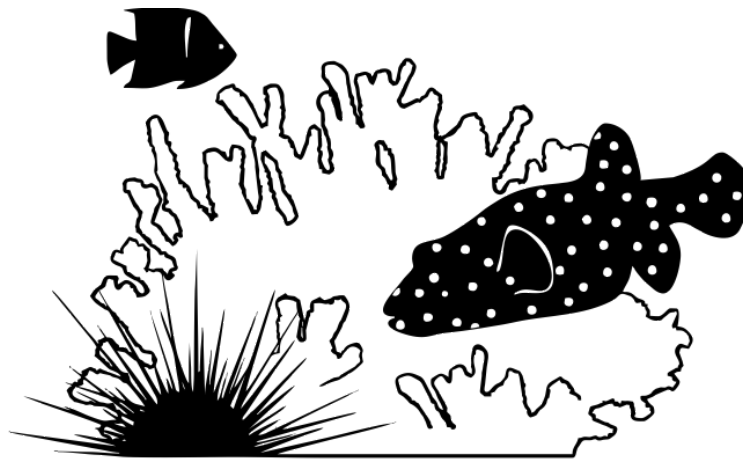


Modos de reclutamiento coralino y efectos de la depredación por *Arothron meleagris* en corales pocilopóridos de Isla Gorgona

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**ECOLOGÍA DE
ARRECIFES
CORALINOS**

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Modos de reclutamiento coralino y efectos de la depredación por *Arothron meleagris* en corales pocilopóridos de Isla Gorgona

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RESUMEN

Los arrecifes coralinos son ecosistemas vulnerables que se han venido deteriorando a escala mundial al desarrollarse en condiciones ambientales restringidas, pero también son sistemas altamente dinámicos al exhibir ciclos naturales de perturbación-recuperación que apenas estamos comenzando a entender. El reclutamiento, o la entrada de nuevos individuos a las poblaciones, determina en gran medida el proceso de recuperación natural después de perturbaciones, y puede darse tanto por asentamiento de larvas derivadas de reproducción sexual, como por fragmentación física de colonias y supervivencia de esos fragmentos. En el Pacífico Tropical Oriental los escasos estudios sobre reclutamiento coralino de origen sexual han sido poco exitosos, y a pesar de la potencial importancia de la reproducción asexual por fragmentación, aspectos básicos sobre la ecología de este proceso aún se desconocen. Esta investigación por medio de un amplio trabajo de campo, aportó información novedosa sobre la ecología reproductiva de los corales del Pacífico colombiano. Se proporcionó por primera vez evidencia sobre la presencia de reclutas coralinos de origen sexual en diversos sitios de Isla Gorgona, y mediante monitoreos y experimentos *in situ* estudiamos algunas causas física y bióticas de la fragmentación de coral en el arrecife de La Azufrada. Se describió la acción de troncos flotantes y la depredación por peces en la producción de fragmentos coralinos, analizando cuantitativamente la coralivoría por el pez *Arothron meleagris* y su efecto sobre el arrecife, al destruir coral pero al mismo tiempo generar reclutas asexuales que al crecer contribuyen a aumentar la cobertura coralina y formar nuevas colonias y, en última instancia, compensar el impacto deletéreo de la coralivoría.

Palabras clave: Coralivoría, Reproducción asexual, Fragmentación, *Pocillopora*, Tetraodontidae.

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CGM

TABLA DE CONTENIDOS

RESUMEN	III
AGRADECIMIENTOS.....	IV
TABLA DE CONTENIDOS.....	VI
LISTA DE TABLAS	VII
LISTA DE FIGURAS	VIII
INTRODUCCIÓN GENERAL.....	1
<i>REFERENCIAS.....</i>	<i>8</i>
CAPÍTULO 1	14
EVIDENCE OF SEXUALLY-PRODUCED CORAL RECRUITMENT AT GORGONA ISLAND, EASTERN TROPICAL PACIFIC.	
.....	14
<i>Abstract.....</i>	<i>14</i>
<i>Resumen.....</i>	<i>14</i>
<i>INTRODUCTION.....</i>	<i>15</i>
<i>METHODS.....</i>	<i>16</i>
<i>RESULTS.....</i>	<i>18</i>
<i>DISCUSSION.....</i>	<i>19</i>
<i>REFERENCES</i>	<i>22</i>
<i>TABLES AND FIGURES.....</i>	<i>26</i>
<i>APPENDIX.....</i>	<i>29</i>
CAPÍTULO 2	30
DRIFT LOGS ARE EFFECTIVE AGENTS OF PHYSICAL CORAL FRAGMENTATION IN A TROPICAL EASTERN PACIFIC	
CORAL REEF.	30
CAPÍTULO 3	33
FISH CORALLIVORY ON A POCILLOPORID REEF AND EXPERIMENTAL CORAL RESPONSES TO PREDATION.....	33
CAPÍTULO 4	46
OPPOSITE EFFECTS OF PUFFERFISH CORALLIVORY ON THE CARBONATE BUDGET OF A POCILLOPORID REEF.	46
<i>Abstract.....</i>	<i>46</i>
<i>Resumen.....</i>	<i>47</i>
<i>INTRODUCTION.....</i>	<i>47</i>
<i>METHODS.....</i>	<i>49</i>
<i>RESULTS.....</i>	<i>55</i>
<i>DISCUSSION.....</i>	<i>58</i>
<i>REFERENCES</i>	<i>64</i>
<i>TABLES AND FIGURES.....</i>	<i>70</i>
DISCUSIÓN GENERAL Y CONCLUSIONES	75
<i>REFERENCIAS.....</i>	<i>80</i>

LISTA DE TABLAS

Tabla 1-1. Checklist of species of coral recruits observed at ten sites in Gorgona National Natural Park (Colombia, Eastern Tropical Pacific) during 2010 - 2017.....	26
Apéndice 1-A. List of sites surveyed looking for coral recruits at Gorgona Natural National Park (Colombia, Eastern Tropical Pacific) during years 2010 – 2017.....	29
Tabla 3-1. Carbonate budget estimated for La Azufrada coral reef, considering only the production of Pocillopora spp. and the destruction by the puffer <i>Arothron meleagris</i>	42
Tabla 3-2. Abundance of the puffer <i>Arothron meleagris</i> on pocilloporid reefs within the Tropical Eastern Pacific.....	42
Tabla 4-1. Pufferfish abundance, and rates of fragmentation by pufferfish, survival of fragments and asexual recruitment in La Azufrada reef.....	70
Tabla 4-2. Substrate cover of live coral, sand and coral rubble/rock in La Azufrada reef, used as the probability of a fragment to land on each substrate1	70
Tabla 4-3. Estimations of coral weight rates (kg m ⁻² yr ⁻¹) involved in the interaction between pufferfish and pocilloporid corals.....	70

LISTA DE FIGURAS

Figura 1-1. Coral recruits derived from sexual reproduction attached to natural substrates at Gorgona Island (Eastern Tropical Pacific). White arrows (A, B and C) point to encrusting base in <i>Pocillopora</i> specimens. A-B) <i>Pocillopora</i> sp. on coral rubble with calcareous algae; C) <i>Pocillopora</i> sp. on rocky wall with filamentous algae; D) <i>Porites panamensis</i> on coral rubble with calcareous-algae; E) <i>Pavona varians</i> on coral rubble with calcareous-algae; F) <i>Pavona gigantea</i> on rocky wall with filamentous algae.	27
Figura 1-2. Size frequency distributions of coral recruits at Gorgona National Natural Park (Eastern Tropical Pacific). The distributions are truncated at 5.0 cm, since juveniles are defined as colonies ≤ 5.0 cm. Distribution for pocilloporid recruits (N = 41) at A) La Azufrada, B) El Laberinto, and C) Playa Blanca. <i>Porites panamensis</i> (N = 170) in D) El Arrecifito. Colony size refers to the largest colony diameter	28
Figura 2-1. Drift logs causing physical coral fragmentation in La Azufrada reef, Eastern Tropical Pacific.....	31
Figura 3-1. Bite marks by the pufferfish <i>Arothron meleagris</i> on <i>Pocillopora</i> spp. colonies: a) scrapes to the coral tissue; b, c) excavating bites where coral tissue and skeleton have been removed, d) pocilloporid colony exhibiting pufferfish bite marks; e) <i>A. meleagris</i> feeding on <i>Pocillopora</i> sp.....	37
Figura 3-2. Treatments considered in the predator exclusion experiment where pocilloporid nubbins were individually exposed or protected from fish corallivores: a) Predation treatment (no cage), b) cage control treatment (half-cage), and c) Predator exclusion treatment (full cage). Half-cages were employed to allow fish predation while controlling for the possible effects of the mesh on the nubbins.....	38

Figura 3-3. Mean (+95 % CI) a) pocilloporid coral cover (%), b) <i>Arothron meleagris</i> abundance (ind ha ⁻¹), and c) standing bite density (bites m ⁻²) across three zones of La Azufrada coral reef, Gorgona Island. Bars with the same lowercase letter did not differ significantly: a, b) two-sample resampling tests with Holm's correction ($\alpha = 0.05$), c) Tukey's multiple comparison test ($\alpha = 0.05$).....	39
Figura 3-4. Observed frequency distribution of standing bite scars within 100 cm ² quadrats on each of three reef zones at La Azufrada coral reef: a back reef, b reef flat, and c reef crest. Dash line histograms correspond to the expected Poisson distribution under the null hypothesis of a random spatial distribution of bite scars.....	40
Figura 3-5. Adjusted mean (+95 % CI) of the change in weight attained by pocilloporid colonies exposed to different levels of simulated bite inflicted damage (control = 0 % or no damage, and 25, 50, or 75 % of colony branch tips damaged). Means of change in weight were adjusted by ANCOVA to the mean initial weight of colonies.....	45
Figura 3-6. Mean (+95 % CI) growth in terms of a normalized linear extension (cm cm ⁻² yr ⁻¹) and b) normalized weight (g cm ⁻² yr ⁻¹) of <i>Pocillopora</i> spp. nubbins in each of three predation treatments (Predation, cage control = CC, and Predation exclusion). c) Average ratio between the normalized weight gained and the increased linear extension of nubbins (normalized) in each treatment. Bars with the same lowercase letter did not differ significantly: a, c) Tukey multiple comparison test ($\alpha = 0.05$), b) two sample resampling tests with Holm's correction ($\alpha = 0.05$).....	45
Figura 3-7. Representative corallum morphologies of pocilloporid nubbins a) exposed and b) protected from fish corallivory in the Predator exclusion experiment carried out at La Azufrada coral reef, Gorgona Island, Colombia.....	45
Figura 4-1. La Azufrada reef at Gorgona Island (left), and its main reef zones (right).....	71

Figura 4-2. (A) Pocilloporid fragment (circled in red) falling during a pufferfish attack on pocilloporid corals. (B) Coral fragments produced by pufferfish predation on pocilloporid corals at La Azufrada reef.....	71
Figura 4-3. Frequency distributions of coral fragments generated by pufferfish predation (A) length, (B) weight. (C) Length-Weight relationship ($W = -0.71 + 8.52L$; $p < 0.05$, $R^2 = 0.88$).....	72
Figura 4-4. (A) Kaplan-Meier plots showing the survival of pocilloporid fragments trajectories among treatments (sand, loose coral rubble and consolidated coral matrix) during one year. (B) Growth of pocilloporid fragments deployed on coral rubble and coral matrix during one year from May 2013 to April 2014. Whiskers denote standard errors	73
Figura 4-5. Annual coral production by the pocilloporid standing crop across the processes of predation, fragmentation, and generation of asexual recruits. Percentage values are shown for the whole reef. 1) Coral affected by pufferfish = Coral fragmentation + Coral consumption; (2) Coral after corallivory = Gross carbonate production – Carbonate affected by pufferfish; (3) Net carbonate production = Growth of recruits + Carbonate after corallivory; (4) Total coral destruction = Mortality of fragments + Coral consumption....	74

INTRODUCCIÓN GENERAL

Los arrecifes coralinos son ecosistemas marinos contruidos principalmente por corales duros (Cnidaria: Hexacorallia: Scleractinea), que sintetizan y acumulan carbonato de calcio para formar un esqueleto. La acumulación de material coralino por cientos o miles de años con la acción combinada de otros procesos (como la cementación por parte de las algas costrosas calcáreas) construyen la matriz estructural arrecifal, base de los ecosistemas arrecifales coralinos (Goreau *et al.* 1979).

Los arrecifes coralinos son considerados vulnerables, debido en parte a que normalmente se desarrollan bajo condiciones ambientales restringidas (Veron 1995; Hubbard 1997), aunque también han sido considerados como ecosistemas altamente dinámicos, al exhibir ciclos naturales de perturbación-recuperación a distintas escalas espaciales y temporales (Connell 1997; Zapata 2017). Desde la década de 1980, existe cada vez un mayor consenso acerca de que los ecosistemas arrecifales coralinos, a pesar de los esfuerzos por conservarlos, se han deteriorado a escala mundial (Bruno y Selig 2007; De'ath *et al.* 2012). Actualmente, los arrecifes coralinos presentan alteraciones que van desde el incremento en la densidad de macroalgas hasta el colapso de comunidades arrecifales completas (Jackson *et al.* 2014). Aunque el deterioro de los arrecifes varía dependiendo de su localización, la última evaluación a nivel mundial (Wilkinson 2008) señaló que hasta ese momento casi un 20% de los arrecifes se encontraban degradados, otro 15% estaba en estado crítico, y un 20% podría desaparecer en las próximas décadas. Estos cambios son consecuencia de múltiples disturbios tanto naturales como antrópicos, que alteran los servicios ecosistémicos y afectan directamente la calidad de vida de las comunidades humanas (Knowlton 2001; Schroeder *et al.* 2008). La disminución de los arrecifes coralinos en el mundo afecta de manera negativa aproximadamente a 500 millones de personas que dependen de éstos para su alimentación, protección costera, obtención de materiales de construcción y empleo producto del turismo; esto incluye aproximadamente a unos 30 millones que dependen total y directamente de los arrecifes coralinos según cálculos publicados hace ya una década (Wilkinson 2008).

El Pacífico Tropical Oriental (PTO) es la región biogeográfica al Occidente del continente americano en el Océano Pacífico, incluyendo las aguas costeras comprendidas entre la península de Baja California (México) hasta el norte de Perú, y oceánicas alrededor de las islas de Clipperton, Revillagigedo, Coco, Malpelo y Galápagos. En general, los arrecifes coralinos en esta región, aunque ampliamente distribuidos, son relativamente pequeños, discontinuos, poco desarrollados y compuestos por pocas especies de coral (Cortés 2003; Glynn *et al.* 2017a). Se considera que son relativamente jóvenes (≤ 5600 años) y que su desarrollo se ha visto limitado por las condiciones geográficas y oceanográficas poco favorables de la región, como un alto grado de aislamiento, una plataforma continental angosta, gran afluencia de agua dulce que aumenta la turbidez y disminuye la salinidad, adicional a temperaturas relativamente frías debido a corrientes marinas y fenómenos de surgencia (Glynn y Wellington 1983; Cortés 2003).

El Parque Nacional Natural Gorgona, ubicado en el PTO, cuenta actualmente con una extensión aproximada de 616.8 km^2 , de los cuales poco más de un 2 % corresponde a área terrestre, mientras que un 98 % es área marina. Isla Gorgona es la porción de área terrestre más grande y está ubicada en las coordenadas $2^{\circ}59'N$ y $78^{\circ}12'W$, mide aproximadamente 9.3×2.6 km y está alejada unos 30 km del punto más cercano en la costa (Díaz *et al.* 2001). Las mareas presentan un ciclo semidiurno alternando dos mareas bajas y dos altas, dentro de un ciclo con mareas de mayor (pujas) y menor amplitud (quiebras) que se intercalan semanalmente; la amplitud mareal está entre un nivel mínimo de marea de -0.6 m y uno máximo de $+5.0$ m (Díaz *et al.* 2001; Zapata y Vargas-Ángel 2003). Gorgona es afectada por la Zona de Convergencia Intertropical (ZCIT), se encuentra en la región más húmeda del continente americano presentando una pluviosidad muy alta excediendo anualmente los 6600 mm (Blanco 2009); tiene dos épocas climáticas marcadas, una muy lluviosa entre mayo y octubre y una menos lluviosa entre diciembre y febrero (Giraldo *et al.* 2008).

En Gorgona se encuentran diversas comunidades coralinas, entre las cuales están los arrecifes más desarrollados y diversos del Pacífico colombiano. El arrecife de La Azufrada es una estructura coralina de aproximadamente de 10 ha de extensión, somero (entre 4 y 10 m de profundidad en marea alta), y ubicado en el lado oriental de la isla a unos 50 m de la línea de costa. La superficie del arrecife está cubierta principalmente por corales de los géneros

Pocillopora, *Pavona*, *Porites*, *Psammocora* y *Gardineroseris*, algas costrosas calcáreas y tapetes de algas filamentosas (Zapata 2001; Muñoz y Zapata 2013). Los corales pocilopóridos dominan el paisaje arrecifal, y se observan creciendo en dos formas principales: como colonias arborescentes dispersas por el sustrato, o como parches de colonias agrupadas formando tapetes homogéneos y continuos de ramas entrelazadas (Zapata 2001). Además, existen tres zonas arrecifales distinguibles distribuidas desde la costa hacia el mar: el tras-arrecife, la planicie arrecifal y el frente arrecifal, donde el tras-arrecife y el frente son los bordes respectivamente interno y externo de la matriz arrecifal. La forma general del arrecife sugiere algunos efectos de la profundidad, del agua dulce y los sedimentos que llegan al arrecife por unos arroyos relativamente estables a lo largo del año, aunque en época de lluvias el agua dulce puede escurrir hacia el mar a lo largo de toda la playa (CGM, Obs. pers.).

Evaluaciones de los ecosistemas arrecifales en Gorgona indican en general, un buen estado de conservación en comparación con arrecifes de otras regiones como el Caribe (Muñoz y Zapata 2013). Es de resaltar que en el último informe sobre el estado de los arrecifes coralinos del mundo, Wilkinson (2008) reportó la calificación total más baja en factores de amenaza para los arrecifes del Pacífico colombiano con 43 de 155 puntos totales, mientras que otros del PTO y Caribe recibieron calificaciones entre 72 y 97 puntos. A pesar de lo anterior, estos arrecifes se encuentran sujetos a las condiciones ambientales particulares de la costa Pacífica colombiana, donde es relativamente bien conocido el impacto de fenómenos como El Niño-Oscilación del Sur (ENSO por sus siglas en inglés) y de exposiciones temporales al aire durante mareas extremadamente bajas, que pueden llevar a eventos de blanqueamiento y mortalidad coralina (Vargas-Ángel *et al.* 2001; Castrillón *et al.* 2017; Zapata 2017). Para el arrecife de La Azufrada, Zapata (2017) reportó una disminución histórica neta de 16.2% en la cobertura de coral vivo entre 1998 y 2014, pasando de 66.9% hasta su punto más bajo en 2008 (39.4%) y luego recuperándose hasta alcanzar un 50.7%; concluyendo que el arrecife exhibe una dinámica cíclica de perturbación-recuperación, resultado de la interacción entre perturbaciones naturales y procesos biológicos como la herbivoría y el reclutamiento coralino.

El reclutamiento, la entrada de nuevos individuos a una población, es un aspecto clave para evaluar el potencial de recuperación y resiliencia de los arrecifes de coral, ya que sirve para

determinar el proceso de recolonización y recuperación después de perturbaciones (Caley *et al.* 1996; Hughes y Tanner 2000). Los patrones de reclutamiento coralino han sido ampliamente estudiados en el Indo-Pacífico y el Caribe, pero pobremente documentados en el PTO. El estudio de la historia de vida temprana en corales, comenzó con el trabajo de Connell (1973) sobre el reclutamiento y las tasas de mortalidad juvenil en sustrato natural de la Gran Barrera Arrecifal en Australia, aunque el trabajo pionero experimental sobre reclutamiento coralino fue realizado por Birkeland (1977) en las costas del Pacífico y Caribe de Panamá utilizando sustratos artificiales (placas de asentamiento) (Mundy 2000). Para el Océano Índico los estudios son aún más recientes (Clark y Edwards 1994; Glassom *et al.* 2006) y es evidente el aumento posterior de las investigaciones en el Pacífico Occidental (*e.g.* Sammarco y Andrews 1989; Dunstan y Johnson 1998, Hughes *et al.* 1999; Hughes y Tanner 2000). Por otro lado, los escasos estudios sobre reclutamiento en el PTO han obtenido pocos resultados para estimar tasas de asentamiento de larvas plánulas sobre placas experimentales, el cual ha sido un método efectivo en otras regiones (Birkeland 1977, Wellington 1982, Richmond 1985, Glynn *et al.* 1996; Medina-Rosas *et al.* 2005, López-Pérez *et al.* 2007; Lozano-Cortés y Zapata 2014).

Para especies del género *Pocillopora* en el PTO, los estudios de reclutamiento sexual han reportado tasas extremadamente bajas, incluso cero reclutas, durante periodos de muestreo hasta de cinco años, por lo que anteriormente se llegó a considerar que estas poblaciones coralinas podrían ser estériles (Birkeland 1977; Wellington 1982; Richmond 1985). Posteriormente, gracias a análisis histológicos publicados a partir de la década de 1990 se sabe que estas poblaciones son fértiles, ya que se ha observado la maduración de gametos en varias especies de la región (Glynn *et al.* 2017b) incluyendo *Pocillopora damicornis* en Isla Gorgona (Castrillón *et al.* 2015). Adicionalmente, las especies de corales pocilopóridos presentan diferencias importantes en sus características de historia de vida, dependiendo de la región donde se encuentren (Harrison 2011). Por ejemplo, en el Pacífico Occidental y Central se ha reportado que *P. damicornis* es una especie incubadora que puede liberar mensualmente plánulas en la columna de agua, mientras que en el PTO la misma especie es considerada liberadora de gametos con un ciclo reproductivo anual (Richmond 1985, 1997; Glynn *et al.* 1991; Castrillón *et al.* 2015).

En adición a los reclutas de coral derivados de la reproducción sexual que dan variabilidad genética y capacidad de adaptación a cambios ambientales, hay una parte significativa del reclutamiento que es derivada de reproducción asexual (Harrison 2011). Actualmente se conocen varios modos de reproducción asexual en corales, como la producción asexual de plánulas, la expulsión de pólipos, y la fragmentación de colonias y supervivencia de estos fragmentos (Highsmith 1982; Sammarco 1982; Stoddart 1983). La reproducción asexual producto de la fragmentación de colonias de coral, es un mecanismo reproductivo para el establecimiento de nuevas colonias que ha despertado interés desde estudios tempranos en corales (*e.g.* Kawaguti 1937), y se considera que puede ser especialmente importante al contribuir a la recuperación de poblaciones locales a corto plazo (Richmond 1997). Highsmith (1982), en una revisión de la reproducción por fragmentación en corales, expuso la importancia de este modo reproductivo asexual concluyendo que la fragmentación debería ser considerada como una adaptación de las estrategias de historia de vida de las especies de coral más exitosas. Más recientemente y aunque sigue siendo un tema de discusión, la reproducción asexual, incluyendo la fragmentación, ha sido considerada en algunos casos como una adaptación a condiciones relativamente estables ya que permite que los genotipos bien adaptados se vuelvan dominantes en ausencia de perturbaciones; y en el caso de condiciones ambientales locales desfavorables permite cierta dispersión cuando las especies no pueden completar sus ciclos reproductivos sexuales (Miller y Ayre 2004; Honnay y Bossuyt 2005).

Como consecuencia de los resultados disponibles sobre reclutamiento coralino en el PTO hasta ahora, es lógico pensar que con un limitado reclutamiento de larvas producto de reproducción sexual, la fragmentación de colonias puede ser una fuente importante de reclutas, en este caso de origen asexual (*e.g.* Glynn *et al.* 1996, Medina-Rosas *et al.* 2005, López-Pérez *et al.* 2007). La reproducción asexual de corales por fragmentación, se presenta principalmente en especies con crecimiento ramificado (*e.g.* familias Acroporidae y Pocilloporidae) las cuales son fácilmente fragmentadas por la acción de agentes externos físicos como tormentas (Foster *et al.* 2007), y biológicos como peces coralívoros o aquellos que rompen corales en búsqueda de los invertebrados que habitan en ellos (Highsmith 1982). Hasta la década de 1970, el efecto de las especies coralívoras se consideraba insignificante para las colonias de coral (*e.g.* Hiatt y Strasburg 1960; Yonge 1968; Stoddart 1969; Robertson 1970), sin embargo, esta idea cambió

con los trabajos de Cox (1986), Littler *et al.* (1989), Grottoli-Everett y Wellington (1997), quienes demostraron que estos peces tienen el potencial de modificar la estructura física de los arrecifes coralinos. La mayoría de los peces coralívoros son peces mariposa (Chaetodontidae), que sólo consumen tejidos blandos (pólipos) y causan poco o ningún daño a las estructuras esqueléticas; sin embargo, algunos peces globo (Tetraodontidae), peces loro (Scaridae) y peces gatillo (Balistidae) raspan, excavan, o rompen los corales, consumiendo tanto el tejido blando como porciones del esqueleto calcáreo subyacente (Cole *et al.* 2008; Enochs y Glynn 2017).

Hasta el momento algunos estudios han intentado cuantificar el material calcáreo removido por peces coralívoros (Glynn *et al.* 1972; Glynn 1985; Cox 1986; Reyes-Bonilla y Calderón-Aguilera 1999; Bellwood *et al.* 2003; Hoey y Bellwood 2008); se sabe por ejemplo que *Arothron meleagris* consume distintas especies de coral como *Pocillopora*, *Psammocora* y *Porites*, son capaces de remover diariamente entre 15 - 20 g de coral arrancando fragmentos de hasta 31 mm de largo y 5 mm de grosor (Guzmán y Robertson 1989; Guzmán y López 1991). No es extraño que en la mayoría de estudios los peces coralívoros sean catalogados como agentes de perturbación, ya que la depredación crónica puede llegar a limitar las tasas de crecimiento, la habilidad de competencia y la distribución de los corales (Neudecker 1977; Wellington 1982; Cox 1986; Littler *et al.* 1989; Grottoli-Everett y Wellington 1997; Glynn *et al.* 1996; Bellwood *et al.* 2006).

Aunque es evidente que la pérdida de tejidos blandos y esqueleto por coralivoría puede representar una inversión energética extra para las colonias afectadas, es posible que esta inversión no sea en vano ya que los fragmentos generados podrían estar contribuyendo a la reproducción asexual de las poblaciones coralinas (Highsmith 1982). Hasta el momento prácticamente ningún estudio ha analizado efectos positivos que algunas especies de peces coralívoros puedan tener sobre los corales; sin embargo, en los arrecifes del PTO es posible que este sea el caso. En ausencia de huracanes o tormentas recurrentes que fragmenten las colonias en el PTO (a diferencia de lo que sucede en el Caribe), es probable que los peces sean una de las fuentes principales de fragmentación de colonias propiciando la reproducción asexual de los corales. Dependiendo del balance entre el efecto negativo y positivo de los efectos de la coralivoría, la percepción de este proceso ecológico podría cambiar significativamente, ya que

además de existir una interacción depredador-presa, es posible que algunas especies de corales y de peces coralívoros mantengan una relación de tipo mutualista donde los peces obtienen alimento, mientras facilitan y promueven la reproducción asexual de los corales.

