fig. 6). Density of *Diadema antillarum* adults ranged from 0.8 ind 10 m^{-2} (R3) to 7.2 ind 10 m^{-2} (R1) (Fig. 7). The mean adult density of this species differed statistically among sectors (ANOVA test, $F = 4.178$, d.f. $= 3$, $P < 0.05$, Table 1). A post-hoc Tukey test showed significant differences between R1 and R3. Rugosity index and *D. antillarum* density were positively and significantly related ($r = 0.61$, $P < 0.05$).

3.3. *1-m^2 scale*

3.3.1. *Coral community structure*

In the impacted sector, there were 282 hard coral colonies belonging to 13 species and 424 soft coral colonies from 18 species plus 11 unidentified colonies (Table A3). In turn, at the non-impacted sector (R1) there were 15 hard coral species with 448 colonies and 10 soft coral taxa with 260 colonies plus 20 unidentified colonies (Table A4). *Porites astreoides* had the highest relative abundance and mean density in both sectors (Tables A3 and A4). For soft coral species, *Eunicea mammosa* and *Eunicea succinea* were the most abundant taxa for both sectors (Tables A3 and A4). One-way PERMANOVA tests for coral abundances, ELT and soft coral heights revealed significant differences among sectors (Table 1), due to variation in the response variables, rather than in community composition (Tables A3 and A4).

3.3.2. *Size class distribution*

For soft corals, only *Eunicea mammosa*, *E. succinea* and *Gorgonia ventalina* had enough colonies to warrant the analysis of size class distribution (Fig. 8). The histogram of relative size frequency distribution showed a normal distribution for *Eunicea mammosa* both under the impacted and non-impacted conditions. Analysis of skewness showed that the size distribution *Eunicea succinea* at the

Table 1
Scales and variables measured at the Cuevones patch reef, Cancún, Mexico, with results of ANOVA and PERMANOVA.

Scale	Variable	(Pseudo-) *F*	Significance
Whole patch reef (among sectors)	Rugosity index (n = 18)	6.150	**
	Coral abundance (n = 18)	1.472	n.s.
	Hard coral linear cover (n = 18)	1.346	n.s.
	Hard coral ELT (n = 18)	1.495	n.s.
	Soft coral height (n = 18)	1.290	n.s.
	Algal cover (n = 89)	4.022	*
	Diadema antillarum density (n = 18)	4.178	*
1-m^2	Coral abundance (n = 58)	4.816	***
	Hard coral ELT (n = 58)	9.128	***
	Soft coral height (n = 58)	5.123	***
0.01-m^2	Algal cover (condition) (n = 720)	13.819	***
	Algal cover (date) (n = 882)	35.915	***

*P < 0.05, **P < 0.01, ***P < 0.001, n.s. not significant. (Pseudo): Pseudo-*F* values apply in those cases where multivariate tests were performed to analyse community structure (see text for details). See Fig. 6 for algal group contribution at patch scale.

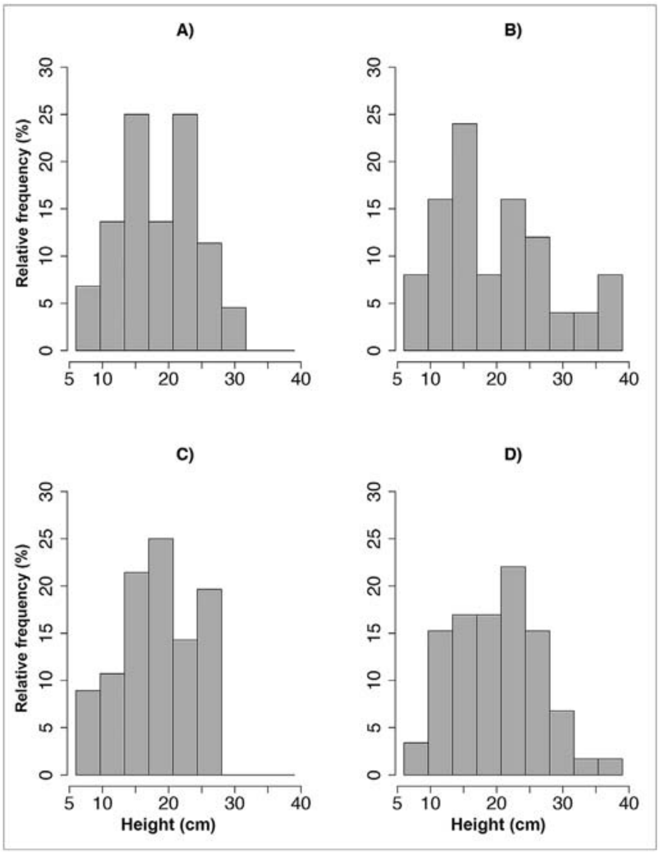

Fig. 5. Size class distribution of *Eunicea mammosa* in the four sectors into which the Cuevones patch reef was subdivided. (A) Impacted; (B) R1; (C) R2; (D) R3.

Table 2
Number of coral recruits by genus recorded in the four sectors of the Cuevones patch reef.

Sector	*Agaricia*	*Eunicea*	*Millepora*	*Porites*
Impacted	0	2	1	4
R1	0	3	0	1
R2	0	7	0	0
R3	1	11	0	2
Total	1	23	1	7

non-impacted sector (skewness = 1.183, $P < 0.05$) and *Gorgonia ventalina* at the impacted sector (skewness = 0.899, $P < 0.05$) were right-skewed, suggesting a higher proportion of young colonies. Only for *Porites astreoides* there were enough colonies in both sectors for analysing size class distribution (Fig. 9). Skewness

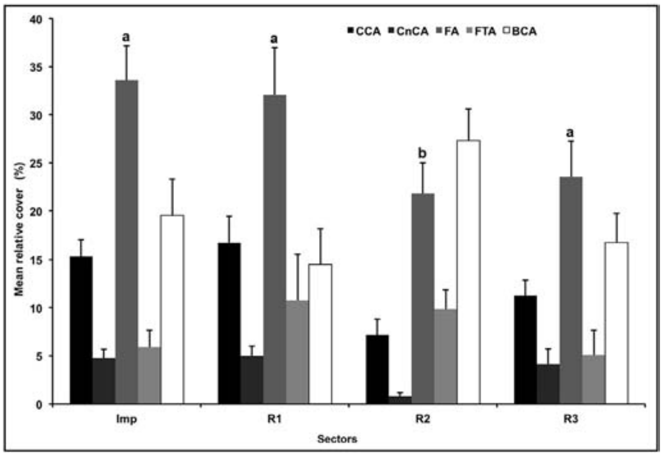

Fig. 6. Mean (±1 S.E.) relative cover of five algal groups (CCA = crustose coralline algae; CnCA = crustose non-coralline algae; FA = fleshy algae; FTA = filamentous turf algae, and BCA = branched calcareous algae) in the four sectors [Impacted (Imp) and three non-impacted sectors (R1-R3)].of Cuevones patch reef, Cancún, Mexico. Different letters denote significant differences after a pairwise multivariate comparison. Imp n = 19; R1 n = 20; R2 and R3 n = 25.

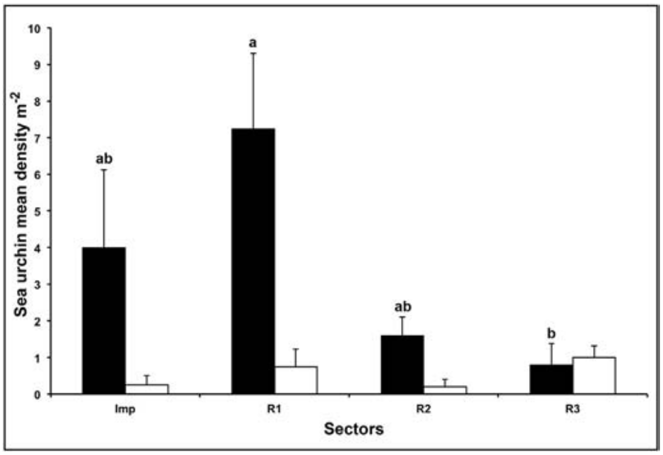

Fig. 7. Mean (+1 SE) density (no. of individuals) 10 m^{-2} of adult (black bars) and young (white bars) individuals of *Diadema antillarum* in the four sectors (Impacted (Imp) and three non-impacted sectors (R1-R3)] of the Cuevones patch reef. Different letters denote significant differences for adults (Tukey HSD test); no test for young individuals was performed.

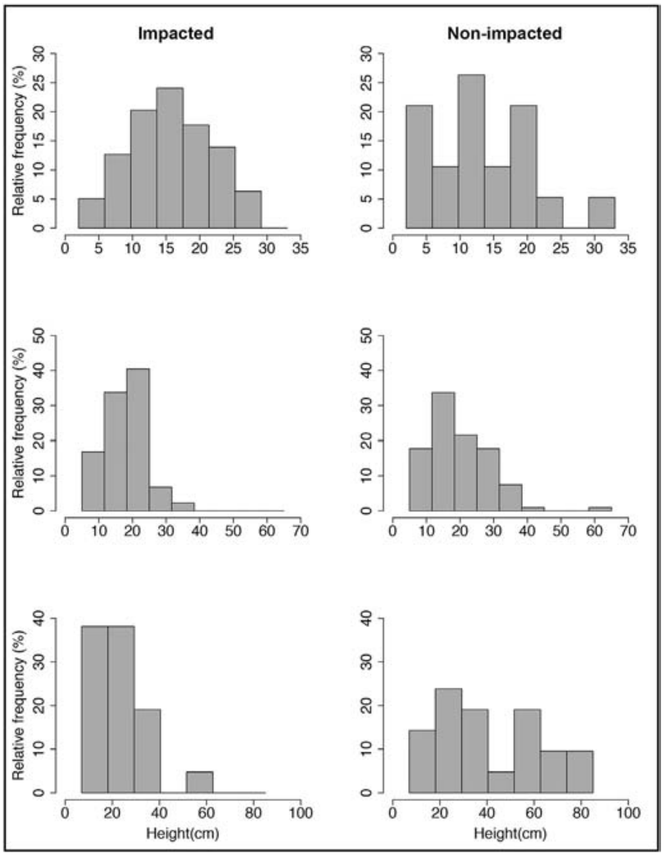

Fig. 8. Size class distribution for *Eunicea mammosa* (top), *E. succinea* (centre) and *Gorgonia ventalina* (bottom) at the impacted (left) and non-impacted (right) sectors in the Cuevones patch reef at the 1-m^2 scale.

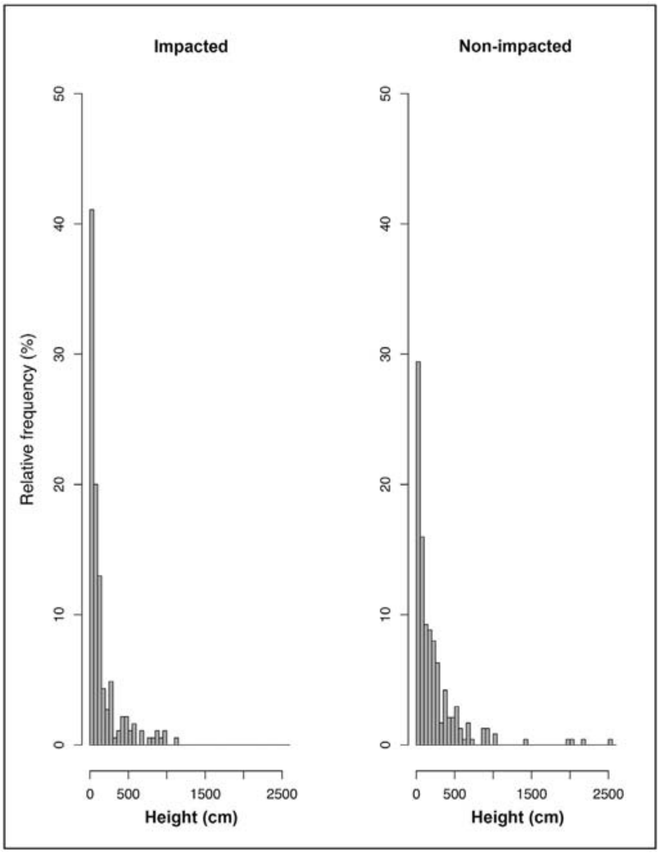

Fig. 9. Size class distributions of *Porites astreoides* at the non-impacted and impacted sectors at the Cuevones patch reef. Data are for the 1-m^2 scale.

analysis also showed that in both sectors size distributions of this species was right-skewed (skewness = 2.325 and 3.652 for the impacted and non-impacted sectors, respectively, $P < 0.05$). *Diadema antillarum* at this scale was scarce, with only 14 individuals at the non-impacted sector and two at the impacted one.

3.4. 0.01-m^2 scale

In October 2012, 50 coral recruits were recorded in the impacted sector ($n = 509$ 10 × 10-cm sampling units). *Eunicea* was the most abundant taxon (27 colonies), followed by *Porites astreoides* (13 colonies). In December 2012, at the impacted sector 18 recruits were recorded, and only 6 survivors were found ($n = 386$ 10 × 10-cm sampling units). At this time, *Eunicea* was again the most frequent taxon. At the non-impacted sector, there were only seven recruits in December 2012, and *Eunicea* was dominant with six colonies (Table 3). For algae cover, a one-way PERMANOVA test between the impacted and non-impacted sectors in December 2012 produced significant differences (Table 1). The SIMPER analysis showed that a higher cover of FA at the impacted sector and of TA at the non-impacted one was responsible for the differences. The one-way PERMANOVA between October and December for the impacted sector again showed significant differences (Table 1). In this case, the SIMPER showed that FA and BCA cover were higher in December, whereas TA cover was higher in October.

4. Discussion

The recovery pathway of a coral reef area affected by an acute physical disturbance, such as a ship-grounding, depends on the ecological history of the pre-disturbance condition, the biotic interactions among structural elements, and the connectivity with the neighbouring non-impacted areas (Smith, 1985; Miller and Barimo, 2001; Fox et al., 2003; Fox, 2004; Fox and Caldwell, 2006). This study combines historical data with recent surveys in an attempt to reconstruct the past trajectory before and after an acute impact in a patch reef. Additionally, it helps understand the effects of the non-touch protection regulation on recovery process of coral reefs.

From the analysis of the historical trajectory, it is inferred that before the impact the patch was already running a shift from corals to algae dominance. In less than one year, algal cover jumped from being slightly higher than corals in 1996, to three times as large in 1997. Two months after the disturbing incident, coral cover fell to ca. 5%, while algae increased to 30% (Fig. 2). Algal cover was higher at the impacted sector than at the non-impacted one, suggesting that the ship grounding accelerated the coral to algal replacement process in this sector. Actually, the period November 2006–May 2007 seems to be an exception to this trend, because at that time a reduction in algal cover and an increase in coral frequencies were reported, However, these changes in cover are likely an artefact due to the different methods used each time: Vega-Zepeda et al. (2007) used line intercept transects and Carriquiry (2010) used point intercept transects.

