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POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

ECOLOGÍA

(PROYECTO)

MECANISMOS NATURALES DE RECUPERACIÓN DE COMUNIDADES CORALINAS AFECTADAS POR EL SÍNDROME BLANCO: EVALUACIÓN DE RECLUTAMIENTO Y RECUPERACIÓN EN COLONIAS AFECTADAS

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

Recovery and Future Perspectives of Juvenile Scleractinian Corals Following a Disease-Induced Mass Mortality Event

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO(A) EN CIENCIAS BIOLÓGICAS

PRESENTA:

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

A T E N T A M E N T E
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Índice

Resumen

Las poblaciones de corales del Caribe han sido afectadas seriamente por diversos factores, aunque las enfermedades son probablemente el efecto más predominante en la región. El brote de la enfermedad de pérdida de tejido de coral duro (SCTLD, siglas del nombre en inglés "Stony Coral Tissue Loss Disease") ha sido una de los más letales, causando mortalidades superiores al 90% en algunas especies. Una afectación de esta magnitud pone de manifiesto la necesidad de evaluar si existe reclutamiento de nuevos individuos, e identificar los mecanismos por los cuales este proceso pudiera guiar la recuperación natural de sus poblaciones. En este estudio se evaluó el estado de las comunidades coralinas jóvenes a lo largo de un gradiente espacial amplio del Caribe Mexicano (≈ 450 km) después del brote de la SCTLD. Se monitorearon 65 sitios afectados, en los cuales, por medio de transectos, se registraron los corales juveniles (15 $m^2 \cdot sitio^{-1}$) y los adultos (60 $m^2 \cdot sitio^{-1}$). Se realizaron análisis multivariados y modelos generalizados para identificar los principales factores que influyen en la presencia, densidad y diversidad de especies en un escenario post-brote. Además, mediante el tamaño y la identidad del coral se estimó la fecha de reclutamiento en los sitios afectados y se comparó la estructura poblacional de las especies susceptibles en los sitios afectados y no afectados. En general, se encontró evidencia de que algunos juveniles de las especies afectadas por la SCTLD lograron sobrevivir o reclutarse después del brote. Además, detectamos patrones ecológicos consistentes en la abundancia y diversidad de especies, a pesar del evento de mortalidad masiva. Nuestros resultados sugieren que ciertas especies susceptibles, como *Pseudodiploria strigosa* y *Eusmilia fastigiata*, podrían recuperarse de manera natural mediante el reclutamiento; sin embargo, el panorama no es tan alentador para las especies más afectadas, como *Dendrogyra cylindrus* y *Meandrina meandrites*. Nuestros resultados confirman que las

poblaciones de varias especies susceptibles sufrieron cambios importantes en su abundancia además de mostrar una tendencia hacia colonias de tallas pequeñas en los sitios afectados. El monitoreo de corales juveniles en escalas espaciales amplias y áreas de muestreo extensas ofrece información crucial sobre los posibles cambios estructurales de las comunidades futuras y su capacidad de recuperación natural. Esta información es esencial para identificar sitios prioritarios donde se pueda conservar la diversidad y abundancia de corales impactados por la SCTLD.

Palabras clave: reclutamiento, supervivencia, recuperación poblacional, cambios ecológicos, brote de enfermedad

Abstract

Diseases are widespread and harmful drivers of coral mortality. The most lethal outbreak ever recorded in the Caribbean is of Stony Coral Tissue Loss Disease (SCTLD), which resulted in mortality rates >90% in some species. This underscores the urgent need to understand the mechanisms that could promote natural recovery. We evaluated the condition of juvenile coral communities across a broad spatial gradient in the Mexican Caribbean following an SCTLD outbreak. We surveyed 65 affected sites and recorded juvenile ($15\ m^2 \cdot site^{-1}$) and adult ($60\ m^2 \cdot site^{-1}$) corals to identify the factors that affected juvenile abundance and diversity after the outbreak. We used size and species identity to estimate when juveniles established themselves in affected sites and compared the population structure of susceptible species in affected and unaffected sites. Overall, we found evidence that some juveniles of the species affected by STCLD endured or recruited after the outbreak, and we identified consistent ecological patterns in the abundance and diversity of species despite the mass mortality event. Our findings suggest that some susceptible species, such as *Pseudodiploria strigosa* and *Eusmilia fastigiata*, might naturally recover through recruitment; however, the diagnosis is not as encouraging for the species that were most severely afflicted, such as *Dendrogyra cylindrus* and *Meandrina meandrites*. Our findings confirm that the populations of several susceptible species underwent severe change in overall number and in a size skew toward smaller colonies. We show that monitoring juveniles over broad spatial scales and extensive sampling areas yields invaluable insights into the potential structural changes of future communities and their capacity for natural recovery. This information is needed to identify priority sites to conserve the diversity and abundance of corals impacted by SCTLD.

Keywords: recruitment, survival, population recovery, ecological shifts, disease outbreak

Introducción General

En las últimas décadas el crecimiento exponencial de las principales ciudades costeras del Caribe ha deteriorado las condiciones ambientales en las que se desarrollan los corales, ya que ha desencadenado procesos de eutrofización, sedimentación, sobreexplotación de los recursos marinos y deterioro de la calidad del agua (Baker *et al*., 2013; Hernández-Terrones *et al*., 2015; Rioja-Nieto *et al*., 2019). Estos fenómenos locales aunados con otros globales, como el cambio climático, han dejado muy vulnerables a los corales propiciando el brote de enfermedades y eventos de blanqueamiento que han provocado grandes eventos de mortalidad en las comunidades coralinas (Bruckner *et al*., 2002; Jackson *et al*., 2014). En consecuencia, se ha registrado una disminución drástica en la cobertura de coral en esta región (cerca del 80%) en las últimas décadas (Gardener *et al*., 2003).

La enfermedad de la SCTLD (SCTLD, siglas del nombre en inglés "Stony Coral Tissue Loss Disease") ha sido la más reciente y las más letal jamás registrada en el Caribe (Álvarez-Filip et al., 2022). El primer brote de esta enfermedad fue registrado por primera vez en el 2014 en las costas de Florida, donde se observaron lesiones graves en los tejidos de los corales, que progresaban rápidamente y provocaban la mortalidad total de las colonias en cuestión de meses (Precht *et al*., 2016). Actualmente el agente causal de esta enfermedad aún se desconoce, sin embargo, las observaciones sugieren que la SCTLD podría ser causada por bacterias pertenecientes a distintos órdenes (Aeby et al., 2019). Esta enfermedad se ha expandido a una velocidad alarmante afectando a más de 20 especies de corales (Precht *et al*., 2016), lo cual ha suscitado preocupación acerca de la posible extinción local de las especies afectadas en un período de tiempo notablemente corto (Chan et al., 2019; Álvarez-Filip et al., 2022). Por ejemplo, especies como *Dendrogyra cylindrus*,

Dichocoenia stokesii, *Eusmilia fastigiata* y *Meandrina meandrites* experimentaron tasas de mortalidad muy altas, algunas de sus poblaciones incluso disminuyeron hasta un 90-100 % (Gintert et al., 2019; Álvarez-Filip et al., 2022; Papke et al., 2024). Aunque otras especies, como el complejo *Orbicella* y *Montastrea cavernosa*, no sufrieron el mismo grado de afectación que las mencionadas anteriormente, también experimentaron pérdidas poblacionales significativas (> 20%) (Álvarez-Filip et al., 2022). Esto resalta la gravedad de la situación y enfatiza la importancia de evaluar el estado actual y futuro de las comunidades coralinas, destacando la importancia de estudiar los procesos naturales de recuperación de las especies afectadas.

Un proceso de recuperación natural de los sistemas arrecifales coralinos requiere del reclutamiento; es decir, de la incorporación de nuevos individuos a poblaciones existentes (Eriksson y Ehrlen, 2008), así como su posterior crecimiento y supervivencia. En las etapas de vida temprana los corales son considerablemente más vulnerables y experimentan tasas de mortalidad elevadas durante los primeros meses de vida, lo que puede crear un cuello de botella importante en el potencial de recuperación de las poblaciones afectadas (Chong-Seng et al., 2014; Vermeij y Sandin, 2008; Sarribouette et al., 2022). Comprender la dinámica de estas etapas puede ofrecer información valiosa sobre los efectos a largo plazo de los disturbios e informar sobre el potencial de recuperación y la resiliencia de las poblaciones y sus dinámicas ecológicas (Gilmour et al., 2013; Doropoulos et al., 2015).

La mortalidad provocada por la enfermedad de la SCTLD, y la pérdida de cobertura asociada a esta, puede poner en amenaza la recuperación natural de las comunidades coralinas. Una reducción de la cobertura coralina de cada especie, así como la disminución en el área viva de la colonia podría estar comprometiendo el potencial reproductivo (Hartmann *et al*., 2017) e impidiendo la recuperación potencial de las especies afectadas. Aunque la reproducción es el principal factor en

el reclutamiento y en la dinámica de las etapas de vida temprana de los corales, estos procesos están influenciados intrincadamente por múltiples factores bióticos y abióticos.

El asentamiento y supervivencia de los propágulos de coral dependen en gran medida del sustrato en el que se establecen; por ejemplo, hay una mayor probabilidad de éxito en superficies que son topográficamente complejas (Doropoulos et al., 2016) y en sustratos cubiertos por algas coralinas incrustantes (CCA, siglas del nombre en inglés "Crustose Coralline Algae"), ya que estas facilitan el asentamiento de las larvas a través de señales químicas (Morse et al., 1988; Webster et al., 2004; Birrell et al., 2008; Jorissen et al., 2021). En contraste, una alta cobertura coralina o condiciones adversas en el bentos, como una alta presencia de macroalgas o sedimentos, tienden a impedir el reclutamiento y a afectar la supervivencia de juveniles debido a la competencia por el espacio, la alelopatía y la abrasión (Wittenberg y Hunte 1992; Birrel et al., 2005; Box y Mumby 2007; Morrow et al., 2017; Couch et al., 2023). Los factores mencionados anteriormente, junto con la composición de la comunidad de los corales y las condiciones ambientales, varían a lo largo del gradiente de profundidad y desempeñan roles críticos en la estructuración de las comunidades juveniles (Bak y Engel, 1979; Rogers 1984; Turner et al., 2018; Doropoulos et al., 2020; Couch et al., 2023). Además, se han observado tendencias positivas consistentes en la densidad y diversidad juveniles conforme aumenta la profundidad (Acosta et al., 2011; Couch et al., 2023). Sin embargo, esta zonación puede ser alterada significativamente por eventos de mortalidad masiva desencadenados por enfermedades (Jackson 1991; Aronson y Precht, 2001), u otros disturbios (Edmunds y Leichter, 2016), lo que plantea la interrogante de si estas tendencias se mantienen después del brote de la SCTLD. Del mismo modo, el reclutamiento y la supervivencia de los corales se han visto sustancialmente afectados por el aumento de las temperaturas del agua (Ritson-Williams et al., 2016; Hughes et al., 2019). Comprender los factores bióticos y abióticos que

determinan la comunidad en regeneración es de crucial importancia para identificar sitios prioritarios de conservación y facilitar la recuperación natural de los arrecifes.