El pez globo *Arothron meleagris* es un pez arrecifal considerado como uno de los principales depredadores de coral en Isla Gorgona (Guzmán y Robertson 1989; Guzmán y López 1991; Palacios *et al.* 2014) donde su abundancia es la más alta de toda la región (Palacios *et al.* 2014). Este pez se alimenta principalmente de corales ramificados pocilopóridos, y debido a su abundancia y comportamiento alimenticio inflige un efecto negativo sobre la producción de carbonato de calcio del arrecife, mientras que potencialmente promueve la reproducción asexual al morder y fragmentar ramas de colonias coralinas (Alvarado *et al.* 2017; Enochs y Glynn 2017).

Actualmente, para los arrecifes del Pacífico colombiano no existen estudios publicados acerca de los patrones de reclutamiento coralino para establecer la importancia relativa del reclutamiento coralino derivado asexualmente, su relación con variables físico-químicas, u otros aspectos ecológicos. Dada la evidente pérdida de cobertura coralina en sitios como Gorgona, es urgente comenzar a estudiar estos procesos. En este estudio se presenta evidencia por primera vez de reclutamiento coralino por asentamiento de larvas en Gorgona (capítulo 1) y del impacto de troncos flotantes en la fragmentación de corales (capítulo 2); posteriormente se centra en el análisis de la relación que existe entre los corales pocilopóridos y el pez *A. meleagris*, en especial sobre cómo se afectan los corales y el arrecife de La Azufrada por coralivoría (capítulo 3), y qué tan efectiva es esta relación promoviendo la reproducción asexual de los corales (capítulo 4). Estos resultados proporcionan información novedosa respecto a la estabilidad, resiliencia y persistencia, de los arrecifes y poblaciones coralinas en la región del Pacífico Tropical Oriental en momentos de perturbaciones naturales recurrentes.

REFERENCIAS

- Alvarado JJ, Grassian B, Cantera-Kintz JR, Carballo J, Londoño-Cruz E. 2017. Coral Reef Bioerosion in the Eastern Tropical Pacific. En: Glynn PW, Manzello DP, IC Enochs (Ed). Coral Reefs of the Eastern Tropical Pacific: Persistence and loss in a dynamic environment. Coral Reefs of the World, Volume 8, Springer.
- Bellwood DR, Hoey AS, Choat JH. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology letters* 6(4): 281-285.
- Bellwood DR, Hoey AS, Ackerman JL, Depczynski M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* 12: 1587–1594.
- Birkeland C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the 3rd International Coral Reef Symposium, Miami* 1: 15-21.
- Blanco JF. 2009. The hydroclimatology of Gorgona Island: Seasonal and ENSO-related patterns. *Actualidades Biológicas* 31(91): 111-121.
- Bruno JF y Selig ER. 2007. Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLoS ONE* 2(8): e711.
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecological Systems* 27: 477-500.
- Castrillón AL, Muñoz CG, Zapata FA. 2015. Reproductive patterns of the coral *Pocillopora damicornis* at Gorgona Island, Colombian Pacific Ocean. *Marine Biology Research* 11:1065-1075.
- Castrillón AL, Lozano-Cortés D, Zapata FA. 2017. Effect of short-term subaerial exposure on the cauliflower coral, *Pocillopora damicornis*, during a simulated extreme low-tide event. *Coral Reefs* 36 (2): 401 – 414.
- Clark S y Edwards AJ. 1994. Use of artificial reef structures to rehabilitate reef flats degraded by coral mining in the Maldives. *Bulletin of Marine Science* 55(2-3): 724-744.
- Cole AJ, Pratchett MS, Jones GP. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9: 286–307.
- Connell J. 1973. Population ecology of reef-building corals. En: Jones OA y Endean R (Ed) *Biology and geology of coral reefs*. Vol. II, Biology 1. Academic Press, NY.
- Connell J. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16(1): S101-S113.

- Cortés J. 2003. Coral reefs of the Americas: an introduction to Latin American coral reefs. En: Cortés J (Ed). Latin American Coral Reefs. Elsevier, Amsterdam.
- Cox EF. 1986. The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *Journal of Experimental Marine Biology and Ecology* 101(1-2): 161-174.
- De'ath G, Fabricius KE, Sweatman H, Puotinen M. 2012. From the Cover: The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences* 109: 17995–17999.
- Díaz JM, Pinzón JH, Perdomo AM, Barrios LM, López-Victoria M. 2001. Generalidades. En: Barrios LM y López-Victoria M (Ed). *Gorgona marina: contribución al conocimiento de una isla única*. INVEMAR, Serie de publicaciones especiales 7, Santa Marta.
- Dunstan PK y Johnson CR. 1998. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. *Coral Reefs* 17(1): 71-81.
- Enochs IC y Glynn PW. 2017. Corallivory in the eastern Pacific. En: Glynn PW, Manzello DP, Enochs IC (Ed). *Coral Reefs of the Eastern Tropical Pacific: Persistence and loss in a dynamic environment*. *Coral Reefs of the World*, Volume 8, Springer.
- Foster NL, Baums IB, Mumby PJ. 2007. Sexual vs. asexual reproduction in an ecosystem engineer: the massive coral *Montastraea annularis*. *Journal of Animal Ecology* 76: 384–391.
- Giraldo A, Rodríguez-Rubio E, Zapata FA. 2008. Condiciones oceanográficas en Isla Gorgona, Pacífico oriental tropical de Colombia. *Latin American Journal of Aquatic Research* 36: 121-128.
- Glassom D, Celliers L, Schleyer MH. 2006. Coral recruitment patterns at Sodwana Bay, South Africa. *Coral Reefs* 25(3): 485-492.
- Glynn PW. 1985. El Nino-associated disturbance to coral reefs and post disturbance mortality by *Acanthaster planci*. *Marine Ecology-Progress Series* 26(295300): 295-300.
- Glynn PW y Wellington GM. 1983. *Corals and coral reefs of the Galapagos Islands*. University of California Press, Berkeley.
- Glynn PW, Stewart RH, McCosker JE. 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geol. Rundsch.* 61: 483.
- Glynn PW, Gassman NJ, Eakin CM, Cortes J, Smith DB, Guzman HM. 1991. Reef coral reproduction in the eastern pacific: Costa Rica, Panama, and Galapagos Islands (ecuador) I. Pocilloporidae. *Marine Biology* 109(3): 355-368.

- Glynn PW, Colley SB, Gassman NJ, Black K, Cortés J, Maté JL. 1996. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador) III. *Agariciidae (Pavona gigantea and Gardineroseris planulata)*. *Marine Biology* 125: 579-601.
- Glynn PW, Alvarado JJ, Banks S, Cortés J, Feingold JS, *et al.* 2017a. Eastern Pacific coral reef provinces, coral community structure and composition: An Overview. En: Glynn PW, Manzello D y Enochs I (Ed). *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment*. *Coral Reefs of the World* 8. Springer Science + Business Media, Dordrecht.
- Glynn PW, Colley SB, Carpizo-Ituarte E, Richmond RH. 2017b. Coral reproduction in the Eastern Pacific. En: P.W. Glynn, D. Manzello y I. Enochs (Ed). *Coral Reefs of the Eastern Pacific: Persistence and Loss in a Dynamic Environment*. *Coral Reefs of the World* 8. Springer Science + Business Media, Dordrecht.
- Goreau TF, Goreau NI, Goreau TJ. 1979. Corals and coral reefs. *Scientific American* 124-136.
- Grottoli-Everett A y Wellington G. 1997. Fish predation on the scleractinian coral *Madracis mirabilis* controls its depth distribution in the Florida Keys, USA. *Marine Ecology Progress Series* 160: 291-293.
- Guzman HM y Robertson DR. 1989. Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Marine Ecology Progress Series* 55: 121-131.
- Guzman HM y Lopez JV. 1991. Diet of the corallivorous pufferfish *Arothron meleagris* (Pisces: Tetraodontidae) at Gorgona Island, Colombia. *Revista de Biología Tropical* 39(2): 203-206.
- Harrison PL. 2011. Sexual reproduction of scleractinian corals. En: Dubinsky Z y Stambler N (Ed). *Coral Reefs: An Ecosystem in Transition*. Springer, Netherlands.
- Hiatt RW y Strasburg DW. 1960. Ecological Relationships of the Fish Fauna on Coral Reefs of the Marshall Islands. *Ecological Monographs* 30: 65-127.
- Highsmith RC. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7(2): 207-226.
- Hoey AS y Bellwood DR. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27(1): 37-47.
- Honnay O y Bossuyt B. 2005. Prolonged clonal growth: escape route or route to extinction? *Oikos* 108: 427-432.
- Hubbard DK. 1997. Reefs as dynamic systems. 43-67. En: Birkeland C (Ed). *Life and death of coral reefs*. Chapman and Hall, NY.

- Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397(6714): 59.
- Hughes TP y Tanner JE. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81: 2250–2263.
- Jackson JBC, Donovan MK, Cramer KL, Lam VV. 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Kawaguti S. 1937. On the physiology of reef corals. III. Regeneration and phototropism in reef corals. *Palao Trop. Biol. Stat. Stud.* 2: 209-216.
- Knowlton N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences* 98(10): 5419-5425.
- Littler MM, Taylor PR, Littler DS. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80: 331.
- López-Pérez R, Mora-Pérez M, Leyte-Morales G. 2007. Coral (Anthozoa: Scleractinia) recruitment at Bahías de Huatulco, Western Mexico: Implications for coral community structure and dynamics. *Pacific Science* 61: 355-369.
- Lozano-Cortés D y Zapata FA. 2014. Invertebrate colonization on artificial substrates in a coral reef at Gorgona Island, Colombian Pacific Ocean. *Revista de Biología Tropical* 62 (Suplem.1): 161-168.
- Medina-Rosas P, Carriquiry JD, Cupul-Magaña AL. 2005. Reclutamiento de *Porites* (Scleractinia) sobre sustrato artificial en arrecifes afectados por El Niño 1997-98, en Bahía de Banderas, Pacífico mexicano. *Ciencias Marinas* 31: 103-109.
- Miller KJ y Ayre DJ. 2004. The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. *Heredity* 92: 557–568.
- Mundy CN. 2000. An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19:124–131
- Muñoz CG y Zapata FA. 2013. Plan de Manejo de los Arrecifes Coralinos del Parque Nacional Natural Gorgona. Parques Nacionales Naturales de Colombia y WWF-Colombia, Cali.
- Neudecker S. 1979. Effect of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60(4): 666-672.
- Palacios MM, Muñoz CG, Zapata FA. 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs* 33: 625–636.

- Reyes-Bonilla H y Calderón-Aguilera LE. 1999. Population Density, Distribution and Consumption Rates of Three Corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. *Marine Ecology* 20: 347–357.
- Richmond RH. 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. *Proceedings of the fifth International Coral Reef Congress* 6: 101-106.
- Richmond RH. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. En: Birkeland C (Ed). *Life and death of coral reefs*. Chapman & Hall, NY.
- Robertson R. 1970. Review of the Predators and Parasites of Stony Corals, with Special Reference to Symbiotic Prosobranch Gastropods. *Pacific Science* 24: 43-54.
- Sammarco PW. 1982. Polyp bail-out: an escape response to environmental stress and a new means of reproduction in corals. *Marine Ecology Progress Series* 65(1): 57-65.
- Sammarco PW y Andrews JC. 1989. The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnology and Oceanography* 34(5): 896-912.
- Schroeder RE, Green AL, DeMartini EE, Kenyon JC. 2008. Long-term effects of a ship-grounding on coral reef fish assemblages at Rose Atoll, American Samoa. *Bulletin of Marine Science* 82: 345–364.
- Stoddart DR. 1969. Ecology And Morphology of Recent Coral Reefs. *Biological Reviews* 44: 433–498.
- Stoddart JA. 1983. Asexual production of planulae in the coral *Pocillopora damicornis* *Marine Biology* 76(3): 279.
- Vargas-Ángel B, Zapata FA, Hernández H, Jiménez JM. 2001. Coral and coral reef responses to the 1997-98 El Niño event on the Pacific coast of Colombia. *Bulletin of Marine Science* 69(1): 111-132.
- Veron JEN. 1995. *Corals in space and time: the biogeography and evolution of the Scleractinia*. Cornell University Press, NY.
- Wellington GM. 1982. Depth Zonation of Corals in the Gulf of Panama: Control and Facilitation by Resident Reef Fishes. *Ecological Monographs* 52: 224-241.
- Wilkinson C. 2008. Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia.
- Yonge CM. 1968. Review Lecture: Living Corals. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 169 (1017): 329-344.

- Zapata FA. 2001. Formaciones coralinas de la Isla de Gorgona. En: Barrios LM y López-Victoria M (Ed). Gorgona Marina: Contribución al Conocimiento de una Isla Única. INVEMAR, Serie de Publicaciones Especiales 7, Santa Marta.
- Zapata FA. 2017. Temporal dynamics of coral and algal cover and their drivers on a coral reef of Gorgona Island, Colombia (Eastern Tropical Pacific). Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 41(160): 298-310.
- Zapata FA y Vargas-Ángel B. 2003. Corals and coral reefs of the Pacific coast of Colombia. En Cortés J (Ed). Latin American Coral Reefs. Elsevier, Amsterdam.

CAPÍTULO 1

Evidence of sexually-produced coral recruitment at Gorgona Island, Eastern Tropical Pacific.

Abstract

Early suggestion that coral populations in the Eastern Tropical Pacific (ETP) did not reproduce sexually was eventually proved wrong, but sexually-produced coral recruitment has typically been very low in this region. We searched for evidence of coral sexual recruitment on coral and rocky reefs of Gorgona Island, Colombia, by thoroughly examining natural substrates for coral juveniles and by using settling plates of different materials. Coral recruits of at least ten species were found on natural substrates at several sites around the island during scuba diving explorations made between 2010 – 2017, but no recruits were found on settlement plates. The two most abundant juveniles belonged to *Porites panamensis*, which occurred at an average density of 5.7 colonies m⁻², and *Pocillopora* spp., whose density varied between 0.05 and 0.85 juveniles m⁻², depending on the site. These results indicate that coral recruitment derived from the sexual reproduction of a diverse set of species is a relatively active process around the island, yet settlement plates do not seem to be as useful to study coral recruitment in the ETP as they are elsewhere.

Keywords: Coral settlement, *Pocillopora*, *Porites*.

Resumen

Aunque ya se ha demostrado como errónea la idea que las poblaciones coralinas en el Pacífico Tropical Oriental (PTO) no se reproducen sexualmente, el reclutamiento coralino de origen sexual ha sido típicamente bajo en esta región. Para conocer este proceso en Isla Gorgona, Colombia, buscamos evidencia de reclutamiento de origen sexual de corales en la isla mediante el examen minucioso de sustratos naturales en diferentes arrecifes coralinos y sitios rocosos, junto con la instalación y revisión de placas de asentamiento de materiales diferentes en uno de los arrecifes coralinos. Encontramos reclutas de coral de al menos diez especies en sustratos naturales en varios sitios alrededor de la isla durante exploraciones de buceo entre 2010 y 2017,

pero no encontramos reclutas adheridos a las placas de asentamiento. Los dos juveniles más abundantes fueron de las especies *Porites panamensis* con una densidad promedio de 5.7 colonias m^{-2} , y *Pocillopora* sp. cuya densidad estuvo entre 0.05 y 0.85 juveniles m^{-2} . Estos resultados indican que el reclutamiento coralino derivado de reproducción sexual de un conjunto diverso de especies es un proceso relativamente activo alrededor de la isla, sin embargo, las placas de asentamiento no parecen ser tan útiles para estudiar el reclutamiento de coral en el PTO como lo son en otros lugares.

INTRODUCTION

Recruitment, the entry of new individuals to populations, is a key demographic process involved in the supply and maintenance of wild populations (Caley *et al.* 1996). In the case of organisms like trees and corals, which are key structural components of forests and coral reefs, recruitment also determines the resilience of the ecosystems (Hughes and Tanner 2000). Understanding coral recruitment is critical given the evident global deterioration in recent decades of coral reefs and their associated goods and services (Richmond 1997; Babcock *et al.* 2003; Hughes *et al.* 2010).

Coral recruitment has been relatively well documented in the Indo-Pacific, Central Pacific and Caribbean regions, and less studied in the Eastern Tropical Pacific (ETP). Early studies in the ETP did not find coral recruits on natural substrates, and sampling with settlement plates resulted in extremely low to nil recruitment (Birkeland 1977, Wellington 1982, Richmond 1985). These first results led researchers to consider that coral populations in the region could be sexually sterile and limited by recruitment, and therefore, coral population replenishment and recovery from perturbations were primarily driven by asexual reproduction such as that resulting from colony fragmentation (Highsmith 1982, Richmond 1985). More recent studies found few – if any – recruits on settlement plates (Medina-Rosas *et al.* 2005; López-Pérez *et al.* 2007; Lozano-Cortés and Zapata 2014), but histological evidence clearly indicated that gonadal maturation is an active process in some of these coral populations, including those at Gorgona Island (Castrillón *et al.* 2015; Glynn *et al.* 2017 and references therein).

Although Gorgona Island is located within a marine protected area so that direct anthropogenic impacts are virtually absent, these reefs are negatively affected by recurring natural disturbances (Zapata and Vargas-Ángel 2003, Fiedler and Lavín 2017). For example, live coral cover at La Azufrada reef declined 26% in one decade, and critically so in shallow areas where coverage decreased from 61% in 1998 to 15% in 2007 (Zapata *et al.* 2008; Zapata 2017). It has, therefore, become urgent to know how resilient these reefs are and how much does coral recruitment contribute to their resilience.

In this study, we present evidence of recruitment derived from larval settlement on natural substrates for ten species of corals at Gorgona Island, but report the absence of coral recruitment on artificial substrates (settlement plates). We also report the density and size frequency distribution of juvenile colonies of *Pocillopora* sp. and *Porites panamensis* observed on natural substrates.

METHODS

Study area

Gorgona Island and Gorgonilla Islet located ~ 30 km off the continental coast (3° 00' 55"N, 78° 14' 30"W), constitute the largest insular territory (13.2 km²) in the Colombian Pacific continental shelf (Muñoz and Zapata 2013). To date, 28 hermatypic coral species are reported for Gorgona, but due to taxonomic difficulties within the genus *Pocillopora*, the true number remains uncertain (Cortés *et al.* 2017).

The Island and surrounding waters are part of “Gorgona National Natural Park”, which harbors some of the largest, most diverse and developed coral reef formations in the ETP (Zapata and Vargas-Angel 2003), along with extensive rocky shorelines and submerged rocky mounts. The average annual rainfall is very high (ranging between 4000 - 7000 mm) with two contrasting climatological seasons, a rainy one from May to October and a dry season between December and March (Diaz *et al.* 2001; Blanco 2009).

Due to heavy rainfall and high mountains at Gorgona, freshwater streams are abundant,

although their flow and discharge location may vary with the seasons, usually affecting sea surface temperature and salinity (CGM and FAZ unpubl. data); turbidity is also highly variable and partially related to rainfall, with visibility ranging between 1 - 30 m. Tidal regime is semidiurnal completing a full cycle every ~12.5 hours, with a maximum tidal range of 5.7 m (Ideam 2017); ocean currents and wave action are stronger on the western, windward side of the main island (Giraldo *et al.* 2008).

Sampling

We implemented different methods to examine recruitment of sexually-produced corals at Gorgona Island: A) a wide search for coral recruits on natural substrates around the island during exploratory dives, B) visual counts on transects, and C) the use of settlement plates to sample coral recruits.

During 2010 - 2017, a total of 19 sites around the island (including both coral reefs and rocky sites) were inspected during exploratory dives, making a special effort to search for juvenile corals. We used different criteria to establish whether small coral colonies were derived from larval settlement: 1) the presence of a wide, flat, and nearly-symmetrical encrusting base, and 2) attachment to steep substrates like rocky walls, where asexual recruits derived from colony fragmentation would not be expected to get attached to (Richmond 1985, Glynn *et al.* 1996). Because pocilloporid coral recruits were difficult to identify to species, they were simply identified as *Pocillopora* sp.

To estimate the abundance of some species of coral recruits, during November 2010 ten visual transects (each transect 20 m²) were examined on two coral reefs (La Azufrada and Playa Blanca). During March 2011 nine similar transects were examined on the rocky shore El Laberinto, and during June 2011 three smaller transects (10 m²) were examined at El Arrecifito. In these transects we recorded the abundance and size (maximum diameter) of coral recruits. To test for size differences between pocilloporid recruits from La Azufrada, Playa Blanca and El Laberinto, we used a one-way ANOVA after testing for compliance with homoscedasticity and normality assumptions. An additional criterion to define coral recruits was a colony-size < 5 cm,

considering that branching corals like pocilloporids achieve sexual maturity at around 2-3 years old, and massive corals like *Porites* at 4-7 years old (Richmond 1997). Considering that pocilloporids have a growth rate $\sim 2.7 \text{ cm y}^{-1}$ (Palacios *et al.* 2014) and *Porites panamensis* $\sim 1.5 \text{ cm y}^{-1}$ (Cabral-Tena *et al.* 2013), colonies up to 5 cm in diameter would be between 1.5 and 3.5 years old respectively, hence could be classified as juveniles.

In October 2010, 54 settlement plates measuring 20 x 20 cm were installed on the reef flat of La Azufrada reef (12 of each of four materials - acrylic, ceramic, concrete, and marble - and six of tarred twisted nylon twine interwoven on a PVC pipe frame). The plates were arranged in pairs, one on top of the other (to provide the cryptic microhabitat often preferred by settling coral larvae (Harriott 1985, Harriott and Fisk 1987), and held together by a steel bar driven into the substrate (Figure 1). To reduce potential effects on corals of competition for space by algae and barnacles (Birkeland 1977), these organisms were removed approximately every 45 days from half of the plates. All plates were photographed with a high-resolution digital camera approximately every 45 days for a period of six months, and the photographs were examined visually on a computer. In April 2011, the plates were recovered from the sea and examined in the laboratory.

RESULTS

We found sexually produced coral recruits at ten out of a total of 19 sites surveyed at Gorgona Island between 2010 and 2017 (Figure 1). Recruits belonged to at least 10 different species from four families (Table 1). A list of surveyed sites with geo-location coordinates is found in Appendix A.

At least two coral species were recorded attached to the natural substrate within transects at La Azufrada, Playa Blanca, El Laberinto and El Arrecifito: *Pocillopora* sp. at the first three sites, and *Porites panamensis* at the last one. We found 41 pocilloporid recruits in total, and observed the highest coral recruitment at La Azufrada reef ($0.85 \text{ recruits m}^{-2}$), followed by the rocky site El Laberinto ($0.08 \text{ recruits colonies m}^{-2}$) and Playa Blanca reef ($0.05 \text{ recruits m}^{-2}$). The

mean colony-size of pocilloporid recruits was similar between the three sites ($F_{2,38} = 0.31$; $p > 0.1$; Fig. 2). The smallest pocilloporid recruit had a diameter ~ 1.0 cm and was observed at El Laberinto. At El Arrecifito we recorded a total of 170 recruits of *Porites panamensis*, with a mean density ($\pm$ SD and hereafter) of 5.7 ± 4.7 recruits m^{-2} and a mean colony-size of 2.3 ± 0.9 cm. The smallest *P. panamensis* recruit was ~ 0.5 cm in diameter, and had between 15 to 20 polyps, each one about 0.1 cm in diameter (Figure 1D).

In contrast with natural substrates, we did not find coral recruits attached to the settlement plates upon completion of the analysis of the photographs and after a thorough direct examination of the plates with a dissecting microscope. However, the plates were colonized by a diverse community of other sessile organisms like bryozoans and polychaetes, which were dominant along with filamentous and calcareous algae.

DISCUSSION

This study reports the occurrence of recruits of at least ten species of coral from five genera (*Pocillopora*, *Porites*, *Pavona*, *Gardineroseris* and *Psammocora*) for the first time in the Colombian Pacific. However, we obtained two conflicting results, similar to those reported by previous studies on coral recruitment in the ETP: despite low densities, coral recruits were found on natural substrates on coral and rocky reefs, but the usual sampling method of settlement plates failed to detect coral recruitment (Birkeland 1977, Wellington 1982, Richmond 1985, Medina-Rosas *et al.* 2005, López-Pérez *et al.* 2007, Lozano-Cortés and Zapata 2014). On coral reefs, the recruits were found attached either to coral rubble or to the consolidated coral reef matrix covered by calcareous algae, while in rocky areas the recruits were found attached to rocky walls, either bare or partially covered by mats of filamentous algae.

While at other reef locations in the ETP recruits of *Pocillopora* sp. and *Porites panamensis* derived from sexual reproduction have been already observed on natural substrates (Richmond 1985, Glynn *et al.* 1991, 1994, Medina-Rosas *et al.* 2005), this study is the first to report the abundance and size distribution of recruits for these species in the region. The

abundance of coral recruits on natural substrates in ETP reefs has been very low (Glynn *et al.*, 1996; 2000), indicating that the abundance reported here for *P. panamensis* is one of the highest in the region, second to that of *Pavona clavus* in Costa Rica (Glynn *et al.* 2011); this high abundance was apparently the result of a recruitment pulse at El Arrecifito in June 2011.

The implication of the results obtained so far in the ETP, including ours, is twofold: first, clearly corals are reproducing sexually in the region; this has been amply corroborated by several histological studies about coral reproduction throughout the ETP (Glynn *et al.* 2017 and references therein). These studies refute the hypothesis that corals in the ETP are sterile, and at the same time challenge the idea that recruitment derives mostly from fragmentation of colonies (Birkeland 1977, Highsmith 1982, Wellington 1982, Richmond 1985). Second, the scarcity of coral recruitment on artificial substrates in the ETP must then be due to some unknown factor that prevents coral larvae from settling or surviving on artificial sampling substrates.

The negative results obtained with the settlement plates could be related to: 1) the use of inappropriate substrate materials, 2) insufficient time after plate deployment for adequate substrate conditioning, and 3) competition, predation, or herbivory, on settlement plates. However, for our study the first case is an unlikely explanation because we used five different materials, including ceramic that has yielded the highest recruitment results in other studies, both in the Indo-Pacific (Harriott and Fisk 1987) and the Caribbean (Tomascik 1991). In the second case, it is well known that artificial substrates require a conditioning period during which an encrusting community develops before coral larvae will settle (Segal *et al.* 2012). While the duration of the conditioning period is not well established and may be highly variable from place to place, in southwestern Mexico coral recruitment occurred 5 – 10 months after plates had been submerged (López-Pérez *et al.* 2007). Since our plates were submerged for six months, it is plausible that the encrusting community that induces or enhances coral settlement had not fully developed. However, in a previous attempt to document recruitment on artificial substrates at La Azufrada reef, the settlement plates were submerged for a full year and yet no juveniles were found (Lozano-Cortés and Zapata 2014). In the third case, it is known that competition, predation or herbivory on settlement plates may prevent coral spats from surviving and actually recruiting

on these substrates (Birkeland 1977, Sammarco 1985, Díaz-Pulido et al. 2010). Although we periodically removed algae and other sessile invertebrates from half of the plates to reduce potential competition with recently settled corals, sea urchins, ophiuroids and gastropods were commonly seen on the plates and may have interfered with coral settlement or survival.