Changes like those described by historical data have been shown across the Caribbean Sea (Alvarez-Filip et al., 2009). Sights of the coral declining started earlier in the 1970's and became more frequent when *D. antillarum* populations collapsed (Carpenter, 1981, 1990). Coral losses have been attributed to several factors,

Table 3
Absolute abundance, density (no. of recruits m^{-2}) and relative survival of coral recruits by genus at the 0.01-m^2 scale.

Genus/group	Impacted					Non-impacted	
	October 2012		December 2012			December 2012	
	Absolute abundance	Mean density m^{-2}	Absolute abundance and (survivors)	Mean density m^{-2}	Survival (%)	Absolute abundance	Mean density m^{-2}
Acropora	1	0.2	NP		0		
Eunicea	27	5.3	9 (4)	3.4	11.81	6	1.7
Gorgonia	3	0.6	NP		0		
Millepora	1	0.2	NP		0		
Porites	13	2.6	(2)	0.5	15.38		
Octocorallia	5	1.0	2	0.5	0		
Muricia	NP		1	0.3	NA		
Agaricia	NP		NP		NA	1	0.3
Total	50	9.9	12 (6)	4.7		7	2.0

Data recorded in October and December 2012 at the impacted sector, and in December 2012 at the R1 non-impacted sector in the Cuevones patch reef. For the impacted sector $n = 509$ in October 2012, $n = 386$ in December 2012. For the non-impacted sector $n = 348$ in December 2012. In all cases n refers to 10 × 10-cm sampling units. (Survivors) = absolute number of individuals recorded both in October and December 2012 at the impacted sector. NP = not present at the sampling time; NA = not available.

mainly anthropogenic (Jackson et al., 2001). Patch reef-scale data before the disturbance indicated similar species composition. After the time of impact, the non-impacted sector showed a larger dissimilarity in subsequent years, while the impacted sector showed the largest dissimilarity (Fig. 3). After the incident, the patch reef was closed to visits in order to allow the community to recover. Non-touch regulations have clearly shown positive impacts on biomass recovery within MPA's (Lester and Halpern, 2008; Mumby and Harborne, 2010). However, this is not the case of Cuevones patch reef, as such strategy did not help to ameliorate the degradation process. On the contrary, despite the implementation of such strategy, the patch appears to have developed a phase shift, since in the long term fleshy algae and *Porites astreoides* have dominated the patch, sending a physical signal of degradation in this reef.

Rugosity index has been related to changes in coral species composition. High rugosity index values are related to the dominance of structurally more complex coral species, such as *Acropora palmata*, *Acropora cervicornis* or *Orbicella annularis*, whilst low values of this index are related to coral species like *Porites astreoides* and *Agaricia agaricites* (Alvarez-Filip et al., 2011). At Cuevones, the Rugosity Index did not differ significantly between the impacted and the non-impacted sectors. This result may be explained by the dominance of opportunistic species, such as *Porites astreoides*, in all sectors. Differences between R1 and R3 were due to the presence of branching coral species such as *A. palmata* and *A. cervicornis* in R1 (Table A1). Besides RI was influenced by the presence of dead standing colonies in R1, which were absent in R3 (Victoria-Salazar per. obs.). Comparing with other coral reefs of the Mexican portion of the Caribbean Sea, Cuevones is as flat as those where structurally relevant hard coral species have been replaced by less complex species (Alvarez-Filip et al., 2009, 2011). The replacement of structurally important hard coral species has been reported as a chronic response in the Caribbean Basin (Aronson and Precht, 2001), which has been concomitant with an overall decline in coral cover (Green et al., 2008). At Cuevones, the adult hard coral community was dominated in all sectors by *Porites astreoides* in terms of colony abundance. Also, *Porites astreoides* dominated the impacted sector in terms of ELT, while other species were dominant in the remaining sectors (*Acropora palmata* in R1, *Orbicella faveolata* in R2, and *Millepora complanata* in R3). Comparable shifts in dominance have been reported for the entire Caribbean Basin, regardless of the protection status of coral reefs and the proximity to human populations (McClanahan and Muthiga, 1998; Green et al., 2008; Schutte et al., 2010; Jackson et al., 2014). For example, over a 25-year period Glovers Reef reduced its coral cover from 80 to 20%, and shifted from coral dominance to algal dominance (McClanahan and Muthiga, 1998). Similarly, Toth et al. (2014) found that *Orbicella annularis* was the species with the largest loss of relative cover over a 14-year period both in protected and unprotected marine areas in coral reefs of Florida. In turn, opportunistic groups such as *Montastraea cavernosa*, *Siderastrea* spp., *Agaricia* spp., *Porites astreoides* and *Millepora* spp. persisted through time and even increased their abundance and relative cover. The potential ecological effects of this shift in dominance include the reduction on carbonate deposition rates and a reduced reef physical complexity (Alvarez-Filip et al., 2013). In this ecological context, even the positive impacts of grazing could become overwhelmed, causing the coral community to perish and thus perpetuating the algae-dominated phase.

The loss of architectural complexity compromises the potential effect of main grazers on coral reefs. The role of grazers in the prevalence of coral reefs is well documented (Carpenter, 1990; Edmunds and Carpenter, 2001). Earlier in the 1980's, when *D. antillarum* decimated, algae (particularly fleshy algae) became rapidly dominant in reefs across the Caribbean (Carpenter, 1990). As a grazer, *D. antillarum* was the main driver of the maintenance of a low algal cover that allowed the coral to dominate the seascape (Carpenter and Edmunds, 2006). In our study though *D. antillarum* density was positively correlated with the physical complexity of the patch reef, fleshy algae also had the highest cover in the same sectors. A likely explanation for this fact is a density-dependent urchin effect (Sammarco, 1980), so that there is a threshold above which algae start to reduce its cover as a consequence of urchin grazing. Urchin density at Cuevones (1–9 ind. m^{-2}) may be below this threshold. Similar results have been reported for other Caribbean reefs. For example, in Puerto Rico algal cover is highly variable (0–100%) when urchin density is below 4 ind. m^{-2} (Mercado-Molina et al., 2014), and densities ranging between 5 and 12 ind. m^{-2} reduced consistently the algal cover to ca. 10% in five Jamaican reefs (Edmunds and Carpenter, 2001).

Downscaling our scope at the1-m^2 scale showed that coral community structure differed significantly between the impacted sector and R1, with a lower number of colonies and coral cover in the former (Tables S3 and S4). This difference is indicative of the persistent altered-state of the benthic community structure in the impacted sector. Small *P. astreoides* colonies, a significant contributor in both sectors, indicate an intense recruitment. Along with a high post-settlement survival and the virtual absence of key coral species, this process may contribute to maintain the dominance of this species. Also, despite the higher number of colonies, the R1 sector has lost the dominance of more structurally complex species, whereas at the impacted sector the newly established species had the lowest structural complexity.

Our data for recruits revealed that *Porites* was the only abundant stony coral genus both at the patch reef and the 0.01 m^2 scales in all sectors (Tables 2 and 3). We expected to find *Acropora* spats, yet only one such spat was recorded in >800 sampling units. As recruits of foundation species (i.e., the *Acropora* and *Orbicella* complex) were virtually absent, we infer a low regenerative potential in the non-impacted sector and a low potential for the development of a physically more complex condition in the impacted one (Hughes and Tanner, 2000; Huntington et al., 2011). Dominance of opportunistic species in coral reef communities has been related to a functional loss in terms of the erosion-accretion balance in the model proposed by Alvarez-Filip et al. (2013). Of course, this possibility is highly discouraging, as its ultimate consequence would be the extinction of Caribbean coral reefs (Bruno, 2013).

The strong similarities in the coral community between the impacted and non-impacted sectors should not be interpreted as evidence of an ongoing recovery process at Cuevones; rather, these similarities provide evidence for a long-term, chronic disturbance, which has progressively led to a new state (Jackson et al., 2001; Bozec et al., 2008; Alvarez-Filip et al., 2009, 2011; Jackson et al., 2014). For the study region such disturbances have been amply documented since the 1970's, and they often result in the loss of former reef-building species (Jordán-Dahlgren and Rodríguez-Martínez, 2003), the loss of grazers like *Diadema antillarum* (McClanahan and Muthiga, 1998), and the exacerbated competition between algae and corals for space (e.g., Quan-Young and Espinoza-Ávalos, 2006; Ferrari et al., 2012). Although the specific causes of coral loss in Cuevones are unknown, the compilation of unpublished data allowed us to identify the trends of change on the cover and presence of key species/groups for reef dynamics. The binary (presence/absence) data used in this study retained enough information to enable an indirect assessment of the effect of a non-touch regulation on the reef community pathway by providing insights on the successional process. A main problem related with the application of this regulation in Cuevones is that surveillance only operates 8 h per day, which leaves a broad window for illegal activities like fishing. However, no information is available of such of negative impacts. Thus, the historical analysis shed light on the synergic effects of multiscale disturbances. For one, the loss of grazers together with coral diseases may have contributed to a shift in community structure from more complex species to less complex ones, and higher algal covers (Weil and Rogers, 2011). Second, concomitant to the urchin loss, the coastal region around Cancún has undergone severe transformations in the past 30 years due to the increasing demand of tourist services; this has exerted a strong human pressure on all adjacent ecosystems, including coral reefs (Ortiz-Lozano et al., 2005). Third, 50% of storms and hurricanes passing through the Mexican Caribbean, in the 1850–2010 period, affected the northern area of the Mexican Caribbean where Cuevones is located (Hernández-Arana et al., 2016). Thus, a reasonable conclusion is that the investigated ship-grounding accelerated community structure transformation in the impacted sector of the patch reef, as suggested by the historical changes in coral composition and the relative absence of structurally relevant species at this sector. However, such degradation process may also potentially obscure the size of the effect of the disturbance. The outcome of the accumulative effects of such large-scale disturbances is the present degraded condition, which has continued despite the establishment of a marine protected area (MPA) and the decision to prohibit all recreational and fishing activities in the patch. Although specific data for our study site have not been formally published, the management program of the MPA and the reports from Reefkeeper International (1999a) clearly demonstrate that the site was dominated by *Acropora palmata*, *Millepora complanata* and *Porites astreoides* before the impact (Ortiz-Lozano et al., 2005), with a consistent presence of *Porites porites*, *Acropora cervicornis* and *Millepora complanata* (Vega-Zepeda et al., 2005, 2006, 2007). In total, this information suggests that the patch reef is in the trajectory of a phase shift, as supported by our data.

In synthesis, use of historical information allowed identified that Cuevones patch reef exemplifies a convergence in community structure between the impacted and the non-impacted areas. By convergence to refer to the process by which the impacted sector is occupied by opportunistic species, and the non-impacted sector undergoes a gradual replacement by the same opportunistic species. From a management perspective, the lack of significant differences between sectors should be pondered carefully, as they do not imply at all a recovery process in the sense of the reestablishment, particularly because of the inability of structurally relevant species, such as *A. palmata*, to remain in the community. In the Caribbean Sea Basin, as in other regions of the World, the rule appears to be that regardless of the outstanding efforts made to establish and conserve marine protected areas, coral reefs are following a worrisome degradation path.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2017.04.009.

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Table A1. Absolute and relative abundances, mean linear cover (cm), and Estimated Live Tissue (ELT) in m^2 of hard corals by species, recorded in the four sectors (impacted plus three non-impacted sectors) of Cuevones patch reef (at the whole patch reef scale), Cancún, Mexico. S.E. = standard error; ¶ = species recorded in all sectors. Figures in bold typeface are the highest values by sector.

Species	Impacted n=4			R1 n=4			R2 n=5			R3 n=5		
	Absolute and (relative) abundance	Mean linear cover (1 S.E.)	ELT (1 S.E.)	Absolute and (relative) abundance	Mean linear cover (1 S.E.)	ELT (1 S.E.)	Absolute and (relative) abundance	Mean linear cover (1 S.E.)	ELT (1 S.E.)	Absolute and (relative) abundance	Mean linear cover (1 S.E.)	ELT (1 S.E.)
Acropora cervicornis	1 (2.78)	0.25 (0.250)	0.004 (0.0036)	4 (9.52)	3.25 (2.287)	0.018 (0.0107)				6 (16.22)	6.60 (3.059)	0.049 (0.0255)
Acropora palmata				2 (4.76)	27.50 (27.500)	**0.264 (0.2643)**						
Agaricia agaricites				3 (7.14)	1.75 (1.750)	0.002 (0.0025)						
Pseudodiploria strigosa				1 (2.38)	0.50 (0.500)	0.009 (0.0093)	1 (4.76)	2.00	0.015 (0.0152)			
Millepora alcicornis¶	1 (2.78)	2.00 (2.000)	0.002 (0.0024)	1 (2.38)	0.25 (0.250)	0.001 (0.0009)	1 (4.76)	1.40 (1.400)	0.001 (0.0013)	5 (13.51)	3.60 (1.913)	0.006 (0.0022)
Millepora complanata¶	4 (11.11)	4.25 (3.614)	0.014 (0.0082)	4 (9.52)	5.25 (1.250)	0.034 (0.0175)	3 (14.29)	5.00 (2.720)	0.006 (0.0027)	5 (13.51)	4.60 (2.561)	**0.085 (0.0383)**
Montastraea cavernosa										1 (2.70)	0.40 (0.400)	0.002 (0.0023)
Orbicella faveolata							1 (4.76)	**31.40 (31.400)**	**0.321 (03214)**	1 (2.70)	5.80 (5.800)	0.022 (0.0220)
Porites astreoides¶	**18 (50.00)**	**46.75 (6.421)**	**0.128 (0.0163)**	**23 (54.76)**	**44.00 (7.842)**	0.143 (0.0332)	**9 (42.86)**	21.40 (10.284))	0.064 (0.0333)	**17 (45.950)**	**28.80 (6.909)**	0.082 (0.0815)
Porites furcata¶	3 (8.33)	2.75 (1.702)	0.010 (0.0059)	3 (7.14)	2.75 (2.750)	0.004 (0.0039)	3 (14.29)	2.00 (0.949)	0.011 (0.0072)	1 (2.70)	0.40 (0.400)	0.001 (0.0013)
Porites porites	7 (19.44)	10 (4.453)	0.067 (0.0374)				2 (9.52)	2.60 (2.600)	0.010 (0.0105)			
Siderastrea siderea¶	2 (5.56)	2 (1.225)	0.003 (0.0017)	1 (2.38)	0.75 (0.750)	0.012 (0.0118)	1 (4.76)	2.40 (2.400)	0.003 (0.0028)	1 (2.70)	0.60 (0.600)	0.001 (0.0006)
Pooled colonies	36 (100)	68.00 (12.682)	0.228 (0.0516)	42 (100)	86.00 (22.616)	0.488 (0.2230)	21 (100)	68.20 (40.322)	0.433 (0.3677)	37 (100)	50.80 (9.682)	0.248 (0.0400)

Table A2. Absolute and relative abundances and mean size (height in cm) of soft corals recorded in four sectors of Cuevones patch reef (at the whole patch reef scale). S.E. = standard error; † measures are mean linear cover under the transects as in hard coral species; ¶ species recorded in all sectors. Figures in bold typeface are the highest values by sector.