La recuperación de los arrecifes coralinos ha tenido una gran variación en distintas regiones; sin embargo, se ha observado una disminución general en el reclutamiento en los trópicos en las últimas décadas (≈ 80 %), lo cual genera dudas sobre la recuperación de estos ecosistemas (Hughes et al., 2019; Price et al., 2019; Edmunds, 2023). Un claro ejemplo se puede observar en los arrecifes del Caribe, en los cuales la drástica disminución de cobertura de coral y su funcionalidad (Gardener et al., 2003; Álvarez-Filip et al., 2013), aunado a las tasas bajas de reclutamiento (Edmunds, 2023), parecen haber impedido su capacidad de recuperación (Huntington et al., 2011; Roff y Mumby, 2012; Adjeroud et al., 2018; Cramer et al., 2020). Además, otra preocupación crítica surge de la identidad y estrategias ecológicas de las especies o grupos funcionales que se están estableciendo con éxito y sobreviviendo hasta la adultez en los arrecifes del Caribe (Kayal et al., 2015). Lo que está sucediendo actualmente en el Caribe es un cambio en las comunidades, en las cuales las especies estructuralmente importantes están siendo reemplazadas por especies más pequeñas con diferentes estrategias y funciones ecológicas. Las especies masivas de coral de crecimiento lento con reproducción liberadora y estructuralmente fundamentales en los arrecifes están siendo reemplazadas por corales más pequeños con reproducción incubadora, tasas de crecimiento rápido y tasas de recambio poblacional elevadas (Knowlton, 2001; Green et al. 2008; Álvarez-Filip et al., 2011; Álvarez-Filip et al., 2013). La SCTLD podría acentuar aún más estas tendencias, ya que se ha observado una clara alteración en la composición de la comunidad juvenil posterior a la enfermedad (Hayes et al., 2022).

La gran mortalidad coralina resultante del brote de la enfermedad causó cambios en la estructura de la comunidad que afectaron aún más y radicalmente la integridad funcional de las comunidades

de coral del Caribe. Esto plantea la pregunta de si los ensamblajes de coral posteriores a la SCTLD se recuperarán y mantendrán funciones ecológicas clave. En este estudio utilizamos datos posteriores a la SCTLD a lo largo de un gradiente espacial amplio (~ 450 km) en el Caribe mexicano para investigar si las especies de coral afectadas por la SCTLD tienen la capacidad de recuperarse naturalmente. En primer lugar, describimos la composición de las comunidades de corales juveniles después del brote en varios sitios con diferentes condiciones geomorfológicas y ambientales. Posteriormente, evaluamos la influencia de posibles factores ecológicos y ambientales en la presencia y diversidad de corales juveniles. Luego, estimamos la fecha de establecimiento de los juveniles de especies altamente susceptibles para inferir si los juveniles de coral sobrevivieron al brote o se reclutaron después del evento. Por último, analizamos la frecuencia de tamaño de colonias de especies afectadas en sitios impactados y saludables, comparando la estructura poblacional de corales afectados por la enfermedad.

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Original Article

Recovery and future perspectives of juvenile scleractinian corals following a disease-induced mass mortality event

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Keywords: recruitment, survival, population recovery, ecological shifts, disease outbreak

***Abstract*:** Diseases are widespread and harmful drivers of coral mortality. The most lethal outbreak ever recorded in the Caribbean is of Stony Coral Tissue Loss Disease (SCTLD), which resulted in mortality rates >90% in some species. This underscores the urgent need to understand the mechanisms that could promote natural recovery. We evaluated the condition of juvenile coral communities across a broad spatial gradient in the Mexican Caribbean following an SCTLD outbreak. We surveyed 65 affected sites and recorded juvenile (15 $m^2 \cdot site^{-1}$) and adult (60 $m^2 \cdot site^{-1}$) corals to identify the factors that affected juvenile abundance and diversity after the outbreak. We used size and species identity to estimate when juveniles established themselves in affected sites and compared the population structure of susceptible

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Introduction

The post-disturbance recovery of coral populations and communities relies heavily on the survival, recruitment, and growth of newly settled individuals (Caley et al., 1996). However, corals often exhibit high mortality during early life stages (Price et al., 2019), which can create bottlenecks in recovering populations (Vermeij and Sandin, 2008; Sarribouette et al., 2022). Thus, understanding the early life stages of corals can provide valuable insights into the long-term effects of disturbances, recovery, and resilience of coral populations (Gilmour et al., 2013; Doropoulos et al, 2015).

Stony Coral Tissue Loss Disease (SCTLD) is the most lethal disease ever recorded in the Caribbean and has threatened the populations of over 20 coral species over a remarkably short time frame (Alvarez-Filip et al. 2022). For instance, species like *Dendrogyra cylindrus*, *Dichocoenia stokesii*, *Eusmilia fastigiata*, and *Meandrina meandrites* experienced staggering mortality rates (>90%), while other species, such as brain corals, the *Orbicella* species complex, and *Montastrea cavernosa*, experienced notable population losses ranging from 20% to 60% (Álvarez-Filip et al., 2022; Papke et al., 2024). Furthermore, on afflicted colonies that survived, the reduction in colony living area and size can

compromise reproductive potential, ultimately hindering offspring numbers and impeding the potential recovery of affected species (Hartmann et al., 2017). The severity of the situation and the high number of affected species highlights the need to assess the natural processes of recovery of affected species, which are led by the incorporation of new individuals into the populations.

Recruitment and early life stage dynamics are the primary drivers of coral recovery, yet multiple biotic and abiotic factors intricately influence these processes. The settlement and recruitment of coral propagules rely heavily on the substrate, with success rates notably higher on topographically complex surfaces (Doropoulos et al., 2016) and those covered with crustose coralline algae (CCA; Jorissen et al., 2021). Conversely, high coral coverage or adverse benthic conditions, such as macroalgae or sediment cover, tend to impede juvenile recruitment and survival due to competition for space, allelopathy, or abrasion (Wittenberg and Hunte 1992; Box and Mumby 2007). Depth also seems to play a relevant role in shaping juvenile communities, as positive trends in juvenile density and diversity have been observed with increasing depth (Bak and Engel, 1979; Turner et al., 2018; Couch et al., 2023). However, the relationship between coral juveniles and these environmental variables can be altered by mass mortality events triggered by diseases (Aronson and Precht, 2001) or disturbances (Edmunds and Leichter, 2016), prompting questions about the persistence of these patterns following SCTLD outbreaks.

Coral reef recovery varies worldwide; however, a notable decrease in coral recruitment has been observed in recent decades, raising doubts of their recovery potential (Price et al., 2019; Edmunds, 2023). A prime example of this can be observed in Caribbean reefs, where rapid declines in coral cover and reef functionality (Alvarez-Filip et al. 2022), coupled with low recruitment rates (Edmunds, 2023), seem to have hampered their ability to recover (Huntington et al., 2011; Roff and Mumby, 2012). Another crucial concern stems from the species or functional groups that successfully establish and their ecological strategies (Kayal et al., 2015). For example, in recent decades, Caribbean coral communities have shifted from being dominated by massive, slow-growing, spawning corals to being increasingly represented by small, rapidly growing, brooding corals with elevated population turnover rates (Alvarez-Filip et al., 2013). Given that SCTLD primarily affects important reef-building species, most sites affected by this

disease are likely to be dominated by opportunistic corals (Alvarez-Filip et al. 2022). This change could further alter community dynamics, given that clear changes in coral recruitment in post-disease communities have already been observed (Hayes et al., 2022).

Wide-spread coral mortality has resulted from SCTLD in the Caribbean, causing non-random changes in community structure that have radically affected the functional integrity of these communities. In this study, we used extensive post-SCTLD data along a 450-km reef track in the Mexican Caribbean to investigate whether coral species affected by SCTLD have the capacity to recover naturally. We described coral communities across sites with different geomorphological and environmental factors to examine whether the patterns and predictors that drive juvenile corals' abundance and diversity still govern the post-outbreak composition of early-stage corals. Then, to gain insights into the impacts of SCTLD on coral recruitment, we estimated the establishment date for juveniles of highly susceptible species and determined whether they survived the outbreak or settled after the event. Lastly, we investigated the broad effects of the outbreak on the population structure of diseased-affected corals by analyzing the colony size frequency (including juveniles and adults) of affected species in both affected and unaffected sites.

Methods

The study area included 75 sites across the Mexican Caribbean (Fig. S1): 65 sites along the mainland and Cozumel Island were affected by SCTLD; the 10 sites of Banco Chinchorro were unaffected by SCTLD (Fig. S1; Alvarez-Filip et al. 2022). The data set included information from 63 fore-reefs and 12 back-reefs (1–24 m; Supplementary Data). Some of these locations were sampled twice, once in 2021 and again in 2022. The data from repeat sampling sites in 2021 were excluded from multivariate, diversity, and density analyses to prevent the sampling effort and year from inflating the data and introducing noise. Conversely, these sites were included in the estimations of settlement dates and size structure. The decision to include these sites was motivated by the goal of identifying the maximum number of species susceptible to SCTLD. The Banco Chinchorro data were used exclusively to compare affected and healthy sites in the size-structure analysis.

Coral community census

In this study, we defined a juvenile coral as any individual polyp or colony with a maximum diameter ≤4 cm (Edmunds, 2007). In each site, we established 4–8 transects for juvenile surveys (10 m × 0.25 m, 15 $m^2 \cdot site^{-1} \approx 1125\ m^2$ total area) and 4–9 transects for adult surveys (10 m × 1 m, 60 $m^2 \cdot site^{-1} \approx 4500\ m^2$ total area) (average of 6 ± 0.76 transects). The sampling effort for juveniles was significantly greater than in other studies and monitoring protocols because we aimed to maximize the possibility of including rare species, many of which have been affected by SCTLD.

We recorded the maximum diameter, minimum diameter, and height of all corals. Additionally, we checked for any signs of partial mortality, bleaching, or disease. All juvenile transects were conducted by highly experienced surveyors. Juvenile and adult densities were calculated for the entire sampling area. Due to the difficulties in identifying juvenile corals in field surveys and the non-destructive nature of our surveys, certain individuals were only classified at the genus level (*Orbicella* species complex, *Porites digitata* complex, *Scolymia* spp., *Madracis* spp., and *Mycetophyllia* spp.). We were unable to identify corals in only 15 cases.

Diversity

We used Hill numbers to represent the diversity patterns of coral juveniles after the SCTLD mass mortality event. The exponent 'q' serves as an indicator of diversity. A 'q' value of 0 makes the Hill number equivalent to species richness; as 'q' increases, greater emphasis is placed on common species over rare ones. When utilizing Hill numbers, diversity should be presented in terms of richness (q = 0), common species (q = 1), and dominant species (q = 2) (Chao and Jost, 2012). Given that sampling effort varied across sites, indices were standardized based on sampling coverage. Following the recommendations of Chao et al. (2014), a coverage of 1 was used to extrapolate the cases of q1 and q2, while a coverage of 0.95 was employed for q0. Extrapolation and rarefaction analyses were conducted using the 'iNext' package in R (R Core Team, 2023).