Additionally, there is a reasonable methodological argument related to the sampling size, whose solution can be impossible in practice: if the abundance of coral recruits is naturally low, then the sampling area should be considerably larger than the one we used to successfully detect coral recruits. While there are several other potential explanations, none of them are general enough to explain the common failure to document coral recruitment on artificial settlement plates in the ETP, and therefore the reason for these results remains obscure.

In conclusion, the results presented here indicate that coral recruitment derived from sexual reproduction occurs at Gorgona Island. This, however, has been overlooked by the failure to observe coral settlement on artificial substrates and the difficulty to differentiate sexual recruits from small surviving coral fragments generated from the fragmentation of adult colonies, particularly in areas with high coral cover. Future research will have to examine the relative contribution of sexual and asexual reproduction to the supply of coral recruits and their role in the recovery and maintenance of coral populations and coral reefs in the Colombian Pacific and ETP.

REFERENCES

- Babcock R, Baird A, Piromvaragorn S, Thomson D, Willis B. 2003. Identification of Scleractinian Coral Recruits from Indo-Pacific Reefs. *Zoological Studies* 42: 211-226.
- Birkeland C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the third International Coral Reef Symposium* 1: 15-21.
- Blanco JF. 2009. The hydroclimatology of Gorgona Island: Seasonal and ENSO-related patterns. *Actualidades Biológicas* 31: 111-121.
- Cabral-Tena RA, Reyes-Bonilla H, Lluch-Cota S, Paz-Garcia DA, Calderon-Aguilera LE, Norzagaray-Lopez O, Balari EF. 2013. Different calcification rates in males and females of coral *Porites panamensis* in the Gulf of California. *Marine Ecology Progress Series* 476: 1-8.
- Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecological Systems* 27: 477-500.
- Castrillón AL, Muñoz CG, Zapata FA. 2015. Reproductive patterns of the coral *Pocillopora damicornis* at Gorgona Island, Colombian Pacific Ocean. *Marine Biology Research* 11:1065-1075.
- Cortés J, Enochs IC, Sibaja-Cordero J, Hernández L, Alvarado JJ, *et al.* 2017. Marine biodiversity of Eastern Tropical Pacific coral reefs. in: Glynn PW, Manzello DP, Enochs IC (Eds). *Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment* (Coral Reefs of the World, Volume 8). Springer, Dordrecht.
- Díaz JM, Pinzon JH, Perdomo AM, Barrios LM, López-Victoria M. 2001. Generalidades. Pp. 17-26 In: Barrios LM and López-Victoria M (Ed). *Gorgona marina, contribución al conocimiento de una isla única*. INVEMAR, Serie de Publicaciones Especiales No. 7. Santa Marta, Colombia.
- Díaz-Pulido G, Harii S, McCook LJ, Hoegh-Guldberg O. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29: 203-208.

- Fiedler PC, Lavin MF. 2017. Oceanographic conditions of the Eastern Tropical Pacific. In: Glynn PW, Manzello DP, Enochs IC (Ed). Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment (Coral Reefs of the World, Volume 8). Springer, Dordrecht.
- Giraldo A, Rodríguez-Rubio E, Zapata F. 2008. Condiciones oceanográficas de Isla Gorgona, Pacífico Oriental Tropical de Colombia. Latin American Journal of Aquatic Research 36: 121-128.
- Glynn PW, Colley SB, Gassman NJ, Black K, Cortés J, Maté JL. 1996. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). III. Agariciidae (*Pavona gigantea* and *Gardineroseris planulata*). Marine Biology 125:579-601.
- Glynn PW, Colley SB, Carpizo-Ituarte E and Richmond RH. 2017. Coral reproduction in the Eastern Pacific. In: Glynn PW, Manzello DP, Enochs IC (Ed). Coral Reefs of the Eastern Tropical Pacific: Persistence and Loss in a Dynamic Environment (Coral Reefs of the World, Volume 8). Springer, Dordrecht.
- Guzmán HM y Cortés J. 2001. Changes in reef community structure after fifteen years of natural disturbances in the eastern Pacific (Costa Rica). Bulletin of Marine Science 69: 133-149.
- Guzmán HM y Cortés J. 2007. Reef recovery 20 years after the 1982-83 El Niño massive mortality. Marine Biology 151: 401-411.
- Harriott V and Fisk D. 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. Marine Ecology Progress Series 37: 201-208.
- Highsmith RC. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7: 207-226.
- Hughes TP and Tanner JE. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81: 2250–2263.
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology and Evolution 25:633-642.

- Kleypas JA, McManus JW, Meñez LAB. 1999. Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39:146–159.
- López-Pérez R, Mora-Pérez M, Leyte-Morales G. 2007. Coral (Anthozoa: Scleractinia) recruitment at Bahías de Huatulco, Western México: Implications for coral community structure and dynamics. *Pacific Science* 61: 355-369.
- Lozano-Cortés D and Zapata FA. 2014. Invertebrate colonization on artificial substrates in a coral reef at Gorgona Island, Colombian Pacific Ocean. *Revista de Biología Tropical* 62 (Suplem. 1): 161-168.
- Medina-Rosas P, Carriquiry JD, Cupul-Magaña AL. 2005. Reclutamiento de *Porites* (Scleractinia) sobre sustrato artificial en arrecifes afectados por El Niño 1997-98, en Bahía de Banderas, Pacífico mexicano. *Ciencias Marinas* 31: 103-109.
- Muñoz CG and Zapata FA. 2013. Plan de Manejo de los Arrecifes Coralinos del Parque Nacional Natural Gorgona. WWF Colombia – Parques Nacionales Naturales de Colombia.
- Palacios MM, Muñoz CG, Zapata FA. 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs* 33:625–636.
- Richmond RH. 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 6: 101-106.
- Richmond RH. 1997. Reproduction and recruitment in corals: Critical links in the persistence of reefs. Pp. 175-197 In: C. Birkeland (Ed). *Life and Death of Coral Reefs*. Chapman and Hall, New York.
- Sammarco PW. 1985. The Great Barrier Reef vs. the Caribbean: Comparisons of grazers, coral recruitment patterns and reef recovery. *Proceedings of the 5th International Coral Reef Congress, Tahiti* 4: 391-397.
- Segal B, Berenguer V, Castro CB. 2012. Experimental recruitment of the Brazilian endemic coral *Mussismilia braziliensis* and conditioning of settlement plates. *Ciencias Marinas* 38(1A): 1-10.
- Tomascik T. 1991. Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. *Marine Ecology Progress Series* 77: 261–269.

Wellington GM. 1982. Depth zonation of corals in the Gulf of Panama: Control and facilitation by resident reef fishes. *Ecological Monographs* 52: 224-241.

Zapata F.A. 2001. Formaciones coralinas de la isla de Gorgona. In: Barrios LM y López-Victoria M (Ed). *Gorgona marina: contribución al conocimiento de una isla única*. INVEMAR, Serie de Publicaciones Especiales No.7. Santa Marta, Colombia.

Zapata FA. 2017. Temporal dynamics of coral and algal cover and their drivers on a coral reef of Gorgona Island, Colombia (Eastern Tropical Pacific). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 41(160): 298-310.

Zapata FA and Vargas-Ángel B. 2003. Corals and coral reefs of the Pacific coast of Colombia. Pp. 419-447. In: Cortés J (Ed). *Latin American Coral Reefs*.

Zapata FA, Rodríguez-Ramírez A, Navas-Camacho R. 2008. Decade-long 1998-2007 Trends in live coral cover in a Tropical Eastern Pacific coral reef at Gorgona Island, Colombia. Abstracts of the 11th International Coral Reef Symposium, Fort Lauderdale.

TABLES AND FIGURES

Table 1. Checklist of species of coral recruits observed at ten sites in Gorgona National Natural Park (Colombia, Eastern Tropical Pacific) during 2010 - 2017.

Site / Survey time	Arrecifito	Azufrada	Muelle	Playa Blanca	Ventana	Farallones	Laberinto	Parguera de Harold	Remanso	Yundigua
	2010-2012	2010-2014	2010-2014	2010-2014	2010-2014	2010-2011	2010-2012	2017	2010-2012	2010-2012
AGARICIIDAE										
<i>Gardineroseris planulata</i>					x		x			
<i>Pavona chiriquiensis</i>						x				
<i>Pavona clavus</i>						x				
<i>Pavona frondifera</i>						x				
<i>Pavona gigantea</i>	x		x						x	x
<i>Pavona varians</i>	x	x	x							
POCILLOPORIDAE										
<i>Pocillopora</i> sp.	x	x		x	x	x	x	x	x	x
PORITIDAE										
<i>Porites panamensis</i>	x			x						
<i>Porites lobata</i>						x	x		x	
PSAMMOCORIDAE										
<i>Psammocora</i> sp.	x					x				
10	5	2	2	2	2	6	3	1	3	2

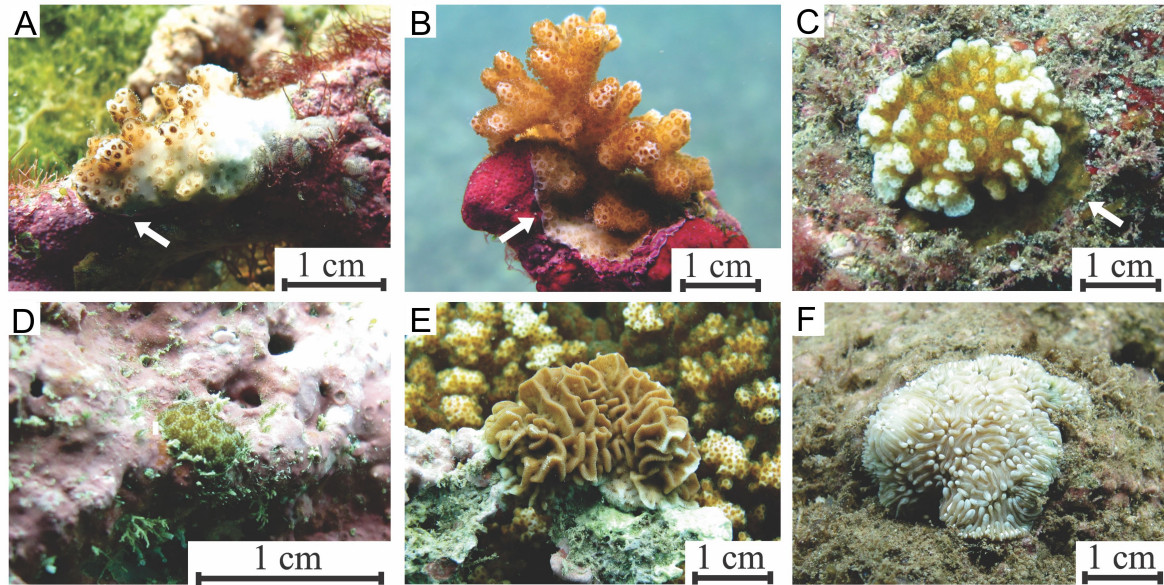


Figure 1. Coral recruits derived from sexual reproduction attached to natural substrates at Gorgona Island (Eastern Tropical Pacific). White arrows (A, B and C) point to encrusting base in *Pocillopora* specimens. A-B) *Pocillopora* sp. on coral rubble with calcareous algae; C) *Pocillopora* sp. on rocky wall with filamentous algae; D) *Porites panamensis* on coral rubble with calcareous-algae; E) *Pavona varians* on coral rubble with calcareous-algae; F) *Pavona gigantea* on rocky wall with filamentous algae.

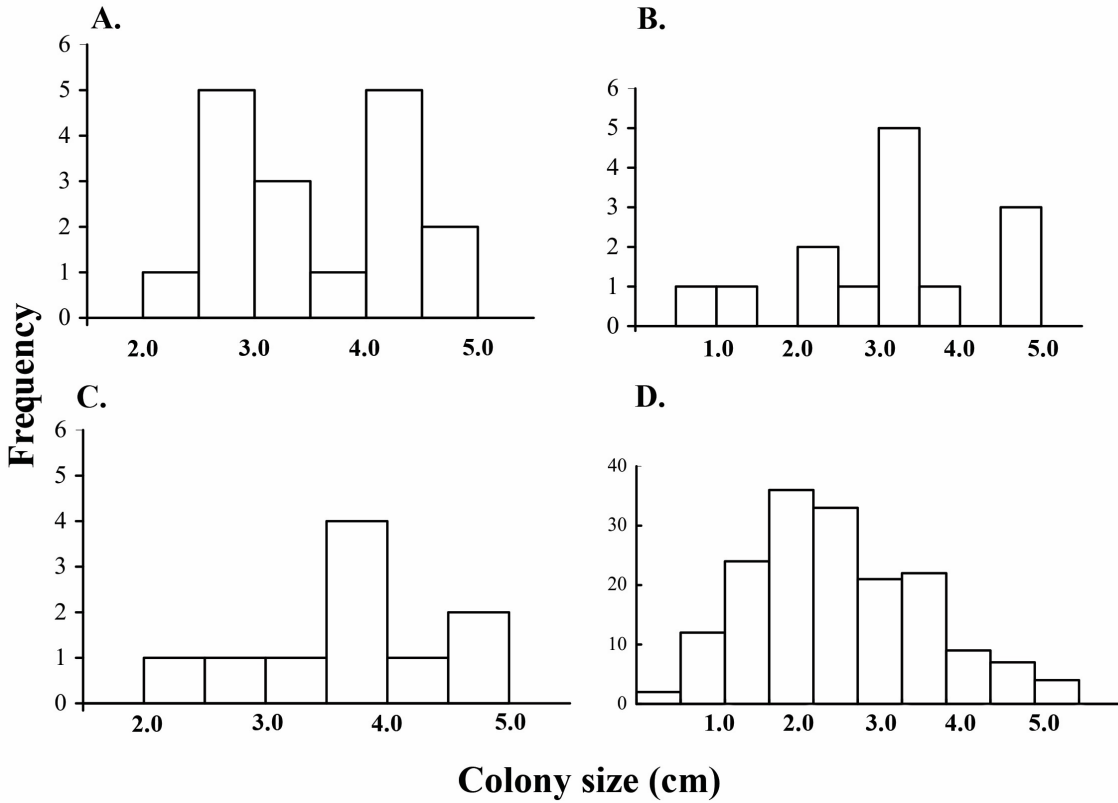


Figure 2. Size frequency distributions of coral recruits at Gorgona National Natural Park (Eastern Tropical Pacific). The distributions are truncated at 5.0 cm, since juveniles are defined as colonies ≤ 5.0 cm. Distribution for pocilloporid recruits ($N = 41$) at A) La Azufrada, B) El Laberinto, and C) Playa blanca. *Porites panamensis* ($N = 170$) in D) El Arrecifito. Colony size refers to the largest diameter of a colony.

APPENDIX

Appendix A. List of sites surveyed looking for coral recruits at Gorgona National Natural Park (Colombia, Eastern Tropical Pacific) during years 2010 - 2017.

Description	Site	Sampling year	Geographic coordinates
Coral reefs	Arrecifito	2010 - 2012	2° 56' 45.0"N 78° 11' 00.3"W
	Azufrada	2010 - 2015	2° 57' 18.4"N 78° 10' 33.5"W
	Muelle	2010 - 2015	2° 57' 38.9"N 78° 10' 25.6"W
	Playa blanca	2010 - 2015	2° 56' 32.2"N 78° 11' 25.2"W
	Ventana	2010 - 2014	2° 55' 43.3"N 78° 12' 17.2"W
Rocky boulders / mounts	Cazuela	2013 - 2014	2° 55' 38.4"N 78° 14' 22.8"W
	Farallones	2010	2° 56' 39.2"N 78° 12' 25.2"W
	Horno	2013 - 2014	3° 00' 16.0"N 78° 09' 52.4"W
	Jardín de las Gorgonias	2017	2° 58' 24.2"N 78° 11' 56.9"W
	Montañita I	2013 - 2014	2° 57' 45.6"N 78° 12' 33.9"W
	Montañita II	2013 - 2014	2° 57' 31.8"N 78° 12' 43.1"W
	Montañita III	2013 - 2014	2° 57' 35.7"N 78° 12' 58.4"W
	Parguera de Harold	2017	2° 56' 27.3"N 78° 13' 12.9"W
Rocky shores	Peña Mora	2013 - 2014	2° 58' 23.7"N 78° 10' 10.9"W
	Laberinto	2010, 2014	3° 00' 15.5"N 78° 10' 09.7"W
	Parguera	2013 - 2014	3° 00' 14.6"N 78° 10' 01.8"W
	Remanso	2010, 2014	3° 00' 04.5"N 78° 09' 58.2"W
	Yundigua (Acuario)	2010, 2014	2° 59' 08.0"N 78° 10' 13.5"W
Sandy shore	Planchón	2013 - 2014	2° 58' 01.8"N 78° 10' 14.3"W

CAPÍTULO 2

Drift logs are effective agents of physical coral fragmentation in a tropical eastern Pacific coral reef.

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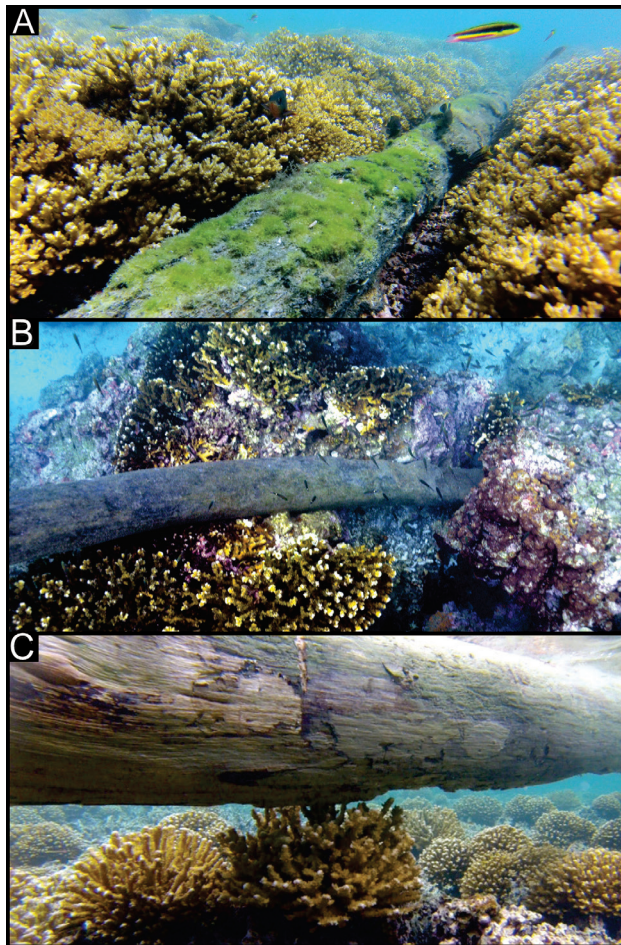
Drift logs are effective agents of physical coral fragmentation in a tropical eastern Pacific coral reef

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Coral reefs of the tropical eastern Pacific (TEP) exhibit high coral cover, but low coral diversity. These reefs are usually dominated by the genus *Pocillopora*, with branching colonies that are highly susceptible to breakage. Fragments of *Pocillopora* are often scattered over the reef bottom even in areas free of human disturbance. A major biological cause of coral natural fragmentation is the feeding activity of certain fish species, like pufferfishes (Tetraodontidae), which feed directly on the corals (Palacios et al. 2014), while triggerfishes (Balistidae) break coral colonies looking for invertebrates dwelling within them (Glynn et al. 1972). Because survival of *Pocillopora* fragments can be high (CG Muñoz, Universidad del Valle, unpubl data), coral asexual reproduction by fragmentation is likely important in these reefs (Highsmith 1982).

The continental landscape adjacent to Gorgona Island, Colombia, is densely covered by rainforests (Chocó/Darién/W. Ecuador—biodiversity hotspot; Myers et al. 2000), where logging is a poorly regulated, but widespread

profitable activity performed by local people. Logs are carried through waterways by small boats pulling many logs tied together with ropes. As a result, logs are frequently lost during transport. Additionally, landslides are common in forests along coastal hills and carry large quantities of vegetation to the sea, including entire large trees. In consequence, logs and other floating plant debris frequently drift at sea before stranding on beaches. Drift logs have drawn some attention, mostly regarding their function as floating structures for long-distance dispersal of marine organisms (Jokiel 1990). Although drift logs “battering” of intertidal communities has received some attention (Dayton 1971), the potential effects on coral reefs have not yet been addressed. Based on direct observations, here we describe the effects of physical impact by drift logs on a TEP coral reef.

La Azufrada reef is a 9.4-ha, shallow coral reef located on the leeward side of Gorgona Island. Extensive areas of the reef flat are located at shallow water depths of approximately 0.5 m during low tide, and subaerially exposed during occasional extreme low tides. We have observed that drift logs can affect this reef in two ways: (1) logs sink and get trapped between corals, which break continually as waves rock the logs back and forth; and (2) logs break corals when they bump against the substrate as logs hover over the reef.

To assess the importance of drift logs as agents of coral fragmentation at La Azufrada reef, in June 2013 we estimated the abundance and dimensions of submerged logs on the reef and of logs stranded on the adjacent beach (which has an extension of approximately 5 ha during low tide). We found 11 submerged logs measuring a mean of 4.0 (SD 2.6) m in length and 0.4 (SD 0.2) m in diameter, all of which were surrounded by broken colonies and numerous coral fragments providing examples of the first type of effect (A, B). Additionally, we found 57 stranded logs on the beach measuring 5.6 (SD 5.4) m in length and 0.3 (SD 0.3) m in diameter, the largest ones (27 and 24 m long; approximately 1 m diameter) had roots and branches. Both types of logs (submerged and stranded) were present during the 10 d of the study, and no additional logs arrived during this period. We hypothesize that logs stranded on the beach had a destructive impact on the reef as a function of the tide level at the time of arrival, their size, and presence of roots and branches (which would maximize their potential for coral fragmentation). Later, in October 2013, one encounter with a large log (13.6 × 0.3 m) drifting over a distance of about 200 m on the reef for 45 min clearly illustrated the second type of effect, when this single log collided with corals at low tide (<0.5 m depth) and under weak wind conditions (C). This log hit and broke at least 13 *Pocillopora* colonies, generating 71 fragments [5.4 (SD 2.6) fragments colony⁻¹ at a rate of 1.6 fragments min⁻¹] between 4 and 12 cm in length. Approximately 60% of the fragments remained on the original colonies and thus could potentially reattach to them. The remaining fragments reached the adjacent bottom, potentially forming new colonies as observed for some species in the TEP (Richmond 1987, Baums et al. 2014). Given the survival advantages of coral fragments conferred by their much larger size in comparison with juvenile colonies derived from recently recruited larvae (Highsmith 1982), these fragments may play an important role in the local coral population replenishment. This assumption is supported by the findings that recruitment by sexually-produced larvae is generally low throughout the TEP region (Richmond 1987, López-Pérez et al. 2007, Lozano-Cortés and Zapata 2014). Thus, logs drifting over reefs may be important physical agents of coral asexual reproduction in similar areas where reefs are shallow, branching corals are common, and where rainforests co-occur with coral reefs (e.g., Coral Triangle).

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LITERATURE CITED

- Baums IB, Devlin-Durante M, Laing BAA, Feingold J, Smith T, Bruckner A, Monteiro J. 2014. Marginal coral populations: the densest known aggregation of *Pocillopora* in the Galápagos Archipelago is of asexual origin. *Front Mar Sci*. 1:59. <http://dx.doi.org/10.3389/fmars.2014.00059>
- Dayton PK. 1971. Disturbance and community organization: the provision and subsequent colonization of space in a rocky intertidal community. *Ecol Monogr*. 41(4):351–389. <http://dx.doi.org/10.2307/1948498>
- Glynn PW, Stewart RH, McCosker JE. 1972. Pacific coral reefs of Panamá: structure, distribution and predators. *Geol Rdsch*. 61:483–519. <http://dx.doi.org/10.1007/BF01896330>
- Highsmith RC. 1982. Reproduction by fragmentation in corals. *Mar Ecol Prog Ser*. 7:207–226. <http://dx.doi.org/10.3354/meps007207>
- Jokiel PL. 1990. Long-distance dispersal by rafting: reemergence of an old hypothesis. *Endeavour*. 14:66–73. [http://dx.doi.org/10.1016/0160-9327\(90\)90074-2](http://dx.doi.org/10.1016/0160-9327(90)90074-2)
- López-Pérez RA, Mora-Pérez MG, Leyte-Morales GE. 2007. Coral recruitment at Bahías de Huatulco, western México: implications for coral community structure and dynamics. *Pac Sci*. 61:355–369. [http://dx.doi.org/10.2984/1534-6188\(2007\)61\[355:CASRAB\]2.0.CO;2](http://dx.doi.org/10.2984/1534-6188(2007)61[355:CASRAB]2.0.CO;2)
- Lozano-Cortés DF, Zapata FA. 2014. Invertebrate colonization on artificial substrates in a coral reef at Gorgona Island, Colombian Pacific Ocean. *Int J Trop Biol*. 62:161–168.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*. 403:853–858. <http://dx.doi.org/10.1038/35002501>
- Palacios MM, Muñoz CG, Zapata FA. 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs*. 33:625–636. <http://dx.doi.org/10.1007/s00338-014-1173-y>
- Richmond RH. 1987. Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral, *Pocillopora damicornis*. *Bull Mar Sci*. 41:595–604.

CAPÍTULO 3

Fish corallivory on a pocilloporid reef and experimental coral responses to predation.

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Fish corallivory on a pocilloporid reef and experimental coral responses to predation

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Abstract This study examined the effects of the Guineafowl pufferfish (*Arothron meleagris*), a major corallivore in the Eastern Pacific, on pocilloporid corals on a reef at Gorgona Island, Colombia. Pufferfish occurred at a density of 171.2 individuals ha⁻¹ and fed at a rate of 1.8 bites min⁻¹, which produced a standing bite density of 366.2 bites m⁻². We estimate that approximately 15.6 % of the annual pocilloporid carbonate production is removed by the pufferfish population. Examination of the predation effect on individual pocilloporid colonies revealed that although nubbins exposed to corallivory had lower linear growth, they gained similar weight and became thicker than those protected from it. Additionally, colonies with simulated predation injuries (on up to 75 % of branch tips) healed successfully and maintained growth rates similar to those of uninjured colonies. Despite the high corallivore pressure exerted by pufferfish on this reef, we conclude that

they have a low destructive impact on *Pocillopora* colonies as corals can maintain their carbonate production rate while effectively recovering from partial predation. Due to its influence on colony morphology, pufferfish predation may increase environmentally induced morphological variability in *Pocillopora*.

Keywords *Arothron meleagris* · Corallivory · Reef fishes · Guineafowl pufferfish · *Pocillopora* spp. · Tropical Eastern Pacific

Introduction

Coral-feeding fishes, represented by at least 128 species (Cole et al. 2008), are an important functional guild within tropical coral reefs as they influence the abundance and distribution of coral species and coral community structure (Neudecker 1979; Wellington 1982; Hixon 1997; Rotjan and Lewis 2008; Lenihan et al. 2011). Most corallivore fishes are butterflyfishes (Chaetodontidae), which only remove live tissue from corals and cause little or no damage to skeletal structures (Cole et al. 2008). However, some pufferfish, parrotfish, and triggerfish scrape, excavate, or break corals removing also portions of the underlying calcareous skeleton. These fishes can have a significant impact on corals because the fitness of injured corals is usually altered through the reallocation of energy resources from growth and reproduction to tissue and skeletal regeneration (Hall 2001; Henry and Hart 2005). Such impact also contributes to determine the physical structure, zonation, and diversity of reef habitats (Wellington 1982; Cole et al. 2008; Jayewardene et al. 2009; Bonaldo and Bellwood 2011).