	Impacted n=4		R1 n=4		R2 n=5		R3 n=5	
Species	Absolute and (relative) abundance	Mean size (1 S.E.)	Absolute and (relative) abundance	Mean size (1 S.E.)	Absolute and (relative) abundance	Mean size (1 S.E.)	Absolute and (relative) abundance	Mean size (1 S.E.)
*Erythropodium caribaeorum**	1 (1.92)	6†	1 (2.86)	12†	2 (2.50)	27.5† (15.500)		
Eunicea mammosa¶	**44 (84.62)**	18.68 (0.910)	**25 (71.43)**	20.16 (1.695)	**56 (70.00)**	18.34 (0.178)	**59 (72.84)**	19.97 (0.833)
Gorgonia flabellum			2 (5.71)	**28.00 (18.000)**	1 (1.25)	**45.00**		
Gorgonia ventalina			1 (2.86)	25.00	2 (2.50)	33.00 (0.522)	1 (1.23)	**64.00**
Muricea muricata	1 (1.92)	16.00					1 (1.23)	20.00
Muriceopsis flavida¶	3 (5.77)	12.67 (3.180)	5 (14.29	13.40 (0.748)	5 (6.25)	20.60 (0.910)	6 (7.41)	26.50 (6.428)
Plexaura flexuosa¶	2 (3.85)	**26.50 (1.500)**	1 (2.86)	22.00	5 (6.25)	31.00 (0.576)	7 (8.64)	25.00 (3.748)
Plexaura homomalla	1 (1.92)	14.00			1 (1.25)	**45.00**	1 (1.23)	21.00
Plexaurella sp					1 (1.25)	33.00		
Pseudoplexaura sp					1 (1.25)	23.00	1 (1.23)	15.00
Pseudopterogorgia americana					1 (1.25)	38.00	2 (2.47)	30.00 (1.000)
Pseudopterogorgia bipinnata					2 (2.50)	16.50 (1.354)		
Pterogorgia citrina					1 (1.25)	16.00	1 (1.23)	13.00
Pterogorgia guadalupensis					2 (2.50)	22.50 (1.160)	2 (2.47)	18.00 (2.000)
Pooled colonies	52 (100)		35 (100)		80 (100)		81 (100)	

* Linear cover was measured due to its growth pattern

Table A3. Absolute and relative abundances, mean density (no. of colonies m^{-2}), and Estimated Live Tissue (ELT) cm^{2} m^{-2} for hard and soft coral species present in the impacted sector (1-m^{2} scale). S.E. = standard error; n = 27 quadrats.

Hard coral				Soft corals		
Hard coral species	Absolute and (relative) abundance	Mean density (1 S.E.)	ELT (1 S.E.)	Soft coral species	Mean density (1 S.E.)	ELT (1 S.E.)
Acropora cervicornis	27 (9.6)	1.00 (0.547)	226.29 (151.286)	*Erythropodium caribaeorum*	12 (2.8)	0.44 (0.154)
Acropora palmata	3 (1.1)	0.11 (0.082)	1.61 (1.240)	*Eunicea mammosa*	79 (18.2)	2.93 (1.790)
Acropora prolifera	2 (0.7)	0.07 (0.051)	4.41 (4.074)	***Eunicea* spp.**	**137 (31.5)**	**5.07 (1.486)**
Agaricia agaricites	2 (0.7)	0.07 (0.051)	6.28 (5.031)	*Eunicea succinea*	89 (20.5)	3.30 (1.063)
Agaricia fragilis	3 (1.1)	0.11 (0.082)	2.38 (1.511)	*Gorgonia flabellum*	2 (0.5)	0.07 (0.051)
Millepora alcicornis	3 (1.1)	0.11 (0.082)	5.61 (5.524)	*Gorgonia marie*	4 (0.9)	0.15 (0.070)
Millepora complanata	15 (5.3)	0.56 (0.269)	62.18 (34.199)	*Gorgonia ventalina*	21 (4.8)	0.78 (0.209)
Porites astreoides	**181 (64.2)**	**6.70 (0.952)**	**885.21 (170.335)**	*Muricea muricata*	6 (1.4)	0.22 (0.163)
Porites divaricata	6 (2.1)	0.22 (0.154)	21.85 (20.813)	*Muriceopsis flavida*	1 (0.2)	0.04 (0.037)
Porites furcata	10 (3.5)	0.37 (0.186)	10.61 (8.267)	*Muriceopsis* spp.	23 (5.23)	0.85 (0.281)
Porites porites	26 (9.2)	0.96 (0.247)	38.74 (12.233)	*Plexaura homomalla*	4 (0.9)	0.15 (0.070)
Siderastrea radians	2 (0.7)	0.07 (0.051)	0.78 (0.549)	*Plexaura* spp.	4 (0.9)	0.15 (0.116)
Siderastrea siderea	2 (0.7)	0.07 (0.051)	1.31 (0.914)	*Plexaurella* spp.	1 (0.2)	0.04 (0.037)
				Pseudoplexaura spp.	17 (3.9)	0.63 (0.170)
				Pseudoterogorgia americana	1 (0.2)	0.04 (0.037)
				Pseudoterogorgia spp.	14 (3.2)	0.52 (0.263)
				Pterogorgia citrina	7 (1.6)	0.26 (0.137)
				Pterogorgia spp.	2 (0.5)	0.7 (0.051
				Unidentified	11 (2.5)	0.41 (0.298)
Pooled colonies	282 (100)	10.44 (1.248)	1267.26 (305.896)	Pooled colonies	435	16.11 (1.898)

Table A4. Absolute and relative abundances, mean density (no. of colonies m^{-2}) and Estimated Live Tissue (ELT) cm^{2} m^{-2} for hard and soft coral species present in R1 non-impacted sector (1-m^{2} scale). S.E. = standard error; n = 31 quadrats.

Hard corals				Soft corals		
Hard coral species	Absolute and (relative) abundance	Mean density (1 S.E.)	ELT (1 S.E.)	Soft coral species	Mean density (1 S.E.)	ELT (1 S.E.)
Acropora cervicornis	5 (1.12)	0.16 (0.082)	38.35 (25.041)	*Erythropodium caribaeorum*	24 (8.57)	0.77 (0.390)
Acropora palmata	19 (4.24)	0.61 (0.184)	921.91 (379.297)	*Eunicea mammosa*	19 (6.79)	0.61 (0.390)
Acropora prolifera	12 (2.68)	0.39 (0.261)	46.34 (21.580)	*Eunicea* spp.	39 (13.93)	1.26 (0.497)
Agaricia agaricites	26 (5.80)	0.84 (0.464)	32.04 (15.495)	***Eunicea succinea***	**107 (38.21)**	**3.45 (0.885)**
Agaricia fragilis	1 (0.22)	0.03 (0.032)	0.61 (0.608)	*Gorgonia flabellum*	17 (6.07)	0.55 (0.179)
Agaricia teunifolia	4 (0.89)	0.13 (0.129)	1.70 (1.697)	*Gorgonia ventalina*	21 (7.50)	0.68 (0.209)
Millepora alcicornis	33 (7.37)	1.06 (0.318)	101.40 (41.228)	*Muricea* spp.	2 (0.71)	0.06 (0.065)
Millepora complanata	52 (11.61)	1.68 (0.386)	392.39 (136.934)	*Plexaura homomalla*	2 (0.71)	0.06 (0.065)
Orbicella annularis	1 (0.22)	0.03 (0.032)	54.72 (54.725)	*Pseudoplexaura* spp.	12 (4.29)	0.39 (0.200)
Orbicella faveolata	1 (0.22)	0.03 (0.03 2)	18.05 (18.051)	*Pseudoterogorgia* spp.	17 (6.07)	0.55 (0.196)
Porites astreoides	**238 (53.12)**	**7.68 (0.801)**	**1514.92 (193.784)**	Unidentified	20 (7.14)	0.64 (0.310)
Porites divaricata	9 (2.01)	0.29 (0.203)	2.63 (1.724)			
Porites furcata	26 (5.80)	0.84 (0.174)	76.16 (20.869)			
Porites porites	20 (4.46)	0.65 (0.177)	99.31 (34.734)			
Siderastrea siderea	1 (0.22)	0.03 (0.032)	0.35 (0.355)			
Pooled colonies	448 (100)	14.45 (1.343)	3300.88 (448.540)		280 (100)	9.03 (1.503)

Succession and resilience of a coral patch reef: insights from an accidental experiment

Introduction

In his seminal paper, Clements (1916) put forward a deterministic model of ecological succession that describes how a community's fate is determined by species' identities and interactions among them. Ecological succession occurs after a substantially large area has been cleared and a re-colonization process has initiated (Clements, 1916; Connell & Slatyer, 1977; Horn, 1974); ultimately, it is a process determined by the availability of space and of species with their differential performances. The key role of disturbance as a fundamental cause of spatio-temporal heterogeneity and of individuals and species turnover, and as overall driver of ecological succession, has been clearly shown (*e.g.*, Bruno & Bertness, 2001; Connell & Keough, 1985; Pickett & White, 1985a; Sousa, 1984). When disturbance attribute (*e.g.*, type, frequency and extent) exceed a community's limits of tolerance (Sousa, 1984, 1985), this may have severe consequences.

Catastrophic disturbances bring profound changes in the dynamics of biological communities, compromising their stability and resilience (Jackson *et al*., 2001). Initially, stability was defined as the community's ability to recover to a previous stable state after a disturbance (Holling, 1973; Lewontin, 1969), whereas the term resilience was employed to refer to the community's ability to cope with the energy added by a disturbance to a community (Holling, 1973). At present, however, stability is inferred when the state variables of a community remain virtually constant in the absence of disturbance (Beisner et al., 2003), while resilience refers mostly to the community's capacity to return to a previous state (Graham *et al*., 2013; Mumby, Chollett, Bozec, & Wolff, 2014). Thus, the faster a community recovers to its previous state, the more resilient it is.

In coral reef ecology, stability and resilience have been at the core of research due to the multifactorial anthropogenic stresses acting on these ecosystems, including eutrophication, overfishing, land-based activities, and physical damage (Fox, 2004; Fox & Caldwell, 2006; Fox *et al.*, 2003; Hatcher, 1984; Jackson *et al.*, 2001; Riegl, 2001; Schroeder *et al.*, 2008). In Caribbean coral reefs, shifts between stable states of coral dominance to dominance by other groups (mainly fleshy algae) have been frequently linked to the loss of herbivorous fish biomass (Mumby, Steneck, Adjeroud, & Arnold, 2016; Steneck, Arnold, & Mumby, 2014; but see, Arias-González *et al.*, 2017; Suchley, McField, & Alvarez-Filip, 2016), along with the decimation of the sea urchin *Diadema antillarum* in the 1980s (Carpenter, 1988). Such shifts have raised questions such as what are the requirements that allow coral reefs to regain dominance, what are the drivers of such recovery, how to identify a recovering coral reef, and how can coral reef resilience be measured.

The possibility to recovery from alternate states to a coral-dominated one depends on the integration of top-down and bottom-up processes. For one, herbivores have a negative impact on algal cover, reducing competition with corals, releasing potential space for recruitment of benthic fauna (Carpenter, 1981; Mumby & Steneck, 2008). Further, coral recruitment is also sensitive to the chemical cues released on the reef surface; when these cues come from a species-specific crustose calcareous algae (CCA) in a healthy reef, settlement and metamorphosis have a higher rate of success (Fabricius *et al*., 2017; Faiz *et al*., 2017; McCook *et al*., 2001). Once settlement occurs, redundancy of functional traits such as coral growth forms determine the future development of coral reefs, with branched forms being particularly efficient in providing essential reef features such as physical complexity, habitat provision and high carbon capture (McWilliams *et al*., 2018; Perry *et al*., 2011). Thus, the synergistic effects of herbivores and chemical cues shape the successional pathway followed by a given coral reef. Moreover, recruits of key coral species (*i.e.*, framework building corals) should survive and possess a high probability to replace any other benthic group. Conversely, if other groups dominate re-colonization, such as seaweeds and other non-framework-building (NFB) corals, the community will likely transit into an alternative state. On top of these biological processes, disturbance is also an important driver of the route followed by ecological succession. When a coral reef suffers physical damage, for example, its successional trajectory is characterized by the growth of undamaged colonies, the production of new tissue in damaged but surviving colonies, the available substrate for recruitment, and supply-side of coral key species (Gittings, Bright, Choi, & Barnett, 1988; Underwood & Keough, 2001).

Understanding the drivers of coral reef ecological succession is therefore essential to determine whether a community is shifting towards an alternative state (Doropoulos, Roff, Visser, & Mumby, 2017), ultimately compromising the ecosystem goods and services they provide (Harborne et al., 2006; Moberg & Folke, 1999). Taking advantage of a ship grounding incident in a Neotropical patch reef within a marine protected area in the Mexican Caribbean, in this study we (1) examined the contribution of framework-building (FB) coral recruits to the community, their relationship with adult colonies, and the cover of crustose coralline algae (CCA), the recruitment-promoting group, (2) assessed the contribution of FB species to coral cover in the impacted reef patch, and (3) analyzed whether the observed successional trajectory in the impacted area directs the system towards a state dominated by FB coral species.

Methods

Study site

This study was conducted in the Cuevones patch reef located within the ‘Parque Nacional Costa Occidental de Isla Mujeres, Punta Cancún y Punta Nizuc’, hereinafter the Cancún National Park (CNP), in the northern portion of Quintana Roo state, Mexico (21º 09’ 41.5’’ N, 86º 44’ 27.6’’ W) (Fig. 1). In 1997 the *Leeward* vessel impacted the patch reef, dislodging the biota of ca. 452 m^2

from its substrate. Since the vessel integrity was not compromised, there was no oil, fuel or cargo spilled in the water; hence, non-physical long-term impacts can be discarded. Historical records show that before this incident, the dominant species in the patch were *Porites astreoides*, *Acropora palmata*, *A. cervicornis* and *Orbicella annularis (Reefkeeper International, 1997, 1999a, 1999b, 2000)*. Yet, prior to the impact the patch already showed signs of transition towards an alternative stable state (Victoria-Salazar *et al*., 2017).

As only one portion of the patch was affected and the impacted sector (IS) was a fringe, a contiguous non-impacted sector (NS), along its longest axis, was used as reference and assumed to be the closest source of larvae for IS (Fox *et al*. 2003; Fig. 1). Every six months (February and August 2013, and February and September 2014) 20 out of 40 1-m^2 permanent quadrats were randomly selected within each sector and used to record the cover of coral recruits, coral adults, algae and the abundance of the sea urchin *Diadema antillarum*.