Predictors of juvenile density and diversity after SCTLD

We examined the factors influencing juvenile coral density patterns following SCTLD mortality in the affected sites. Our focus encompassed a range of biotic and abiotic variables, and we identified several

critical factors affecting early life stages (Table S1). To obtain information on benthic characteristics, we evaluated coral density and the coverage of CCA, algae, hydrocorals, and sediments. These variables were selected based on their negative or beneficial impacts on coral recruitment (Table S1). Additionally, we evaluated the influence of anthropogenic pressures, which have been shown to adversely impact coral survival and recruitment, such as population density, rising water temperatures, and thermal stress (i.e., maximum degree heating week). We also assessed the effects for some environmental conditions such as depth, latitude, and reef complexity.

First, we conducted a redundancy analysis (RDA) with all the covariates. Then, we performed an analysis of variance (ANOVA) to evaluate the impact of each predictor on the response matrix through sequential hypothesis tests. Based on these results, we refined the model to include only the variables that demonstrated a significant effect; these were adult coral density, depth, sediments, CCA, population density, and latitude (Fig. S2). Using these pre-selected variables of the RDA, we constructed linear models and a binomial logistic generalized linear mixed model to assess their effects on the density and presence of the most affected and the most abundant species, as well as species diversity. These models were built using the 'lmer()' function from the 'lme4' package in R (R Core Team, 2023).

Recruitment among dominant and highly susceptible species before and after the SCTLD outbreak

We used colony size and species to estimate when every juvenile coral established itself in the affected sites. First, we conducted an extensive literature review to obtain the growth rates for juvenile coral species (Table S2). When species-specific information was unavailable, we used the growth rate of the genus; if no information was available for the juvenile stage, we used data from the adults. We estimated the number of days that passed since recruitment by multiplying the maximum observed diameter by the daily growth rate of the species. We determined whether an individual recruited before or after the onset of SCTLD. For this, we assumed the outbreak started in Puerto Morelos in July 2018 and subsequently spread from north to south (Alvarez-Filip et al. 2019; Alvarez-Filip et al. 2022). We also assumed a spread rate of 1 $km \cdot day^{-1}$, as this rate was previously estimated for our study region (Estrada-Saldívar et

158 al., 2021). With this information, we were able to define a specific date for the onset of the SCTLD
159 outbreak in all sampling sites (Supplementary Data). If the number of days since recruitment was greater
160 than the estimated outbreak date for a coral, then the recruitment of that coral occurred prior to the
161 SCTLD outbreak. This standardization allowed us to effectively compare the recruitment dates of all the
162 observed corals.

163 ## Population size structure after SCTLD

164 To investigate the impacts of SCTLD on the size structure of the populations of the most affected
165 species, we calculated the total living area for all juvenile and adult corals in all sites, including those
166 impacted by SCTLD and those in Banco Chinchorro, which served as a control site as SCTLD was not
167 present. To ensure consistency despite variations in sampling size, we extrapolated juvenile records to
168 align with the adult sampling area.

169 We assumed that all colonies had a hemispheric shape and calculated the living surface area of
170 each following the methods of González-Barrios and Álvarez-Filip (2018). We log-transformed the living
171 surface area of each colony and assigned a size category (Vermeij and Bak 2002). The log transformation
172 increased the number of smaller size classes while reducing the number of larger size classes (Bak and
173 Meesters 1998), resulting in a relatively normal distribution of the data.

174 We then use the skewness, the coefficient of variation, mean colony size, and standard deviation to
175 describe distributions across various species susceptible species in affected and unaffected sites (Vermeij
176 and Bak 2002). In particular, skewness indicates the shape of the data distribution around the mean,
177 where a value different from 0 indicates that the distribution is asymmetric. This asymmetry can be
178 interpreted in two ways. If the skewness value is negative, the tail is skewed to the left, and most of the
179 size classes are large; in contrast, if the value is positive, most of the size classes are small (Vermeij and
180 Bak 2002). Skewness is also related to the input of new individuals into populations and coral longevity
181 (Bak and Meesters, 1998)

182

Results

Density and composition of juvenile corals in SCTLD-affected sites

After the SCTLD outbreak in the Mexican Caribbean, we recorded 4,209 juvenile corals (33 species, mean density of 4.18 ± 1.86 individuals·m^{-2}) in the affected sites. Additionally, we observed 22,254 adult colonies belonging to 43 species (average density of 5.34 individuals·m^{-2} ± 2.13) across all sampling sites. For some very rare species, such as *D. cylindrus* and *Mussa angulosa*, we found no juveniles and very few adults (we only observed adult *D. cylindrus* in the non-affected sites of Banco Chinchorro). Post-outbreak communities of juvenile and adult corals were dominated by three species: *Agaricia agaricites*, *Porites astreoides*, and *Siderastrea siderea* (Fig. 1a). Collectively, these species accounted for nearly 70% of all recorded individuals (Fig. 1). It is noteworthy that in the case of specific species, such as *S. siderea*, *E. fastigiata*, and *D. stockesii*, the density of juvenile individuals surpassed that of adults (Fig. 1a). In general, recruit density was positively influenced by adult density (Fig. 1b).

Post-outbreak dynamics of SCTLD in juvenile coral communities

The density of conspecific adults stands out as a key determinant of juvenile presence across various susceptible species and the density of the most abundant species (Fig. 2). This observation persisted regardless of the reproductive strategy of the species and susceptibility to SCTLD. Interestingly, while a positive relationship between conspecific juveniles and adults was evident at the species level (Fig. 2), a negative relationship was observed when analyzing the broader community. At the community level, the diversity indices (q1 and q2) declined with higher adult density (Fig. S3d, f).

Our analysis also shows that depth was strongly correlated with the presence of juveniles of nearly half of the species susceptible to SCTLD (Fig. 2a b). Moreover, depth was positively associated with higher diversity values across all Hill numbers (Fig. S3a, c, e). Additionally, in terms of species richness (q0), the presence of CCA also exhibited a positive effect on juvenile presence, although slightly less pronounced than depth (Fig. S3b), as this effect was only observed in two species: *A. agaricites* (Fig. 2a) and *P. strigosa* (Fig. 2b). Notably, for *S. siderea* and *A. agaricites*, latitude had a significant, yet opposite effect. Specifically, *S. siderea* exhibited an increase in juvenile density in southern reefs, whereas *A. agaricites* juvenile density increased towards the north (Fig. 2a). It is worth mentioning that,

while these variables were significant, their impacts were subtle (Table S3).

It is important to acknowledge the challenges in drawing definitive conclusions for certain species, such as *Diploria labyrinthiformis*, *M. meandrites*, and *Colpophyllia natans*, given the limited data points and resulting uncertainty in the calculated odds ratios. This underscores the necessity for further investigation and careful interpretations of the observed patterns in the post-outbreak scenario (Fig. 2b).

Recruitment among dominant and highly susceptible species

Overall, we found that almost all species affected by STCLD recruited before and after the outbreak. However, it is important to note that the majority of individuals for most species were recorded before the outbreak (Fig. 3). This makes the behavior of certain species, such as *E. fastigiata* and *D. stokesii*, particularly notable, as they showed significantly higher recruitment after the outbreak (92% and 62% of individuals recruited post-outbreak, respectively). Although not as pronounced as in the previously mentioned species, it is also noteworthy that nearly half of the recruits of *P. strigosa* established themselves after the outbreak. The pattern shown by this species hints at a potential recovery response to the substantial mortality experienced by the adult colonies.

We also found a clear difference in the recruitment of *A. agaricites* (n = 1659), *P. astreoides* (n = 1121), and *S. siderea* (n = 1002), which exhibited significantly greater numbers of recruits compared to the other species that were present in almost all sites. This difference became even more pronounced when we considered the low representation of juveniles from highly affected species, such as *M. meandrites* (n = 6), *C. natans* (11), and *D. labyrinthiformis* (10), as well as moderately affected species like *Orbicella* (20). This lack of juveniles was concerning and may suggest recruitment failure in these species (Fig. 3).

Comparison of size structure in SCTLD-affected and healthy sites

The size structure comparisons among the most susceptible species in affected and unaffected (i.e., Banco Chinchorro) sites revealed clear differences. Average colony size values were notably higher in Banco Chinchorro compared to the affected sites (Table S5). Additionally, skewness was evidently higher in the

sites affected by the disease (Table S5). Notably, highly affected species, such as *C. natans*, *D. labyrinthiformis*, *E. fastigiata*, and *M. meandrites*, showed pronounced changes. It is evident how the larger size categories were lost, affecting the average values in the impacted sites (Fig. 4c, d, f, h). This transformation was particularly conspicuous in *C. natans* (Fig. 4f); the differences between the means nearly doubled, and the skewness value was the highest recorded (Table S5). This clearly illustrates a change in the size structure of certain species due to SCTLD, with populations transitioning toward domination by smaller colonies.

Other species showed similar albeit subtler trends, including moderately affected species such as *P. strigosa*, *Montastrea cavernosa*, and *S. siderea* (Fig. 4a, b, i). While differences in average sizes and skewness were discernible (Table S5), these differences were less pronounced than those observed in the previously mentioned species. It is also important to highlight that the size distribution of *S. siderea* in affected and unaffected sites was skewed towards smaller sizes. In addition, colony size diminished even further following the onset of SCTLD (Fig. 4i).

In contrast, *Orbicella* was the only species with nearly identical average size and distribution values (Fig. 4i). Similarly, this species showed the lowest skewness, indicating a significant inclination towards larger sizes. Although the average size of *D. stokesii* remained comparable in affected and unaffected sites (Fig. 4i), the skewness indicated a reduction in population size.

Discussion

Stony Coral Tissue Loss Disease represents a breakpoint for the ecological integrity of Caribbean reefs. Given the magnitude of the resulting losses, understanding the roles of recruitment and juvenile dynamics is crucial to identify the natural recover potential of the affected species. Our findings confirm that the populations of several susceptible species underwent severe changes, not only in overall number but also in terms of the skewness of their size distributions, resulting in disproportionately smaller colonies. We recorded juveniles of most of the affected species during our surveys and identified consistent ecological patterns regarding the abundance and diversity of species, despite the mass mortality event. Overall, we found evidence that suggests that some species might naturally recover through recruitment, including

some species that are highly susceptible to SCTLD, such as *P. strigosa* and *E. fastigiata*. In these species, we found that a high proportion of juveniles had recruited to the population following the peak of the SCTLD outbreak, revealing that the surviving adults were still capable of sexually reproducing despite drastic decreases in their abundance (Quiroz et al., 2023). However, the prognosis is not as encouraging for the species that were most severely afflicted by SCTLD, such as *D. cylindrus* and *M. meandrites*. Indeed, we did not observe any living colony (either juvenile or adult) of *D. cylindrus* in the affected sites, and we only observed a small number of juvenile *M. meandrites*, which did not allow us to explore any trends for this species.