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Studies on fish corallivory have examined the pressure and effects of predators on corals at different levels of organization. Some studies have determined the extent of damage inflicted or tissue removed by corallivores (Reyes-Nivia et al. 2004; Bonaldo and Bellwood 2011; Cole et al. 2011; Bonaldo et al. 2012;) and their effects on the growth or recovery of individual coral colonies (Jayewardene et al. 2009; Edmunds and Lenihan 2010; Lenihan and Edmunds 2010; Shantz et al. 2011). Others have examined the broader impacts of fish predation on coral species composition and coral community diversity (Cox 1986; Littler et al. 1989; Rotjan and Lewis 2006; Lenihan et al. 2011). While studies in the Caribbean and Indo-Pacific have focused on butterflyfishes and parrotfishes as major coral predators, those in the Tropical Eastern Pacific (TEP) have concentrated on the Guineafowl pufferfish *Arothron meleagris*—a generalist corallivore that ingests between 16 and 20 g $\text{CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ by constantly scraping and breaking off the branch tips of the abundant pocilloporid colonies (Glynn et al. 1972, 1982; Guzmán and López 1991; Reyes-Bonilla and Calderon-Aguilera 1999). This pufferfish, despite being perhaps the most important fish corallivore in the region (Guzmán and Robertson 1989), appears to have no significant negative impact on coral abundance, reef development, or community structure of pocilloporid coral reefs (Guzmán and López 1991; Reyes-Bonilla and Calderon-Aguilera 1999). It is unknown why the effect of puffers in the TEP differs from the common negative impact that corallivorous fishes exert on other coral reef regions (e.g., Rotjan et al. 2006; Bonaldo and Bellwood 2011; Shantz et al. 2011). Addressing this issue requires an understanding of the effects of fish predation on the growth and recovery of individual *Pocillopora* spp. colonies as well as basic information on the predator's feeding behavior, feeding rate, and the resulting predation pressure on the reef.

Considering that pocilloporid reefs in the TEP region differ greatly in species richness and composition from those in the Caribbean and Indo-Pacific, and that the pressure and effects of corallivory vary according to the characteristics of the fish predator and the coral prey (Rotjan and Lewis 2008; Lenihan and Edmunds 2010), conclusions from one system in a particular region cannot be easily extended to different systems in other regions. Before any generalizations can be made, specific studies must be undertaken. Additionally, as pocilloporid reefs in the TEP offer a simplified predator–prey system (only one important fish predator—*A. meleagris* and one main coral prey—*Pocillopora* spp.), it may be possible to have a better understanding of the interaction and the process of corallivory. This study examined corallivory by the puffer *A. meleagris* on pocilloporid reefs from the TEP and addressed the following: (1) What is the predator's (*A. meleagris*)

density, feeding behavior, and predation pressure on branching pocilloporid colonies (coral prey)?, (2) What is the effect of puffer predation on the growth of coral colonies?, (3) What is the tolerance of coral colonies to injuries inflicted by the pufferfish?, and (4) What is the rate of destruction by puffers in relation to the rate of annual carbonate production by pocilloporid corals?.

Methods

Study site

This study was conducted from April to December 2012 at La Azufrada reef, a fringing coral reef located at Gorgona Island (2°58'27"N and 78°11'13"W) off the Colombian coast in the TEP region. La Azufrada reef is a shallow (4–12 m depth at high tide) calcareous framework extending over 9.4 ha, dominated by branching coral species of the genus *Pocillopora* (*P. capitata*, *P. damicornis*, *P. eydouxi*). Despite having relatively high coral cover (~40–75 %; Zapata et al. 2010), La Azufrada reef (like other reefs of the TEP) occurs within suboptimal and highly variable environmental conditions, such as an intense rainfall regime (resulting in frequent low salinity episodes and high water turbidity), sporadic extreme low tides, that cause subaerial exposure of corals and temperature alterations by ENSO events (Zapata and Vargas-Ángel 2003). During the time of the study, however, mean water temperature remained stable (27.7 ± 0.4 °C; mean $\pm$ SD) and oceanographic conditions corresponded to neutral/weak El Niño conditions (NOAA 2013).

Based on substrate cover composition and reef topography, three main reef zones can be distinguished at La Azufrada reef: (1) the back reef, which comprises a soft sediment bottom with many unattached coral colonies; (2) the reef flat, which is the largest reef zone and has a relatively thick (>8 m; Glynn et al. 1982) carbonate matrix where *Pocillopora* colonies are found both individually and in patches; and (3) the reef crest, where *Pocillopora* spp. form a dense, continuous stand that can cover up to 80–90 % of the substrate. As a result of the large variability in the abundance and distribution of pocilloporid colonies (preferred prey species for *A. meleagris*; Glynn et al. 1982; Guzmán and López 1991) throughout the coral reef, we considered observations from each of the three reef zones separately to account for variability in the pufferfish population and corallivore pressure.

Prey abundance (*Pocillopora* spp.)

Pocilloporid coral cover was estimated using 1 m² quadrats divided into 100 sub-quadrats of 10 × 10 cm². In each

zone, 30 quadrats were haphazardly placed and pocilloporid percentage cover was calculated for each as the number of sub-quadrats that were occupied by *Pocillopora* spp. (1 sub-quadrat = 1 % of cover). Differences in mean percentage of pocilloporid cover (arcsine-transformed) among reef zones (back reef, reef flat, and reef crest) were assessed using a resampling one-way ANOVA as the data did not satisfy the assumptions of normality and homoscedasticity required by standard parametric procedures. Subsequently a two-sample resampling test with Holm's correction ($\alpha = 0.05$) was used as a post hoc analysis to detect which means were significantly different from each other. The software Rndom Pro version 3.14 (Jadwiszczak 2009) was used to perform all the resampling analyses in this study.

Predator abundance (*Arothron meleagris*)

To estimate the population density of the puffer *A. meleagris*, we conducted 150 visual surveys along 50×5 m belt transects ($N = 50$ transects per reef zone). On each of the three reef zones, half of the surveys were conducted in the morning (09:22–11:55 h) and half in the afternoon (12:10–17:40 h) in order to obtain a uniform distribution of observations during the activity hours of *A. meleagris* (from ~6:00 h to ~18:30 h; personal observation). The number and the total length (TL; visually estimated to the nearest centimeter) of all puffers seen within transects were recorded. Puffer densities (ind ha^{-1}) were compared across reef zones (back reef, reef flat, and reef crest) through a resampling one-way ANOVA and a two-sample resampling test with Holm's correction ($\alpha = 0.05$). As data from fish sizes (TL) satisfied the assumptions normality and homoscedasticity of parametric tests, they were compared between the reef zones through a one-way ANOVA and a Tukey's multiple comparison test ($\alpha = 0.05$) as a post hoc test. We used the software STATISTICA version 8 (Stat-Soft Inc. 2007) to perform all parametric analyses in this study.

Standing bite density

All open lesions (exposed coral skeleton) on *Pocillopora* branch tips were considered to be bites made by the puffer *A. meleagris*, since preliminary field observations indicated that all conspicuous scars on coral branch tips were inflicted by *A. meleagris* (Fig. 1). No other fish species at Gorgona Island feeds in the same way, except for the congeneric *A. hispidus*, which is less abundant (23.7 ± 35.3 ind ha^{-1} , mean $\pm$ SD), occurs on deeper or sandy areas, and is rarely seen feeding on corals. Preliminary observations on the regeneration rate of coral tissue at La Azufrada reef indicated that superficial injuries

heal in approximately 2 weeks and deeper lesions take about 2 months to recover. Consequently, we assumed that the standing density of feeding scars recorded in this study was the result of the puffers' feeding activity during the past few weeks.

The standing density of fish bite marks on *Pocillopora* colonies (bites m^{-2}) was estimated ($N = 90$ for the entire reef) with the 1 m^2 quadrats previously used to calculate coral cover (see "Prey abundance" section). Each time the large quadrat was haphazardly placed over the substrate, and bite marks were counted within those 10×10 cm sub-quadrats along the diagonal that had living coral (between three and ten sub-quadrats). Counts within the sub-quadrats in each quadrat were averaged and used as a replicate estimate of the standing bite density ($N = 30$ per reef zone). Standing bite density data were Log_{10} transformed to satisfy assumptions of normality and homoscedasticity. Differences in standing bite densities between reef zones (back reef, reef flat, and reef crest) were examined using a one-way ANOVA and a Tukey's multiple comparison test as a post hoc analysis ($\alpha = 0.05$). The spatial distribution of bite scars within each reef zone was analyzed by examining the fit to a Poisson distribution of the frequency distribution of the mean number of bites (rounded to the nearest integer) in the $10 \times 10 \text{ cm}^2$ sub-quadrats. Lack of fit was determined using the Index of Dispersion (ID or variance to mean ratio), which follows a chi-square distribution with $N - 1$ degrees of freedom (Ludwig and Reynolds 1988).

Feeding rate

To determine the feeding rate of *A. meleagris*, we followed 120 haphazardly selected puffers ($N = 40$ puffers per reef zone) for ten min each while recording the number of bites taken from the substrate. The behavior and size of the fish were recorded, as well as the substrate type/species from which bites were taken. Fish feeding behavior was classified as active (≥ 1 bites 10 min^{-1}) or inactive (0 bites 10 min^{-1}). Half of the fish observations on each reef zone were conducted during the morning (08:40–11:40 h) and the other half during the afternoon (14:40–17:30 h). Puffer feeding rates (bites min^{-1}) were compared among reef zones (back reef, reef flat, and reef crest), among periods of the day (morning, 08:40–11:40 h and afternoon, 14:40–17:30 h) and among size classes of puffers (small: ≤ 17 cm TL, medium: 18–24 cm TL, and large: ≥ 25 cm TL) using resampling one-way ANOVAs as the data did not satisfy the assumptions of standard parametric tests.

Tolerance to corallivory experiment

The tolerance of pocilloporid colonies to different levels of damage caused by simulated pufferfish biting was

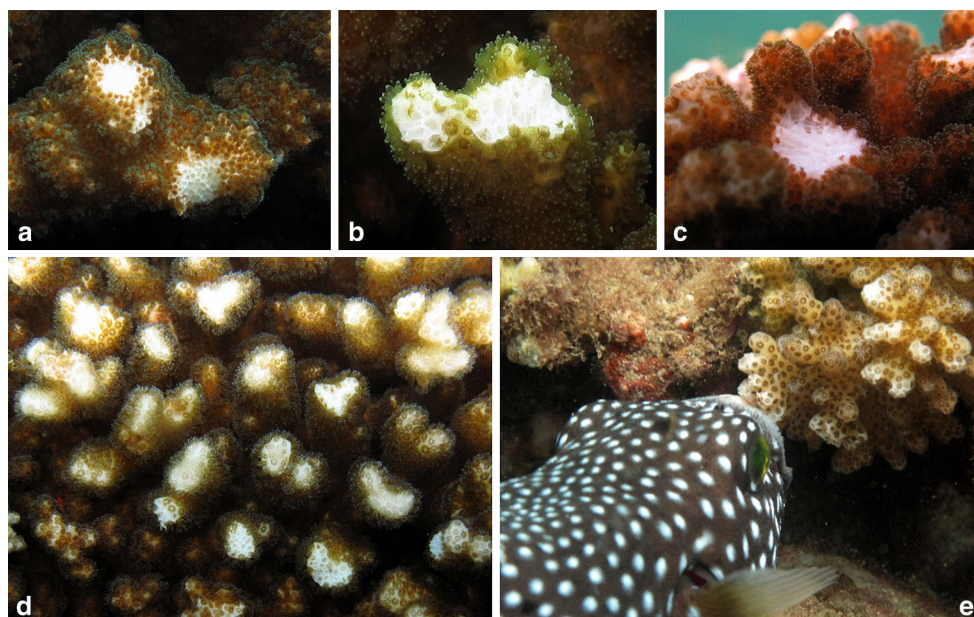


Fig. 1 Bite marks by the pufferfish *Arothron meleagris* on *Pocillopora* spp. colonies: **a** scrapes to the coral tissue, **b**, **c** excavating bites where coral tissue and skeleton have been removed, **d** pocilloporid colony exhibiting pufferfish bite marks, **e** *A. meleagris* feeding on *Pocillopora* spp.

determined through a field experiment conducted in the reef crest of La Azufrada. We monitored the tissue regeneration and growth of 40 small colonies of *Pocillopora* spp. (75–325 g) after exposure to four experimental treatments ($N = 10$ colonies per treatment) that differed in the percentage of branch tips per colony that was artificially damaged by simulated puffer bites: 0 % (control), 25, 50, and 75 % of branch tips scraped/tissue removed. Based on preliminary field observations, these damage treatments were designed to mimic the wide range of standing bite densities observed on pocilloporid colonies (47.7 ± 23.0 % of coral branches assessed had bite marks, mean $\pm$ SD, $N = 3,263$ branches) and to resemble the natural injuries inflicted by puffers (Fig. 1). Measurements with calipers (to the nearest 0.1 mm) of bite marks made by puffers on *Pocillopora* spp. revealed that bites were small (area = 0.47 ± 0.38 cm²; mean $\pm$ SD; $N = 362$ bites) and that most often puffers inflicted only shallow injuries (mean bite depth = 0.19 ± 0.08 mm, $N = 50$ bites) on branch tips (although they also can occasionally break weak branches). In this experiment, artificial injuries made with pliers were similar in area to those measured in the field and although they were deeper (between 0.1 mm and 0.5 cm depth) than natural ones, we haphazardly made a large proportion of shallow scars (≤ 0.3 mm) to resemble the natural pattern. Considering that many puffer bite marks are superficial injuries that do not represent a significant removal of coral skeleton (Fig. 1a), the aim of our treatments was to injure the branch tips (resembling natural

bite marks) in different densities, but not necessarily to remove specific weights of coral tissue/skeleton.

All colonies employed in this experiment were haphazardly collected from the reef and kept in tanks with fresh seawater, while they were being tagged, treated (according to the four experimental groups), and weighed (to the nearest 0.01 g). In <2 h from the time of collection, all colonies were taken to the reef and placed inside ten mesh cages ($35 \times 20 \times 25$ cm; 1.5 cm mesh size), so that each cage contained one colony from each treatment. Cages had previously been installed on the reef crest and were monitored periodically throughout the duration of the experiment to remove any fouling organisms and algae from the mesh. At the end of the experiment (122 d later), each colony was weighed for a second time. To assess pocilloporid tolerance to bite injuries and measure the degree to which coral fitness (in terms of growth) was affected, we compared the mean change in colony weight (g) among the four experimental groups (0, 25, 50, and 75 % of the branch tips injured by simulated puffer feeding) with a one-way ANCOVA using the initial colony weight as a covariate.

Predator exclusion experiment

The effect of puffer predation on the growth (measured as linear extension and weight change) of *Pocillopora* spp. was assessed in situ by exposing 30 nubbins, each ~ 4 cm long, to three experimental treatments ($N = 10$ per treatment): (1) predation treatment in which nubbins were kept

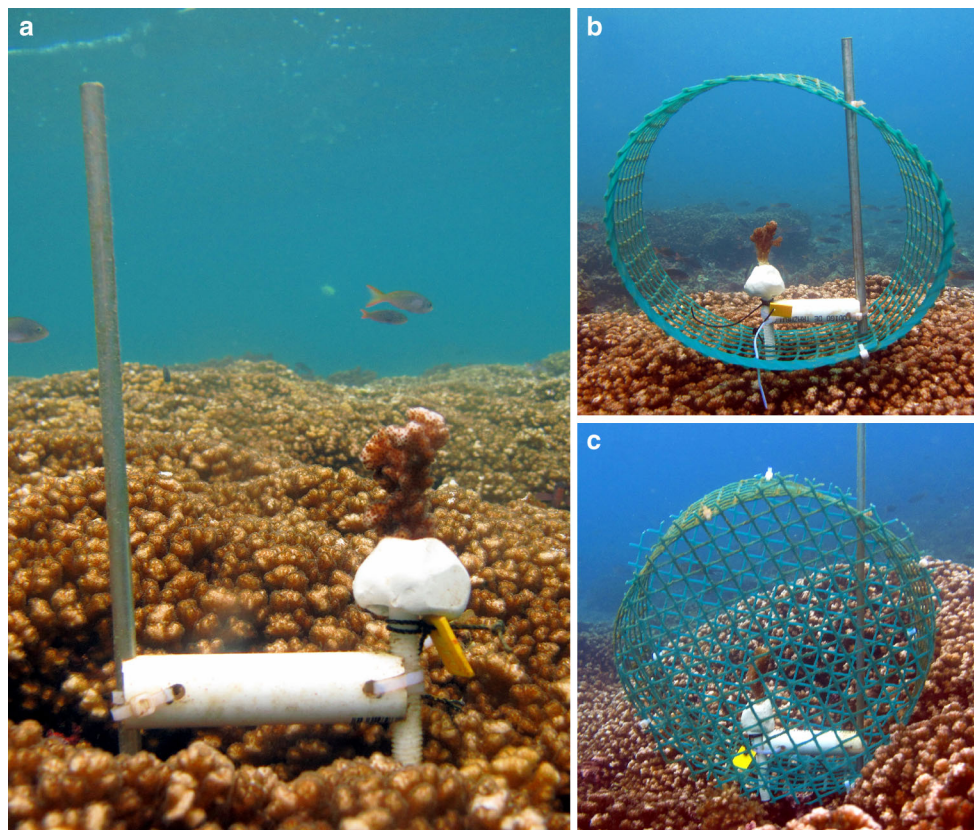


Fig. 2 Treatments considered in the Predator exclusion experiment where pocilloporid nubbins were individually exposed or protected from fish corallivores: **a** Predation treatment (no cage), **b** cage control

treatment (half-cage), and **c** Predator exclusion treatment (full cage). Half-cages were employed to allow fish predation while controlling for the possible effects of the mesh on the nubbins

in the open, exposed to corallivory; (2) predator exclusion treatment in which mesh cages ($25 \times 25 \times 11.5$ cm; 1.5 cm mesh size) protected nubbins from fish corallivores; and (3) cage control treatment in which nubbins were kept within half-open cages (mesh cages lacking two sides) and therefore exposed to corallivory; this controlled possible effects of the full cage on the nubbins (Fig. 2). To conduct this experiment, haphazardly collected nubbins were individually glued (with epoxy cement) to plastic screws (Fig. 2), tagged, measured with calipers (lengthwise; from the base of the epoxy to the tip of the nubbin) to the nearest 0.01 cm, and weighed on a scale (including the screw and the tag) to the nearest 0.01 g. Afterward, they were placed on the reef flat at 5-m intervals, where the three treatments were systematically assigned to them in sequence. After 183 d, the nubbins were collected, measured, weighed, and examined closely for bite marks. Annotations were made on the number of the fish bites that each nubbin presented.

Changes in the length and weight of coral nubbins were normalized to surface area ($\text{cm cm}^{-2} \text{ yr}^{-1}$ and $\text{g cm}^{-2} \text{ yr}^{-1}$) using the wax-dipping technique (Stimson and Kinzie 1991) to account for any differences in the size or surface area of the nubbins that might affect growth. To

compare the normalized linear extension rate ($\text{cm cm}^{-2} \text{ yr}^{-1}$) among the three treatments (predation treatment, predator exclusion treatment, and cage control treatment), we used a one-way ANOVA followed by a Tukey post hoc analysis. In contrast, as data from the normalized weight gained ($\text{g cm}^{-2} \text{ yr}^{-1}$) did not satisfy the assumptions of parametric tests, differences between treatments were analyzed through a resampling one-way ANOVA. Additionally, because treatment-related changes in nubbin morphology (colony weight/length ratio) were apparent, we ran a parametric one-way ANOVA and Tukey's post hoc test to compare, across the three treatments, the average ratio of the normalized weight gain to the linear extension of nubbins ($\Delta \text{ weight} / \Delta \text{ length ratio}$).

The effect of puffers on the pocilloporid carbonate budget

We considered the effect of puffers on the pocilloporid standing crop as the percentage of the carbonate produced by pocilloporids that is removed by puffers. The carbonate production ($\text{kg m}^{-2} \text{ yr}^{-1}$) of *Pocillopora* spp. was calculated as follows:

Pocillopora Carbonate Production

$$= \text{Coral Cover (\%)} \times \text{Growth Rate (cm yr}^{-1}\text{)} \\ \times \text{Colony Density (g cm}^{-3}\text{)}$$

where coral cover and growth rates were obtained as described previously (see the “Prey abundance” section for coral cover and the “Predator exclusion experiment” section for growth rate). Colony density was employed instead of skeletal density, as the latter should only be employed to calculate the carbonate production of massive coral colonies (where the density and volume of a colony are constant per unit of coral cover; Perry et al. 2012). Because ramose pocilloporid species have spaces between branches that do not contribute to carbonate production (discussed by Heiss 1995), we used the density of pocilloporid colonies and subtracted the volume of empty space to approximate carbonate production. Colony density (g cm^{-3}) was determined for five *Pocillopora* colonies that were individually wrapped with plastic film, weighed (g), and submerged in a container with water to estimate their volume (cm^3). Wrapping the entire colony in plastic film served to include the empty volume between branches in the estimation of the colony volume and thus colony density (Adams et al. 1985; Vytopil and Willis 2001).

On the other hand, the rate of Puffer Destruction ($\text{kg m}^{-2} \text{yr}^{-1}$) was obtained as:

$$\text{Puffer destruction} = \text{population density (ind ha}^{-1}\text{)} \\ \times \text{destruction rate per fish (g min}^{-1}\text{)} \\ \times \text{feeding correction factor.}$$

Data on puffer density were obtained from the fish surveys made in this study (see “Predator abundance” section), whereas the destruction rate per fish was calculated following fish bioerosion studies (e.g., Bellwood 1995; Bruggemann et al. 1996), in which the fish feeding rate (bites min^{-1} ; see “Feeding rate” section) is multiplied by the mass of coral removed per bite (g bite^{-1}). To estimate the mean weight of coral removed per bite (g bite^{-1}), we followed the method used by Bellwood (1995) in which the volume of a bite mark (calculated by its length, width, and depth) is combined with the substratum density. Although the depth of bite marks is difficult to measure in branching pocilloporid species (original branch tip length is unknown), we did not deem appropriate the approach used by Glynn et al. (1972) as the puffers significantly change their feeding behavior when enclosed in mesh cages (personal observation). For our calculations, we used the bite mark measures taken for the “Tolerance to coral-livory experiment” and the mean skeletal density of 30 *Pocillopora* spp. branches collected in the field. To obtain the density estimates (g cm^{-3}), branches were individually weighed with a digital scale to the nearest 0.001 g and

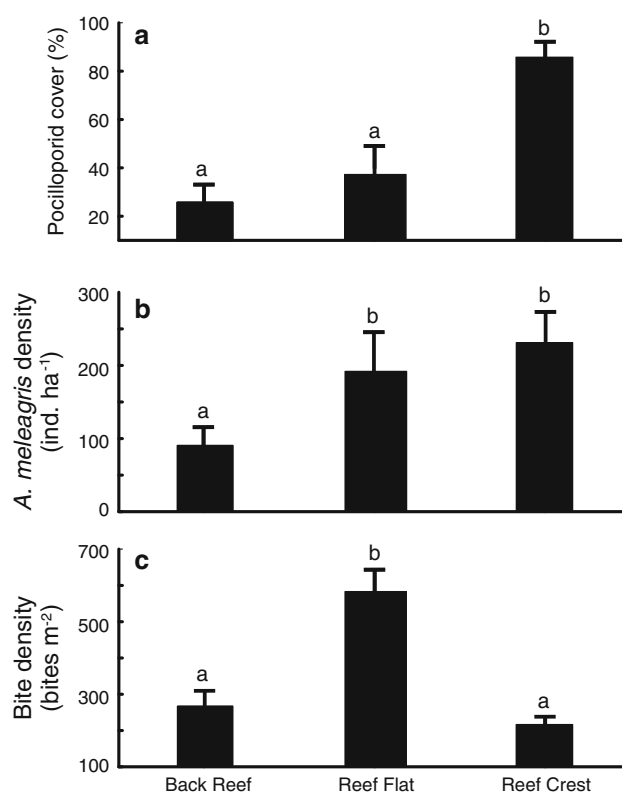


Fig. 3 Mean ($\pm 95\%$ CI) **a** pocilloporid coral cover (%), **b** *Arothron meleagris* abundance (ind ha^{-1}), and **c** standing bite density (bites m^{-2}) across three zones of La Azufrada coral reef, Gorgona Island. Bars with the same lowercase letter did not differ significantly: **a**, **b** two-sample resampling tests with Holm's correction ($\alpha = 0.05$), **c** Tukey's multiple comparison test ($\alpha = 0.05$)

volume was calculated as the water displaced by each branch in a 50-ml graduated cylinder (± 0.1 ml). Finally, the feeding correction factor in the formula reflects the proportion of puffers actively feeding at a given time and was calculated from our field observations (see “Feeding rate” section).

Results

Prey abundance (*Pocillopora* spp.)

The average cover of pocilloporid colonies at La Azufrada reef was $49.6 \pm 37\%$ (mean $\pm$ SD, $N = 90$). *Pocillopora* spp. cover varied significantly across reef zones ($F_{2,87} = 43.3$, $P < 0.001$; Fig. 3a), with the highest cover recorded on the reef crest, where a dense and continuous stand of interlinked pocilloporid colonies occupied $85.8 \pm 18.7\%$ ($N = 30$) of the substrate. Both the back reef and the reef flat had a coral cover of $< 40\%$ as the back reef was dominated by sand and rubble, and the reef flat was characterized by large areas of calcareous matrix

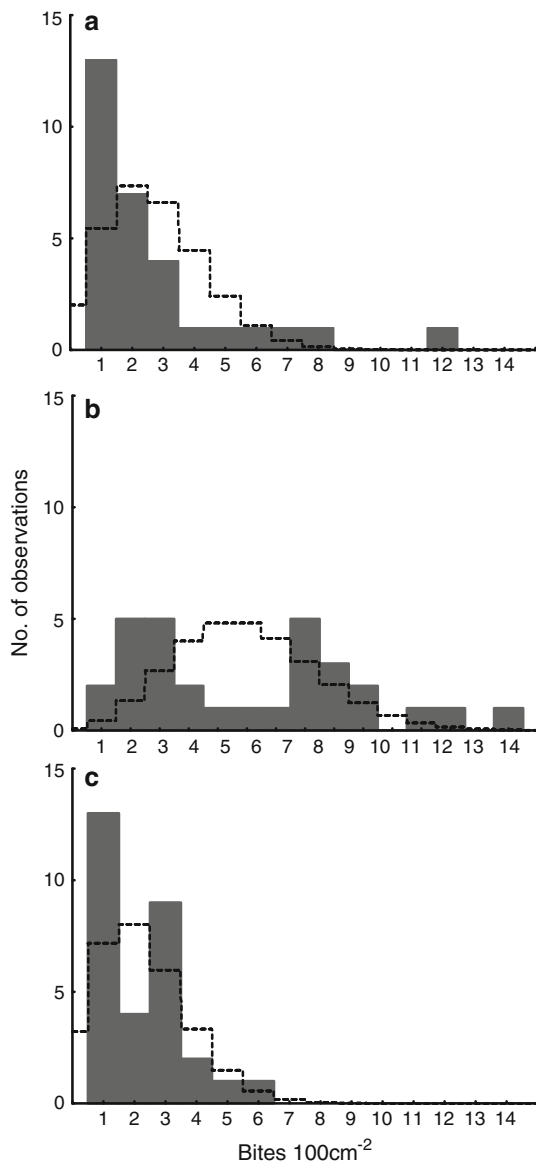


Fig. 4 Observed frequency distribution of standing bite scars within 100 cm² quadrats on each of three reef zones at La Azufrada coral reef: **a** back reef, **b** reef flat, and **c** reef crest. Dash line histograms correspond to the expected Poisson distribution under the null hypothesis of a random spatial distribution of bite scars

(composed of coral rubble tightly cemented by encrusting calcareous algae) and scattered coral patches.