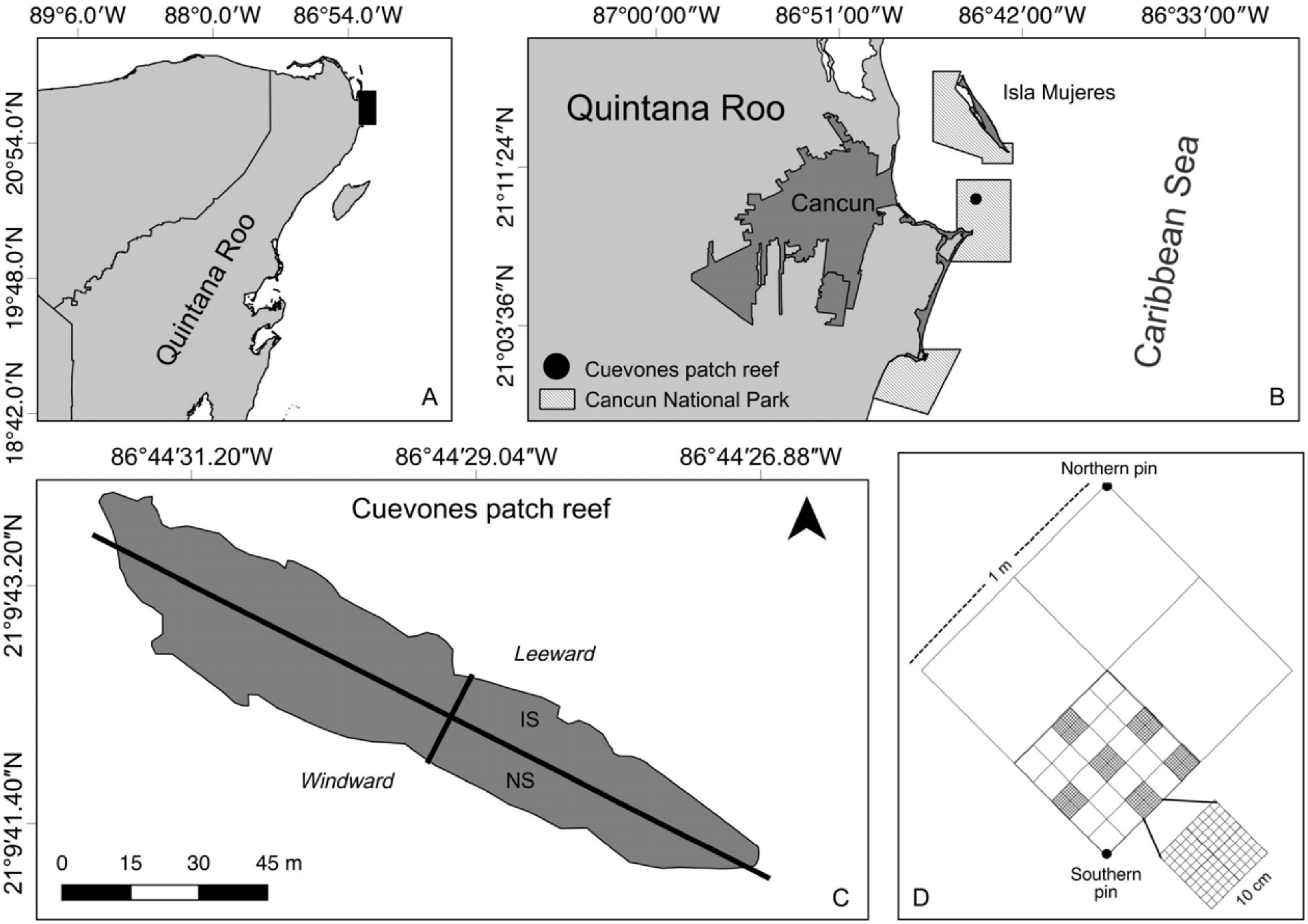

Figure 1. (A) Cancun National Park, (B) Cuevones patch reef within CNP, (C) location of the impacted (IS) adjacent to the non-impacted (NS) sectors, and (D) sampling details for recruits and algae.

Data collection

Adult coral cover and sea urchin abundance

The area of the randomly selected 1-m^2 quadrats was carefully delimited with the aid of a nylon square. All complete or fractional adult coral colonies located within the quadrats were recorded and identified. The cover of each coral colony was estimated as an ellipse using the lengths of the longest axis and the perpendicular one to it, to the nearest centimeter. In the case of colony fractions within quadrats, cover was obtained by subtracting the fraction from the total colony area. The proportion of coral cover was obtained by dividing coral cover (cm^2) by the area of the quadrat (i.e., 10 000 cm^2). All *Diadema antillarum* individuals (i. e, adults and juvenile) roaming whiting the quadrats were tallied.

Coral recruits

In order to search for recruits, a 50 × 50 cm PVC frame was attached to the southern pin of the 20 1-m^{-2} quadrats in each sector (Fig. 1B, inset). The PVC frame was divided into 10 × 10 cm units (25 in total). Within each quadrat an exhaustive search was carried out for all hard coral recruits; a recruit was defined as an individual colony ≤ 4 cm in diameter (Bak & Engel, 1979). Colonies were identified to genus level. Recruit cover was calculated as a circle and coral recruits cover proportion (cp) was calculated for each genus as:

$$\mathrm{cp} = \frac{\sum_{i=1}^{n} cc_i}{as} \times 4$$

(Eq. 1)

where cc_i is the cover (cm^2) of each recruit i, as is the quadrat area (i.e., 2500 cm^2), and n is the number of recruits for each type.

Algal cover

In order to assess algal cover, five 10 × 10 cm units were randomly selected and the cover of the underneath benthic groups was recorded to the nearest cm^2 with the aid of a 1-cm resolution grid. Algal cover was classified into two categories according to five functional groups: (1) algae promoting coral recruitment, which only include CCA; and (2) algae deterring coral recruitment, which include fleshy macroalgae (FA), turf algae (TA; Doropoulos *et al*., 2017), branched coralline algae (BCA; Olsen *et al*., 2016), and crustose non-coralline algae (CnCA). From these data, we calculated independently the percent contribution of both algal categories to reef surface within each quadrat in the space not occupied by adults or recruits coral colonies, as follows:

$$ap_i = \frac{\sum_{i=1}^{5} ac_j}{500} \times (1\text{-}\ cp)$$

(Eq. 2)

where ap_i is the algal cover proportion of category j, ac_j is the cover of the algae in each sampling unit and the term $1 - cp$ denotes the proportion of space not occupied by corals.

Data analysis

Benthic community structure

In order to determine whether the benthic community developing in the impacted sector 16 years after the ship grounding could still be differentiated from that in the non-impacted sector, a multivariate approach was used. Using a dissimilarity matrix based on the Bray-Curtis index, a two-way PERMANOVA test was computed (9999 permutations), with time and condition as fixed factors. When significant differences were detected, pairwise comparisons were computed. A Principal Coordinate Analysiss (PCO) of mean values for time and condition was used for visualization. Data homogeneity was tested with a PERMDISP test. As data were inhomogeneous, even after square-root transformation, a conservative $\alpha < 0.01$ was used as significance threshold. All tests were computed with PRIMER V6 and PERMANOVA+ add-on for Primer (Clarke & Gorley, 2006).

Relationship between coral recruits and adult cover

In order to determine the relationship between adult and recruit cover proportions, and since proportions can exclusively be expressed between two boundary values, beta regressions were performed with the betareg package (Cribari-Neto & Zeileis, 2010) in R (R Core Team, 2017) for FB corals and NFB corals. Because the beta regression requires that data range to be in the standard unit interval (0,1), and our proportions included the extreme values of this interval, we transformed the data using the equation:

$$p' = \frac{p \times (n - 1) + 0.5}{n}$$

(Eq. 3)

where p is the observed proportion, and n is the sample size (Cribari-Neto & Zeileis, 2010).

Successional trajectories

The cover proportions of the surveyed benthic groups were grouped into four categories: (i) proportion of coral cover, irrespective of its contribution to reef development; (ii) proportion of reef-building coral cover; (iii) proportion of algae, irrespective of their capability to promote coral recruitment; and (iv) proportion of algae promoting coral recruitment. All proportion data were transformed to fit the standard interval unit (using Eq. 3), except for algae cover proportion, which fitted the interval in their original form. The proportion of each category was modeled using a mixed beta regression, with quadrat as random intercept (Zuur, Hilbe, & Ieno, 2015). To fit the model to the data, Markov Chain Monte Carlo (MCMC) method was performed using Just Another Gibbs Sampler (JAGS, Plummer, 2003) software via the R2jags package (Su & Yajima, 2015) in R (R Core Team, 2017). For each posterior distribution 60 chains were used, each with 50 000 iterations (a burning of 10 000 and a thinning of 10). Diffuse normal priors were used for the fixed and random parameters. In turn, for the standard deviation a half-Cauchy distribution was used. Selection of the best model was based on Bayessian Information Criterion (BIC) and, if more than one model were good candidates, a full averaging approach was followed (Symonds & Moussalli, 2011). In total eight models were fitted (Table 1).

Table 1. Covariate matrices evaluated.

Model	Code
M1	Semester + Condition
M2	Semester + Condition + Semester*Condition
M3	Semester + Condition + Sea urchins
M4	Semester + Condition + Sea urchins + Semester*Condition
M5	Semester + Condition + Sea urchins + Condition*Sea urchins
M6	Semester + Condition + Sea urchins + Condition*Sea urchins + Semester*Sea urchins
M7	Semester + Condition + Sea urchins + Semester*Condition*Sea urchins
M8	Semester + Condition + Sea urchins + Semester*Condition + Semester*Sea urchins + Condition*Sea urchins + Condition*Sea urchins + Semester*Condition*Sea urchins

Results

Benthic community structure

The community structure of both the impacted and non-impacted sectors of the Cuevones patch reef differed significantly (Pseudo-*F* = 6.59, d.f. = 1, *P* < 0.001), and varied along time (Pseudo-*F* = 3.60, d.f. = 3, *P* < 0.001). These differences are readily observed by the separation between sectors and sampling times in the principal coordinate analysis (Fig. 2). Over the entire duration of the study, fleshy algae dominated in both sectors, followed by turf algae (Fig. S1 and S2). With respect to corals, *Porites astreoides* was the most important contributor to benthic cover of all recorded species (Figs. S1 and S2). Contribution of FB corals to benthic cover was modest in both sectors (Fig. S1 and S2).

Coral recruitment

Over the study period, 79 coral recruits were recorded. *Acropora* was the only FB genus occurring in both sectors and its contribution to recruitment was low, 6 individuals in total (Fig. S3). In turn, *Porites* was the genus dominating the recruit community in both sectors at all sampling times (Fig. S3). Other genera recorded were *Agaricia* (9 colonies) and *Millepora* (4 colonies) (Fig. S3). The proportional cover of the two categories of coral recruits (i.e., FB and

NFB corals) were neither related to the cover proportion of adult colonies in their respective categories, nor to the sector condition, nor to the recruitment algae proportional cover (Table 2).

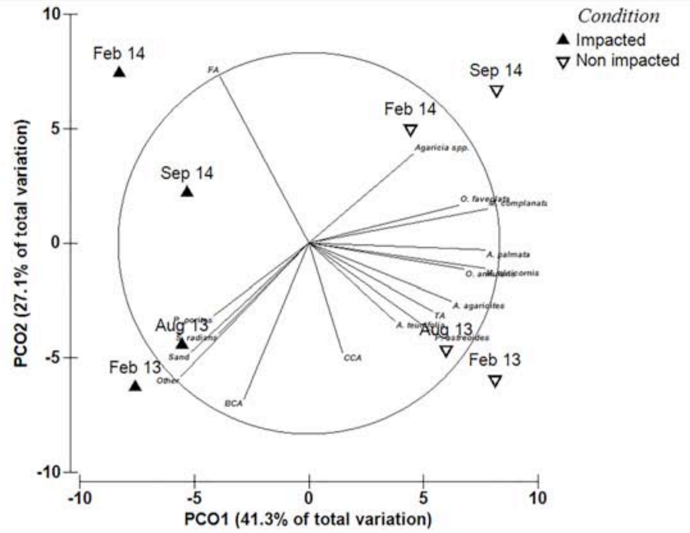

Figure 2. Principal coordinate analysis of the community cover in impacted and non-impacted sectors in the Cuevones patch reef along sampling dates. BCA = branched coralline algae, CCA = crustose coralline algae, FA = Fleshy algae, and TA = turf algae. For species names see Fig. S3.

Table 2. Results of the beta regression between recruits and adults cover proportion for FB and NFB coral species. BIC: Bayesian Information Criterion, N: number of samples, and S.D. = standard deviation.

Parameter	Mean (S.D)	Goodness of fit	
		R^2_{pseudo}	BIC
FB (n=159)			
Intercept	-5.716 (0.018)	0.02	-2013.3
Adults cover proportion	0.047 (0.134)		
Condition (Non-impacted)	-0.031 (0.020)		
RP Algae	-0.046 (0.140)		
NFB (n=159)			
Intercept	-5.463 (0.063)	0.01	-1579.2
Adults cover proportion	0.0521 (0.238)		
Condition (Non-impacted)	-0.007 (0.063)		
RP Algae	-0.465 (0.438)		

Succession of functional groups

Algae were the main contributors to cover (~70 %) in the four sampling times (Fig. 3). Non-recruitment promoting (NRP) algae were the main contributors to algae cover with > 50 % of the area in both sectors at all sampling times. In turn, CCA did not exceed the 15 % threshold of proportional cover in both sectors at the four sampling times (Fig. 3). Mean coral cover ranged between 10-16 % in the impacted sector, and 20-26 % in the non-impacted sector. FB corals had the lowest proportional cover during the entire study period, with a mean cover between 1.3-3.4 % in the impacted sector, and 5-10 % in the non-impacted one. NFB corals had a mean cover between 10-14 % in the impacted sector, while in the non-impacted sector the mean cover of this group varied between 14-21 %. Regarding the density of *D. antillarum* in the 1-m^2 quadrats, it ranged between 0.045-0.62 ind. m^{-2} in the impacted sector, and 0.4-0.81 ind. m^{-2} in the non-impacted sector.

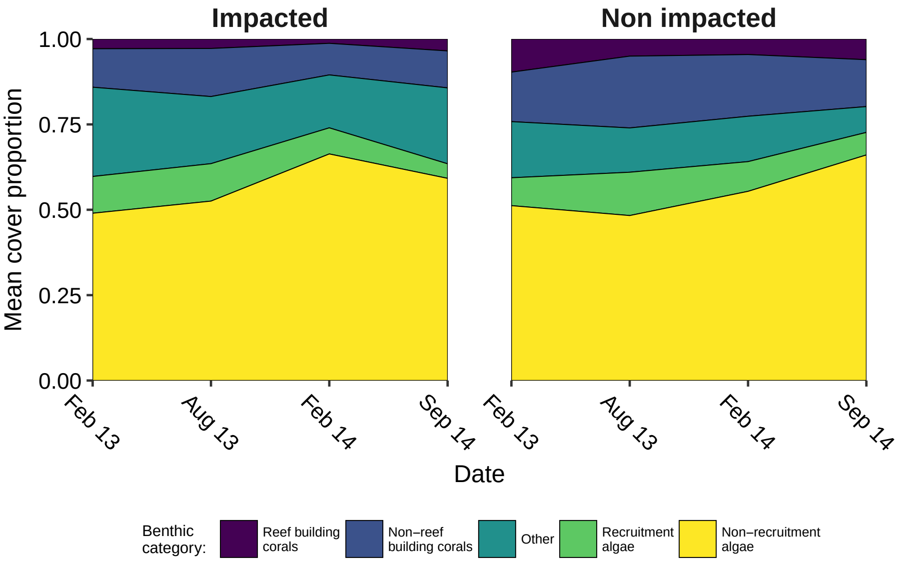

Figure 3. Recorded proportional cover of the four analyzed response variables.