The juvenile community post-SCTLD was disproportionately dominated by three species: *A. agaricites*, *P. astreoides*, and *S. siderea*. The dominance of a few coral species within juvenile communities is not surprising, as similar patterns have been documented since the early 1980s (e.g., Bak and Engel, 1979; Rogers, 1984) and more recently following the SCTLD outbreak (Hayes et al., 2022). While *A. agaricites* and *P. astreoides* are brooder species and only mildly affected by the disease, *S. siderea* is a spawner and was moderately affected by SCTLD (40%) (Álvarez-Filip et al., 2021). Despite this, *S. siderea* shares similar traits with brooder species, such as high rates of population turnover and sexual maturity at small sizes that enables the larvae of this species to extensively settle near adult colonies, even under marginal conditions (Szmant, 1986; Edmunds, 2010; Gelais et al., 2016). These life history traits allow these three species to rapidly colonize space and dominate juvenile communities. This dynamic may create a positive feedback loop between adults and juveniles in the community (Hughes et al., 2000) and account for the positive relationship we observed between conspecific adults and juvenile density in these three species.

The widespread mortality of corals caused by SCTLD led to changes in species composition and a decrease in coral diversity. Despite these impacts, it is noteworthy that our study still identified certain consistent patterns in juvenile community structure; notably, we observed a positive relationship between depth and diversity, as shown in previous studies (Huston, 1985; Cornell and Karlson 2000). This trend persisted despite SCTLD affecting all depths similarly (Álvarez-Filip et al., 2022). The continued

presence of these patterns may indicate a form of ecosystem resilience and may suggest a hierarchy of environmental filters for the impacts caused by the disease (O'Neill et al., 1989). Similar to depth, benthic composition played a crucial role in structuring juvenile communities. We found that CCA coverage and adult density played significant yet contrasting roles in determining diversity and juvenile density patterns in different species. Higher CCA coverage may facilitate the establishment of various coral species (Vermeij & Sandin, 2008), thereby increasing site richness. On the other hand, high adult density could potentially reduce diversity due to competition for space among the adults and juveniles of different species (Connell et al., 2004).

However, it is also important to note that at the species level, we observed a positive effect of conspecific adult density on the density and presence of several species, including those affected by SCTLD. These findings suggest that recruitment in most coral species, regardless of their reproductive strategy, relies more on the local group of adults within the same site than on larval input from colonies at other sites. Contrary to previous assumptions, this may imply that Caribbean coral populations exhibit a more closed recruitment system, which is consistent with several studies showing a greater reliance on local recruitment over external recruitment (Caley et al., 1996; Roberts, 1997; Cowen et al., 2000). However, these results also prompt the question of whether this population behavior is typical or if the observed recruitment restriction may be partially attributed to historical disturbances and changes in environmental conditions (O'Connor et al., 2007; Cowen and Sponaugle, 2009).

Juveniles from most species were observed in our surveys post-SCTLD outbreak, although our results indicate that this proportion is significantly lower compared to pre-outbreak levels. Nevertheless, the recruitment of new individuals following the outbreak implies that despite substantial declines in population size and colony damage, adults retained some capacity for sexual reproduction (Quiroz et al., 2023). Our findings also show that some juveniles of the most afflicted species survived through the outbreak. This inference is supported by the fact that virtually no juvenile exhibited signs of the disease during our post-outbreak surveys. This can be interpreted as a differential resistance to the disease based on the life history stage and suggests that juveniles are less affected than adults (Green et al., 2016; Glynn

314 and Moss 2020). However, this interpretation does not agree with the available evidence regarding the
315 susceptibility of different life stages to SCTLD. Williamson et al. (2022) found that recruits of *C. natans*
316 and *D. labyrinthiformis* recruits and adults were similarly susceptible to SCTLD controlled conditions.
317 Additionally, Hayes et al. (2022) and Croquer et al. (2022) reported that small colonies and recruits were
318 equally prone to infection. Considering this evidence, it is likely that our observations reflect only the
319 surviving recruits without extending to the survival and resistance of all recruits. This suggests that the
320 abundance of juvenile corals from afflicted species may have been higher before the outbreak, and the
321 severity of the disease may have been comparable to that experienced by the adults.
322 One key question is whether the affected species will be able to recover naturally after the
323 SCTLD outbreak. Overall, we observed corals in early life history stages of most of the affected species,
324 which either resisted the outbreak or recruited after the mortality event. In both cases, our results are
325 positive and show some level of resilience of the affected populations at the regional scale. Furthermore,
326 we identified different population mechanisms that could lead to the potential recovery of some of the
327 affected species, at least in the short-term. A response marked by a considerable focus on recruitment
328 amidst mass mortality events could suggest a *Boom or Bust* strategy. Such a strategy would entail
329 prioritizing resource allocation towards reproduction rather than individual maintenance (Graham and
330 van Woesik 2013; Gelais et al., 2016). This could be the case for species like *E. fastigiata*, in which we
331 observed that most individuals recruited after the outbreak (Fig. 4). While species employing this strategy
332 in the Indo-Pacific have demonstrated recovery, it is important to note that they exhibit distinct
333 morphologies and ecological strategies than *E. fastigiata* (Edmunds 2018, Morais et al., 2021). Another
334 population mechanism that could promote recovery is the ability to tolerate disturbances and chronic
335 stressors in different life stages. Species like *P. strigosa* show remarkable longevity in large colonies,
336 resistance to fission, lower annual mortality rates for juveniles compared to other Caribbean corals (Bak
337 & Engel 1979, Edmunds 2004), and great adaptability to adverse conditions (Bumann et al., 2021; Coles
338 et al., 2018). These characteristics could explain the high survivorship of their juveniles and the capacity
339 of this species to sexually reproduce following the outbreak.

The remarkably low values and lack of juveniles for some other species are concerning and noteworthy and may be attributed to two reasons that are not necessarily mutually exclusive. The low juvenile values may be intrinsic to these species, as their life histories may not heavily rely on a consistent supply of juveniles for population turnover. Species that are crucial for the structure of the reef, such as the *Orbicella* species complex, could exhibit a *storage* effect (Warner and Chesson, 1985; Edmunds and Elahi, 2007) and recruit through infrequent "masting" events that unfold at broad temporal scales that have not yet been detected by ecological studies. However, even if this recruitment strategy is at work, some researchers question its capability for restoring populations to previous levels due to the extensive damage they have suffered in recent decades (Edmunds and Elahi, 2007).

The chronic stressors and frequent disturbances in the Caribbean compromise the recovery of species that were more prominent in previous decades such as *C. natans*, *M. meandrites*, *D. cylindrus*, and *D. labyrinthiformis*. The absence of juveniles of these species seems intricately tied to the decline in their populations, their colony sizes, and even the mortality of recruits rather than reflecting a specific ecological strategy that results in these notably low values (Williamson et al., 2022). This is evident in the striking disparity in juvenile density for these species from the 1980s to the present (Bak and Engel et al., 1979; Rogers, 1984). *Diploria labyrinthiformis* serves as a prime example to further illustrate this point. Although this species reproduces by spawning, it exhibits multiple reproductive events per year, a short planktonic phase, and rapid settlement, which have been associated with brooder reproduction and high recruitment rates (Chamberland et al., 2016). The exceptionally low abundance of individuals of this species cannot be solely explained by its reproductive strategy but also by the extensive population damage that it has suffered.

Our findings show a reduction in the size distribution of the affected species compared to those in sites not affected by SCTLD. This might have population-level implications. First, a decrease in the size distribution of a population might limit their reproductive capacity (Hartmann et al., 2017). This is particularly important as colony size plays a pivotal role in determining gamete production capabilities (Szmant, 1986). Furthermore, this mass mortality event unfolded in the context of a pre-existing

366 population decline of several species affected by the disease (Gardener et al., 2003). This historical trend,
367 coupled with the high mortality attributed to the disease, exacerbates the already notable decrease in
368 population size (Álvarez-Filip et al., 2022).

369 More specifically, the observed size distributions and skewness in species like *D. stokesii*, *E.*
370 *fastigiate*, and *S. siderea* illustrates that large colonies are relatively rare in the populations of affected
371 and unaffected sites. However, their sizes in affected sites diminished further. This aligns with the
372 findings reported by Lewis (1997) and suggests that skewness could be a consequence of biotic and
373 abiotic disturbances. For species like *P. strigosa* and *M. cavernosa*, the survival of large-sized colonies is
374 crucial for maintaining healthy populations (Edmunds, 2004). Our study also revealed a decline of these
375 specific size classes within sites affected by SCTLD. This observation underscores that despite the
376 occurrence of relatively high recruitment, a notable segment of the population characterized by larger
377 sizes was adversely affected, which poses a considerable challenge for this species to recover.

378 Ultimately, the recovery of affected species will rely on the survival into adulthood of some of
379 the juveniles and their ability to successfully reproduce. Consequently, conducting long-term monitoring
380 that follows the trajectories of these populations is crucial for drawing more robust conclusions and
381 generating a deeper understanding of post-disturbance dynamics in coral juvenile communities. One of
382 the key highlights from our findings is the potential to identify priority conservation sites to conserve
383 diversity and protect the populations of the species that were impacted the most by SCTLD. We suggest
384 prioritizing sites with depths ≥10 m that contain adults of the affected species. These sites could serve as
385 crucial refuges to safeguard the diversity and populations of the affected species (Bongaerts and Smith,
386 2019).

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395 **Author contributions**

396 RDT and LAF conceived the ideas, EPC and LAF designed the methodology; RDT, EPC and LAF
397 collected the data; EPC processed and systematized the data, RDT analyzed the data; and RDT and LAF
398 led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval
399 for publication.