Predator abundance (*Arothron meleagris*)

The puffer *A. meleagris* had an average density of 171.2 ± 166.9 ind ha⁻¹ (mean $\pm$ SD, $N = 150$) and an estimated total population size of 1,606 individuals (on a 9.4 ha reef). Significant differences in puffer abundance were found among reef zones ($F_{2,147} = 10.7$, $P < 0.001$; Fig. 3b), with the reef crest (231.2 ± 160.7 ind ha⁻¹,

$N = 50$) and the reef flat (192 ± 199.7 ind ha⁻¹, $N = 50$) being the zones with the highest puffer density. The abundance of puffers increased toward the outer edge of the reef, where puffers usually aggregate in groups of up to 15 individuals and hide in caves within the pocilloporid framework (Glynn et al. 1982). Puffer size at La Azufrada ranged between 10 and 30 cm TL and had a mean TL of 20.5 ± 3.9 cm ($N = 642$). Puffers from the back reef were significantly smaller than the ones from the reef flat and the reef crest ($F_{2,612} = 5.3$, $P < 0.05$).

Standing bite density

At La Azufrada reef, the average puffer-inflicted standing bite density on *Pocillopora* spp. colonies was 366.2 ± 329.7 bites m⁻² (mean $\pm$ SD, $N = 90$). However, standing bite density differed significantly among the three reef zones ($F_{2,87} = 15.5$; $P < 0.001$; Fig. 3c). The reef flat, which occupies the most area (58 %) of La Azufrada reef, had a higher standing bite density (608.6 ± 383.7 bites m⁻², $N = 30$) than the other reef zones (< 300 bites m⁻²), indicating a higher feeding pressure by the puffers on the pocilloporid patches occurring on the reef flat. The spatial distribution of bite scars was aggregated on the back reef and the reef flat (back reef: ID = 2.45, $P < 0.005$, $df = 29$; reef flat: ID = 2.47, $P < 0.05$, $df = 29$), but uniform on the reef crest (ID = 0.82, $P < 0.005$, $df = 29$; Fig. 4) where coral cover was the highest.

Feeding rate

The majority of *A. meleagris* bites was made on live *Pocillopora* spp. colonies (86.6 % of all bites), although *Psammocora stellata* (especially in the back reef, where it is more abundant), coral rubble, and other invertebrates (e.g., sponges) were also bitten by the fish. Sixty percent of the 150 pufferfish we followed were actively feeding, so we used this value to estimate the rate of coral consumption by puffers. During the feeding activity, the puffers' average feeding rate on *Pocillopora* was 1.8 ± 1.4 bites min⁻¹ (mean $\pm$ SD, $N = 72$) with no significant differences among fish size classes ($F_{2,69} = 0.8$, $P > 0.3$), reef zones ($F_{2,69} = 0.98$, $P > 0.3$), or periods of the day, ($F_{1,70} = 0.13$, $P > 0.9$).

Tolerance to corallivory experiment

Uninjured control colonies of *Pocillopora* spp. were slightly heavier than injured colonies at the end of the experiment; however, their change in weight was not statistically different from the weight changes of colonies in any of the damage treatments ($F_{3,31} = 1.12$, $P > 0.1$;

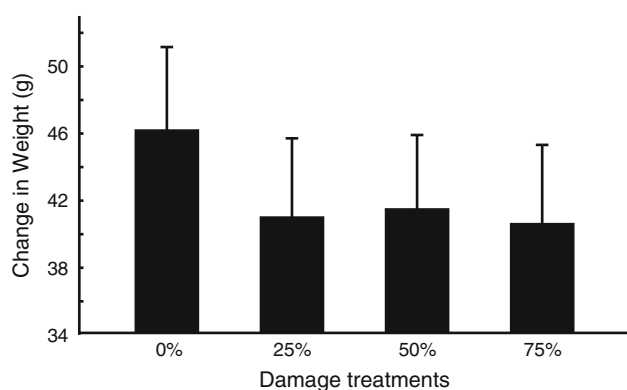


Fig. 5 Adjusted mean (+95 % CI) of the change in weight attained by pocilloporid colonies exposed to different levels of simulated bite-inflicted damage (control = 0 % or no damage, and 25, 50, or 75 % of colony branch tips damaged). Means of change in weight were adjusted by ANCOVA to the mean initial weight of colonies

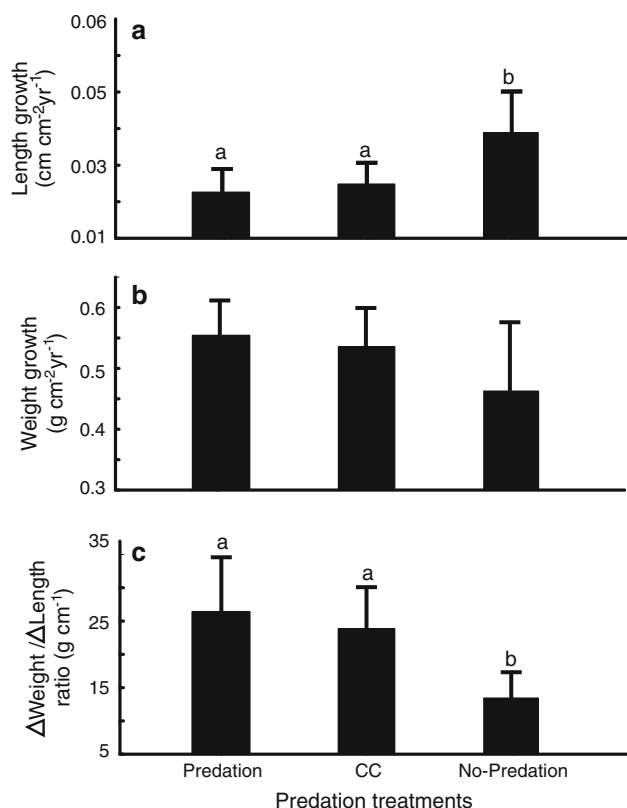


Fig. 6 Mean (+95 % CI) growth in terms of **a** normalized linear extension (cm cm⁻² yr⁻¹) and **b** normalized weight (g cm⁻² yr⁻¹) of *Pocillopora* spp. nubbins in each of three predation treatments (Predation, cage control = CC, and Predation exclusion). **c** Average ratio between the normalized weight gained and the increased linear extension of nubbins (normalized) in each treatment. Bars with the same lowercase letter did not differ significantly: **a, c** Tukey multiple comparison test ($\alpha = 0.05$), **b** two-sample resampling tests with Holm's correction ($\alpha = 0.05$)

Fig. 5). Growth rate of pocilloporid colonies seemed not to be affected significantly by the levels of injury we examined (25, 50, or 75 % of the branch tips injured by

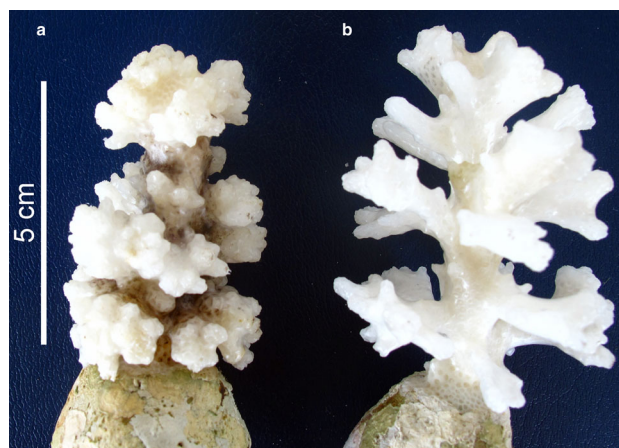


Fig. 7 Representative corallum morphologies of pocilloporid nubbins **a** exposed and **b** protected from fish corallivory in the Predator exclusion experiment carried out at La Azufrada coral reef, Gorgona Island, Colombia

simulated puffer feeding). All injuries had healed successfully after 2 months with no apparent negative effects on the colony branches. Thus, pocilloporid colonies appear to tolerate bitelike injuries on up to 75 % of their branches.

Predator exclusion experiment

Pocilloporid nubbins exposed to corallivory (predator and cage control treatments) had an average of 15.2 ± 9.3 fish bites nubbins⁻¹ (mean $\pm$ SD, $N = 20$) and a significantly lower normalized linear growth than the protected nubbins ($F_{2,26} = 5.1$, $P < 0.05$; Fig. 6a). Remarkably, nubbins in all treatment groups had a similar normalized weight gain ($F_{2,26} = 1.7$, $P = 0.2$; Fig. 6b). Nubbins in the half-cage treatment did not differ in linear growth or weight gain from those in the predator (uncaged) treatment, so it was assumed that the mesh did not affect growth of the fully caged nubbins (predator exclusion treatment).

Results from the Predator exclusion experiment provided evidence that the presence/absence of predation influenced the morphology (colony weight/length ratio) and normalized growth rates (Δ weight/ Δ length ratio) of pocilloporid nubbins: Corals exposed to corallivory were usually thick and short and had a greater rate of increase in weight for a given rate of linear extension than corals protected from fish predation ($F_{2,26} = 6.2$, $P < 0.01$; Figs. 6c, 7). Nubbins in the predator exclusion treatment showed the opposite morphology (long thin branches).

Effect of puffers on the pocilloporid carbonate budget

The puffer *A. meleagris* removed 15.8 % of the carbonate produced by the pocilloporid stands at La Azufrada reef, assuming a mean carbonate production rate of 5.5 kg

Table 1 Carbonate budget estimated for La Azufrada coral reef, considering only the production of *Pocillopora* spp. and the destruction by the puffer *Arothron meleagris*

<i>Pocillopora</i> spp. production				Destruction by <i>A. meleagris</i>			
Growth rate (cm yr ⁻¹)	Colony density (g cm ⁻³)	Cover (%)	Production (kg m ⁻² yr ⁻¹)	Density (ind ha ⁻¹)	Destruction per fish (g d ⁻¹)	CF	Destruction (kg m ⁻² yr ⁻¹)
2.70	0.42	49	5.56	171.2	233.28	0.6	0.87

The destruction rate per fish was calculated taking into account a carbonate removal of 0.18 ± 0.14 g bite⁻¹ (mean $\pm$ SD), a feeding rate of 1.8 ± 1.4 bites min⁻¹ and 12 h of feeding activity per day (based on field observations). CF is a correction factor representing the proportion of the pufferfish population actively feeding at a given time

Table 2 Abundance of the puffer *Arothron meleagris* on pocilloporid reefs within the Tropical Eastern Pacific

Site	Date of survey	Reef size (ha)	Coral cover (%)	<i>A. meleagris</i> (ind ha ⁻¹)	References
Colombia					
Azufrada reef	1979	15	36.5	12	Glynn et al. (1982)
Azufrada reef	1987/1988	15	48.5	34	Guzmán and Robertson (1989)
Playa Blanca reef	1989	8	32.6	21.9	Guzmán and López (1991)
Azufrada reef	1989	15	50.2	25.8	Guzmán and López (1991)
Azufrada reef	1993	10	–	80	Zapata and Morales (1997)
Azufrada reef	2012	9.4	49.6	171.2	This study
Mexico					
Cabo Pulmo reef	1991/1992	220	30	39	Reyes-Bonilla and Calderon-Aguilera (1999)
Playa Mora reef	2002/2004	2.5	–	43.7	Galván-Villa et al. (2011)
Panama					
Señora Is. reef	1971	0.8	75	40	Glynn et al. (1972)
Uva Is. reef	1981/1984	2.4	45	55	Glynn (1985)
Uva Is. reef	1986/1988	2.4	28.2	55	Guzmán and Robertson (1989)
Secas Is. reef	1986/1988	7.6	13.8	27	Guzmán and Robertson (1989)
Señora Is. reef	1987	0.8	49.5	0	Guzmán and Robertson (1989)

The location, reef size, percentage of live cover, date of survey and sources are shown. Modified from Guzmán and Robertson (1989)

CaCO₃ m⁻² yr⁻¹ and a puffers' destruction rate of 0.87 kg CaCO₃ m⁻² yr⁻¹ (Table 1).

Discussion

This study determined that a large proportion of La Azufrada pocilloporid reef is under intense corallivore pressure from the puffer *A. meleagris*. Coral colonies on the reef flat, the largest reef zone at La Azufrada reef (58 % of the entire reef's area), are consumed intensely by puffers. The mean standing bite density observed on pocilloporid colonies (~ 600 bites m⁻²) was greater than the median of the mean bite densities reported for several massive and branching coral species around the world (4–952 bites m⁻²; Rotjan and Lewis 2006; Jayewardene et al. 2009; Bonaldo and Bellwood 2011; Roff et al. 2011).

Although corallivore pressure is influenced by several factors (e.g., predator feeding rates, abundance, bite size), the impact recorded here is mainly due to the high density of *A. meleagris* (the highest ever reported for this species on any coral reef within the TEP; Table 2), as estimates of its feeding rate (1.8 bites min⁻¹) and carbonate removal per bite (0.18 g bite⁻¹) are similar to or lower than estimates for excavating parrotfishes (*Chlorurus gibbus*, *C. sordidus*, and *Sparisoma viride*; 6.7–18.0 bites min⁻¹ and 0.05–2.7 g bite⁻¹; Bellwood 1995; Reyes-Nivia et al. 2004). As expected, high densities of *A. meleagris* cause the greatest standing bite density when coral cover is relatively low and patchy. Although the reef crest and reef flat had similar puffer densities, the pocilloporid colonies on the reef flat exhibited greater bite densities as predators concentrated their feeding on the limited coral patches (Jayewardene et al. 2009; Shantz et al. 2011). The spatial

distribution of bite scars further supports this idea, since bites were aggregated on the reef flat, but uniformly distributed on the reef crest where coral cover was greatest. Together, this body of information suggests that *A. meleagris* exert a substantial impact to the distribution and growth of corals in La Azufrada.

While pufferfish predation affects the linear growth and morphometrics of *Pocillopora* spp. colonies, these colonies have the capacity to tolerate and recover from the high intensity levels of injury. As was expected, the constant pruning and trimming of branch tips by fish corallivores (Glynn et al. 1982) meant that nubbins exposed to predation increased their length at a lower rate than those protected from predation. However, similar to results reported for *Porites porites* in the Caribbean (Fig. 5b in Miller and Hay 1998), *Pocillopora* spp. appear to tolerate partial predation as the colony carbonate production (in terms of weight gain) and recovery were not negatively affected, despite corallivory causing ~ 15 bites nubbin⁻¹ or damage on up to 75 % of all branch tips in a colony. In contrast to massive corals, in which injuries are highly deleterious because their growth is relatively slow and recovery requires the deposition of new skeleton within the lesion (compensatory growth; sensu Henry and Hart 2005), pocilloporid corals can tolerate injuries because their healing process is not regenerative *per se*, but occurs through stimulation of the apical points of growth (branch tips) or reoriented growth (Lenihan and Edmunds 2010). Our results support the “reoriented growth hypothesis” as the morphology of pocilloporid nubbins exposed to predation changed significantly as shown by the redistribution of growth (Δ weight/ Δ length ratio).

The propensity of *Pocillopora* spp. to change their phenotype in response to environmental conditions (e.g., sediment, light, or depth; Veron 1995; Todd 2008) means that an important biological stressor such as corallivory is very likely to change morphometric proportions of pocilloporid colonies. Predator-induced phenotypic variation has been reported in several clonal-marine organisms (Gaulin et al. 1986; West 1997; Hill and Hill 2002). For instance, polyp withdrawal and changes in nematocyst density have been observed as responses to predation in hard corals (Gochfeld 2004; Rotjan and Dimond 2010). However, a recent review of morphological plasticity in scleractinian corals (Todd 2008) found no previous evidence of morphological skeletal change induced by fish predation in *Pocillopora* spp. The thick and short shape of nubbins that were exposed to corallivory (Fig. 7) results from the accumulation of carbonate through the thickening of the branches given their reduced linear growth (as the branch tips are constantly being cropped).

Despite intense feeding, puffer predation is not having a major effect on the carbonate production of individual

pocilloporid colonies (measured as weight gain) or on the carbonate budget of the entire pocilloporid reef. As in other pocilloporid reefs within the TEP (Glynn et al. 1972; Reyes-Bonilla and Calderon-Aguilera 1999), this study has shown that the destruction rate of *A. meleagris* ($0.87 \text{ kg m}^{-2} \text{ yr}^{-1}$) is not that high (<16 %) compared with the annual pocilloporid carbonate production at La Azufrada reef ($5.5 \text{ kg m}^{-2} \text{ yr}^{-1}$). However, it should be noted that our estimates of puffer impact and carbonate production rates were different from those reported in other studies, probably due to methodological differences. For instance, we estimated carbonate production rates using a colony density of 0.42 g cm^{-3} , however, if we had used data from Eakin (1996) our carbonate production would have been lower ($2.2 \text{ kg m}^{-2} \text{ yr}^{-1}$). In terms of the impact by *A. meleagris*, Glynn et al. (1972) and Reyes-Bonilla and Calderon-Aguilera (1999) used daily ingestion rates from puffers held in aquaria to estimate the daily mass removed from colonies ($16\text{--}20 \text{ g m}^{-2} \text{ d}^{-1}$). If we use such estimates (which may be an underestimate due to changes in the feeding behavior of puffers in aquaria; personal observation), the puffers’ destruction rate at La Azufrada would be eight times lower ($0.1 \text{ kg m}^{-2} \text{ yr}^{-1}$). In a scenario where the carbonate production is the lowest ($2.2 \text{ kg m}^{-2} \text{ yr}^{-1}$; using the colony density from Eakin 1996) and the puffers’ destruction is the highest (using all of our data), the annual pocilloporid production removed by *A. meleagris* predation would correspond approximately to 39.5 %. Such an increase in the estimate suggests that where corallivory is intense, a relatively high carbonate production appears to be essential for a significant reef accretion and persistence.

In conclusion, despite of the fact that high corallivory limits their linear growth, *Pocillopora* colonies can withstand partial predation. Colonies can easily recover from injuries and maintain their carbonate production rate through the thickening of branches. Under the ecological conditions in this study, pufferfish predation does not prevent reef accretion. Predation by *A. meleagris* may only pose a risk to the *Pocillopora* colonies or the reef framework when coincident with major coral mortality or the presence of acute environmental stressors (e.g., aerial exposure, ENSO events; Zapata and Vargas-Ángel 2003). At these times, predators will tend to concentrate on the remaining live coral colonies (causing increased bite density) and corals will be less physiologically capable of responding to the impact of tissue and skeletal damage. A noteworthy finding of this work was that corallivory causes phenotypic changes in hard corals and consequently can be the source of irregular morphologies reported in these organisms (Jayewardene and Birkeland 2006). In the case of Pocilloporid corals, which are already known for their morphological variability and phenotypic plasticity, this issue exacerbates the difficulties inherent in taxonomic

studies (Veron 1995; Pinzón et al. 2013; Schmidt-Roach et al. 2014). Determining the extent to which predation affects morphological variability will be an important step in understanding phenotypic plasticity in this group. A more complete understanding of the importance of coral-livory in pocilloporid reefs will involve assessing the effects of predation on sexual and asexual coral reproduction, including their relative contribution to population replenishment, and a complete carbonate budget of La Azufrada coral reef that includes other producers and bioeroders.

In contrast with other important processes such as herbivory, the role of corallivory on coral reefs has only recently received attention. While the importance of corallivory has perhaps been underestimated, it is now becoming apparent that corallivores can have diverse impacts on coral fitness, coral population and community structure, reef structure, and ecosystem function (Rotjan and Lewis 2008). Given the increasing levels of natural and anthropogenic disturbances on coral reefs, it is important to examine the full spectrum of impacts by corallivores on corals and coral reefs, and whether they contribute to decrease reef resilience. Our study provides one example from the TEP, where reefs are somewhat simple, low diversity systems, in which intense predation by a major corallivore does not seem to negatively affect reef resilience. Studies of corallivory in locations that differ in coral diversity and patterns of disturbance are required to fully understand the role of corallivory on coral reefs.

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References

- Adams J, Edwards AJ, Emberton H (1985) Sexual size dimorphism and assortative mating in the obligate coral commensal *Trapezia ferruginea* Latreille (Decapoda, Xanthidae). *Crustaceana* 48:188–194
- Bellwood DR (1995) Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Mar Biol* 121:419–429
- Bonaldo RM, Bellwood DR (2011) Parrotfish predation on massive *Porites* on the Great Barrier Reef. *Coral Reefs* 30:259–269
- Bonaldo RM, Welsh JQ, Bellwood DR (2012) Spatial and temporal variation in coral predation by parrotfishes on the GBR: evidence from an inshore reef. *Coral Reefs* 31:263–272
- Bruggemann JH, Van Kessel AM, Van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Mar Ecol Prog Ser* 134:59–71
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish Fish* 9:286–307
- Cole AJ, Lawton RJ, Pratchett MS, Wilson SK (2011) Chronic coral consumption by butterflyfishes. *Coral Reefs* 30:85–93
- Cox EF (1986) The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *J Exp Mar Biol Ecol* 101:161–174
- Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reefs* 15:109–119
- Edmunds PJ, Lenihan HS (2010) Effect of sub-lethal damage to juvenile colonies of massive *Porites* spp. under contrasting regimes of temperature and water flow. *Mar Biol* 157:887–897
- Galván-Villa CM, López-Urriarte E, Arreola-Robles JL (2011) Diversidad, estructura y variación temporal del ensamble de peces asociados al arrecife coralino de Playa Mora, Bahía de Tenacatita, México. *Hidrobiológica* 21:135–146
- Gaulin G, Dill L, Beaulieu J, Harris LG (1986) Predation induced changes in growth form in a nudibranch-hyroid association. *Veliger* 28:389–393
- Glynn PW (1985) Corallivore populations sizes and feeding effects following El Niño (1982–1983) associated coral mortality in Panama. *Proc 5th Int Coral Reef Symp* 4:183–188
- Glynn PW, Stewart RH, McCosker JE (1972) Pacific coral reefs of Panama: structure, distribution and predators. *Geol Rundsch* 61:483–519
- Glynn PW, Prah H, Guhl F (1982) Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on community structure and reef development. *Anales del Instituto de Investigaciones Marinas de Punta de Betín* 12:185–214
- Gochfeld DJ (2004) Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes. *Mar Ecol Prog Ser* 267:145–158
- Guzmán HM, López JD (1991) Diet of the corallivorous pufferfish *Arothron meleagris* (Pisces: Tetraodontidae) at Gorgona Island, Colombia. *Rev Biol Trop* 39:203–206
- Guzmán HM, Robertson DR (1989) Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Mar Ecol Prog Ser* 55:121–131
- Hall VR (2001) The response of *Acropora hyacinthus* and *Montipora tuberculosa* to three different types of colony damage: scraping injury, tissue mortality and breakage. *J Exp Mar Biol Ecol* 264:209–223
- Heiss GA (1995) Carbonate production by scleractinian corals at Aqaba, Gulf of Aqaba, Red Sea. *Facies* 33:19–34
- Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals: a review. *Int Rev Hydrobiol* 90:125–158
- Hill MS, Hill AL (2002) Morphological plasticity in the tropical sponge *Anthiosigmella varians*: responses to predators and wave energy. *Biol Bull* 202:86–95
- Hixon MA (1997) Effects of reef fishes on corals and algae. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman & Hall, New York, pp 230–248

- Jadwiszczak P (2009) Rndom Pro version 3.14. <http://pjadw.tripod.com/>
- Jayewardene D, Birkeland C (2006) Fish predation on Hawaiian corals. *Coral Reefs* 25:499–506
- Jayewardene D, Donahue MJ, Birkeland C (2009) Effects of frequent fish predation on corals in Hawaii. *Coral Reefs* 28:499–506
- Lenihan HS, Edmunds PJ (2010) Response of *Pocillopora verrucosa* to corallivory varies with environmental conditions. *Mar Ecol Prog Ser* 409:51–63
- Lenihan HS, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Influence of corallivory, competition, and habitat structure on coral community shifts. *Ecology* 92:1959–1971
- Littler MM, Taylor PR, Littler DS (1989) Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80:331–340
- Ludwig JA, Reynolds JF (1988) Statistical ecology: a primer of methods and computing. Wiley Press, New York
- Miller MW, Hay ME (1998) Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* 113:231–238
- Neudecker S (1979) Effects of grazing and browsing on the zonation of corals in Guam. *Ecology* 60:666–672
- NOAA (2013) Cold and Warm episodes by season: Changes to the Oceanic Niño Index (ONI). http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml
- Perry CT, Edinger EN, Kench PS, Mumby PJ, Murphy G, Steneck RS, Smithers SG (2012) Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* 31:853–868
- Pinzón JH, Sampayo E, Cox E, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013) Blind to morphology: genetics identifies several widespread ecological common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *J Biogeogr* 40:1595–1608
- Reyes-Bonilla H, Calderon-Aguilera LE (1999) Population density, distribution and consumption rates of three corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. *Mar Ecol* 20:347–357
- Reyes-Nivia MC, Garzón-Ferreira J, Rodríguez-Ramírez A (2004) Depredación de coral vivo por peces en el Parque Nacional Natural Tayrona, Caribe colombiano. *Rev Biol Trop* 52:883–895
- Roff G, Ledlie MH, Ortiz JC, Mumby PJ (2011) Spatial patterns of parrotfish corallivory in the Caribbean: the importance of coral taxa, density and size. *PLoS One* 6(12):e29133
- Rotjan RD, Lewis SM (2006) Parrotfish abundance and selective corallivory on a Belizean coral reef. *J Exp Mar Biol Ecol* 335:292–301
- Rotjan RD, Lewis SM (2008) Impact of coral predators on tropical reefs. *Mar Ecol Prog Ser* 367:73–91
- Rotjan RD, Dimond JL (2010) Discriminating causes from consequences of persistent parrotfish corallivory. *J Exp Mar Biol Ecol* 390:188–195
- Rotjan RD, Dimond JL, Thornhill DJ, Leichter JJ, Helmuth B, Kemp DW, Lewis SM (2006) Chronic parrotfish grazing impedes coral recovery after bleaching. *Coral Reefs* 25:361–368
- Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N (2014) With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zool J Linn Soc* 170:1–33
- Shantz AA, Stier AC, Idjadi JA (2011) Coral density and predation affect growth of a reef-building coral. *Coral Reefs* 30:363–367
- StatSoft Inc. (2007) STATISTICA (data analysis software system), version 8.0. www.statsoft.com
- Stimson JS, Kinzie RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J Exp Mar Biol Ecol* 153:63–74
- Todd PA (2008) Morphological plasticity in scleractinian corals. *Biol Rev* 83:315–337
- Veron JEN (1995) Corals in space & time: The biogeography & evolution of Scleractinia. Cornell University Press, New York
- Vytopil E, Willis BI (2001) Epifaunal community structure in *Acropora* spp. (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* 20:281–288
- Wellington GM (1982) Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecol Monogr* 52:224–241
- West JM (1997) Plasticity in the sclerites of a gorgonian coral: tests of water motion, light level, and damage cues. *Biol Bull* 192:279–289
- Zapata FA, Morales YA (1997) Spatial and temporal patterns of fish diversity in a coral reef at Gorgona Island, Colombia. *Proc 8th Int Coral Reef Symp* 1:1029–1034
- Zapata FA, Vargas-Ángel B (2003) Corals and coral reefs of the Pacific coast of Colombia. In: Cortés J (ed) *Latin America coral reefs*. Elsevier Science, Amsterdam, pp 419–447
- Zapata FA, Rodríguez-Ramírez A, Caro-Zambrano C, Garzón-Ferreira J (2010) Mid-term coral-algal dynamics and conservation status of a Gorgona Island (Tropical Eastern Pacific) coral reef. *Rev Biol Trop* 58:81–94

CAPÍTULO 4

Opposite effects of pufferfish corallivory on the carbonate budget of a pocilloporid reef.