All 60 MCMC chains attained a good mixing and model validation did not show any problem. Model fitting showed that M1 (i.e., sector condition and time, Table 1) had the highest weight for almost all the four variables (Table 3). Moreover, M1 represents the only candidate model for the proportion of coral cover with a weight of 1 (w in Table 3). In the case of FB corals, algae and CCA algae, several models were candidates to the best model (Table 3).

Hence the full averaging approach was followed (Table S1) and showed that condition and time were the strongest covariates explaining changes in the all the benthic categories examined (Table S1). In the case of FB and NFB coral categories, proportional covers for the non-impacted sector were larger than those for the impacted sector. However, in both cases cover proportion decreased with time (Fig. 4). Regarding algae categories, NRP algae increased their cover proportion with time and were larger in the impacted sector (Fig. 5a). In turn, cover proportion of CCA decreased with time although the impacted sector had higher cover in all sampling times (Fig. 5b). For all four variables assessed, the effect of *D. antillarum* over them was modest (Figs. 4 and 5, and Table S1).

Table 3. Model selection between eight models and four variables considered. Boldface shows the best model for each variable. *w*: BIC weight; Δ: delta BIC.

Model	Response variables							
	Coral		FB corals		Algae		CCA algae	
	Δ	*w*	Δ	*w*	Δ	*w*	Δ	*w*
M1	**0**	**1.00**	**0**	**0.34**	**0**	**0.62**	7.6	0.02
M2	46.5	0.0	0.2	0.30	1.8	0.25	**0**	**0.65**
M3	54	0.0	1.5	0.16	4.5	0.07	10.2	0.00
M4	55.9	0.0	1.5	0.16	6.4	0.03	1.4	0.32
M5	56.2	0.0	4.9	0.03	6.7	0.02	11.4	0.002
M6	58.4	0.0	8.3	0.005	8.9	0.007	12.2	0.002
M7	58.6	0.0	8.2	0.006	9.4	0.006	11.9	0.002
M8	67.6	0.0	10.8	0.002	16.5	0.00	9.7	0.005

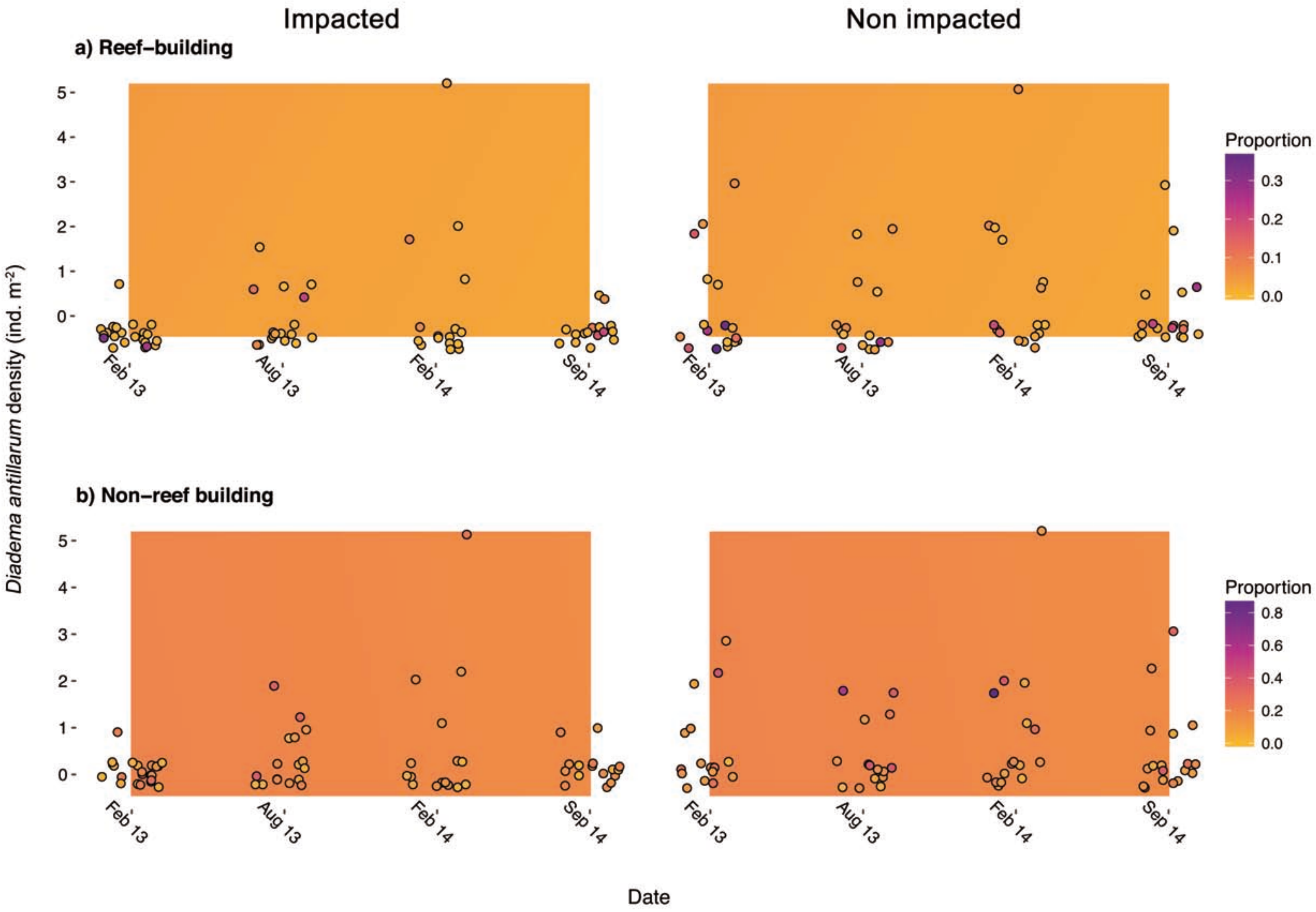

Figure 4. Heat plot of estimated cover proportion for (a) FB, and (b) NFB corals as a function of time, sector condition, and *D. antillarum* density. Circles denote the observed proportions. Note that some jittering has been added to reduce circle overlapping.

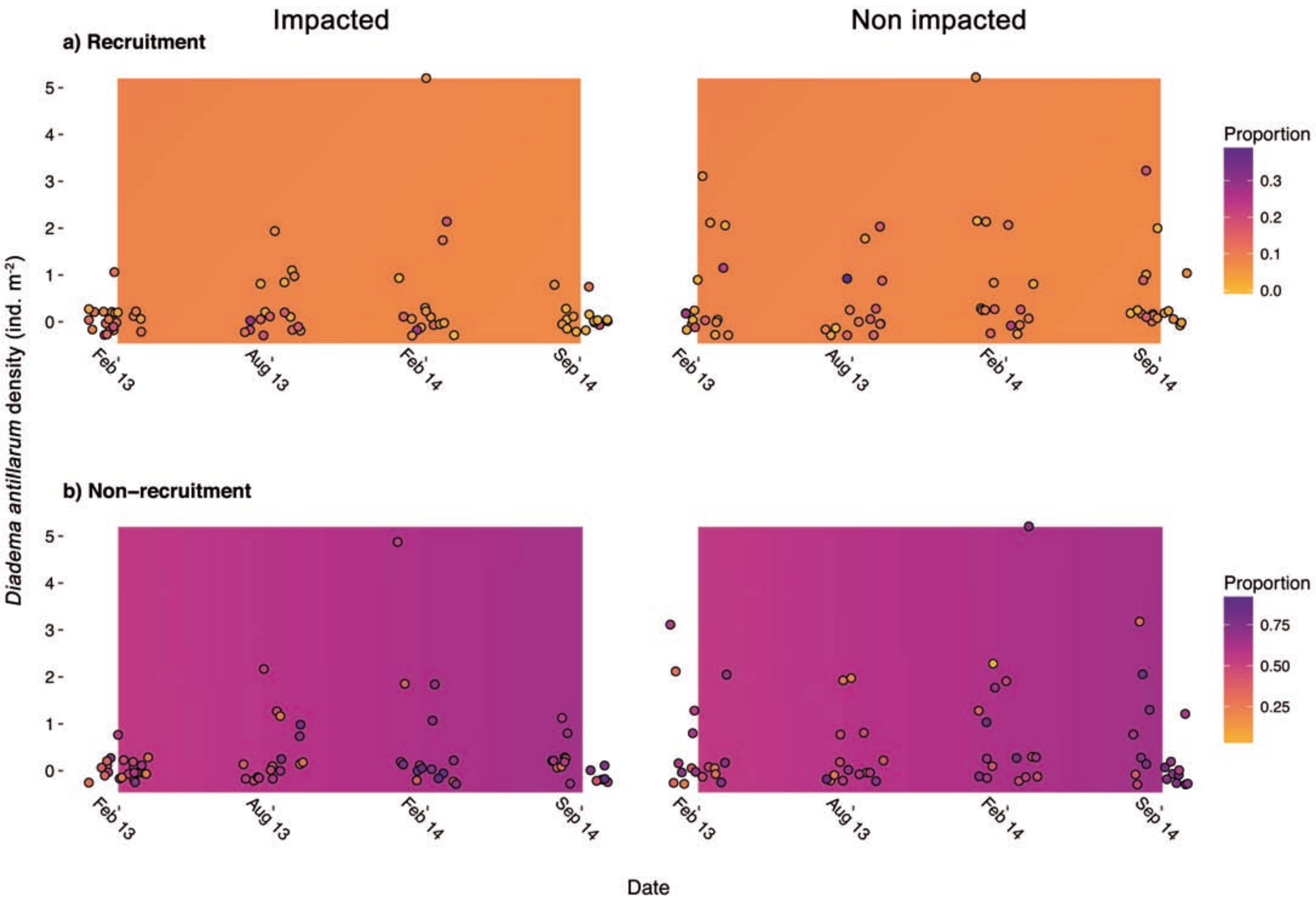

Figure 5. Heat plot of estimated proportional cover for (a) recruitment- and (b) non-recruitment- algae as a function of time, sector condition, and *D. antillarum* density. Circles denote the observed proportions. Note that some jittering has been added to reduce circle overlapping.

Discussion

The results of this study show that the Cuevones patch reef, which was affected by a ship grounding 16 years ago and is under non-take protection (*i.e.*, fishing and tourism are forbiden) status ever since, is currently displaying an alternative state dominated by NFB corals and is transiting to a state dominated by algae. The ongoing successional process in both sectors seems to promote the shift from this NFB coral stable state towards an algae stable state, regardless of whether the ship grounding impacted, the protection status of this marine area, or NFB coral species, such as *Porites astreoides*, dominate. This process also seems to act even in the fraction of Cuevones that is under a coral restoration programm, where coral cover has increased as a result of the introduction of coral fragments but contribution of key species to recruits community is low, being consistent with the patterns found in this research (Perera-Valderrama *et al*. 2016; Perera-Valderrama *et al*., 2017). In Caribbean reefs, loss of resilience and the consequent development of alternative stable states have been driven by reductions of population sizes of key coral species and the decrease in biomass of herbivore species. These phenomena respectively release space available for algal colonization and release algae from negative feedbacks from herbivory. In turn, dominance of fleshy and turf algae, which deter coral recruitment and reduce coral recruit survival (Olsen, Sneed, & Paul, 2016; Steneck *et al*., 2014), promotes, until certain threshold, the dominance of highly disturbance-tolerant coral species with broad ecological plasticity. This has serious ecological implications for reef accretion and the ecosystem services they provide (Alvarez-Filip *et al*., 2013; Kennedy *et al*., 2013; Perry *et al*., 2013; Perry *et al*., 2015). The ultimate consequences of this replacement are the reduction in the calcification of reefs (Alvarez-Filip *et al*., 2013; Perry *et al*., 2015) and the reduction in the availability of refuges for other reef species (Green et al., 2008; Vermeij, 2006).

Previously, Victoria-Salazar et al. (2017) showed that the role of the ship grounding on the Cuevones patch reef was to catalyze the transition in the impacted sector to an alternative stable state from FB corals to NFB ones. In this alternative stable state, species such as *Porites astreoides* were able to colonize reef surface due to its ability to develop healthy populations in harsh environments (Green *et al*., 2008; Olsen *et al*., 2016). However, the modeled dynamics reveals that this potential is being lost. In our study, the analysis of the recruitment patterns showed that abundances of FB species (i.e., *Acropora* and *Orbicella annularis* complex) are so low that their contribution to the coral community is virtually null. Instead, NFB species are the main contributors to the community of recruits.

Several factors have been recognized to drive coral larval settlement, among which sedimentation, interspecific competition with fleshy algae and other groups, available space for settlement, chemical cues, and connectivity with other reef communities that supply coral propagules are noteworthy (Birrell, McCook, & Willis, 2005; Dixson, Abrego, & Hay, 2014; Ferrari, Gonzalez-Rivero, *et al*., 2012; Ferrari, González-Rivero, Ortiz, & Mumby, 2012; Suchley & Alvarez-Filip, 2017). In the Cuevones patch reef, the lack of FB species in the recruit community seems to derive from the combination of several factors. First, the low cover of FB species seems to result from the low abundance of colonies within each sector (Fig. S1), which in turn translates into a limited number of potential autogenic recruits. Second, the connectivity with healthy FB coral populations, a feature that plays an important role by increasing coral reef resilience (Elmhirst, Connolly, & Hughes, 2009; Manikandan *et al*., 2017), appears to be absent. In fact, such lack of connectivity appears to be common to the northern portion of the Mesoamerican Reef System, where only one site (Limones reef) has been recorded to possess a healthy population of *A. palmata* (Rodríguez-Martínez, Banaszak, McField, Beltrán-Torres, &

Alvarez-Filip, 2014), with a high potential fertilization, albeit a low recruitment (Acevedo-Rosas, 2017). The third factor involved seems to be the low cover of recruitment substrate available for FB species, which also diminished with time (Fig. 5). This last factor could be playing an enhanced role in the case of Cuevones: despite the abundance of NFB species and their high reproductive, the available space for coral settlement is reducing and turning into non-recruitment substrate (Figs. 5).

Increasing the chances of settlement, survivorship and growth of FB coral recruits (*e.g.*, *A*. *palmata*, *Orbicella annularis* complex), which are more selective in choosing a settlement substrate than NFB species (Olsen *et al*., 2016), depends strongly on the grazer-mediated reduction of algal cover (Doropoulos, Roff, *et al*., 2017; Suchley & Alvarez-Filip, 2017). In this study, some quadrats had urchin abundances as large as 5 ind. m^{-2}; however, these abundances were not related with a low cover of NRP algae. Noteworthy, the frequency of quadrats recorded with this sea urchin abundance was low, and that most of the quadrats had abundances between 0 and 3 ind. m^{-2} (see figs. 4 and 5). It has been shown that the distribution of sea urchins depends on the identity of the colony, with species having physically more complex colonies offering more refuge space (Dunn, Altieri, Miller, Yeager, & Hovel, 2017). Thus, given that in Cuevones the sub-massive coral species dominate, the only available space for sea urchins are the crevices and the few remaining standing *A*. *palmata* skeletons. Such low refuge availability increases the exclusion of these herbivores, with negative impacts on coral recruitment (Doropoulos, Roff, *et al*., 2017).