400 **Conflict of interest**

401 On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Figure 1

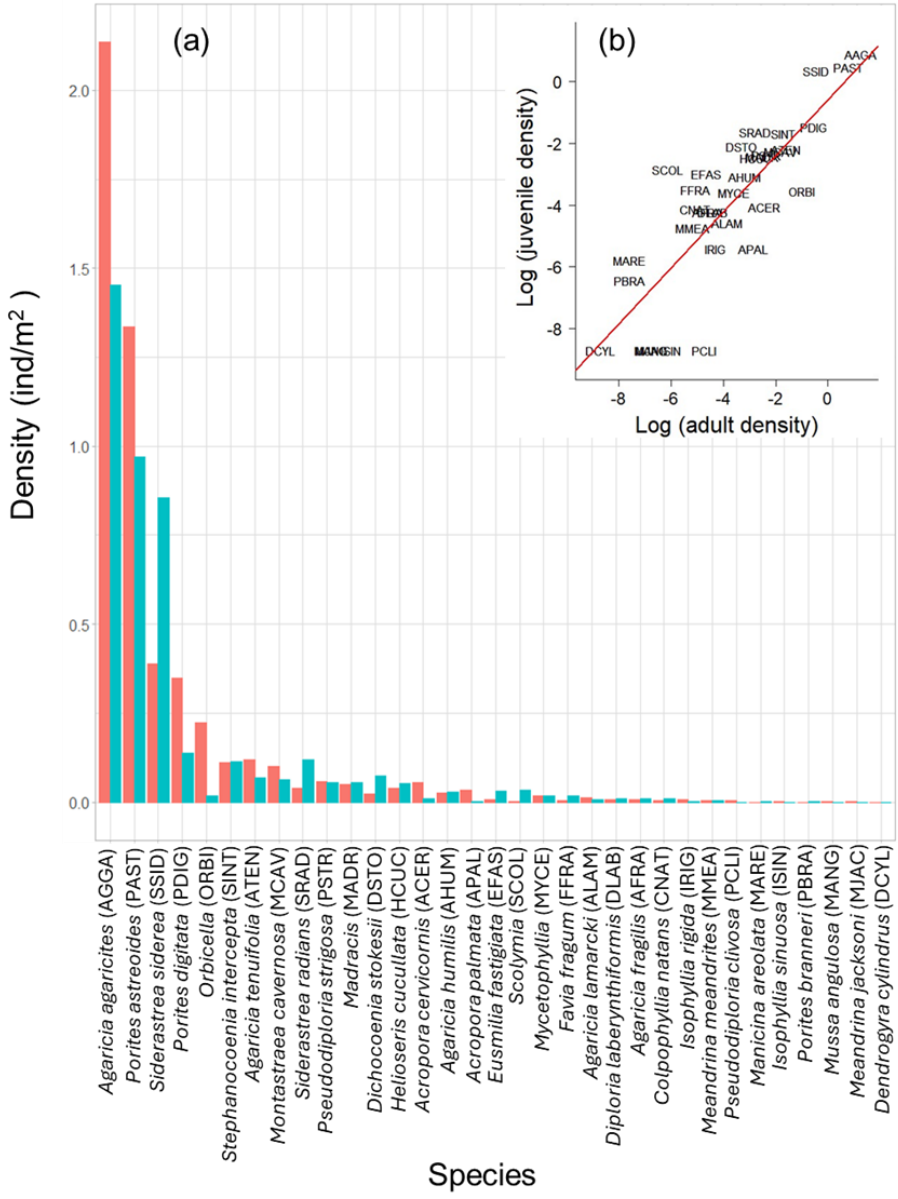


Figure 1. Post- Stony Coral Tissue Loss Disease (SCTLD) community composition in the affected sites of the Mexican Caribbean. (a) The density of juveniles (blue) and adults (red) of different species along a broad spatial gradient in the Mexican Caribbean post-SCTLD. (b) Positive relationship between adult and juvenile density. The red line represents the values predicted from a linear model of juvenile density as a function of adult density for each species.

Figure 2

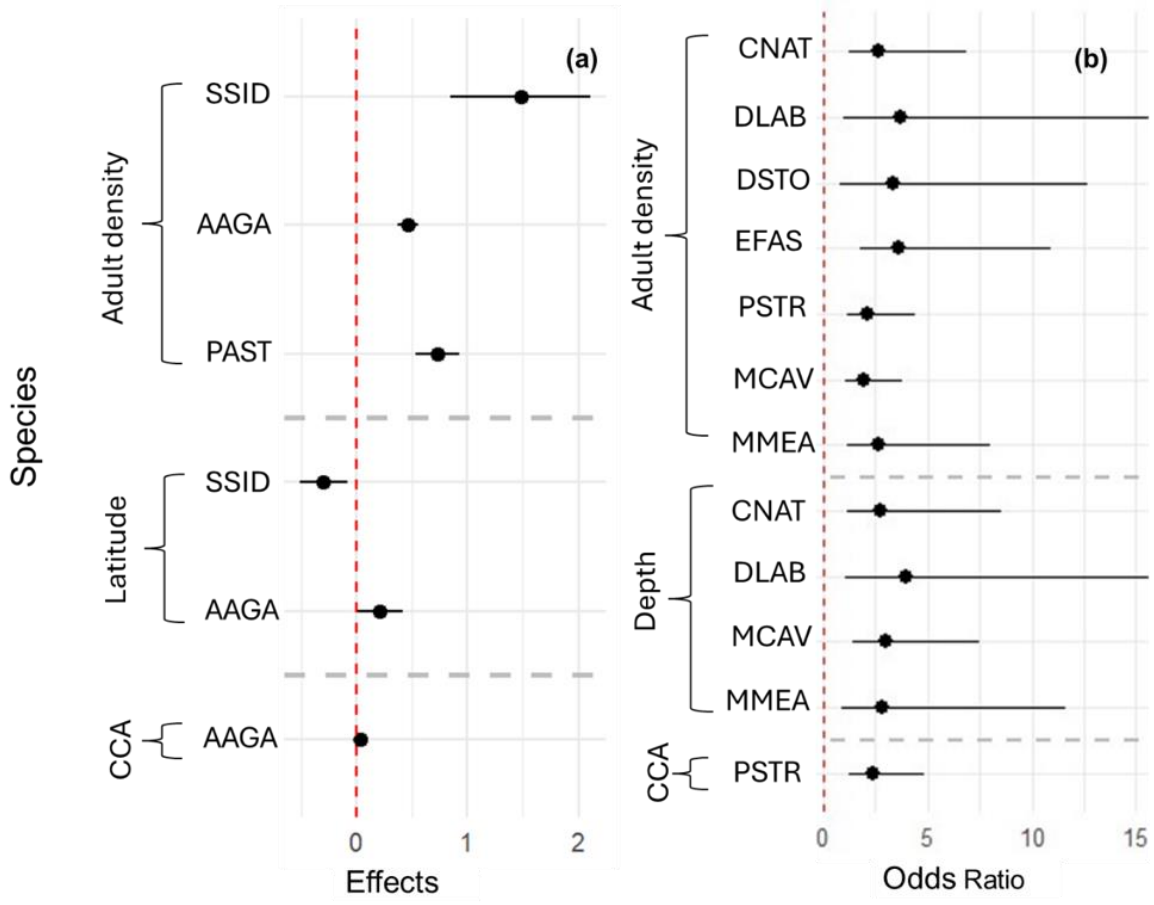


Figure 2. Covariates determining the density and presence of juveniles of the most abundant and highly susceptible species to Stony Coral Tissue Loss Disease (SCTLD) in the affected sites of the Mexican Caribbean. (a) Effects of the significant predictors for density; these estimates were calculated from linear models for species with adequate sample sizes (Table S3). (b) The odds ratio associated with the significant predictors of the presence of highly susceptible species to SCTLD; the presence probabilities were estimated from generalized linear models with a binomial distribution for species with adequate sample sizes (Table S4). The dots and lines represent the means and 95% intervals. Species codes are the same as in Figure 2.

Figure 3

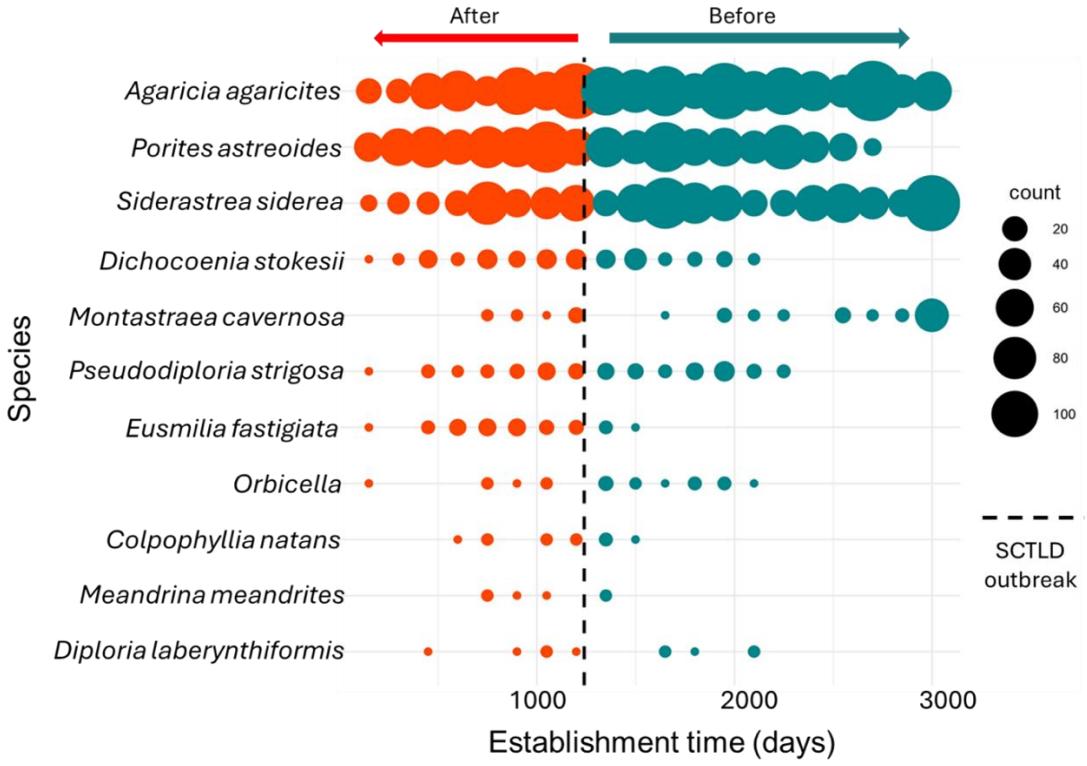
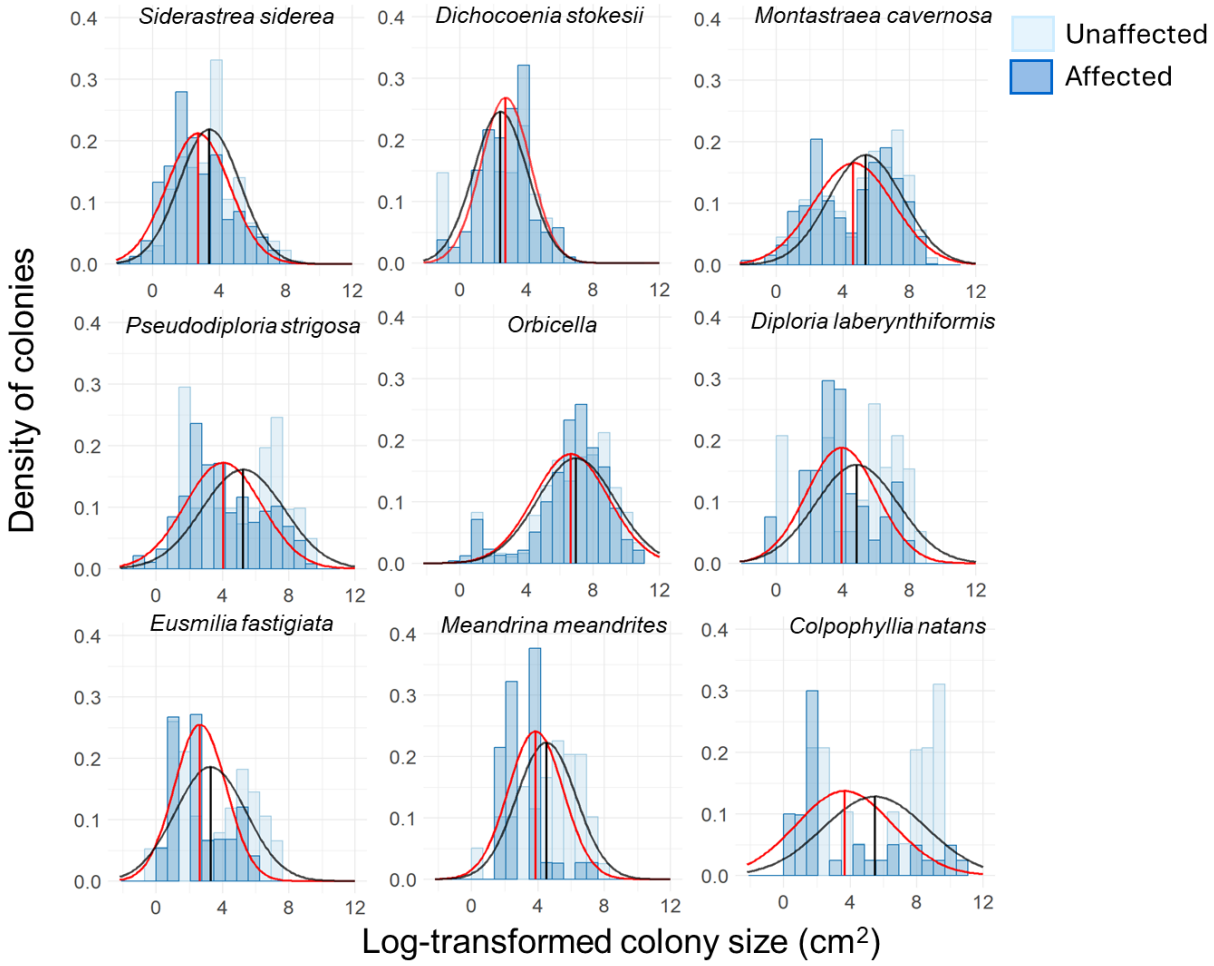