Abstract

Corallivorous fishes can often fragment the branches of coral colonies from which they feed. There is, however, limited understanding of the survival and fate of coral fragments and their importance as a source of asexual recruitment for coral populations and reefs. In this study, we quantified *in situ* the fragmentation and generation of coral asexual recruits by the feeding activity of the pufferfish *Arothron meleagris*, and how this process can affect the carbonate budget of a pocilloporid reef of the Eastern Tropical Pacific (ETP). We found that 1.7% of pufferfish bites directly break pocilloporid branches, generating potentially viable fragments with a mean ($\pm$ SE) length of 3.2 ± 0.2 cm. Fragments that fall on the consolidated coral matrix, or on coral rubble have relatively high survival ($> 75\%$) and are likely to become asexual recruits. In contrast, fragments that fall on sand die within 12 months. Considering their abundance, we estimate that pufferfish can generate $54 \text{ fragments m}^{-2} \text{ yr}^{-1}$, of which ~ 21 are successful asexual recruits that grow and produce calcium carbonate at a rate of $0.9 \text{ kg m}^{-2} \text{ yr}^{-1}$. At the same time, pufferfish predation removes calcium carbonate from live coral at a rate of $0.9 \text{ kg m}^{-2} \text{ yr}^{-1}$, which in addition to the death of fragments produced ($0.2 \text{ kg m}^{-2} \text{ yr}^{-1}$) results in a total rate of carbonate destruction by the pufferfish population of $1.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ or $\sim 20 \%$ of the annual carbonate produced by pocilloporid corals. Therefore, the successful generation of asexual recruits by fragmentation nearly compensates for the carbonate removal exerted by the pufferfish on the reef. We conclude that even though the pufferfish *A. meleagris* is a major bioeroder, it is also an important agent of asexual reproduction through colony fragmentation for pocilloporid corals in the ETP. These findings underscore the importance of fish corallivory, the role that fishes can play in the asexual reproduction of corals, and the dual impact of fish corallivores on coral reefs.

Keywords: Coral asexual reproduction by fragmentation, Recruitment, Tropical Eastern Pacific, *Pocillopora*, *Arothron*.

Resumen

Los peces coralívoros a menudo pueden fragmentar las ramas de las colonias de coral de las que se alimentan. Sin embargo, hay una comprensión limitada de la supervivencia y el destino de estos fragmentos de coral y su importancia, como fuente de reclutamiento asexual para las poblaciones coralinas y arrecifes. En este estudio se cuantificó *in situ* la fragmentación y generación de reclutas asexuales de coral por la actividad alimentaria del pez globo *Arothron meleagris* y cómo este proceso puede afectar el presupuesto de carbonato de un arrecife pocilopórido del Pacífico Tropical Oriental (PTO). Se encontró que el 1.7% de las mordeduras de estos peces rompieron directamente las ramas pocilopóridas, generando fragmentos potencialmente viables con una longitud media ($\pm$ SE) de 3.2 ± 0.2 cm. Los fragmentos que caen sobre la matriz coralina consolidada o sobre escombros de coral, tuvieron una supervivencia relativamente alta ($> 75\%$) y probablemente se convertirán en reclutas asexuales. Por el contrario, los fragmentos que caen sobre la arena murieron antes de 12 meses. Teniendo en cuenta su abundancia, estimamos que *A. meleagris* puede generar 54 fragmentos $\text{m}^{-2} \text{año}^{-1}$, de los cuales 21 fueron reclutas asexuales exitosos que crecieron produciendo carbonato de calcio a una tasa de $0.9 \text{ kg m}^{-2} \text{año}^{-1}$. Al mismo tiempo, la depredación de *A. meleagris* eliminó carbonato de calcio de los corales vivos a una tasa de $0.9 \text{ kg m}^{-2} \text{año}^{-1}$, lo que, además de la muerte de los fragmentos producidos ($0.2 \text{ kg m}^{-2} \text{año}^{-1}$) da como resultado una tasa total de destrucción de carbonatos por la población de *A. meleagris* de $1.1 \text{ kg m}^{-2} \text{año}^{-1}$, aproximadamente un 20 % del carbonato anual producido por los corales pocilopóridos. Por lo tanto, la generación exitosa de reclutas asexuales por fragmentación compensa la eliminación de carbonato ejercida por el pez en el arrecife. Concluimos que aunque *A. meleagris* es un bio-erosionador importante, también lo es como agente promotor de la reproducción asexual por fragmentación de colonias de corales pocilopóridos en el PTO. Estos hallazgos subrayan la importancia de la coralivoría por peces, el papel que estos peces pueden desempeñar en la reproducción asexual de los corales, y su impacto dual sobre los arrecifes de coral.

INTRODUCTION

Predation is the total or partial consumption of one organism by another one (Pianka 2000). In coral reefs, the predation of corals (*i.e.* corallivory) is an interaction usually limited to the partial

consumption of colonies. Fish corallivores can cause two main types of damage to corals; (a) they exclusively remove soft coral tissues, or (b) they remove both soft tissues and skeletal material (Hiatt and Strasburg 1960; Rotjan and Lewis 2008). For example, butterflyfishes pluck individual coral polyps from colonies while pufferfishes break and ingest pieces of coral branches (Alvarado *et al.* 2017; Enochs and Glynn 2017). Depending on the type, magnitude and frequency of the damage caused, corallivory can affect coral populations to the extent of destroying entire coral communities, as in the case of crown-of-thorns starfish (*Acanthaster planci*) outbreaks (Colgan 1987; Moran *et al.* 1988; Bruno and Selig 2007). In addition to the direct removal of coral biomass, corallivory can indirectly impact corals by facilitating the colonization of algae or the spread of diseases (Bonaldo *et al.* 2011, Nicolet *et al.* 2013, Katz *et al.* 2014). Therefore, corallivory is usually considered a biological stressor and a detrimental process, which can negatively affect the health and fitness of coral colonies, and the resilience and calcium carbonate budget of entire reefs (Knowlton *et al.* 1990; Cole *et al.* 2008; Rotjan and Lewis 2008; Alvarado *et al.* 2017; Enochs and Glynn 2017).

In some circumstances, fish corallivory and the fragmentation of coral derived from fish predatory activity can have positive effects. In the Eastern Tropical Pacific (ETP) reef fishes are believed to play key roles in the asexual reproduction of corals (Glynn *et al.* 1972; Glynn *et al.* 1982; Guzmán and López 1989; Guzmán and Cortés 1989; Alvarado *et al.* 2017; Enochs and Glynn 2017). Pufferfishes (Tetraodontidae), triggerfishes (Balistidae), and filefishes (Monacanthidae), commonly break coral colonies while directly consuming coral or while hunting for invertebrates dwelling within colonies. Coral fragments that survive are expected to be viable asexual recruits. For example, the triggerfish *Pseudobalistes naufragium* is believed to favor the asexual reproduction of the coral *Porites evermanni* by generating many coral fragments (*e.g.* while searching for endolithic bivalves) that could potentially survive and establish on the reef (Guzmán 1988; Guzmán and Cortés 1989; Boulay *et al.* 2013).

The pocilloporid coral reefs of the ETP are ideal for examining the role of fish corallivory in coral asexual reproduction. First, corallivorous pufferfish reach extremely high abundances here and are known to voraciously forage and fragment pocilloporid colonies. Second, the pocilloporid colonies preyed upon by pufferfish are not negatively affected, but instead thrive

forming large dense mats (Palacios *et al.* 2014). Finally, the asexual reproduction of pocilloporid corals is considered their main source of replenishment within the ETP, as many studies attempting to estimate their sexual recruitment have reported low settlement rates or total absence of settling larvae (Birkeland 1977; Wellington 1982; Richmond 1985; Guzmán and Cortés 1989; Medina-Rosas *et al.* 2005; López-Pérez *et al.* 2007; Lozano-Cortés and Zapata 2014). In contrast, it is often believed that when coral fragments land on suitable substrate they survive and become asexual recruits that develop into new colonies (Guzmán 1988; Enochs and Glynn 2017). Despite a growing interest on corallivory, there are only few detailed descriptions and quantitative studies examining the ecological consequences of coral fragmentation by corallivorous fish (Rotjan and Lewis 2008).

The importance of asexual reproduction in the life cycle of pocilloporid corals in the ETP, and particularly at Gorgona Island, highlights the need for understanding the role of natural agents of coral fragmentation. Here, we examined fragmentation by the pufferfish *Arothron meleagris* on pocilloporid colonies, and to accomplish this we estimated *in situ* the fragmentation rates caused by pufferfish, along with the yearly survival of pocilloporid fragments on different natural substrates and explored how the pufferfish population impacts the carbonate budget of the reef. These results extends a previous study by the authors (Palacios *et al.* 2014), where the rate of coral consumption by the pufferfish population was estimated and compared to the rate of carbonate production of the pocilloporid standing crop.

METHODS

Study Site

This study was conducted at La Azufrada reef (Fig. 1), located at Gorgona Island (2°58'27''N, 78°11'13''W), ~ 30 km off the Colombian coast in the Eastern Tropical Pacific. La Azufrada is a fringing coral reef that extends for ~ 9.4 ha in relatively shallow waters (4-10 m depth at high tide). Like most other coral reefs in the region, it is built and dominated by the branching corals of the genus *Pocillopora* (Glynn 1976) whose species often form tight mono-specific stands. Other coral genera such as *Pavona*, *Porites*, *Gardineroseris* and *Psammocora* also occur on the

reef, but always at lower densities. La Azufrada exhibits three distinguishable reef zones (Fig. 1), the back reef, which comprises ~14.3 % of the total area of the reef, is composed of patches and loose colonies of pocilloporids interspersed among small aggregations of the sub-massive coral *Psammocora stellata*. The reef flat, which comprises ~ 68.2% of the reef, is mostly a consolidated coral framework where pocilloporid colonies occur either individually or in large patches. Every few years, extreme low tides sub-aerially expose the shallowest portions of the reef flat killing corals and forming algal patches of varying size. The fore reef, comprises ~ 17.5 % of the reef, and is formed almost exclusively by a continuous, dense pocilloporid mat that extends seaward into a moderate slope bordered by scattered colonies of *Pocillopora*, *Psammocora* and massive colonies of *Pavona* and *Gardineroseris* over sand and coral rubble. Detailed descriptions of La Azufrada reef can be found in Glynn *et al.* (1982), Zapata (2001), and Zapata and Vargas-Ángel (2003). During the time of the study (April 2012 to April 2014) oceanographic conditions in the region corresponded to ENSO neutral/weak El Niño conditions (NOAA, 2014).

Study species

The guineafowl pufferfish *Arothron meleagris* is the main corallivorous fish in the ETP (Glynn *et al.* 1972; Palacios *et al.* 2014). At La Azufrada reef it reaches densities of up to ~170 ind. ha⁻¹, the highest population density reported within the region (Palacios *et al.* 2014). *Arothron meleagris* is a facultative corallivore known to feed mostly on hard corals of the genera *Pocillopora* and *Psammocora*, and occasionally on other organisms such as echinoderms, sponges and coralline algae (Glynn *et al.* 1982; Guzmán and Robertson 1989; Guzmán and López 1991; Palacios *et al.* 2014). At La Azufrada, *A. meleagris* targets predominantly pocilloporid colonies, which represent ~ 90 % of the live coral cover (Guzmán and López 1991; Palacios *et al.* 2014). Given that this reef is relatively free of pollution and closed to most human activities (*i.e.* only small research groups and park managers visit the reef sporadically for short periods of time), the pufferfish population is virtually undisturbed. Preliminary observations of *A. meleagris* at La Azufrada showed that they occur alone or in groups of up to ~15 individuals, are active during daylight hours from ~ 6:00 to 18:00 h, and can be easily approached up to a distance of ~1.5 m by cautious snorkelers or divers without altering their foraging behavior.

Fragmentation of pocilloporid colonies by pufferfish

Coral fragmentation rate

Pufferfish individuals between 15 and 30 cm total length (TL) were haphazardly chosen and observed by snorkelers (CGM and MMP). After a 2-min habituation period, snorkelers recorded (a) the number of bites on pocilloporid corals and (b) the number of conspicuous fragments (> 1 cm) generated in a 10-min lapse. A total of 120 individuals were observed; observations were evenly distributed throughout the three reef zones ($N = 40$ per zone) and time of day ($N = 60$ from 6:00 to 12:00; $N = 60$ from 12:01 to 18:00 h). From the behavioral observation data, we calculated (i) the proportion of the population that was actively engaged in feeding activities at a given time during daylight hours (see correction factor in Palacios *et al.* 2014) and (ii) the rate of coral fragmentation per pufferfish (fragments fish⁻¹ min⁻¹) using the number of pocilloporid fragments generated during 1200 minutes of direct field observations of the pufferfish feeding behavior. We considered each fragment as an asexually-produced coral recruit as each had the potential to become a fully grown, independent adult colony.

Size of coral fragments

Pocilloporid fragments generated by pufferfish were collected from the reef immediately after being broken off from colonies. During several visits to the reef we searched for pufferfish groups, selected pufferfish that were actively feeding and followed them to recover the fragments they produced. All fragments collected ($N = 100$) were transported to the laboratory where they were measured along the growth axis (± 0.1 cm), wet weighed (± 0.01 g) and examined for pufferfish bite marks. We used this information to calculate the size frequency distribution of the fragments and their length–weight relationship. While we strived to collect all fragments produced, in practice the fragments collected were ≥ 1.0 cm, even though smaller fragments are produced. Therefore, the rate of asexual recruit production by fragmentation is likely to be an underestimate.

Survival of coral fragments

We conducted a field experiment to estimate the survival and growth of recently generated pocilloporid fragments across three natural substrates of the reef flat: (a) sand, (b) loose coral rubble, and (c) consolidated carbonate matrix. Although fragments could also land on live coral, preliminary observations indicated that these fragments survived and reattached to the parent colony; hence we did not consider live coral as a substrate in this experiment. Fragments were generated by gently hammering off branches of *Pocillopora damicornis* colonies. Coral fragments similar to those naturally generated by pufferfish (*i.e.*, single branch and approximately ~ 3 cm long; see results) were collected, measured along the growth axis (± 0.1 cm), and attached with nylon string (~1 m long) to metal rods at each of the assigned substrates (N = 27 fragments per substrate). Strings were used to prevent the loss of fragments while allowing some movement by waves and currents. All coral fragments were carefully handled underwater *in situ* to minimize manipulation effects on survival.

Pocilloporid fragments were examined one, four, six and twelve months after their deployment. At these times, we visually estimated partial mortality (surface with loss of soft tissue) and searched for signs of bleaching in each fragment. Fragments with > 0 % of live tissue were classified as alive, while those with 0 % were considered dead. Survival trajectories of fragments were analyzed with a Kaplan-Meier analysis (Kaplan and Meier 1958). The linear growth rate of the fragments in this experiment was calculated as the difference in linear extension between final and initial length. The growth rate of fragments on coral rubble and carbonate matrix was compared with a one-way analysis of variance (ANOVA) after testing the assumptions of normality and homoscedasticity.

Generation of coral asexual recruits

To explore how the reef's carbonate budget is affected by pufferfish corallivory, we estimated the rate of generation of asexual recruits as a consequence of coral fragmentation by the pufferfish population, as follows:

Generation of asexual recruits = Coral fragmentation rate (1) x Probability of fragment survival
(2)

1. The rate of coral fragmentation by the pufferfish population (fragments m⁻² yr⁻¹) was calculated as:

$$\begin{aligned} \text{Coral fragmentation rate} &= \text{Pufferfish density (fish m}^{-2}\text{)} \\ &\quad \times \text{Proportion of pufferfish actively feeding at a given time} \\ &\quad \times \text{Fragmentation per pufferfish (fragments fish}^{-1} \text{ min}^{-1}\text{)} \end{aligned}$$

Pufferfish density was visually estimated along 50 x 5 m belt-transects (N = 150) distributed evenly among the reef zones (N= 50 per zone) and activity hours (N= 75 from 6:00 to 12:00; N= 75 from 12:01 to 18:00) during April, June, August, October and December 2013 (N= 30 per date). The proportion of active pufferfish was obtained from Palacios *et al.* (2014), and the fragmentation per pufferfish from results presented here.

2. The survival of pocilloporid fragments depended on the substrate on which they fall:
 - a) Fragments that fall on live coral survive and do not become asexual recruits because they reattach to live coral (very often to the parent colony), and do not generate a new colony or produce carbonate independently afterwards.
 - b) Fragments that fall outside live coral and die were considered as coral destroyed indirectly by pufferfish corallivory.
 - c) Fragments that fall outside live coral and survive become asexual recruits; they can produce carbonate independently from the parental colonies and develop into new colonies. These fragments enter the reef as asexual recruits originating clone colonies.

We assumed that fragments landing on live coral had a 100% survival probability, and used the results of our survival experiment for fragments landing on sand, coral rubble and carbonate matrix; also that the probability of a fragment falling in a specific substrate was proportional to the percentage of cover by each substrate on the reef.

Substrate cover was estimated using 1 m² quadrats divided into 100 sub-quadrats of 10 x 10 cm. Quadrats were haphazardly placed 30 times in each reef zone, and percentages of cover were calculated as the number of sub-quadrats in a quadrat occupied by each substrate (1 sub-quadrat = 1 % of cover). Because the coral rubble and consolidated carbonate matrix were substrates commonly mixed on the reef, their data were pooled into a single category named “coral rubble/matrix”.

Effects on the reef carbonate budget

To analyze the total impact of pufferfish corallivory on the carbonate budget of La Azufrada reef, we used the multiple effects of the interaction to calculate net coral production and total carbonate destruction. In our model, we split the process into four steps:

- 1) Coral affected by pufferfish = Coral fragmentation (a) + Coral consumption (b)
- 2) Coral after corallivory = Gross carbonate prod. (c) – Carbonate affected by puffers (1)
- 3) Net carbonate production = Growth of recruits (d) + Carbonate after corallivory (2)
- 4) Total coral destruction = Mortality of fragments (e) + Coral consumption (b)

In step 1, the coral fragmentation (a) was estimated in terms of coral weight (kg m⁻² yr⁻¹) by multiplying the rate of fragmentation by the average weight of pocilloporid fragments generated by pufferfish (see “size of coral fragments” section). Coral consumption (b) refers to coral ingested by the pufferfish population, and was calculated in Palacios *et al.* (2014) as follows:

$$\begin{aligned} \text{Coral consumption (b)} &= \text{Population density (fish ha}^{-1}\text{)} \\ &\quad \times \text{Proportion of pufferfish actively feeding at a given time (correction} \\ &\quad \text{factor)} \\ &\quad \times \text{Consumption rate per pufferfish (g d}^{-1}\text{)} \end{aligned}$$

The consumption rate per pufferfish was obtained by multiplying the pufferfish feeding-rate (bites min⁻¹) by the weight of coral removed per bite (g bite⁻¹) from Palacios *et al.* (2014).

In Step 2, gross carbonate production (c) refers to the annual production of the pocilloporid standing crop, and was calculated as:

$$\begin{aligned} \text{Gross carbonate production (c)} &= \text{Growth rate of the standing crop (cm yr}^{-1}\text{)} \\ &\quad \times \text{Colony density (g cm}^{-3}\text{)} \\ &\quad \times \text{Live coral cover (\%)} \end{aligned}$$

The growth rate of the standing crop and colony density were estimated previously by Palacios *et al.* (2014). Colony density was calculated as average weight / volume of water displaced by colonies wrapped in plastic film, to include the empty space between branches.

In step 3, the growth of recruits (d) refers to an estimation of the weight gain of surviving pocilloporid fragments after one year of growth. The weight of a fragment after one year was calculated with the Length-Weight relationship for an average fragment after adding the annual growth to its length. Finally, in step 4 the mortality rate of fragments (e) was calculated as the probability of fragments landing on sand, coral rubble/matrix times the mortality associated to each substrate based on the survival rate of fragments on each substrate.

RESULTS

Fragmentation of pocilloporid colonies by pufferfish Coral fragmentation rate

Field observations of the pufferfish feeding activity (Fig. 2) evidenced that 1.7% of the pufferfish bites on pocilloporids resulted in branches breaking off from colonies. The rate of fragmentation caused per fish was 0.02 ± 0.004 fragments fish⁻¹ min⁻¹ (mean $\pm$ SE); sixty percent of the 150 pufferfish we followed were actively feeding, so we applied a correction factor of 0.6 to the fragmentation rate per fish in further calculations. Therefore, a single pufferfish of average size (20.5 ± 0.35 cm TL) feeding on corals during an entire day would generate 8.6 fragments.

Size of coral fragments

Pocilloporid fragments generated by pufferfish were on average 3.2 ± 0.2 cm long, ranging between 1 and 9 cm; and had an average weight of 26.6 ± 1.4 g, ranging between 6.4 and 80.4 g (Fig. 3). Fragment weight was significantly related with fragment length ($R^2 = 0.88$, $p < 0.05$) and the relationship was described by the linear function: $\text{Weight} = -0.71 + 8.52 \text{ Length}$ (Fig. 3C). Most of the pocilloporid fragments generated during pufferfish feeding consisted of a single axis (78%), while 22% were bifurcated or presented more ramifications. We found 1.5 ± 0.07 bite-scars per fragment, and 63% of the fragments had only one bite-scar, while 37 % had two or three major bite-scars.

In addition to conspicuous fragments (> 1 cm), we observed smaller coral pieces generated by pufferfish feeding (Fig. 2). These coral pieces had some living tissue and resembled coral crumbs left by the biting process; they were barely attached by soft tissue to the edges of the bitten branch tip and separated easily by currents and wave action. Due to their small size (0.1 - 0.5 cm long) it was not possible to properly sample or manipulate these fragments; hence, they are not considered hereafter.

Survival of coral fragments

Pocilloporid fragments had an average survival of 54.3% after twelve months. However, the survival trajectories of the fragments significantly differed according to the substrate treatments ($\chi^2 = 55.7$ $df = 2$; $p < 0.01$). Consolidated carbonate matrix and loose coral rubble were suitable substrates on which coral fragments survived, while sand proved to be a lethal substrate (Fig. 4A). Mortality of fragments on sand was higher during the first month when 55% of the fragments died, reaching 92 % mortality by the sixth month and full mortality by the end of the study. In contrast, all fragments on the carbonate matrix and coral rubble survived during the first month, and most deaths occurred during the last six months. After twelve months, the survival of fragments on these two substrate treatments was not significantly different ($Z = -0.6$; $p > 0.1$), with 85.2 % fragment survival recorded on the carbonate matrix and 77.8 % on coral rubble.

The average linear growth rate of the surviving fragments on the different substrates was $2.1 \pm 0.1 \text{ cm yr}^{-1}$ (mean $\pm$ SE) (Fig. 4B), with no significant differences between fragments growing on the carbonate matrix and on coral rubble (ANOVA, $F_{1,42} = 0.047$, $p > 0.1$). Partial mortality was observed on 52.3 % and 17.4 % of the surviving fragments on coral rubble and carbonate matrix, respectively; by the twelfth month, signs of partial mortality persisted on 14.2 % of surviving fragments on coral rubble and on 8.7 % of surviving fragments on the carbonate matrix. Signs of partial bleaching were observed on 19% and 13% of surviving fragments on coral rubble and the carbonate matrix, respectively; signs of bleaching disappeared by the sixth month.

Generation of coral asexual recruits

The pufferfish population generated 54 pocilloporid fragments $\text{m}^{-2} \text{ year}^{-1}$ at La Azufrada reef. This fragmentation rate was higher on the fore reef and reef flat than on the back reef (Table 1). According to the percentages of substrate cover per reef zone (Table 2), the rate of fragmented coral landing onto suitable substrate (*i.e.* coral rubble/matrix) and thus likely to become asexual recruits on the reef flat was ~ 3.5 times higher than on the fore reef, and ~ 18 times higher than on the back reef. With a 100% probability of survival for fragments falling on live coral, 0 % on sand and 81.5 % on coral rubble/matrix, we estimated that the survival of fragments was highest on the fore reef, followed by the reef flat and lowest on the back reef. Combining the probabilities of landing and surviving on each substrate, the recruitment rate of pocilloporids asexually generated by pufferfish was 21 recruits $\text{m}^{-2} \text{ yr}^{-1}$ for the whole reef; this recruitment rate was, however, highest on the reef flat, followed by the back reef, and lowest on the fore reef (Table 1).

Effects on the reef carbonate budget

Figure 5 illustrates the effects of pufferfish corallivory on pocilloporids and how they affect the carbonate budget of La Azufrada reef. Rates of carbonate production or removal ($\text{kg m}^{-2} \text{ yr}^{-1}$) involved in the interaction between pufferfish and pocilloporids and their effects are presented in Table 3.

The total annual gross rate of carbonate produced by pocilloporid coral growth was $5.6 \text{ kg m}^{-2} \text{ yr}^{-1}$ (Palacios *et al.* 2014). Of this, $\sim 0.9 \text{ kg m}^{-2} \text{ yr}^{-1}$, or 16 % of the gross annual carbonate production was consumed by the pufferfish population. While feeding, pufferfish fragment coral at a rate of $1.4 \text{ kg m}^{-2} \text{ yr}^{-1}$, equivalent to 25.8 % of the carbonate produced by pocilloporid stands. Adding the rate of consumption to the rate of fragmentation by pufferfish, we obtained that $2.3 \text{ kg m}^{-2} \text{ yr}^{-1}$ of coral was affected by the pufferfish population, which represents 41.8 % of the annual coral production (step 1).