From a mechanistic perspective, ecological succession on coral reefs takes place in one of two ways. First, facilitation (sensu Connell & Slatyer, 1977) occurs when crustose calcareous algae dominate the reef surface. Second, inhibition mechanisms act when the earlier colonizers prevent the establishment of the coral larvae, considered the late successional dominant species. The dilemma of which mechanism of ecological succession operates in a coral reef depends largely on the earlier colonizers, *i.e.*, algal identity (Doropoulos, Roff, *et al*., 2017; Mumby *et al*., 2007). In our study, CCA were scarcer than NRP algae in both sectors; models show that CCA decreased with time. Hence, it seems that settlement success is reduced not only by the lack of propagules, but also by the loss of recruitment space. The type of benthic earlier succession groups is strongly coupled with herbivore densities (Doropoulos *et al*., 2016; Mumby *et al*., 2016; Steneck *et al*., 2014). Models also show that, for the Cuevones patch reef, the ecological succession in both sectors is driven by an inhibition mechanism promoted not only by the dominance of fleshy algae, but also by the reduction in coral cover and suitable space for coral recruitment. Switching between successional mechanisms in this ecological context seems difficult. Densities of the herbivore *D*. *antillarum* in both sectors along the study time were so low that the effect is negligible, which would explain the increase in the proportion cover of NRP algae.

There is evidence supporting that inhibition mechanism is occurring elsewhere in the Caribbean. Appart from the widely well documented increments on fleshy algae cover across the region, lack of recruitment of FB coral species has also been reported. For example, in Belizean reefs, where recruitment has failed for ten years despite the establishment of MPA (Huntington, Karnauskas, & Lirman, 2011), and in Mexico where even when a healthy population of *A. palmata* is present, recruitmen within Puerto Morelos MPA is practically null (Acevedo-Rosas, 2017). In the US Virgin Islands, the successional trajectory of the coral community partially coincides with the patterns found in this study. There, *P. astreoides* has reduced its recruitment success and coral cover while *Siderastrea* spp. increses them (Edmunds, 2018).

In summary, this study shows that the damaged sector of the Cuevones patch reef has been following a successional trajectory that seems to be in accordance with the inhibition mechanism (sensu Connell and Slatyer 1977), which also seems to operate at the Caribbean scale. Cover of NRP algae, consisting of fleshy and turf algae, has increased over time, occupying the largest portion of space and reducing the space adequate for coral establishment. In turn, CCA, which are required for the successful establishment of FB coral larvae, showed a decrease in their cover with time. These algal patterns are not exclusive of the impacted sector: the non-impacted one has also shown an increase in NRP algae, and a reduction in the CCA over time. Previous studies have shown that shifts between inhibition and facilitation mechanisms are mediated by herbivores (Doropoulos *et al*. 2017). At Cuevones, the increase of *D. antillarum* abundances was associated with reductions in NRP algae; however, most of the quadrats had no single sea urchin. Quadrats having abundances between 1 and 3 sea urchins showed a high variation in algae cover, suggesting that the abundance of this herbivore was below the threshold in which there is an impact on the algal cover (Edmunds and Carpenter 2001, Mercado-Molina *et al*. 2014). The analysis of ecological succession not only allows to understand how a community lose resilience facilitating the transition to an alternative state but also allows to understand why dinamycs of this new state makes difficult to recover the lost optimal state.

Supplemental Information

Table S1. Estimated parameters (± S.D.) for the eight proposed models and the full model averaging.

Response variable	Model	Intercept	Semester	Non Impacted	Sea urchins	Semester: Non impacted	Semester: Sea urchins	Non Impacted: Sea urchins	Semester: Impacted: Sea urchins	Semester: Non impacted: Sea urchins
Coral	M1	**-1.7044 (0.21707)**	**-0.1058 (0.04939)**	**0.6941 (0.26424)**	**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**
Late Corals	M1	-2.3794 (0.34954)	-0.0346 (0.06981)	0.7576 (0.42405)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	M2	-2.6438 (0.39650)	0.0731 (0.10160)	1.2510 (0.54340)	0 (0)	-0.2019 (0.13932)	0 (0)	0 (0)	0 (0)	0 (0)
	M3	-2.3703 (0.35210)	-0.0351 (0.06994)	0.7317 (0.42814)	0.0904 (0.10879)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	M4	-2.6142 (0.40190)	0.0668 (0.10310)	1.1912 (0.55380)	0.075 (0.10980)	-0.1905 (0.14165)	0 (0)	0 (0)	0 (0)	0 (0)
	M5	-2.3684 (0.35538)	-0.0352 (0.07061)	0.7301 (0.42839)	0.0817 (0.17050)	0 (0)	0 (0)	0.0091 (0.22566)	0 (0)	0 (0)
	M6	-2.3419 (0.35837)	-0.0409 (0.07166)	0.7204 (0.42750)	0.2221 (0.32805)	0 (0)	-0.0479 (0.09466)	-0.0047 (0.23203)	0 (0)	0 (0)
	M7	-2.3441 (0.35472)	-0.041 (0.07113)	0.7223 (0.42651)	0.222 (0.28918)	0 (0)	0 (0)	0 (0)	-0.0500 (0.10824)	-0.0483 (0.09637)
	M8	-2.7487 (0.49620)	0.1117 (0.14270)	1.3212 (0.62180)	-0.3142 (0.83320)	-0.2324 (0.17308)	0.1278 (0.27547)	0.4824 (0.89710)	0 (0)	-0.1626 (0.29506)
Full model averaging	**Mean (β)**	**-2.4956 (0.39562)**	**0.0144 (0.10139)**	**0.9722 (0.54283)**	**0.0306 (0.09093)**	**-0.0921 (0.11992)**	**-0.00006 (0.014134)**	**0.0010 (0.05781)**	**-0.0003 (0.00889)**	**-0.0005 (0.01538)**
Algae	M1	0.7211 (0.1817)	0.1309 (0.04454)	-0.2443 (0.0936)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	M2	0.8234 (0.20912)	0.0862 (0.06263)	-0.4541 (0.30021)	0 (0)	0.089 (0.08853)	0 (0)	0 (0)	0 (0)	0 (0)
	M3	0.7118 (0.18144)	0.1305 (0.04480)	-0.2269 (0.21436)	-0.0457 (0.06843)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

	M4	0.8101 (0.21137)	0.0888 (0.06349)	-0.4276 (0.30622)	-0.0382 (0.06932)	0.0834 (0.09023)	0 (0)	0 (0)	0 (0)	0 (0)
	M5	0.7000 (0.184)	0.1330 (0.04517)	-0.2245 (0.21536)	-0.0768 (0.10244)	0 (0)	0 (0)	0.0595 (0.13836)	0 (0)	0 (0)
	M6	0.6781 (0.18716)	0.1385 (0.04586)	-0.2166 (0.21756)	-0.2155 (0.20068)	0 (0)	0.048 (0.0595)	0.0702 (0.14079)	0 (0)	0 (0)
	M7	0.6922 (0.18467)	0.1350 (0.04521)	-0.2200 (0.21744)	-0.1627 (0.17903)	0 (0)	0 (0)	0 (0)	0.0341 (0.06717)	0.0506 (0.06103)
	M8	0.7456 (0.26841)	0.1097 (0.08432)	-0.3622 (0.34795)	-0.2302 (0.48252)	0.06074 (0.10636)	0.0545 (0.16038)	0.1320 (0.52504)	0 (0)	-0.022 (0.17462)
Full model averaging	**Mean (β)**	**0.7477 (0.19553)**	**0.1186 (0.05413)**	**-0.3000 (0.21013)**	**0.0082 (0.04292)**	**0.0246 (0.05765)**	**-0.00036 (0.00684)**	**-0.0018 (0.02675)**	**0.00019 (0.00566)**	**-0.0003 (0.00635)**
Recruitment algae	M1	-1.6003 (0.18607)	-0.2264 (0.04902)	0.1703 (0.20625)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	M2	-1.2971 (0.20826)	-0.3693 (0.06952)	-0.4451 (0.29802)	0 (0)	0.2703 (0.09473)	0 (0)	0 (0)	0 (0)	0 (0)
	M3	-1.5976 (0.18723)	-0.2266 (0.04932)	0.1642 (0.20789)	0.0128 (0.07586)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	M4	-1.2793 (0.21023)	-0.3742 (0.07026)	-0.4763 (0.30259)	0.0370 (0.0741)	0.2780 (0.09594)	0 (0)	0 (0)	0 (0)	0 (0)
	M5	-1.6002 (0.19063)	-0.2268 (0.04963)	0.1676 (0.20890)	0.0026 (0.11764)	0 (0)	0 (0)	0.0078 (0.15680)	0 (0)	0 (0)
	M6	-1.6470 (0.18958)	-0.2173 (0.04985)	0.1805 (0.20778)	-0.3196 (0.21771)	0 (0)	0.1122 (0.06461)	0.0302 (0.15051)	0 (0)	0 (0)
	M7	-1.6422 (0.18788)	-0.2172 (0.18788)	0.1802 (0.20681)	-0.3081 (0.19658)	0 (0)	0 (0)	0 (0)	0.1212 (0.07353)	0.1079 (0.06645)
	M8	-1.4407 (0.30244)	-0.3189 (0.10293)	-0.2963 (0.37318)	-0.4000 (0.58256)	0.2152 (0.12259)	0.1483 (0.19480)	0.3056 (0.62283)	0 (0)	-0.1044 (0.20755)
Full model averaging	**Mean (β)**	**-1.2994 (0.21484)**	**-0.3672 (0.07351)**	**-0.4398 (0.31348)**	**0.0090 (0.07149)**	**0.2661 (0.09453)**	**0.0009 (0.01809)**	**-0.0016 (0.05028)**	**0.0002 (0.00582)**	**0.0004 (0.01735)**

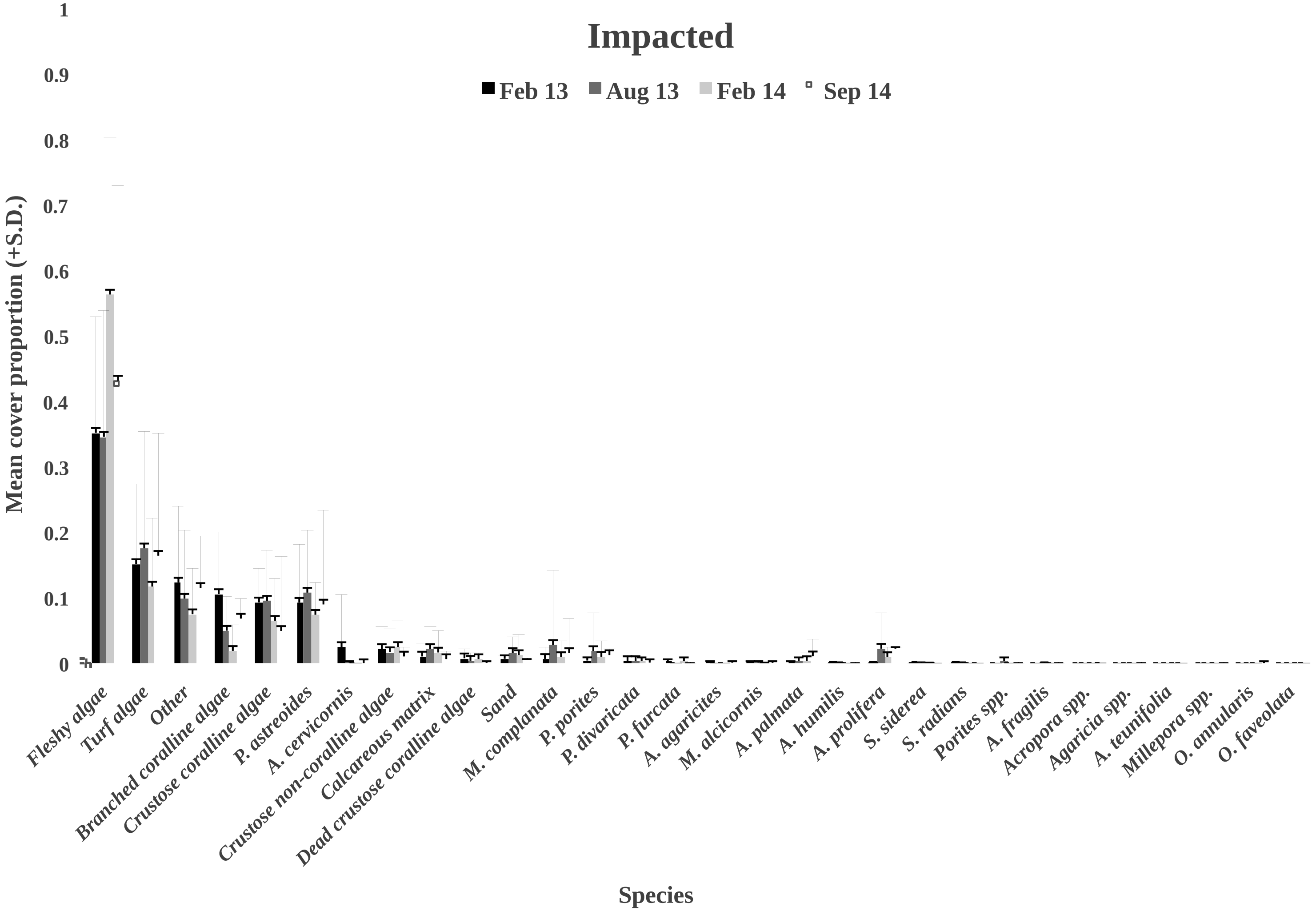

Figure S1. Mean cover proportion of benthic groups recorded in the impacted sector in Cuevones patch reef.