Figure 3. Distribution of establishment time (days) following recruitment for the juveniles of dominant and highly susceptible species to Stony Coral Tissue Loss Disease (STCLD) and the three most abundant species in the Mexican Caribbean. Each circle represents a class of days since recruitment; the size of each circle indicates the number of individuals in each class. The blue circles represent the individuals recruited after the onset of STCLD, while the red circles represent individuals already present in the community. The dotted line indicates the onset of the disease outbreak in relation to the sampling date (see methods).

598 **Figure 4**



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601 **Figure 4. Colony size decline post- Stony Coral Tissue Loss Disease (SCTLD)**. Log-transformed size-
602 density distributions of the colonies or individual polyps of the most susceptible species to STCLD in the
603 affected sites (solid blue) and unaffected sites (transparent blue) in the Mexican Caribbean. The predicted
604 normal distributions are displayed for the affected sites (red) and unaffected (black); the solid vertical
605 lines in the middle of each distribution represent the mean log-size of that species.

606

607 **Supplemental information**

608 **Table S1. Variables used as predictors in the models.**

Variable	Description	Justification	Data source
Adult Density	Density of all stony coral species in the site	High adult density can limit substratum space for coral recruits; competition via allelopathy can also occur (Chadwick and Morrow 2011)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
Depth	Mean site depth	Light is one of the main factors affecting reef growth and species depth distributions can be influenced by the substrate preferences of larvae at settlement (Baird et al., 2003; López-Londoño et al 2021)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
Turf algae-sediment mat	Sum of turf algae and sediments	High sediment conditions tend to impede juvenile recruitment and survival (Wittenberg and Hunte 1992	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
Fleshy macroalgae	Coverage of all fleshy macroalgae in the site	High algae coverage can limit substratum space for coral recruits; competition via allelopathy can also occur (Box and Mumby 2007)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
Calcareous macroalgae	Coverage of all calcareous macroalgae in the site	High algae coverage can limit substratum space for coral recruits; competition via allelopathy can also occur (Box and Mumby 2007)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
CCA	Coverage of all CCA in the site	CCA facilitate coral recruitment through microbial or chemical cues (Jorissen et al., 2021).	Data collected by the Biodiversity and Reef Conservation Laboratory during

			the 2021–2022 census
Hydrocoral	Coverage of all hydrocorals in the site	High hydrocoral coverage can limit substratum space for coral recruits; competition via allelopathy can also occur (Chadwick and Morrow 2011)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census
Population Density	Total population density in different sites along Mexican Caribbean coast	Coastal development can negatively influence coral reefs (Burke et al., 2011)	Population Explorer (2020)
DHW max	Maximum DHW	DHW is correlated with coral bleaching, which increases coral stress (Kayanne, 2017)	National Oceanic and Atmospheric Administration (NOAA)
Latitude	Latitude	Different sub-regions in geographical terms can be recognized by latitude (Jordán-Dahlgren 1993), and different management and costal impacts can be observed (Suchley and Alvarez-Filip, 2018)	Data collected by the Biodiversity and Reef Conservation Laboratory during the 2021–2022 census

609 *CCA: crustose coraline algae; DHW: degree heating week

610

Table S2. Caribbean species growth rates ($mm \cdot year^{-1}$) used in the study. Among all available sources for growth data on juveniles, we prioritized those containing the most recent information, as Edmunds (2007) suggested that current juvenile growth rates could be significantly lower than those observed several decades ago.

Species/Genera	Growth rate ($mm \cdot year^{-1}$)	Reference
Agaricia agaricites	5.2	Edmunds 2007
Colpophyllia natans	8.6	Schelten 2002
Diploria labyrinthiformis	7	Edmunds 2007
Dichocoenia stokesi	7.8	Schelten 2002
Eusmilia fastigiata	10.2	Schelten 2002
Montastrea cavernosa	2.7	Schelten 2002
Meandrina meandrites	12.3	Schelten 2002
Orbicella	7.6	Torres y Morelock 2002
Porites astreoides	6.1	
Pseudodiploria strigosa	7	Edmunds 2007
Siderastrea siderea	4.2	Edmunds 2007

Table S3. Parameters of the linear models used to determine the presence of juveniles of the most abundant species in sites affected by Stony Coral Tissue Loss Disease (SCTLD) in the Mexican Caribbean. Only the 65 affected sites were included in this analysis (Banco Chinchorro sites were excluded). Asterisks (*) indicate significant values ($p > 0.10$).

Predictor	Estimate	Standard Error	t value	Pr(>|z|)
	Siderastrea siderea			
Intercept	6.26	2.24	2.795	0.007*
Adult density	1.48	0.315	4.7	1.65×10^{-5}*
Depth	-0.003	0.017	-0.214	0.831
Turf algae-sediment mat	0.005	0.007	0.682	0.499
CCA	0.006	0.011	0.557	0.579
Latitude	-0.299	0.108	-2.774	0.007*
Population density	-2.95×10^{-7}	3.47×10^{-7}	-0.848	0.39975
	Agaricia agaricites			
Intercept	-4.23	2.25	-1.877	0.066*
Adult density	0468	0.048	9.675	1.04×10^{-13}*
Depth	-0.02	0.018	-1.19	0.239
Turf algae-sediment mat	0.003	0.006	0.611	0.544
CCA	0.043	0.011	4.109	0.0001*
Latitude	0.210	0.108	1.942	0.057
Population density	-3.43×10^{-7}	3.41×10^{-7}	-1.008	0.318
	Porites astreoides			
Intercept	-0.486	2.25	-0.216	0.83
Adult density	0.735	0.095	7.685	2.07×10^{-7}*
Depth	0.03	0.018	1.657	0.103
Turf algae-sediment mat	0.006	0.006	0.855	0.396
CCA	-0.018	0.012	-1.471	0.147
Latitude	0.001	0.108	0.088	0.93
Population density	1.02×10^{-7}	3.45×10^{-7}	0.296	0.768

Table S4. Parameters from generalized linear models with binomial distributions used to determine the presence of juveniles of highly susceptible species in sites affected by Stony Coral Tissue Loss Disease (SCTLD) in the Mexican Caribbean. Only the 65 affected sites were included in this analysis (Banco Chinchorro sites were excluded). Asterisks (*) indicate significant values ($p > 0.10$).

Predictor	Estimate	Standard Error	z value	Pr(>|z|)
	Colpophyllia natans			
Intercept	-2.68	0.598	-4.484	0*
Adult density	0.985	0.416	2.368	0.018*
Depth	1.017	0.494	2.061	0.039*
Turf algae-sediment mat	-0.223	0.509	-0.439	0.661
CCA	-0.139	0.581	-0.24	0.811
Latitude	0.382	0.574	0.666	0.505
Population density	-0.535	0.768	-0.697	0.486
	Pseudodiploria strigosa			
Intercept	-0.174	0.283	-0.614	0.539
Adult density	0.745	0.338	2.206	0.027*
Depth	0.030	0.328	0.093	0.926
Turf algae-sediment mat	-0.444	0.325	-1.367	0.172
CCA	0.854	0.336	2.538	0.011*
Latitude	0.110	0.377	0.293	0.770
Population density	0.151	0.327	0.461	0.645
	Montastraea cavernosa			
Intercept	-0.203	0.306	-0.665	0.506
Adult density	0.643	0.327	1.965	0.049*
Depth	1.097	0.418	2.627	0.009*
Turf algae-sediment mat	-0.170	0.315	-0.540	0.589
CCA	-0.112	0.324	-0.347	0.729
Latitude	-0.129	0.396	-0.324	0.746
Population density	0.107	0.392	0.274	0.784
	Meandrina meandrites			
Intercept	-3.305	0.798	-4.140	0.000*
Adult density	0.967	0.466	2.075	0.038*

Depth	1.046	0.616	1.699	0.089*
Turf algae-sediment mat	0.160	0.542	0.296	0.768
CCA	0.239	0.660	0.362	0.717
Latitude	1.171	1.119	1.047	0.295
Population density	-0.312	0.923	-0.338	0.736
	Dichocoenia stokesii			
Intercept	-0.262	0.310	-0.842	0.400
Adult density	1.204	0.597	2.018	0.0436 *
Depth	0.306	0.317	0.966	0.334
Turf algae-sediment mat	0.421	0.297	1.420	0.156
CCA	-0.346	0.331	-1.047	0.295
Latitude	-0.473	0.365	-1.295	0.196
Population density	-0.542	0.437	-1.239	0.215
	Eusmilia fastigiata			
Intercept	-3.737	1.750	-2.135	0.033*
Adult density	1.653	0.753	2.196	0.028*
Depth	-0.038	0.524	-0.072	0.943
Turf algae-sediment mat	-0.588	0.652	-0.901	0.368
CCA	-0.343	0.568	-0.603	0.547
Latitude	-0.505	0.516	-0.979	0.328
Population density	-3.753	3.608	-1.040	0.298

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Table S5. Descriptive statistics of log-transformed size-density distributions of colonies or individual polyps of the species most susceptible to Stony Coral Tissue Loss Disease (STCLD) in affected sites and unaffected sites in the Mexican Caribbean.