The weight of surviving fragments that fell on all substrates during a year was $1.2 \text{ kg m}^{-2} \text{ yr}^{-1}$. After reintegrating the weight of all fragments that fell on live coral, we obtained that the coral produced in one year that remained live on the reef after corallivory was $3.9 \text{ kg m}^{-2} \text{ yr}^{-1}$, equivalent to 71.2 % of the annual gross carbonate production by pocilloporids (step 2).

The fragments that fell on suitable substrates and survived to become asexual recruits, increased their average length after one year from 3.2 to 5.3 cm, and their weight from 26.6 to 44.0 g. Therefore, we calculated that the weight of surviving asexual recruits after one year of growth was $0.9 \text{ kg m}^{-2} \text{ yr}^{-1}$, and after reintegrating it to the coral remaining after corallivory ($3.9 \text{ kg m}^{-2} \text{ yr}^{-1}$), the net rate of coral production for the whole reef was $4.8 \text{ kg m}^{-2} \text{ yr}^{-1}$, equivalent to 87.2 % of coral produced by the pocilloporid stands during one year (step 3); leading to a first estimation of net carbonates loss equal to 12.8 %. However, the rate of fragment mortality was $0.2 \text{ kg m}^{-2} \text{ yr}^{-1}$ that added to the rate of coral consumed by the pufferfish ($0.9 \text{ kg m}^{-2} \text{ yr}^{-1}$), results in a second estimation of total carbonate destruction of $1.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ (step 4); an amount that represents approximately 19.1 % of the coral production instead of 12.8 % (a difference of + 6.3 % with the first estimation).

DISCUSSION

This study provides quantitative evidence that the population of the corallivorous pufferfish *Arothron meleagris* is an effective promoter of coral asexual reproduction by fragmentation in an Eastern Pacific pocilloporid reef. Also, this study describes the process of coral fragmentation

involved in the interaction between pufferfish and pocilloporids. Finally, our study shows how the guinea-fowl pufferfish has opposite effects on the reef carbonate budget by removing coral carbonate material while simultaneously generating asexual recruits that contribute to increase coral cover and ultimately compensate for the deleterious impact of corallivory.

Several authors refer to fish predation as one of the causes of natural coral fragmentation (Highsmith *et al.* 1980; Knowlton *et al.* 1981; Richmond 1985, 1987a, 1987b). However, most studies have focused on physical disturbances like storms, hurricanes or rough weather as the main causes of fragmentation (Lirman and Fong 1997; Lirman 2000; Lirman *et al.* 2001; Álvarez-Filip and Gil 2006; Aranzeta-Garza 2012). Hence, the process of coral fragmentation has been widely presented as caused by stochastic events that usually cause extensive damage to coral reef systems (Adjeroud and Tsuchiya 1999; Smith and Hughes 1999; Brandt *et al.* 2013; Roth *et al.* 2013). In contrast, our observations on the feeding behavior of *A. meleagris* showed that predation by a single pufferfish can generate an important number of pocilloporid fragments. The rate of fragmentation of pocilloporids by a single pufferfish may seem small in comparison to fragmentation of *Porites evermanni* by the triggerfish *Pseudobalistes naufragium*, which produces ~75 fragments in a few minutes (Guzman 1988; Boulay *et al.* 2013). But when we consider the constant feeding and size of the entire pufferfish population on the reef, the result is a high rate of carbonate removal and constant fragmentation of pocilloporid corals. Yet, we fail to see major reef destruction at the ecosystem level.

Coral fragmentation might be an effective mode of asexual reproduction in pocilloporids, only if the survival of fragments is high (Highsmith 1982; Williams *et al.* 2008). Our results support this expectation, and suggest that many of the coral fragments resulting from pufferfish predation are likely to develop into new colonies. There is a high probability of fragments landing on suitable substrates, and their survival on these substrates is high (81.5 %). This result contrasts with studies reporting high (90 – 100%) fragment mortality (Knowlton *et al.* 1981; Bak and Crieens 1981; Cox 1992), and with results of studies reporting positive size-dependent survival of coral fragments (Loya 1976; Highsmith *et al.* 1980; Rogers *et al.* 1982; Heyward and Collins 1985; Wallace 1985; Liddle and Kay 1987; Lasker 1990; Smith and Hughes 1999). Nonetheless, fragment survival is substrate dependent and fragments on sand have the highest

mortality, as it has been previously reported for *Acropora palmata* in the Caribbean (Lirman 2000). In our study, remaining live tissue of fragments placed on sand was observed only on unburied portions of the fragments; when fully covered by sediment the fragments always presented full mortality. This suggests that fragments on sand died by a mix of asphyxiation and abrasion, something that could be avoided by larger fragments (Tunncliffe 1981; Smith and Hughes 1999). Partial mortality and signs of bleaching on fragments placed on coral rubble and the carbonate matrix were usually located on the side of fragments in direct contact with the substrate, suggesting that the affections were in this case due to lack of light or abrasion (including some manipulation during collection and deployment).

Pocilloporid colonies are considered resistant to some physical damage mainly by their growth form, in the sense that a tight branching morphology permits access only to the branch tips while limiting access to inner structural sections of colonies (Wellington 1982). Jayewardene and Birkeland (2009) reported effective and complete regeneration of coral tissues after fish predation on pocilloporids in Hawaii. Likewise, Palacios *et al.* (2014) found at Gorgona Island that pocilloporids tolerate simulated bite injuries on up to 75% of colony branch tips without affecting growth rates, and with no other negative effects like algae colonization or signs of bleaching on experimental injured colonies. The latter results question whether the overall impact of the pufferfish population is detrimental for La Azufrada reef ecosystem, since this interaction might have opposing short and long-term consequences.

Bioerosion is an antagonistic force that interplaying with accretion determines the carbonates production-destruction balance of coral reefs (Alvarado *et al.* 2017); when bioerosion is sustained larger than accretion, reefs tend to shrink and dramatic changes in biodiversity are expected, along with ecological phase shifts (Done 1992; Hatcher *et al.* 1989). Comparisons of carbonate destruction rates by pufferfish in this study, against known destruction rates by other organisms (between 0.05 and 10 kg m⁻² y⁻¹) suggest that pufferfish in Gorgona are bioeroders with similar impact to other fish species in Gorgona (Cantera *et al.* 2001), a similar to lower impact than echinoderms, and due to larger densities, exert higher destruction rates than the same species in other localities in the ETP, ranging from 0.1 to 0.3 kg m⁻² y⁻¹ (Toro-Farmer *et al.* 2004; Reyes-Bonilla and Calderón-Aguilera 1999; Glynn 1988; Eakin 1992, 1996, 2001). Although some

analyses in this study involved wide assumptions and simplified systems, like the carbonate production estimations based only on pocilloporids, the substrate assignments of the survival model, and the fragment re-attachment to parental colonies, amongst others; the disparity of the carbonate destruction between the two estimations (6.3 %), should coincide with carbonates gained by the growth of clonal recruits, representing a quantifiable positive effect of pufferfish corallivory in the carbonate budget. If fragmentation by pufferfish is indeed traceable on simplified models of bioerosion and carbonate dynamics, as evidenced in our results, the general importance of fish corallivory and coral fragmentation by fish, is at least highlighted among the processes responsible for the ecosystem resilience.

Many studies have examined the role of predation by fishes in determining the structure of benthic communities, since fishes can affect the local distribution and abundance of benthic organisms (Neudecker 1979; Wellington 1982; Cox 1986; Littler *et al.* 1989; Grottoli-Everett and Wellington 1997). It has been proposed that pufferfish boost reef coral cover at different temporal scales by promoting faster asexual propagation and dominance by certain coral species, actively selecting those tolerant to predation, presumably of high nutritive value and fast-growing species, like pocilloporid corals (Enochs and Glynn 2017). All those features could be potentially beneficial in the short term after perturbations, a chance to overcome negative balances in carbonate budgets. However, the genetic diversity within the local pocilloporid population could be impoverished by propagation of clonal colonies, which in turn could have contrasting consequences: it might reduce the genetic pool to few genetic lineages tolerant to environmental disturbances, while at the same time diminish the population capability to withstand diseases. Additionally, partially fragmented colonies of *Pocillopora damicornis* produce significantly less planula larvae and delay the timing of larval release, according to studies in Hawaii by Zakai *et al.* (2000). If fragmentation of pocilloporids in Hawaii has a similar effect in the ETP, this might help to understand the low levels of sexual recruitment historically recorded at La Azufrada reef and across the region. Additionally, constant pocilloporid fragmentation by a large pufferfish population could be one of the driving forces promoting dominance by certain thin-branched pocilloporid colonies at La Azufrada reef and other reefs in the region.

Pollination and seed dispersal assisted by predators are well-known mutualistic interactions in terrestrial plants (Schupp *et al.* 2010). A main aspect of this type of interaction is that even

though the initial impact of the predator on the prey is negative, the ultimate net impact is positive, hence the interaction is mutualistic. Because water currents serve as effective means of dispersal for larvae (Szmant and Meadows 2006; Vermeij *et al.* 2010), assisted dispersal in marine organisms seems unnecessary. However, coral predators that fragment colonies indeed have the potential to enhance asexual reproduction of corals. Our results on the impact of pufferfish at La Azufrada, and those of related studies on other reefs in the ETP as well as studies on triggerfish (Guzmán 1988; Enochs and Glynn 2017; Boulay *et al.* 2013), indicate that different fish species can play a similar role to ichthyocory in riparian and flooded forests (Pollux 2011; Parolin *et al.* 2013). Coral fragmentation by fish and seed dispersal in plants by animals, are rather different processes that nonetheless share a common consequence: the reproduction of structural sessile organisms. In plants, specialized adaptive structures derived by natural selection like fruits, attract predators leading to dispersal and settlement of sexual propagules (Howe and Smallwood 1982; Traveset *et al.* 2014). In contrast, corals have neither specialized structures nor conspicuous adaptations for assisted reproduction or dispersal. Whether certain colony features that facilitate fragmentation are an adaptation or not (*i.e.* resulting from the action of natural selection) is unclear, fragmentation remains an important trait in the life history of many coral species. Also, this interaction is difficult to be considered as mutualistic in a strict sense, although pocilloporids represent the main component of the pufferfish diet, and these corals in turn are subject to the constant generation of new recruits by the pufferfish feeding activity. Many new questions arise for future research, for example: what would be the asexual reproduction by pocilloporid fragmentation, in the absence of coral-eating fish such as *Arothron* or the action of *Pseudobalistes*? In other words, what is the total fragmentation and what part of it fish causes?

Coral fragmentation, understood as the generation of asexual recruits, relies on the interaction of corals with abiotic or biotic factors. In the case of the interaction between pufferfish and pocilloporid corals, the fish plays an important role providing the necessary mechanical action to separate coral pieces off the parental colonies. In systems with limited recruitment of planulae and that depend mostly on asexual reproduction, like La Azufrada and most reefs in the ETP, pufferfish predation plays an important role assisting coral reproduction through coral fragmentation. Pufferfish at Gorgona Island are coral predators that remove a significant amount of calcium carbonate from La Azufrada reef, but at the same time constantly

produce a large number of fragments that increase coral asexual reproduction, so that in the end the negative impact of predation on corals is compensated by the generation of new colonies and the increase of coral cover.

REFERENCES

- Adjeroud M and Tsuchiya M. 1999. Genetic variation and clonal structure in the scleractinian coral *Pocillopora damicornis* in the Ryukyu Archipelago, southern Japan. *Marine Biology* 134(4): 753-759.
- Alvarado JJ, Grassian B, Cantera-Kintz JR, Carballo J, Londoño-Cruz E. 2017. Coral Reef Bioerosion in the Eastern Tropical Pacific. In: Glynn PW, Manzello DP and Enochs IC (Ed). *Coral Reefs of the Eastern Tropical Pacific: Persistence and loss in a dynamic environment*. Coral Reefs of the World, Volume 8, Springer, Dordrecht.
- Alvarez-Filip L and Gil I. 2006. Effects of Hurricanes Emily and Wilma on coral reefs in Cozumel, Mexico. *Coral Reefs* 25(4): 583-583.
- Aranceta-Garza F, Balart EF, Reyes-Bonilla H, Cruz-Hernández P. 2012. Effect of tropical storms on sexual and asexual reproduction in coral *Pocillopora verrucosa* subpopulations in the Gulf of California. *Coral Reefs* 31(4): 1157-1167.
- Bak R and Criens SR. 1981 Survival after fragmentation of colonies of *Madracis mirabilis*, *Acropora palmata* and *A. cervicornis* (Scleractinia) and the subsequent impact of coral disease Proc. 4th Int. Coral Reef Symp. 2: 221-227.
- Birkeland C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc. 3rd Int. Coral Reef Symp. 1: 15-21.
- Bonaldo RM, Krajewski JP, Bellwood DR. 2011. Relative impact of parrotfish grazing scars on massive *Porites* corals at Lizard Island, Great Barrier Reef. *Marine Ecology Progress Series* 423: 223-233.
- Boulay JN, Hellberg ME, Cortés J, Baums IB. 2013. Unrecognized coral species diversity masks differences in functional ecology. *Proceedings of the Royal Society of London B: Biological Sciences* 281: 1776.
- Brandt ME, Smith TB, Correa AM, Vega-Thurber R. 2013. Disturbance driven colony fragmentation as a driver of a coral disease outbreak. *PLoS One* 8(2): e57164.
- Bruno JF and Selig ER. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2(8): e711.
- Cantera JR, Zapata FA, Forero P, Francisco V, Jiménez JM, Londoño E, *et al.* 2001. Organismos bioerosionadores en arrecifes de la isla Gorgona. PAGES. In: Barrios LM, López-Victoria M (Ed). *Gorgona marina: Contribución al conocimiento de una isla única*. INVENAR, Serie Publicaciones Especiales, Santa Marta.

- Cole AJ, Pratchett MS, Jones GP. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* 9(3): 286-307.
- Colgan MW. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* 68(6): 1592-1605.
- Cox EF. 1992. Fragmentation in the Hawaiian coral *Montipora verrucosa*. *Proc. 7th Int. Coral Reef Symp.* 1: 513-516.
- Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247(1-3): 121.
- Enochs IC and Glynn PW. 2017. Corallivory in the eastern Pacific. In *Coral Reefs of the Eastern Tropical Pacific*. In: Glynn PW, Manzello DP and Enochs IC (Ed). *Coral Reefs of the Eastern Tropical Pacific: Persistence and loss in a dynamic environment*. *Coral Reefs of the World, Volume 8*, Springer, Dordrecht.
- Guzmán HM. 1988. Distribución y abundancia de organismos coralívoros en los arrecifes coralinos de la Isla del Caño, Costa Rica. *Rev. Biol. Trop.* 36(2A): 191-207.
- Guzmán HM and Cortés J. 1989. Coral reef community structure at Caño Island, Pacific Costa Rica. *Marine Ecology* 10(1): 23-41.
- Guzman HM and Robertson DR. 1989. Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Marine Ecology Progress Series* 55: 121-131.
- Guzmán HM and López JD. 1991. Diet of the corallivorous pufferfish *Arothron meleagris* (Pisces: Tetraodontidae) at Gorgona island, Colombia. *Revista de Biología Tropical* 39(2): 203-206.
- Glynn PW. 1988. El Nino warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7: 129-160.
- Glynn PW, Stewart RH, McCosker JE. 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geologische Rundschau* 61(2): 483-519.
- Glynn PW, Colley SB, Gassman NJ, Black K, Cortés J, Maté JL. 1996. Reef coral reproduction in the eastern Pacific: Costa Rica, Panama, and Galapagos Islands (Ecuador). III. *Agariciidae* (*Pavona gigantea* and *Gardineroseris planulata*). *Marine Biology* 125:579-601.
- Glynn PW, Colley SB, Carpizo-Ituarte E, Richmond RH. 2017. Coral Reproduction in the Eastern Pacific. In: Glynn PW, Manzello DP, Enochs IC (Ed). *Coral Reefs of the Eastern Tropical Pacific: Persistence and loss in a dynamic environment* (*Coral Reefs of the World, Volume 8*). Springer, Dordrecht.

- Grottoli-Everett AG and Wellington GM. 1997. Fish predation on the scleractinian coral *Madracis mirabilis* controls its depth distribution in the Florida Keys, USA. *Marine Ecology Progress Series* 291-293.
- Hatcher BG, Johannes RE, Robertson AI. 1989. Review of research relevant to the conservation of shallow water tropical marine ecosystems. *Oceanogr. mar. biol. ann. Rev.* 27: 337–414.
- Szmant AM and Meadows MG. 2006. Developmental changes in coral larval buoyancy and vertical swimming behavior: implications for dispersal and connectivity. In: *Proc 10th Int Coral Reef Symp Vol. 1*: 431-437.
- Heyward AJ and Collins JD. 1985. Fragmentation in *Montipora ramosa*: the genet and ramet concept applied to a reef coral. *Coral Reefs* 4(1): 35-40.
- Hiatt RW and Strasburg DW. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* 30(1): 65-127.
- Highsmith RC. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7: 207-226.
- Highsmith RC, Riggs AC, D'Antonio CM. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* 46(3): 322-329.
- Howe HF and Smallwood J. 1982. Ecology of seed dispersal. *Annual review of ecology and systematics* 13(1): 201-228.
- Jayewardene D, Donahue MJ, Birkeland C. 2009. Effects of frequent fish predation on corals in Hawaii. *Coral Reefs* 28(2): 499-506.
- Kaplan EL and Meier P. 1958. Nonparametric estimation from incomplete observations. *J. Amer. Statist. Assn.* 53(282): 457–481.
- Katz SM, Pollock FJ Bourne DG, Willis BL. 2014. Crown-of-thorns starfish predation and physical injuries promote brown band disease on corals. *Coral Reefs* 33(3): 705-716.
- Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32(6): 674-682.
- Lasker HR. 1990. Clonal propagation and population dynamics of a gorgonian coral. *Ecology*, 71(4): 1578-1589.
- Liddle MJ and Kay AM. 1987. Resistance, survival and recovery of trampled corals on the Great Barrier Reef. *Biological Conservation* 42(1): 1-18.

- Lirman D. 2000. Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology* 251(1): 41-57.
- Lirman D and Fong P. 1997. Patterns of damage to the branching coral *Acropora palmata* following Hurricane Andrew: damage and survivorship of hurricane-generated asexual recruits. *Journal of Coastal Research* 67-72.
- Lirman D, Glynn PW, Baker AC, Leyte-Morales GE. 2001. Combined effects of three sequential storms on the Huatulco coral reef tract, Mexico. *Bulletin of Marine Science* 69(1): 267-278.
- Littler MM, Taylor PR, Littler DS. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80(3): 331-340.
- López-Pérez RA, Mora-Pérez MG, Leyte-Morales GE. 2007. Coral (Anthozoa: Scleractinia) recruitment at Bahías de Huatulco, Western México: Implications for coral community structure and dynamics. *Pacific Science* 61(3): 355-369.
- Loya Y. 1976. Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57(2): 278-289.
- Lozano-Cortés D and Zapata FA. 2014. Invertebrate colonization on artificial substrates in a coral reef at Gorgona Island, Colombian Pacific Ocean. *Revista de Biología Tropical* 62 (suplem. 1): 161-168.
- Neudecker S. 1979. Effect of grazing and browsing fishes on the zonation of corals in Guam. *Ecology*, 60(4): 666-672.
- Medina-Rosas P, Carriquiry JD and Cupul-Magaña AL. 2005. Reclutamiento de *Porites* (Scleractinia) sobre sustrato artificial en arrecifes afectados por El Niño 1997-98 en bahía de Banderas, Pacífico mexicano. *Ciencias Marinas* 31(1a): 103-109.
- Muñoz CG and Zapata FA. 2013. Plan de Manejo de los Arrecifes Coralinos del Parque Nacional Natural Gorgona. *Parques Nacionales Naturales de Colombia y WWF-Colombia*, Cali. 68 pp.
- Nicolet KJ, Hoogenboom MO, Gardiner NM, Pratchett MS, Willis BL. 2013. The corallivorous invertebrate *Drupella* aids in transmission of brown band disease on the Great Barrier Reef. *Coral Reefs* 32(2): 585-595.
- Palacios MM, Muñoz CG, Zapata FA. 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs* 33: 625–636.
- Parolin P, Wittmann F, Ferreira LV. 2013. Fruit and seed dispersal in Amazonian floodplain trees—a review. *Ecotropica* 19: 15-32.

- Pianka ER. 2011. Evolutionary Ecology. 7th edition, e-book.
- Pollux BJA. 2011. The experimental study of seed dispersal by fish (ichthyochory). *Freshwater Biology* 56(2): 197-212.
- Reyes-Bonilla H and Calderon-Aguilera LE. 1999. Population Density, Distribution and Consumption Rates of Three Corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. *Marine Ecology* 20: 347–357.
- Richmond RH. 1985. Variations in the population biology of *Pocillopora damicornis* across the Pacific. *Proceedings of the fifth International Coral Reef Congress* 6: 101-106.
- Richmond RH. 1987a. Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Marine Biology* 93(4): 527-533.
- Richmond RH. 1987b. Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. *Bulletin of Marine Science* 41(2): 594-604.
- Rogers CS, Suchanek TH, Pecora FA. 1982. Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, US Virgin Islands. *Bulletin of Marine Science* 32(2): 532-548.
- Roth L, Muller EM, van Woesik R. 2013. Tracking *Acropora* fragmentation and population structure through thermal-stress events. *Ecological Modelling* 263: 223-232.
- Rotjan RD and Lewis SM. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* 367: 73-91.
- Schupp EW, Jordano P and Gómez JM. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188(2): 333-353.
- Smith LD and Hughes TP. 1999. An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology* 235(1): 147-164.
- Toro-Farmer G, Cantera JR, Londoño-Cruz E, Orozco C, Neira R. 2004. Patrones de distribución y tasa de bioerosión del erizo *Centrostephanostraea coronatus* (Diadematoidea: Diadematidae), en el arrecife de Playa Blanca, Pacífico colombiano. *Rev Biol Trop* 52: 67–76.
- Traveset A and Richardson DM. 2014. Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 45: 89-113.
- Tunncliffe V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. *Proceedings of the National Academy of Sciences* 78(4): 2427-2431.

- Vermeij MJ, Marhaver KL, Huijbers CM, Nagelkerken I, Simpson SD. 2010. Coral larvae move toward reef sounds. *PloS one* 5(5): e10660.
- Wallace CC. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology* 88(3): 217-233.
- Wellington GM. 1982. Depth Zonation of Corals in the Gulf of Panama: Control and Facilitation by Resident Reef Fishes. *Ecological Monographs* 52: 224-241.
- Williams DE, Miller MW, Kramer KL. 2008. Recruitment failure in Florida Keys *Acropora palmata*, a threatened Caribbean coral. *Coral Reefs* 27(3): 697-705.
- Zapata FA. 2001. Formaciones coralinas de la isla de Gorgona. In: Barrios LM and López-Victoria M (Ed). *Gorgona marina: contribución al conocimiento de una isla única*. INVEMAR, Serie de Publicaciones Especiales No 7. Santa Marta, Colombia.
- Zapata FA and Vargas-Ángel B. 2003. Corals and coral reefs of the Pacific coast of Colombia. In: J. Cortés (Ed). *Latin American Coral Reefs*. Elsevier, Amsterdam. 497 pp.

TABLES AND FIGURES

Table 1. Pufferfish abundance, and rates of fragmentation by pufferfish, survival of fragments and asexual recruitment in La Azufrada reef.

	Back reef	Reef flat	Fore reef	Whole reef
Fish abundance (fish ha ⁻¹)	90.4	192	231.2	171.2
Fragmentation rate (Fragments m ⁻² yr ⁻¹)	28.5	60.5	72.9	54.0
Surviving fragments (Fragments m ⁻² yr ⁻¹)	22.6	53.4	69.5	47.4
Asexual recruitment (Recruits m ⁻² yr ⁻¹)	15.5	31.3	8.8	21.0

Table 2. Substrate cover of live coral, sand and coral rubble/rock in La Azufrada reef, used as the probability of a fragment to land on each substrate.

	Back reef	Reef flat	Fore reef	Whole reef
Live coral cover (%)	25.7	36.4	83.2	49.0
Sand cover (%)	7.4	0.2	2.0	3.2
Coral rubble/matrix (%)	66.9	63.4	14.8	47.8

Table 3. Estimations of coral weight rates (kg m⁻² yr⁻¹) involved in the interaction between pufferfish and pocilloporid corals.

	Back Reef	Reef Flat	Fore Reef	Whole Reef
Coral consumption	0.46	0.98	1.18	0.87
Coral fragmentation	0.76	1.61	1.94	1.44
Gross coral production	2.84	4.2	9.64	5.56
Growth of recruits	0.68	1.38	0.39	0.93
Mortality of fragments	0.15	0.19	0.09	0.17
Coral affected by pufferfish	1.22	2.59	3.12	2.31
Coral after interaction	1.82	2.2	8.13	3.96
Net coral production	2.5	3.57	8.52	4.88
Total coral destruction	0.61	1.17	1.27	1.04

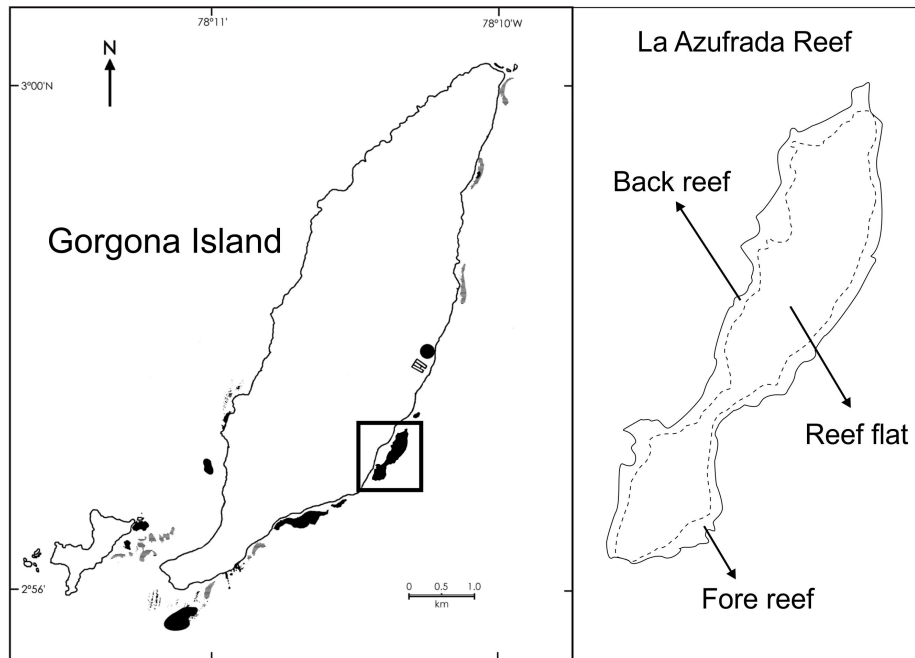


Figure 1. La Azufrada reef at Gorgona Island (left), and its main reef zones (right).