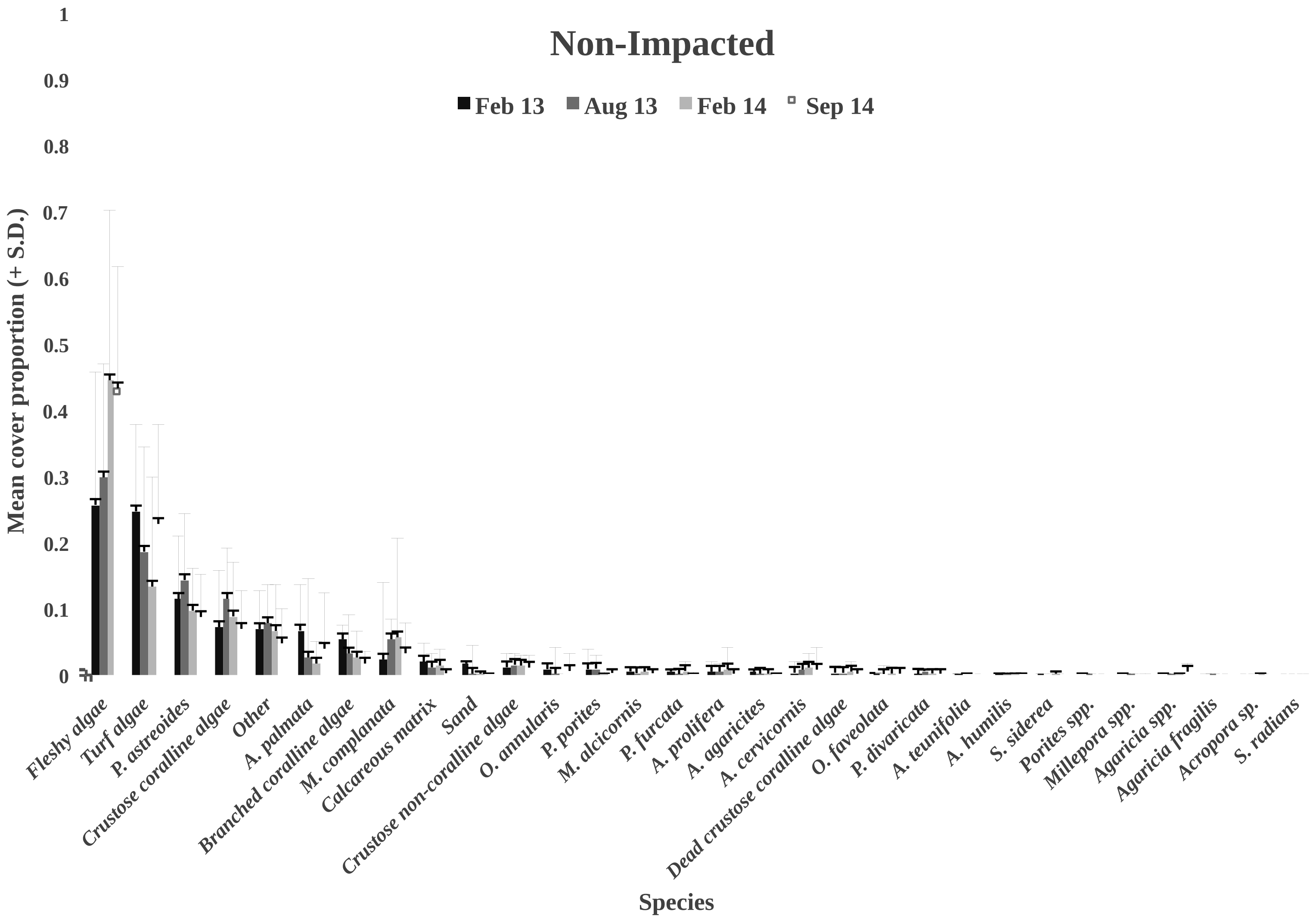

Figure S2. Mean cover proportion of benthic groups recorded in the non-impacted sector in Cuevones patch reef.

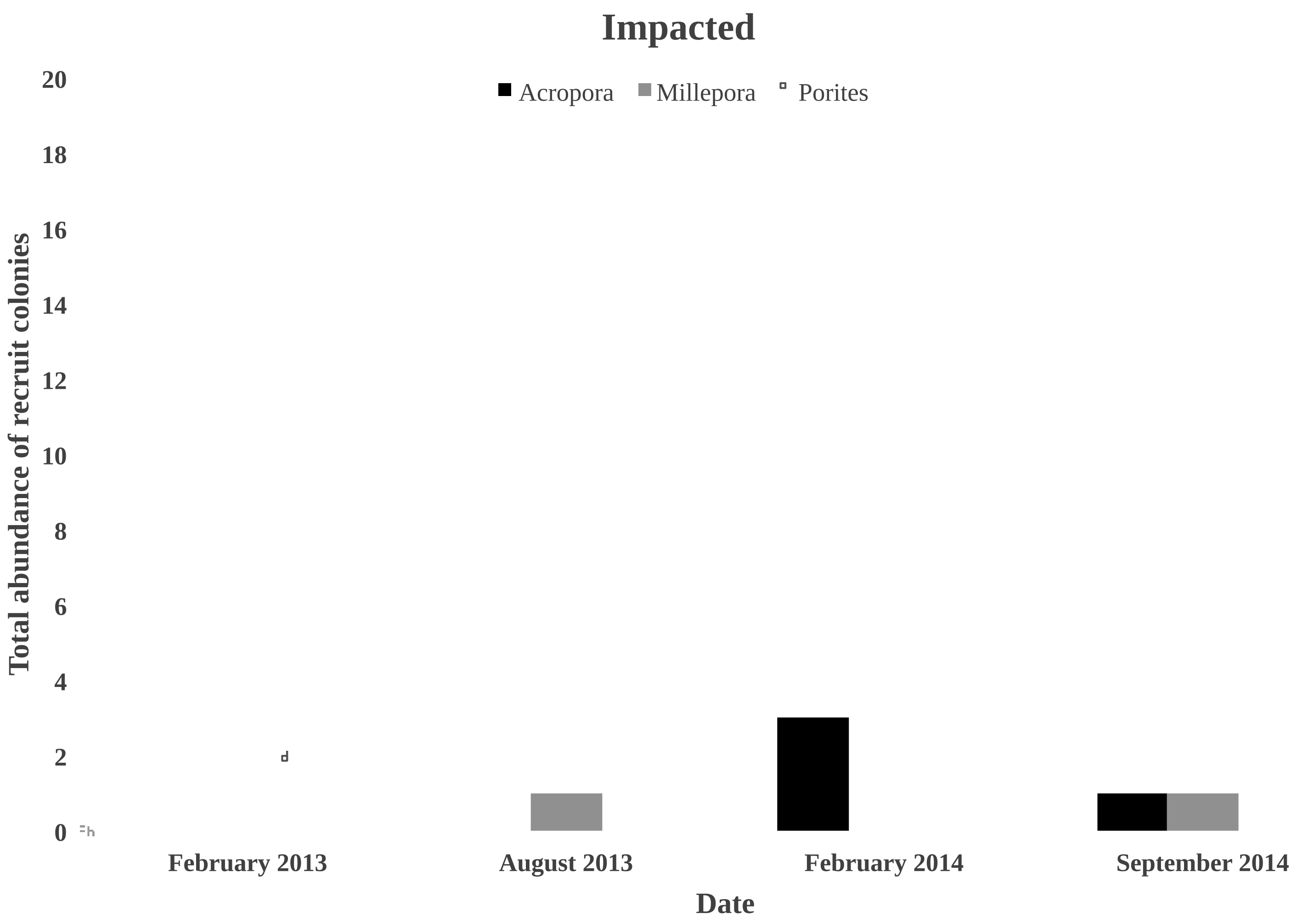

Figure S3. Abundance of coral recruits in the impacted sector of Cuevones patch reef.

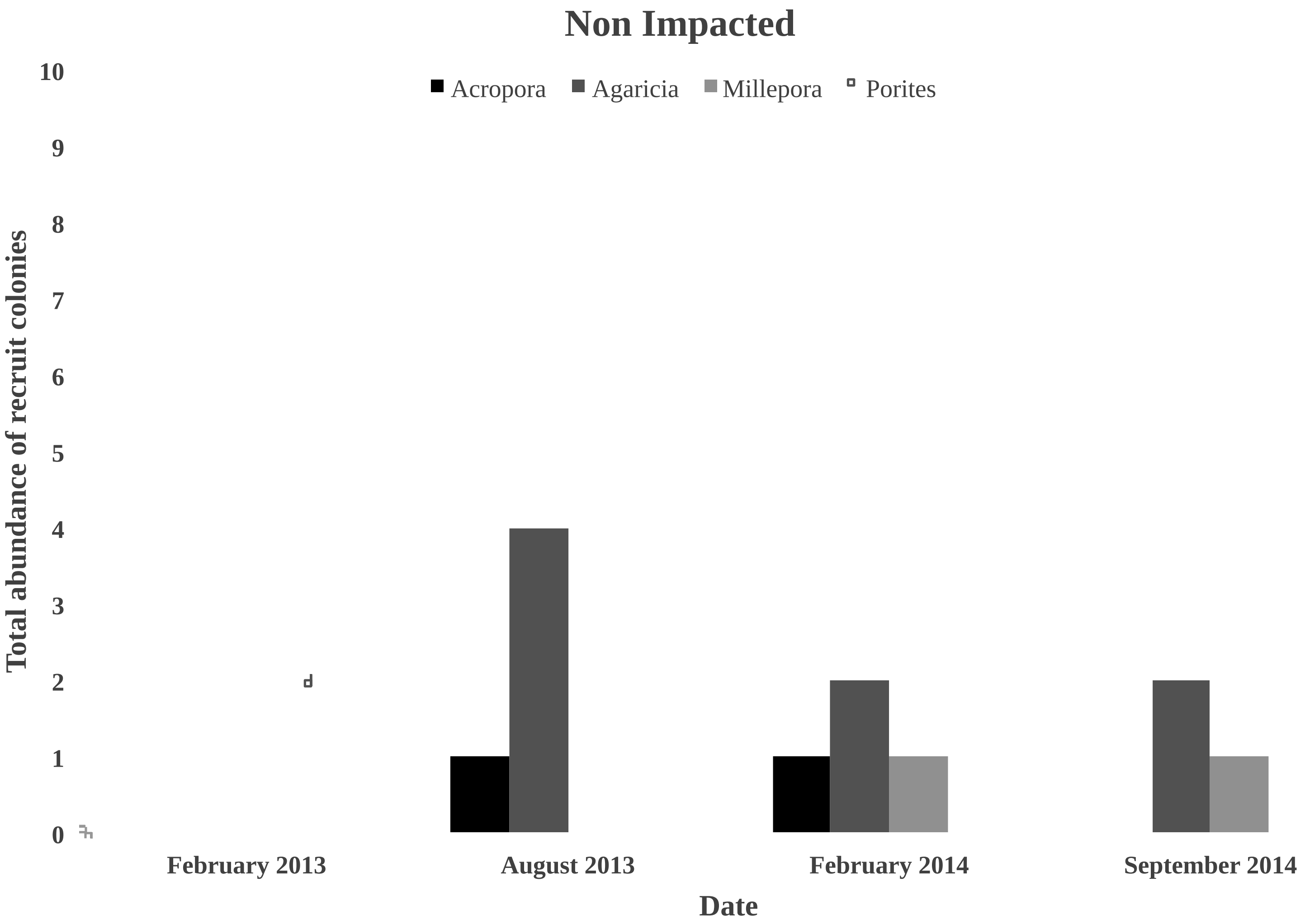

Figure S4. Abundance of coral recruits in the non-impacted sector of Cuevones patch reef.

DISCUSIÓN Y CONCLUSIONES GENERALES

La degradación de los arrecifes de coral en la región del Caribe fue percibida inicialmente en la década de 1960, pero se agudizó a partir de 1980 (Alvarez-Filip *et al*., 2011; Jackson *et al*., 2014; Jackson *et al*., 2001). Esta situación resaltó la urgente necesidad de averiguar qué tipo de transiciones estaban ocurriendo en estos sistemas, así como de reconocer las variables que pudieran indicar la posible pérdida de la capacidad de recuperación de la comunidad arrecifal. Al mismo tiempo que ocurría la transformación de los arrecifes, se formularon las primeras preguntas sobre la capacidad de los sistemas arrecifales de desarrollar estados estables alternativos, y en particular, sobre si dichos estados eran permanentes o no (Bruno, 2014). Los hallazgos de los primeros estudios enfocados a analizar estas preguntas mostraron que, en efecto, los arrecifes de coral desarrollan estados alternativos estables (Done, 1992; Knowlton, 1992; McManus, Menez, Kesner-Reyes, Vergara, & Ablan, 2000; McManus & Polsenberg, 2004). Sin embargo, sigue habiendo un debate enriquecedor acerca de cuáles características de los arrecifes permiten identificar que la comunidad está transitando hacia un estado alternativo (Bruno *et al*., 2009) y sobre su resiliencia en general. En el contexto de estas interrogantes, esta investigación se desarrolló con el objetivo de ofrecer nuevas respuestas. En particular, esta tesis aprovechó la oportunidad que brindó la incidencia de un encallamiento en el pasado para avanzar en el estudio de la sucesión ecológica, tema que ha recibido muy poca atención en el contexto de los sistemas arrecifales, y en última instancia para intentar entender su estabilidad y resiliencia con mayor profundidad.

Relación de la trayectoria sucesional y los estados estables

Durante el periodo de mayor degradación arrecifal mencionado arriba, una de las preguntas que más atención atrajo por parte de los investigadores de sistemas arrecifales fue cuáles atributos de los mismos arrecifes podrían indicar con mayor certidumbre la transición de un sistema arrecifal hacia un estado alternativo. En teoría, uno de las primeras consecuencias de un proceso de cambio de estado es la existencia de una condición definida por Anthony *et al*. (2014) como biestabilidad. En condiciones óptimas los arrecifes de coral sólo pueden ser atraídos hacia un solo estado, caracterizado por la dominancia de corales. Sin embargo, cuando las condiciones dejan de ser óptimas, se presenta la posibilidad de que la comunidad transite hacia un estado estable alternativo. En última instancia, ante la persistencia o agudización de estos cambios negativos en las condiciones sólo es posible la existencia del segundo estado estable, en el cual se pierde la dominancia de los corales. En la búsqueda de indicios de la existencia de este segundo estado estable, la relación entre la cobertura de coral y la de las algas se convirtió en una de las medidas más recurrentes para determinarlo (*e.g*., Fung *et al*., 2011; Knowlton, 1992). Esta práctica se basó en el postulado de que mientras mayor sea la cobertura de las algas y menor la de coral, es más probable que la comunidad se encuentre en un estado estable alternativo. Sin embargo, en realidad esta relación es poco frecuente en las escalas regional y global, y sólo ha sido demostrada claramente en casos muy concretos, como algunos arrecifes de Jamaica (Bruno *et al*., 2009), los cuales por sus respuestas únicas no pueden ser considerados un buen modelo para entender los procesos que ocurren en el resto de los arrecifes del Caribe (Côte *et al*., 2013). Por el contrario, en la mayoría de los arrecifes los cambios en la cobertura de coral no necesariamente están asociados con el incremento de la cobertura de algas (Bruno *et al*., 2009; Kuempel & Altieri, 2017); esto representa una fuente de incertidumbre, ya que significa que la variación intrínseca del sistema hace confusa la expresión de estados alternativos. Además de la relación coral-alga, la abundancia y la biomasa de los herbívoros son variables también usadas con frecuencia para explicar la dinámica potencial de degradación-recuperación de los arrecifes.

Los grupos de herbívoros intervienen directamente en la remoción de la biomasa algal, creando espacios para el reclutamiento. Sin embargo, al igual que en el caso de la relación coral-alga, la evidencia reciente indica que el incremento en la abundancia de los herbívoros no necesariamente produce una reducción en la cobertura de las algas (*e.g*., Arias-González *et al*., 2017; Suchley *et al*., 2016), y por lo tanto el reconocimiento de umbrales críticos de la cobertura algal también está rodeado de confusión (Bruno, 2014).