Site	Species	n	Mean colony size (cm^2)	SD	CV	Skewness
Affected	MCAV	761	4.624	2.413	52.184	-0.211
Unaffected	MCAV	349	5.376	2.233	41.533	-0.500
Affected	PSTR	542	4.046	2.312	57.147	0.297
Unaffected	PSTR	58	5.236	2.474	47.258	-0.237
Affected	CNAT	63	3.664	2.905	79.289	1.105
Unaffected	CNAT	23	5.488	3.108	56.625	-0.062
Affected	EFAS	111	2.644	1.564	59.159	1.077
Unaffected	EFAS	106	3.281	2.147	65.436	0.132
Affected	DSTO	456	2.737	1.484	54.205	-0.083
Unaffected	DSTO	39	2.421	1.623	67.038	-0.469
Affected	DLAB	81	3.925	2.123	54.081	0.189
Unaffected	DLAB	24	4.827	2.492	51.621	-0.462
Affected	ORBI	1125	6.668	2.248	33.716	-1.000
Unaffected	ORBI	226	6.975	2.334	33.466	-0.794
Affected	MMEA	77	3.860	1.656	42.894	0.860
Unaffected	MMEA	91	4.509	1.791	39.718	-0.405
Affected	SSID	6005	2.722	1.878	68.989	0.495
Unaffected	SSID	1305	3.402	1.824	53.606	0.167

n:sample size; SD: standard deviation; CV: coefficient of variation; SSID: *Siderastrea siderea*; ORBI: *Orbicella*; MCAV: *Montastraea cavernosa*; PSTR: *Pseudodiploria strigosa*; DSTO: *Dichocoenia stokesii*; EFAS: *Eusmilia fastigiata*; DLAB: *Diploria laberynthiformis*; CNAT: *Colpophyllia natans*; MMEA: *Meandrina meandrites*.

Figure S1

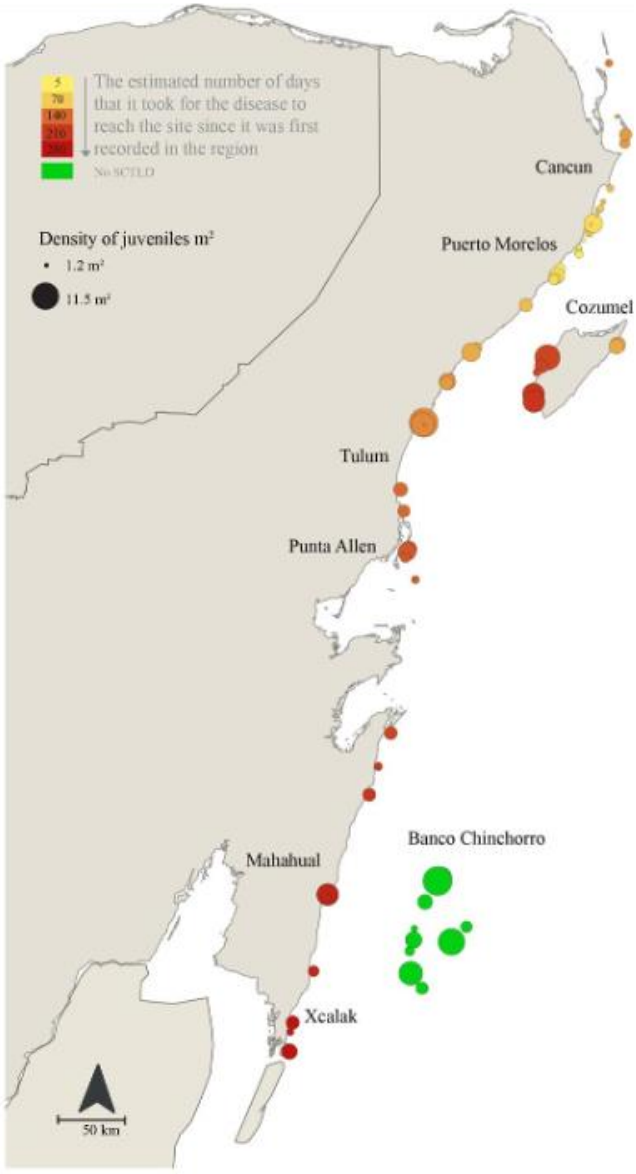

Figure S1. Juvenile Density and Outbreak Timeline in Surveyed Sites of the Mexican Caribbean Post- Stony Coral Tissue Loss Disease (SCTLD). Locations of the 75 monitored reef sites: 65 were affected by STCLD, and the 10 sites in Banco Chinchorro were not affected. The circles represent each site; circle size indicates juvenile density; circle color indicates the estimated number of days until SCTLD reached the site following the first report of the disease in the region.

Figure S2

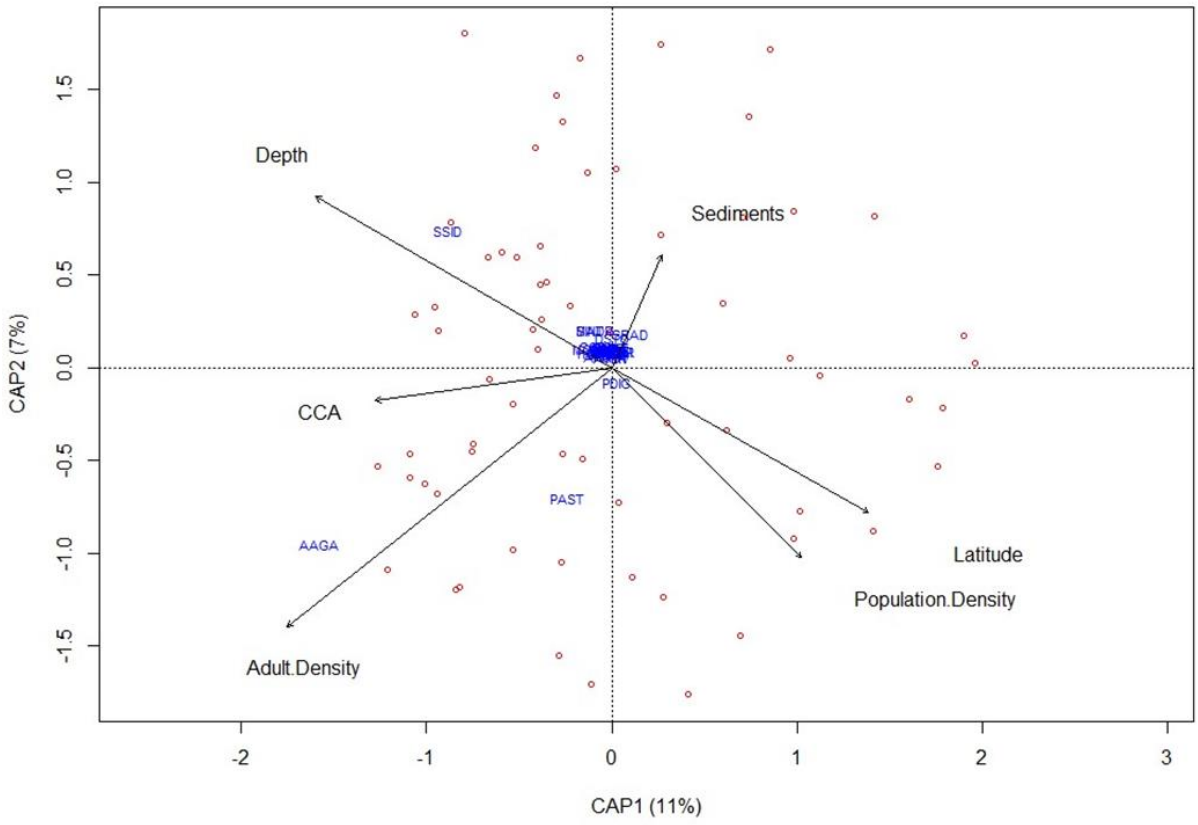

Figure S2. Redundancy analysis (RDA) of the sampling sites based on a matrix of species densities and biotic and abiotic variables. The variation explained by the two axes was 18%. The sites are represented by the red dots; the species are represented by the blue letters. CCA, crustose coralline algae; AAGA, *Agaricia agaricites*; SSID, *Siderastrea siderea*; PAST, *Porites astreoides*.

Figure S3

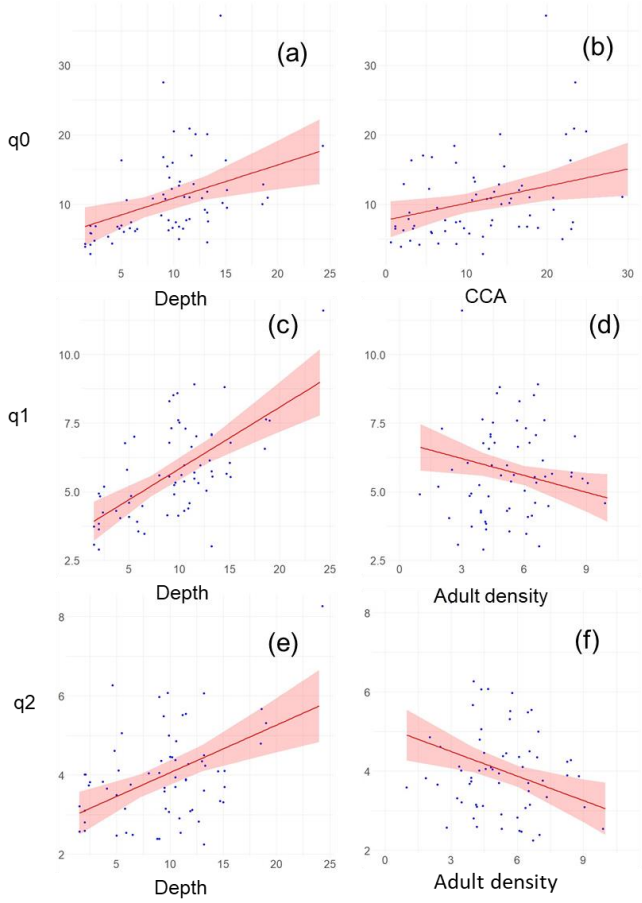

Figure S3. Diversity predictors of coral juveniles after a mass mortality event. Diversity of different orders as a function of depth (a,c,d), CCA (b), and adult density (d,f); only significant covariates are represented. The blue dots represent the rarefied or extrapolated values of diversity per site, and the red line represents the predicted value of the model. The shaded red bands represent the confidence intervals for each model.

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Discusión General

En nuestro estudio registramos juveniles de la mayoría de las especies de coral del Caribe Mexicano. Encontramos una densidad media por sitio de 4.18 juveniles/m^2, estos valores son mucho más bajos que los reportados a inicios de la década de los 80´s, en donde se reportaban valores de cerca de 15 y 17 juveniles/m^2 (Bak y Engel 1979, Rogers, 1984); sin embargo, son consistentes con los valores encontrados en arrecifes más actuales del Caribe (Chiappone y Sullivan, 1996; Ruiz-Zárate y Arias-González, 2004; Lozano-Cortés y Zapata 2015). La disminución del reclutamiento en el Caribe es un fenómeno que ha estado ocurriendo durante décadas (Chiappone y Sullivan; Arnold y Steneck, 2011; Price et al., 2019). Varios factores han contribuido a este problema, entre ellos están la reducción de la cobertura coralina y la pérdida de colonias grandes, lo cual afecta directamente la capacidad reproductiva de las poblaciones (Hartmann et al., 2017). Asimismo, la degradación del hábitat y la disminución de herbívoros han favorecido la colonización y competencia por el espacio de organismos incapaces de formar la estructuras necesarias para sostener los arrecifes (Precht et al., 2020; Estrada-Saldivar et al., 2021).