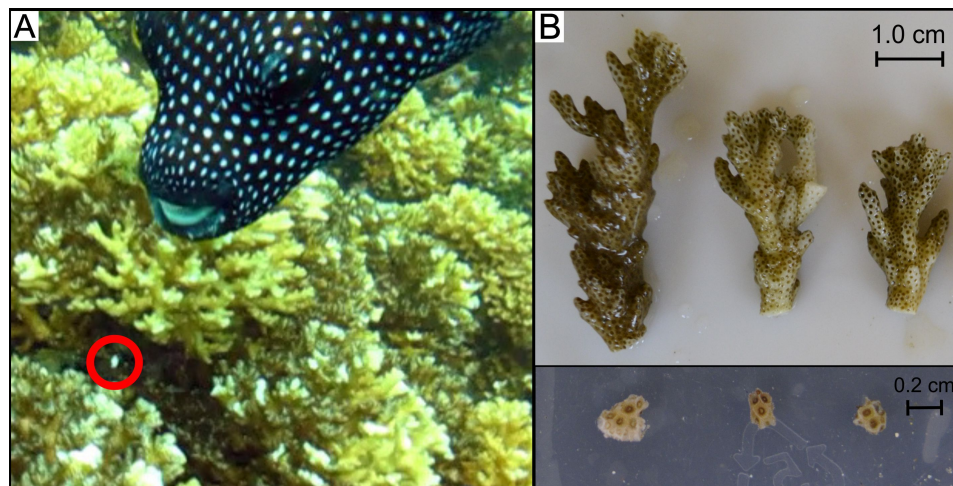


Figure 2. (A) Pocilloporid fragment (circled in red) falling during a pufferfish attack on pocilloporid corals. (B) Coral fragments produced by pufferfish predation on pocilloporid corals at La Azufrada reef.

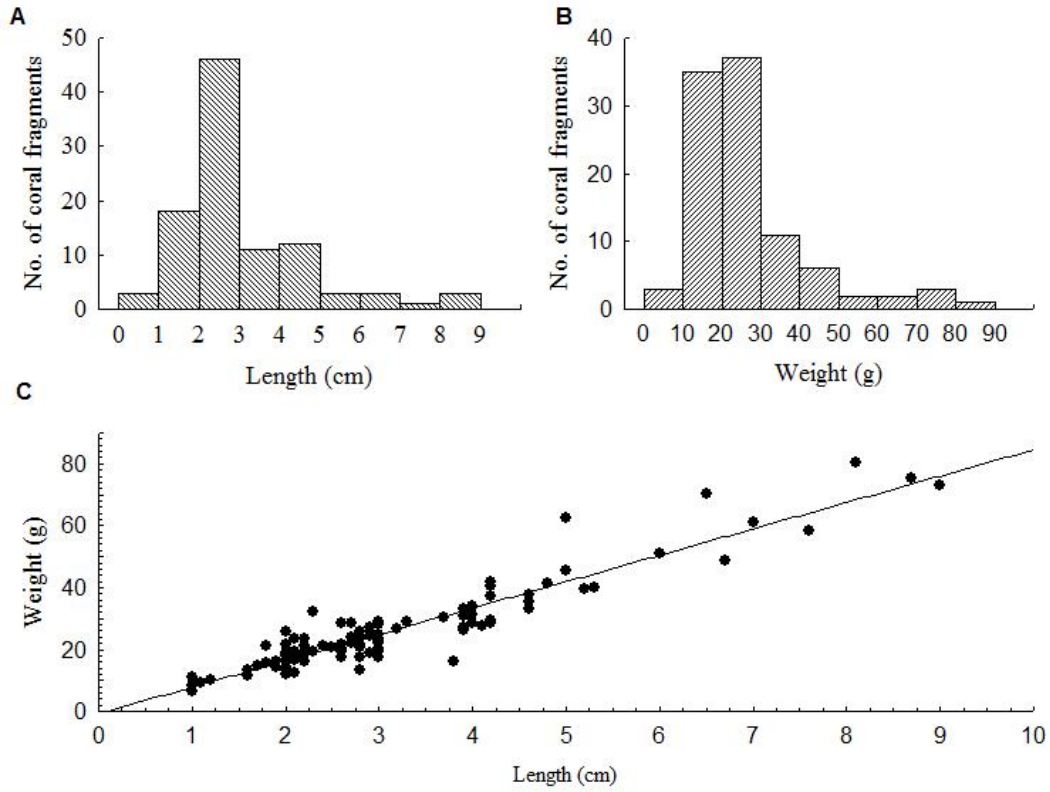


Figure 3. Frequency distributions of coral fragments generated by pufferfish predation (A) length, (B) weight. (C) Length-Weight relationship ($W = -0.71 + 8.52L$; $p < 0.05$, $R^2 = 0.88$).

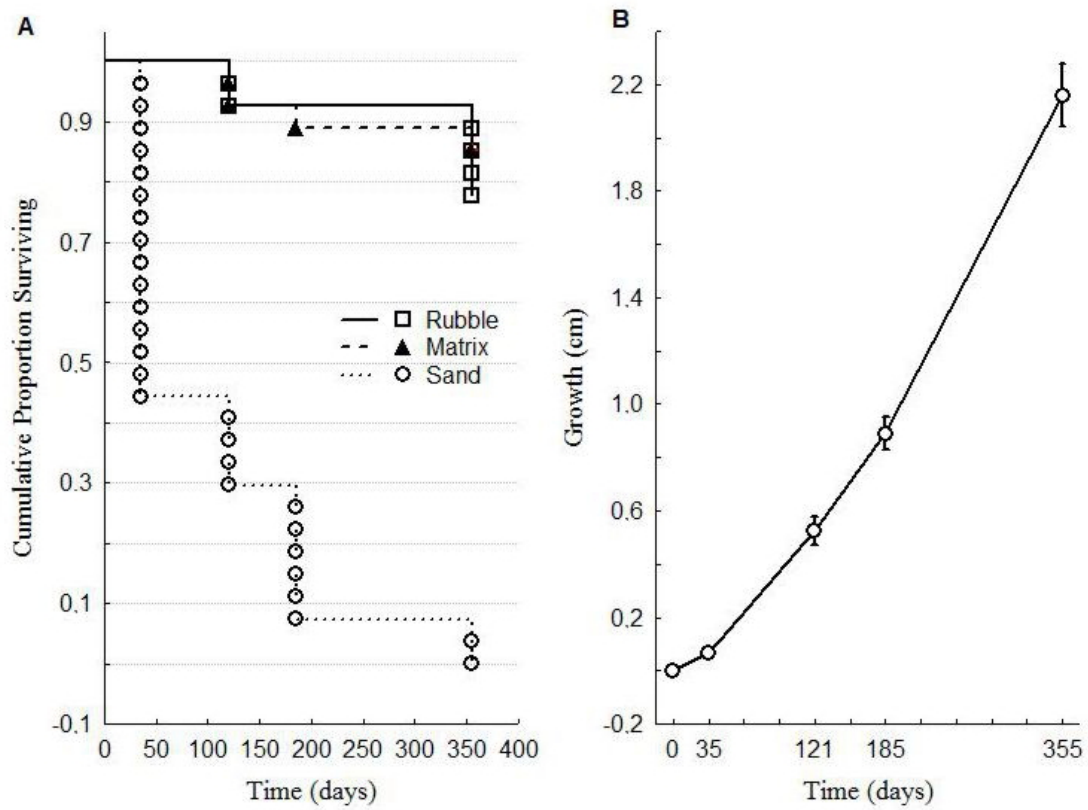


Figure 4. (A) Kaplan-Meier plots showing the survival of pocilloporid fragments trajectories among treatments (sand, loose coral rubble and consolidated coral matrix) during one year. (B) Growth of pocilloporid fragments deployed on coral rubble and coral matrix during one year from May 2013 to April 2014. Whiskers denote standard errors.

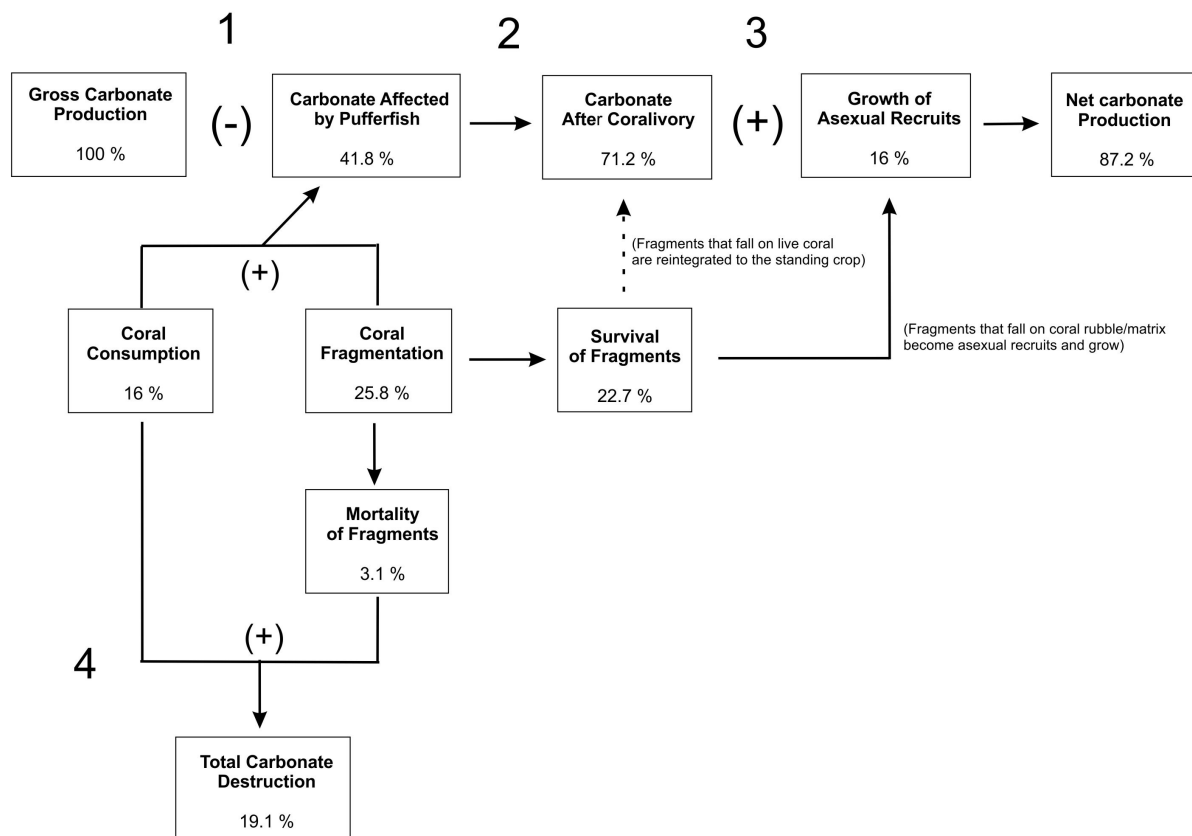


Figure 5. Annual coral production by the pocilloporid standing crop across the processes of predation, fragmentation, and generation of asexual recruits. Percentage values are shown for the whole reef. (1) Coral affected by pufferfish = Coral fragmentation + Coral consumption; (2) Coral after corallivory = Gross carbonate production – Carbonate affected by pufferfish; (3) Net carbonate production = Growth of recruits + Carbonate after corallivory; (4) Total coral destruction = Mortality of fragments + Coral consumption.

DISCUSIÓN GENERAL Y CONCLUSIONES

Esta investigación presenta resultados novedosos sobre la ecología reproductiva de los corales del Pacífico colombiano. Primero, presenta evidencia de la ocurrencia de reclutamiento coralino de origen sexual en Isla Gorgona, en el Pacífico Tropical Oriental (PTO). Segundo, analiza algunos de los agentes causantes de la reproducción asexual por fragmentación en corales pocilopóridos, enfocándose en el sistema trófico de coralivoría por el pez *Arothron meleagris* y sus efectos sobre los corales y arrecifes coralinos de Isla Gorgona. Tercero, examina el papel de la coralivoría por peces sobre el presupuesto de carbonato de un arrecife típico de la región; y cuarto, demuestra que la coralivoría por peces puede generar efectos opuestos sobre el balance de carbonato en el arrecife.

Se observó por primera vez evidencia de reclutamiento coralino producto del asentamiento de larvas para un conjunto diverso de especies en Isla Gorgona, lo que sugiere que la reproducción sexual y el reclutamiento subsiguiente son procesos activos en los arrecifes coralinos del Pacífico colombiano. El reclutamiento coralino de origen sexual por asentamiento y metamorfosis de larvas, tal como se demostró en este estudio sí se da en diversos arrecifes coralinos y ecosistemas rocosos de Isla Gorgona. Sin embargo, los resultados generales respecto al reclutamiento de origen sexual en Gorgona, fueron similares a los encontrados por otros estudios sobre reclutamiento coralino en el PTO, los cuales reportan ausencia o muy bajas densidades de reclutas de coral en sustratos naturales (Glynn *et al.* 2017). Cabe resaltar que aunque los factores que determinan el reclutamiento en los diversos sitios de Gorgona aún se desconocen, la profundidad y el sustrato disponible seguramente juegan un papel importante. Por otro lado, los resultados negativos con las placas de asentamiento permanecen sin una explicación satisfactoria, y aumentar el tamaño y distribución del muestreo para detectar reclutas de coral con abundancias naturalmente bajas, podría ser una solución lógica pero muy difícil de llevar a cabo en la práctica.

Igualmente, se describió un caso de interacción entre elementos de la biota terrestre y marina, como son los troncos flotantes y los corales, y cómo estos troncos bajo ciertas

circunstancias pueden afectar un arrecife tanto por su potencial destructivo, como por su capacidad para promover la reproducción asexual por fragmentación. De los diversos agentes que fragmentan a los corales (Highsmith 1982), los casos de fragmentación en los arrecifes coralinos pocilopóridos por troncos flotantes son eventos fortuitos (Muñoz *et al.* 2015), mientras que otros como el caso de peces globo, son procesos continuos (Palacios *et al.* 2014). La magnitud y frecuencia de la fragmentación coralina pueden variar dependiendo del agente involucrado, pero todos los casos tienen como resultado común la generación de reclutas asexuales con potencial para sobrevivir, desarrollarse y crecer, formando nuevas colonias. En términos prácticos e inmediatos, la fragmentación puede producir nuevas colonias que aumentan la cobertura de coral vivo en el arrecife, siendo un mecanismo rápido y efectivo para el repoblamiento y recuperación de este. Sin embargo, una frecuente y sostenida reproducción asexual por fragmentación, puede resultar en un arrecife constituido por unos pocos clones coralinos disminuyendo a largo plazo la diversidad genética local. Adicionalmente, la fragmentación ha sido señalada como causante de disminución en la producción de larvas en *Pocillopora damicornis* en Hawái (Zakai *et al.* 2000), y si bien esto no ha sido demostrado aún en Gorgona, esto podría ayudar a explicar las bajas tasas de reclutamiento sexual observado en la isla y en el PTO: si el arrecife está formado por pocos individuos genéticos es posible que aunque las colonias sean fértiles, la fecundación se vea limitada por mecanismos que evitan autofecundación, y gran parte de la producción de gametos se pierda. Este efecto podría verse amplificado si la constante fragmentación de las colonias está disminuyendo la capacidad de producción de gametos o larvas.

Se analizó experimentalmente el impacto que tiene una población numerosa de un organismo coralívoro como el pez *Arothron meleagris* sobre algunos aspectos biológicos de los corales, como el crecimiento, la recuperación en colonias tras sufrir remoción de tejidos blandos y esqueleto, y los efectos en los presupuestos de carbonatos del arrecife. Este pez globo es un coralívoro importante en Isla Gorgona, tanto por su alta tasa de depredación como por su alta densidad poblacional, ejerciendo efectos negativos notables en el arrecife al remover directamente carbonato de calcio que se encuentra haciendo parte de la cobertura de coral vivo (Palacios *et al.* 2014). En ese sentido podemos considerar a *A. meleagris* como una especie coralívora única en este ecosistema, ya que consume tanto tejido blando coralino como lo hacen algunos moluscos y equinodermos, pero a diferencia de éstos invertebrados, también afecta

dramáticamente la estructura esquelética de las colonias, removiendo fragmentos de esqueleto de manera similar a como lo hacen otros peces (*e.g.* Balistidae, Monacanthidae), los cuales rompen las colonias buscando presas ocultas, pero no consumen precisamente coral (Alvarado *et al.* 2017; Enochs y Glynn 2017).

La destrucción del material arrecifal, como los esqueletos coralinos de carbonato por acción de otros organismos, es un proceso conocido como bioerosion (Alvarado *et al.* 2017); el cual en oposición a la acreción, está involucrado en la dinámica de construcción-destrucción de los arrecifes coralinos. La importancia de *A. meleagris* como organismo bioerosionador, puede ser analizada, por un lado en el contexto de los presupuestos de carbonatos del arrecife, y por otro lado examinando las tasas de remoción de carbonato de otros organismos. Se mostró cómo la interacción *A. meleagris* y corales pocilopóridos tiene un efecto complejo en el arrecife y en los presupuestos de carbonato, al destruir coral pero al mismo tiempo generar reclutas asexuales que al crecer contribuyen a la formación de nuevas colonias y, en última instancia, a compensar el impacto deletéreo de la coralivoría. Se estimó que la depredación de *A. meleagris* eliminó carbonato de calcio de los corales vivos a una tasa de $0.9 \text{ kg m}^{-2} \text{ año}^{-1}$, lo que, además de la mortalidad de los fragmentos producidos ($0.2 \text{ kg m}^{-2} \text{ año}^{-1}$), da como resultado una tasa total de destrucción de carbonatos de $1.1 \text{ kg m}^{-2} \text{ año}^{-1}$, o 20 % del carbonato anual producido por los corales pocilopóridos en el arrecife. Debido a la supervivencia de los fragmentos pocilopóridos, altamente relacionada con el sustrato donde se encuentran, son al menos dos los componentes del efecto total que tiene el depredador (*A. Meleagris*) sobre la presa (*Pocillopora* spp.) en términos del presupuesto de carbonato de calcio del arrecife: 1) un efecto negativo directo resultado de la remoción de material coralino por parte de la población de *A. meleagris* al ingerir trozos de coral vivo incluyendo esqueleto, y de la mortalidad asociada a aquella población de fragmentos generados en la interacción; 2) un efecto positivo secundario resultado de la supervivencia y crecimiento de los fragmentos de *Pocillopora* que son continuamente generados, y que cayendo en sustratos adecuados pueden crecer y acumular carbonato de calcio independientemente de su colonia parental.

La bioerosión, considerada como alta en el PTO, es promovida por las condiciones oceanográficas regionales y locales: altas cargas de nutrientes, alta productividad primaria,

eventos recurrentes de mortalidad, alto pCO₂, bajo pH, y un estado de saturación bajo de aragonita (Alvarado *et al.* 2017); llevando a considerar estos arrecifes como ecosistemas modelos en escenarios de cambio climático. La tasa de remoción de carbonatos para el arrecife de La Azufrada por *A. meleagris* en este estudio (0.9 kg m⁻² y⁻¹) fue similar o menor a lo reportado para otros organismos como equinodermos, pero fue alta comparada con las tasas para la misma especie en otros estudios; por ejemplo para Isla Gorgona, se han reportado tasas de bioerosión por erizos (*Diadema mexicanum*) entre 0.05 y 0.1 kg m⁻² y⁻¹ (Toro-Farmer *et al.* 2004), de 3.3 kg m⁻² y⁻¹ en las costas de México (Reyes-Bonilla y Calderón-Aguilera 1999) y superior a 10 kg m⁻² y⁻¹ en arrecifes de Panamá (Glynn 1988; Eakin 1992). Las tasas de erosión por peces en otros estudios han sido similares, con 0.6 kg m⁻² y⁻¹ para *Pseudobalistes naufragium* y hasta de 1.1 kg m⁻² y⁻¹ para *Sufflamen verres* en Isla Gorgona (Cantera *et al.* 2001). Mientras que la destrucción para la especie *A. meleagris* en otras localidades ha sido más baja, siendo estimada en 0.1 y 0.3 kg m⁻² y⁻¹, para localidades en Panamá y México respectivamente (Reyes-Bonilla y Calderón-Aguilera 1999).

Adicionalmente, se analizó el rol y la efectividad de *A. meleagris* como promotor de la reproducción asexual de corales pocilopóridos en el Arrecife La Azufrada, describiendo el proceso de fragmentación de las colonias y la supervivencia de los fragmentos resultado de la interacción con el depredador (Alvarado *et al.* 2017; Enochs y Glynn 2017). Un aspecto llamativo de la interacción depredador-presa entre el pez *A. meleagris* y corales del género *Pocillopora*, radica en el rol ecológico de los peces como facilitadores en la reproducción asexual de los corales, promoviendo el aumento de la cobertura coralina viva en arrecifes tras perturbaciones. No sería el primer ejemplo de una relación depredación-reproducción que involucra peces (Pollux 2011, Parolin *et al.* 2013), y aunque algunos estudios han examinado el papel de la depredación por peces en la determinación de la estructura de las comunidades bentónicas (Neudecker 1979, Wellington 1982, Cox 1986, Grottoli-Everett y Wellington 1997), es difícil definir estrictamente esta interacción como mutualista, debido a la naturaleza facultativa de la coralivoría en *A. meleagris* y a dificultades conceptuales para considerar como adaptativo el mecanismo asexual de la reproducción por fragmentación en corales pocilopóridos. Sin embargo, los resultados sugieren que la reproducción asexual por fragmentación puede ser una de las

causas que permiten a los corales pocilopóridos propagarse rápidamente y dominar los arrecifes someros en Gorgona.

Los resultados indican además que los corales pocilopóridos resisten relativamente bien el daño asociado a la depredación al menos de dos formas: a) la colonia se recupera relativamente rápido, y b) los fragmentos generados tienen altas probabilidades de sobrevivir. Adicionalmente, los efectos de la coralivoría, tal como en el caso de *A. meleagris* sobre *Pocillopora* spp. pueden tener consecuencias aún más complejas, como alteraciones morfológicas en las colonias coralinas. Lo que a su vez es una nueva dificultad a tener en cuenta para la correcta identificación y taxonomía de Pocilloporidae (Glynn *et al.* 1982, Lenihan y Edmunds 2010; Palacios *et al.* 2014).

Teniendo en cuenta que los resultados de este estudio están involucrados con los ciclos de vida de los corales y la resiliencia de los arrecifes coralinos, aspectos fundamentales para su conservación, es necesario esclarecer el porqué de los resultados del bajo reclutamiento sexual coralino en el PTO. Aspectos como el efecto de la coralivoría y la propagación de clones en la reproducción sexual coralina, merecen más atención y deberían ser estudiados en detalle tanto en el Pacífico colombiano como en otros lugares de la región. Adicionalmente, una comprensión más completa del acrecimiento y la bioerosión, que incluya a otros grupos de organismos productores y peces coralívoros, ayudará a entender mejor la dinámica entre erosión y acrecimiento arrecifal (Alvarado *et al.* 2017). Esto implicaría continuar con evaluaciones detalladas de la producción de carbonato en el arrecife, incluyendo a otras especies de coral y otros grupos importantes como las algas costrosas coralinas.

Finalmente, como medida de manejo para el Parque Nacional Natural Gorgona en caso de considerar intervenir la recuperación natural de los arrecifes coralinos mediante esfuerzos de restauración, se recomienda maximizar la supervivencia de los fragmentos coralinos que se producen naturalmente en el arrecife. Esto puede ser realizado de manera periódica con los fragmentos que se encuentran normalmente en los arrecifes, simplemente reubicándolos desde los alrededores o zonas arenosas de la periferia arrecifal a sustratos más adecuados donde tendrían mayores probabilidades de sobrevivir.

REFERENCIAS

- Alvarado JJ, Grassian B, Cantera-Kintz JR, Carballo JL, Londoño-Cruz E. 2017. Coral Reef Bioerosion in the Eastern Tropical Pacific. En: Coral Reefs of the Eastern Tropical Pacific. Springer Netherlands.
- Cantera JR, Zapata FA, Forero P, Francisco V, Jiménez JM, Londoño E, *et al.* 2001. Organismos bioerosionadores en arrecifes de la isla Gorgona. In: Barrios LM, López-Victoria M (eds) Gorgona marina: Contribución al conocimiento de una isla única. Inst Invest Mar Cost “José Benito Vives de Andreis”. Ser Publ Esp, Santa Marta, pp 79–92.
- Cox EF. 1986. The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *Journal of Experimental Marine Biology and Ecology* 101: 161–174.
- Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247(1-3): 121.
- Eakin CM. 1992. Post-El Niño Panamanian reefs: less accretion, more erosion and damselfish protection. *Proceeding of the 7th International Coral Reef Symposium, Guam* 1: 387-396.
- Enochs IC y Glynn PW. 2017. Corallivory in the eastern Pacific. En: Coral Reefs of the Eastern Tropical Pacific. Springer Netherlands.
- Glynn PW. 1988. El Nino warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7: 129-160.
- Glynn PW, Prahl H, Guhl F. 1982. Coral reefs of Gorgona Island, Colombia, with special reference to corallivores and their influence on community structure and reef development. *Anales del Instituto de Investigaciones Marinas de Punta de Betín* 12:185–214.
- Glynn PW, Colley SB, Carpizo-Ituarte E, Richmond RH. 2017. Coral reproduction in the Eastern Pacific. En: Coral Reefs of the Eastern Tropical Pacific. Springer, Netherlands.
- Grottoli-Everett AG y Wellington GM. 1997. Fish predation on the scleractinian coral *Madracis mirabilis* controls its depth distribution in the Florida Keys, USA. *Marine Ecology Progress Series* pp 291-293.
- Highsmith RC. 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series* 7(2): 207-226.
- Lenihan HS y Edmunds PJ 2010. Response of *Pocillopora verrucosa* to corallivory varies with environmental conditions. *Marine Ecology Progress Series* 409: 51–63.

- Neudecker S. 1979. Effects of grazing and browsing on the zonation of corals in Guam. *Ecology* 60: 666-672.
- Muñoz CG, Wild C y Zapata FA. 2015. Drift logs are effective agents of physical coral fragmentation in a tropical eastern Pacific coral reef. *Bulletin of Marine Science* 91(3).
- Palacios MM, Muñoz CG y Zapata FA. 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs* 33(3): 625-636.
- Parolin P, Wittmann F y Ferreira LV. 2013. Fruit and seed dispersal in Amazonian floodplain trees—a review. *Ecotropica* 19: 15-32.
- Pollux BJA. 2011. The experimental study of seed dispersal by fish (ichthyochory). *Freshwater Biology* 56(2): 197-212.
- Reyes-Bonilla H and Calderon-Aguilera LE. 1999. Population Density, Distribution and Consumption Rates of Three Corallivores at Cabo Pulmo Reef, Gulf of California, Mexico. *Marine Ecology* 20: 347–357.
- Toro-Farmer G, Cantera JR, Londoño-Cruz E, Orozco C, Neira R. 2004. Patrones de distribución y tasa de bioerosión del erizo *Centrostephanostraea coronatus* (Diadematoida: Diadematidae), en el arrecife de Playa Blanca, Pacífico colombiano. *Rev Biol Trop* 52:67–76.
- Wellington GM. 1982. Depth Zonation of Corals in the Gulf of Panama: Control and Facilitation by Resident Reef Fishes. *Ecological Monographs* 52: 224-241.
- Zakai D, Levy O, Chadwick-Furman N.E. 2000. Experimental fragmentation reduces sexual reproductive output by the reef-building coral *Pocillopora damicornis*. *Coral Reefs* 19(2): 185-188.