En el caso de Cuevones, el parche arrecifal donde se llevó a cabo esta investigación, el periodo que transcurrió entre el encallamiento y el inicio de este trabajo (*ca*. 15 años) dio lugar a la pregunta de si esta comunidad había transitado a un estado alternativo, o si por el contrario, ya había recuperado su condición pre-disturbio. Afortunadamente, existe información histórica para este arrecife que incluye datos sobre los cambios de cobertura de coral, de algas y la composición de la comunidad durante dicho periodo, y esto hizo posible reconstruir la ruta sucesional de los diferentes sectores definidos en función del encallamiento (*i.e*., sector impactado *vs*. no impactado). La integración de esa información con datos actuales también permitió hacer algunas inferencias sobre los procesos que posiblemente actuaron sobre la dinámica de la comunidad arrecifal previa a este estudio. El análisis realizado en el Capítulo 2 mostró que la comunidad ya estaba inmersa en una dinámica de construcción de un nuevo estado estable, situación que se ha vuelto cada vez más común en los arrecifes de coral de la región del Caribe (Jackson *et al*., 2014; Jackson *et al*., 2001). Antes del encallamiento, la cobertura de las macroalgas era mayor que la de coral, oscilando entre 40 y 70 %. El encallamiento ocasionó que la cobertura de coral se redujera a un valor tan bajo como *ca*. 5 % en el sector impactado, mientras que en el no impactado se mantuvo alrededor de 30 %, a la vez que la cobertura de las algas se incrementó de manera sostenida en cada sector (Capítulo

2). Así, aunque la reducción de la cobertura de coral es congruente con el incremento de la cobertura de algas, son las tendencias sostenidas a través del periodo las que constituyen evidencia robusta del tránsito hacia un estado alternativo. Con respecto al encallamiento, los resultados del primer estudio particular muestran una convergencia en las trayectorias de sucesión en ambas condiciones (*i.e.*, afectado y no afectado por el encallamiento); en última instancia, este hallazgo indica el papel del disturbio como agente catalizador del proceso sucesional en el sector impactado, pero no hacia una ruta de recuperación sino de transición hacia un estado alternativo.

Otro aspecto que proporcionó evidencia adicional sobre el desarrollo de un estado estable alternativo en Cuevones lo constituyen los cambios en la composición a través del tiempo, situación que se vio reflejada en el escalameinto multidimensional no métrico (NMDS, Capítulo 2) de los tiempos de muestreo en las diferentes condiciones analizadas. Por ejemplo, antes del encallamiento la composición de la comunidad de corales permaneció más o menos homogénea y esto resultó en una agrupación de los muestreos en la ordenación (Capítulo 2). Después del encallamiento, la composición en el sector impactado originó la mayor dispersión en la agrupación de los periodos de muestreo, mientras que en el sector no impactado la dispersión fue un poco menor. En realidad, la dispersión de los muestreos evaluada a través de los cambios en la composición específica puede ser explicada tanto por la variación espacial como por un cambio temporal. En caso de haber cambios temporales en la composición, éstos pueden interpretarse como un cambio de estado. Por el contrario, en el caso de la variación espacial, la dispersión en la ordenación podría estar asociada a un factor que produzca confusión, como podría ser la dinámica de parches (sensu Pickett & White, 1985b); sin embargo, la existencia de un grupo compacto en términos de la composición antes del encallamiento da robustez a la interpretación de un cambio de estado, tanto en la porción afectada como en la no afectada por el encallamiento.

Por lo general los estudios de dinámica de los arrecifes de coral a mediano y largo plazo se enfrentan a la carencia de información histórica. Por esta razón, es difícil relacionar otras características arrecifales con los estados estables alternativos en el corto plazo de manera confiable. En este sentido, la riqueza y la composición específica, así como su contribución a la complejidad física arrecifal, representan una posible solución a este problema. La riqueza y la composición específica contribuyen de manera importante tanto a la estabilidad como a la resiliencia de las comunidades debido a su estrecha relación con la diversidad y la redundancia funcional (Nyström, 2006; Peterson, Allen, & Holling, 1998), ya que esto permite inferir el estado hacia el cual se dirige una comunidad. En general, se reconoce que mientras mayor sea el número de especies que componen una comunidad no sólo será mayor el número de funciones que ellas tengan (McWilliam *et al*., 2018), sino también mayor el número de especies que desempeñan determinada función (Tilman *et al*., 1997). En el Caribe y en condiciones ambientales óptimas, la construcción de la matriz arrecifal depende básicamente de una tercia de especies (*Acropora palmata*, *A. cervicornis* y el complejo de *Orbicella annularis*; Perry *et al*., 2015; Aronson , Precht, & Toth, 2012), las cuales a su vez son las que confieren una mayor complejidad física a estos sistemas. Con el cambio de las condiciones ambientales, el incremento en la frecuencia de enfermedades y la consecuente reducción drástica de esas especies, los corales oportunistas (como es el caso de *Porites astreoides*), cuya riqueza específica es mayor, dominan el sustrato (Green *et al*., 2008).

Otro de los factores que limita la recuperación de los sistemas arrecifales es el aporte de sedimentos y nutrientes que las actividades humanas originan en la costa. El incremento de sedimentos reduce la cantidad de luz disponible limitando la diversidad de corales que se pueden establecer y sobrevivir (Fabricius, 2005, Roberts, Hanley, Williams, & Cresswell, 2017). En el caso de Cuevones, el desarrollo de Cancún, la zona de mayor desarrollo costero de Quintana Roo, en conjunto con la pérdida generalizada de especies clave de coral y de hérbívoros en el Caribe pueden estar actuando de manera sinérgica favoreciendo la permanencia de condiciones de desarrolo subóptimas, propiciando la virtual ausencia crónica de las especies clave y favoreciendo la dominancia de las especies oportunistas, primordialmente de *Porites astreoides*, las cuales han configurado la comunidad actual. Esta combinación de factores es parte fundamental de un proceso de retroalimentación positiva que favorece la persistencia de un estado alternativo estable, ya que este tipo de especies se reclutan con mayor frecuencia y mantienen una estructura poblacional acorde. En otras palabras, está ocurriendo un proceso de reclutamiento intenso que resulta en un incremento de colonias de tallas grandes de especies oportunistas; dichas especies poseen estrategias reproductivas que les permiten incorporar nuevos individuos al sustrato arrecifal con mayor frecuencia de lo que ocurre con las especies constructoras de arrecifes. Por otra parte, las especies oportunistas contribuyen muy poco al desarrollo de la estructura física arrecifal, tanto por su menor tasa de acumulación de carbonatos (Perry *et al*., 2015), como por su incapacidad de desarrollar estructuras tridimensionales complejas, lo que reduce la disponibilidad de refugios para otras especies. Por lo tanto, la permanencia de las especies oportunistas como elementos dominantes en una comunidad, además de ser sintomática de la degradación del sitio, refleja cambios profundos en el funcionamiento de la comunidad (Álvarez-Filip *et al*., 2009).

Resiliencia del estado estable alternativo

Importancia del reclutamiento

Al igual que los atributos de las colonias de coral adultas, los cambios en la riqueza y la composición de especies en la comunidad de reclutas de coral permiten identificar el desarrollo de trayectorias de sucesión hacia estados estables alternativos. Para que el proceso de recuperación de los arrecifes se lleve a cabo es fundamental que el aporte de elementos de propagación sea suficiente (Fox & Caldwell, 2006; Fox, 2004; Fox *et al*., 2003). Por ejemplo, Tanner, Hughes, y Connell (1994) mostraron, por medio de un ejercicio de modelación para *Orbicella annularis*, que un aporte subóptimo de larvas tiene consecuencias negativas severas tanto para la población, por ejemplo impidiendo el recambio de colonias, como para la comunidad, al inducir la incapacidad de generar estructuras físicas que brinden refugio, con la consecuente pérdida de complejidad física.

La comunidad de reclutas en Cuevones está dominada por colonias del género *Porites*, probablemente *P*. *astreoides* (es imposible obtener una determinación taxonómica precisa en esta etapa del desarrollo); estos reclutas tienen una mayor supervivencia que la correspondiente a las especies hermatípicas. En el contexto de la degradación ambiental de los arrecifes del Caribe, *P. astreoides* se ha consolidado como una especie conspicua, por lo general dominante, gracias al decremento de la cobertura de tejido vivo de otras especies, en combinación con una frecuencia mayor de periodos reproductivos, la presencia de incubación de larvas y, aparentemente, una menor especificidad en la selección del sustrato de establecimiento (Green *et al*., 2008). Además de la dominancia -a veces extrema- de esta especie oportunista o de otras similares ecológicamente, cabe destacar que el proceso de reclutamiento de esta misma especie puede ser poco exitoso. Esto se debe a una reducción importante de los espacios de establecimiento para nuevos reclutas causada por el incremento de la cobertura de algas carnosas. Los modelos estadísticos desarrollados en esta investigación (Capítulo 3) mostraron que las algas calcáreas incrustantes, necesarias para el establecimiento de los reclutas, están perdiendo espacio para cederlo a las algas carnosas; estas últimas ejercen una fuerte competencia sobre los corales, llegando a reducir de manera importante sus tasas de crecimiento (Ferrari, Gonzalez-Rivero, *et al*., 2012; Suchley & Alvarez-Filip, 2017). En el largo plazo, aunque alguna especie de coral mantenga la capacidad de producir estructuras de propagación y, por lo tanto, de reintegrarse a la comunidad, la pérdida sostenida de espacios adecuados para el establecimiento, es decir, los que incrementan la probabilidad de establecimiento y supervivencia, dificulta la recuperación de la comunidad, reduciendo en última instancia su resiliencia.

La contribución de los herbívoros

Entre los principales actores en la regulación de la cobertura de las algas y, en consecuencia, de la trayectoria del proceso sucesional en los arrecifes, están los herbívoros (Belliveau & Paul, 2002; Doropoulos, Evensen, Gómez-Lemos, & Babcock, 2017; Doropoulos, Roff, *et al*., 2017). En las condiciones óptimas de funcionamiento de un arrecife de coral, los peces herbívoros son los principales responsables de regular la cobertura de macroalgas, y la importancia de su papel como consumidores ha sido probado robustamente (Jackson *et al*., 2014; Jackson *et al*., 2001). Sin embargo, en el Caribe, donde las condiciones ambientales están en una situación subóptima en la actualidad, la biomasa y la abundancia de estos organismos no tiene una relación clara con la cobertura de las algas (Arias-González *et al*., 2017; Suchley *et al*., 2016). Incluso dentro de las áreas marinas protegidas, se ha producido evidencia de que las poblaciones de peces herbívoros se están reduciendo, aunque a una velocidad menor que en áreas no protegidas, de modo que su importancia en el mantenimiento de los arrecifes es cada vez más limitada (Schmitter-Soto *et al*., 2017). En contraste, en un contexto arrecifal caracterizado por la dominancia de especies oportunistas de coral, los herbívoros de menor talla, como los erizos, parecen incrementar su importancia (Dunn *et al*., 2017). Así, la estructura física y los consecuentes espacios limitados de refugio construidos por las especies de coral oportunistas, constituyen los únicos escenarios donde puede tener continuidad los procesos ecológicos clave en los arrecifes. Si bien ésta es una posibilidad teórica interesante, la información obtenida en Cuevones no resaltó la importancia del erizo *Diadema antillarum*, la especie de herbívoro que fue analizada como parte de la dinámica sucesional de este sistema. Esto puede deberse a las densidades encontradas de este equinodermo (Capítulos 2 y 3) en ambos sectores posiblemente están por debajo de un umbral en el que el efecto positivo del consumo de algas se traduce en un incremento efectivo del espacio disponible para el establecimiento de corales.

Consideraciones finales

El análisis integral de los resultados obtenidos en los dos estudios particulares incluidos en esta investigación permite concluir de forma general que las similitudes en la estructura y trayectoria sucesional entre la porción afectada y la no afectada por el encallamiento en este parche arrecifal del Caribe no debe ser interpretada como evidencia de recuperación, sino como un claro indicio de la convergencia en el desarrollo de todas estas condiciones hacia un estado estable alternativo.

La definición formal del término resiliencia en ecología describe la capacidad de las comunidades para regresar a un estado previo (Holling, 1973), pero la realidad es que ésta es un atributo complejo que está integrado por varios componentes. Uno de estos componentes es la resistencia que los sistemas biológicos oponen, de manera diferencial, ante un disturbio para alcanzar un estado estable alternativo. Dado el intervalo entre el comienzo de la transición hacia un estado alternativo y esta investigación, así como el tipo de disturbio, este componente no fue factible de análisis para el parche arrecifal Cuevones. Por lo tanto, la pregunta sobre las características que un disturbio debe tener para rebasar los límites de la tolerancia de una comunidad arrecifal representa aún una interrogante por contestar. Otro de los componentes de la resiliencia es el mecanismo que gobierna el proceso sucesional. La ruta de sucesión que favorece el estado dominado por corales, requiere que en las etapas muy tempranas las algas calcáreas incrustantes deben de ocupar el espacio para favorecer el establecimiento de los corales (Doropoulos, *et al*., 2017) ya que éstos una vez establecidos forman parte de la comunidad durante toda la sucesión, siendo los cambios en sus abundancias y sus coberturas las que determinan el grado de avance de este proceso, hasta que ocurra una situación en la que tales cambios son menos frecuentes (Grigg, 1983); este mecanismo es conocido como facilitación (Connell & Slatyer, 1977). El análisis de los datos de esta investigación muestran que el procesos sucesional es acorde con el mecanismo conocido como inhibición; denominado también como anti-sucesional. En los arrecifes de coral tal mecanismo está caracterizado por una reducción en la superficie disponible para el establecimiento de larvas de coral y una reducción en el número de reclutas de las especies clave (Capítulo 3).

Entre las interrogantes que en esta investigación no obtuvieron una respuesta concreta resalta la contribución de los erizos como herbívoros y su influencia en el proceso sucesional. La importancia de entender el papel de los erizos en el funcionamiento de los arrecifes del Caribe es resultado de los cambios que en las redes tróficas han tenido lugar, como consecuencia de las actividades humanas, y que aún siguen influyendo sobre éstas; en particular la reducción en la abundancia de los peces herbívoros (Jackson *et al*., 2014; Jackson *et al*., 2001; Schmitter-Soto *et al*., 2017). En este contexto, los erizos ofrecen, como alguna vez lo hicieron, la posibilidad de mantener el control de la productividad primaria en los arrecifes (Carpenter, 1981); por lo que entender los detalles de sus cambios poblacionales es fundamental. Otro aspecto que genera interés, y que queda pendiente de análisis en esta investigación, es la relación que guardan las coberturas de las algas calcáreas costrosas (ACC) y las macroalgas carnosas (MAC); es posible que ciertos atributos de las ACC tengan efectos negativos sobre las MAC (Vermeij, Dailer, & Smith, 2011). La dirección en que esta interacción ocurre en el Caribe permanece incógnita y desvelar el alcance de ésta en los arrecifes cambiaría nuestra perspectiva sobre las causas que contribuyen a la reducción de resiliencia y a la permanencia de los estados estables alternativos de estos sistemas arrecifales.

Aunque el punto final en la discusión de la resiliencia no se vislumbra a través de esta investigación, la incorporación explícita del proceso sucesional como componente de la resiliencia de los sistemas biológicos permite ampliar la manera en que percibimos este atributo complejo de los arrecifes de coral; incorpora elementos del funcionamiento de la comunidad arrecifal en función de las diferentes escalas a las que ocurren. Además, nos permite reflexionar sobre las variables que se consideran óptimas para determinar que un arrecife mantiene un estado estable deseado. Por último, la resiliencia, y sus componentes, también son resultado de las condiciones y procesos que ocurren a escalas mayores a la extensión de los arrecifes, por lo que mantener o recuperar un estado estable deseado requiere que los procesos que ocurren en escalas regionales o globales sean acordes con dicho estado.

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