La comunidad juvenil está claramente dominada por tres especies: *Agaricia agaricites*, *Porites astreoides* y *Siderastrea sidereae*. Esta tendencia no es sorprendente, ya que desde principios de los años 80 se reportan resultados similares (Bak y Engel 1979; Rylaarsdam, 1983; Rogers, 1984) y estudios más recientes también respaldan esta observación (Chiappone y Sullivan, 1996; Ruiz-Zárate y Arias-González, 2004; Lozano-Cortés y Zapata 2015), incluso después de la SCTLD (Hayes et al 2022).

A pesar de este evento de mortalidad masiva, es importante destacar que en nuestro estudio se siguen observando ciertos patrones relacionados con la estructura comunitaria; por ejemplo, una relación positiva entre la profundidad y la diversidad de juveniles (Huston, 1985; Cornell y

Karlson 2000). El mantenimiento de estas tendencias sugiere que existe un tipo de resiliencia del ecosistema (Nystrom et al 2000), y también podría indicar una jerarquía de estos filtros ambientales sobre los impactos causados por la enfermedad (O´Neill et al., 1989). Al igual que la profundidad, la composición del bentos es determinante en la estructuración de las comunidades coralinas (Vermeij y Sandin, 2008; Chadwick y Morrow, 2011; Sandin y McNamara, 2011). En nuestro estudio observamos que las CCA y la densidad de adultos tuvieron un papel importante, aunque contrastante, en los patrones de diversidad y la densidad de juveniles de las distintas especies. Por un lado, una mayor cobertura de CCA puede facilitar el asentamiento de distintas especies de coral (Morse et al 1988; Vermeij y Sandin 2008; Price, 2010), y así aumentar la riqueza del sitio. Por el otro, una alta densidad de adultos, principalmente de especies pequeñas con reproducción incubadora y con alto recambio poblacional, podría generar una menor diversidad como resultado de la competencia por el espacio entre los adultos y los juveniles de las distintas especies (Connell et al., 2004; Chadwick y Morrow, 2011; Manikandan et al., 2017).

Sin embargo, es interesante observar que la densidad de adultos conespecíficos también tuvo un efecto positivo en la presencia de juveniles en la mayoría de las especies susceptibles a la SCTLD. Estos resultados sugieren que el reclutamiento de la mayoría de las poblaciones de coral, independientemente de su tipo de reproducción, depende más del grupo local de adultos en el mismo sitio que del suministro de larvas de colonias en otros sitios. Esto parecería indicar que las poblaciones de coral en el Caribe son más cerradas que abiertas, lo cual coincide con varios estudios en los que se ha visto una mayor dependencia del reclutamiento local que del externo, contrario a lo que se pensaba antes (Caley et al., 1996; Roberts, 1997; Swearer et al 1999; Cowen et al 2000; Almany, 2007; Manikandan et al., 2017). Sin embargo, estos resultados también plantean la pregunta de si este comportamiento en las poblaciones es normal o si la restricción

observada en el reclutamiento es en parte producto del disturbio histórico y de los cambios en las condiciones ambientales (O'Connor et al 2007; Cowen y Sponaugle, 2009).

Nuestros resultados ilustran claramente la alteración que hubo en las estructuras de tamaños de las distintas especies afectadas por el síndrome blanco. Es evidente que hay una disminución en el tamaño de las colonias en los sitios que fueron afectados. Esta pérdida podría limitar de manera importante su capacidad reproductiva, ya que el tamaño de la colonia influye determinantemente en la capacidad de producción de gametos (Szmant, 1986; Hartmann et al., 2017). Además, este evento de mortalidad masiva se da en un contexto en el cual previamente ya existía un decrecimiento poblacional para varias de las especies que fueron afectadas por la enfermedad (Gardener et al., 2003; Edmunds y Elahi 2007; Jackson *et al*., 2014). Esta tendencia histórica, aunada a la mortalidad tan alta ocasionada por la enfermedad, generó una disminución aún más marcada en el tamaño de las poblaciones (Álvarez-Filip et al., 2022).

Nuestras estimaciones indican que, aunque la mayoría de las especies tuvieron reclutamiento después de la SCTLD, la proporción observada es notablemente menor en comparación con los niveles previos a la enfermedad. Sin embargo, la presencia de este reclutamiento sugiere que las especies conservan alguna capacidad de reproducirse sexualmente, incluso después de los estragos ocasionados a sus poblaciones (Quiroz et al., 2023). Asimismo, nuestros resultados indican que la mayoría de los juveniles registrados en campo se establecieron antes del brote de la enfermedad, sugiriendo así su capacidad de sobrevivir al síndrome blanco. Esta suposición se ve reforzada al observar que prácticamente ningún juvenil presentó signos de la enfermedad. Esto podría interpretarse como una resistencia diferencial a la enfermedad según la etapa de vida del coral, indicando que los juveniles fueron afectados de menor manera que los adultos (Green et al., 2016;

Glynn y Moss 2020). Sin embargo, esta interpretación contrasta con la evidencia disponible sobre la susceptibilidad de diferentes etapas de vida ante la SCTLD. Williamson y colaboradores (2022) encontraron, en condiciones controladas, que los reclutas de Colpophyllia natans y Diploria labyrinthiformis fueron afectados de igual manera que los adultos. Además, Hayes y colaboradores (2022) encontraron en sus muestreos que las colonias pequeñas (5 – 14 cm de diámetro) fueron impactadas de manera similar que las colonias grandes; y, del mismo modo, Croquer y colaboradores (2022) encontraron lo mismo para los reclutas de especies afectadas en Puerto Rico. Tomando en cuenta esta evidencia, es muy probable que en nuestros resultados estemos registrando los reclutas que sobrevivieron, en lugar de implicar la supervivencia y resistencia de todos los reclutas al STCLD. Esto sugiere que la cantidad de juveniles de especies afectadas podría haber sido mucho mayor antes del brote, y podríamos estar subestimando su abundancia inicial y el impacto de la enfermedad, el cual podría haber sido comparable al experimentado por los adultos. También es importante mencionar que los cálculos de la edad de los juveniles y la estimación de las fechas de brote conllevan una incertidumbre importante, por lo cual hay que interpretar estos resultados con cautela.

Con base en el número de juveniles registrados post-síndrome blanco, solo se identifica una posible recuperación en las poblaciones de algunas especies afectadas mediante el reclutamiento, al menos en una escala temporal corta. Estas especies incluyen a *Dichocoenia stokesii*, *Eusmilia fastigiata*, *Pseudodiploria strigosa* y *Siderastrea siderea*. El caso de *Siderastrea siderea* es interesante ya que, aunque fue una especie afectada por el síndrome blanco (prevalencia del 40%) (Álvarez-Filip et al., 2021), fue una de las tres especies con mayor densidad de juveniles en todo el Caribe Mexicano. La gran abundancia de esta especie puede ser resultado de su capacidad de reproducirse sexualmente incluso en tamaños muy pequeños (desde 1 cm de diámetro) y de retener

localmente las larvas, además de su capacidad de sobrevivir y asentarse en condiciones marginales (Gelais et al., 2016). A pesar de que *Pseudodiploria strigosa* fue una de las especies más afectadas por la STCLD (Álvarez-Filip et al., 2022), es sorprendente ver que también fue una de las especies con mayor número de juveniles. Los mecanismos poblacionales por los cuales esta especie parece mantenerse son: gran longevidad de las colonias grandes, resistencia a la fisión, así como una mortalidad anual de los juveniles relativamente más baja que otros corales del Caribe (Bak & Engel 1979, Edmunds 2004). Tendencias similares se observan para *Eusmilia fastigiata*. Sin embargo, para esta especie resalta la proporción de individuos que se reclutaron después del Síndrome Blanco, y los pocos que sobrevivieron o se reclutaron antes del brote. Esta respuesta particular, en la cual se observa una apuesta importante por el reclutamiento ante eventos de mortalidad masiva, podría sugerir una estrategia Boom-Bust (Morais et al 2021, Edmunds, 2023). Dicha estrategia significaría optar por una mayor distribución de los recursos a la reproducción y no al mantenimiento del individuo (Graham y van Woesik 2013; Gelais et al., 2016).

Es preocupante la falta de juveniles de *Dendrogyra cylindrus* y la poca representación de otras especies como *Colpophyllia natans*, *Meandrina meandrites*, *Diploria labyrinthiformis* y el complejo *Orbicella*. Los valores tan bajos de juveniles en estas especies pueden deberse principalmente a dos razones no necesariamente excluyentes entre sí: 1) Estos valores bajos son normales para estas especies ya que en su historia de vida no es tan importante que haya una fuente abundante de juveniles constantemente para el recambio poblacional y dependan de otras estrategias para el mantenimiento de las poblaciones adultas y/o 2) la capacidad reproductiva de las poblaciones de las especies está comprometida por los grandes daños a sus poblaciones y por eso no se observan muchos juveniles de estas especies.

Conclusiones

Los monitoreos de juveniles en escalas espaciales amplias, así como en áreas extensivas de muestreo son cruciales, ya que ofrecen información invaluable acerca de los posibles cambios estructurales en las comunidades futuras y de su posible capacidad de recuperación natural. Esto cobra particular importancia en el contexto de disturbios como enfermedades y blanqueamiento en el que se encuentra el Caribe actualmente. Aunque los monitoreos realizados en un único momento en el tiempo no pueden reflejar las trayectorias de cambio (Condit et al. 1998), la combinación de factores como la mortalidad, la disminución en la estructura de tamaños y la falta de juveniles sugiere una situación crítica para el mantenimiento de las poblaciones de estas especies, *Colpophyllia natans*, *Meandrina meandrites*, *Diploria labyrinthiformis* y *Orbicella* tanto en el presente como en el futuro. Sin embargo, por el lado positivo, nuestros resultados nos permitieron reconocer algunas especies que podrían tener una recuperación natural en los arrecifes del futuro, como *Sideratsrea siderae*, *Pseudodiploria strigosa*, *Eusmilia fastigiata* y *Dichocoenia stokesii*. En última instancia, la recuperación de estas especies dependerá de la supervivencia de algunos de estos juveniles hasta la edad adulta y de su capacidad de dejar descendencia. En consecuencia, es crucial llevar a cabo un monitoreo a largo plazo y seguir la trayectoria de estas poblaciones para obtener conclusiones más fehacientes y asi lograr una comprensión más profunda de la dinámica post-disturbio en las comunidades juveniles de coral. Uno de los puntos más importantes de nuestros resultados es la posible identificación de sitios prioritarios para la conservación de la diversidad y de las poblaciones de las especies más afectadas por la enfermedad. Con base en lo que encontramos se recomendaría la selección de sitios con profundidades de 10 m o más y con presencia de adultos de las especies afectadas. Estos lugares podrían servir como una especie de refugio para el mantenimiento de la diversidad y de las poblaciones de estas especies (Bongaerts y Smith 2019).

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