

1 Historical and modern data sources reveal long-term declines in Caribbean
2 coral reef water quality

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26 coastal zone management

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36 **Abstract**

37 Although it is suspected that the widespread death of Caribbean corals is associated with
38 declining reef water quality from land-based pollution, this link has been difficult to quantify due
39 to a dearth of reef water quality data. To assess the role of land-based pollution in recent coral
40 declines, we synthesized paleoecological, historical, and modern data on reef water quality
41 across the Caribbean region from 1970-2021. We focused on two aspects of water quality that
42 have been most consistently collected in the Caribbean and have been shown to have direct
43 impacts on corals: nutrients (nitrogen and phosphorous) and water clarity. We analyzed trends
44 in water quality across the wider Caribbean and within individual well-studied countries or reefs,
45 providing insights into how the differing histories of land use and contrasting oceanographic
46 conditions have influenced the varying trajectories of reef water quality change and ecosystem
47 health. On a regional scale, nutrient concentrations had already exceeded established
48 thresholds beyond which coral health was compromised by the 1970s, nutrient levels increased
49 and water clarity decreased between the 1970s-2000, and nitrogen to phosphorous ratios were
50 negatively correlated with coral cover. Case study sites revealed that coral cover declines were
51 often related to water quality declines even in marine protected areas and at offshore reefs
52 previously thought to be less influenced by land-based pollution. This synthesis of long-term
53 historical data confirms the urgent need to mitigate land-based pollution to improve reef health
54 and resilience in the face of increasing alteration of coastal zones and climate change impacts.

55 **Author Summary**

56 The survival of reef-forming corals is threatened by climate change and local human stressors.
57 As climate impacts accelerate, interventions to improve coral health are imperative. Land-based
58 pollution negatively affects coral health via several pathways, but this stressor is understudied

59 due to a lack of reef water quality monitoring. Here, we synthesize reef water quality data from
60 historical and modern sources across the Caribbean to assess the role of land-based pollution in
61 recent coral losses. We find that nutrient concentrations associated with land-based pollution
62 have increased since the 1970s, water clarity has declined since the 1990s, and a nutrient
63 imbalance is correlated with coral losses during this period. These trends highlight the need for
64 improved water quality monitoring and integrated management of land and sea to promote
65 coral persistence.

66 **Introduction**

67 Caribbean coral reefs are under duress from multiple human stressors¹⁻³. Reefs in this region
68 have lost between 50-80% of their living coral cover since the late 1970s when systematic
69 ecological monitoring began, and reef-building corals have been largely replaced by benthic
70 macroalgae^{4,5}. Although accelerated coral loss has occurred via disease outbreaks and
71 anthropogenic climate change-driven bleaching⁶⁻⁹, historical and paleoecological data show
72 that the loss of coral species that are highly sensitive to water quality change were initiated
73 decades before the first recorded instances of these outbreaks¹⁰⁻¹². Since these early coral
74 losses, declining reef water quality has been chronically affecting Caribbean reefs^{13,14}, likely
75 exacerbating the recorded negative effects of overfishing, climate change, and diseases and
76 reducing the capacity of coral communities to recover from acute disturbances^{15,16}. The early
77 timing, taxonomic patterns, and unprecedented nature of recent coral community change¹⁷⁻¹⁹
78 implicate declining water quality as an important driver of these declines.

79 Increased levels of nutrients (both dissolved and sediment bound) and sediments from land-
80 based runoff due to increasing development and poor land management can affect reef corals
81 via several mechanisms. High levels of nutrients and sediment can interfere with the

82 physiological processes of the coral holobiont (coral, symbionts, and microbiome). For example,
83 nitrogen (in the form of dissolved inorganic nitrogen, DIN) and phosphorus (in the form of
84 soluble reactive phosphorus, SRP) from human sewage, manure, and fertilizers can increase
85 growth rates and abundance of algal endosymbionts^{20,21} and reduce the transfer of energy to
86 the coral host^{22,23}. Elevated DIN without a balanced supply of SRP can induce phosphorus
87 starvation in corals that are adapted to N-limitation and low N:P ratios, exacerbate coral
88 disease, and reduce the temperature and light thresholds for bleaching^{24–32} but see³³. Elevated
89 N:P ratios are now a common feature of many Caribbean coral reefs experiencing an oversupply
90 of N relative to P, as reported for the Florida Keys²⁸, Jamaica^{34,35}, the Mexican Yucatán region
91^{36,37}, and the Belize Barrier Reef³⁸. Increased levels of DIN and SRP and high N:P ratios can also
92 lead to growth and competitive advantage for benthic macroalgae, algal turfs, and crustose
93 coralline algae (CCA), which can smother, overgrow, reduce available surface area, and/or
94 reduce light availability to reef-building coral colonies^{35,39,40}. The replacement of corals by algae
95 is the most evident and consistent pattern observed on reefs across the Caribbean since large-
96 scale monitoring efforts began in the 1980s^{5,41}. Eutrophication can also drive deoxygenation of
97 reef waters and increase microbialization and microbial pathogenicity that can kill corals^{42–44}.

98 Increases in land-based or terrigenous sediments, often bound with nutrients, reduce light
99 penetration via increases in suspended particles and/or via stimulating phytoplankton blooms.
100 This results in reduced water clarity and light availability for algal symbionts and reduces the
101 phototrophic contribution of algal symbionts to the coral host metabolism, impacting their
102 growth and calcification rates^{45–47}. Terrigenous sediments can also negatively affect coral health
103 by smothering and abrading coral polyps, requiring corals to divert energy to sloughing off
104 sediments, and by inhibiting the settlement and survival of coral larvae^{48–51}. Along with

105 sediments and nutrients, land-based runoff can contain additional constituents that are harmful
106 to corals, including freshwater, heavy metals, microbial pathogens, toxins, pesticides,
107 herbicides, and endocrine disruptors ⁵².

108 Nutrient pollution has also been shown to affect disease resistance in corals ^{24,53,54}. via two
109 mechanisms: by increasing the density of algal symbionts (Family Symbiodiniaceae) which can
110 depress the expression of coral immune-related genes ^{20,23,55} and by disrupting the coral's
111 microbiome composition ⁵⁶, leading to increases in pathogenic bacteria ^{57,58}. These combined
112 effects can not only leave corals more susceptible to disease but can also reduce coral
113 reproductive success ⁵⁹, settlement rates ⁶⁰, growth rates ⁶¹, and resilience to thermal stress
114 ^{16,31,62}. Given that different coral species have different susceptibilities to the effects of increased
115 nutrients and sediments in the water column ⁶³, it is likely that these effects ultimately result in
116 changes in the community composition and physical structure of afflicted reefs ^{14,64,65}.

117 While the negative effects of land-based pollution on Caribbean reef health have been
118 documented by researchers for decades, the long-term cumulative effects of this stressor tend
119 to be generally overshadowed by the impact of acute catastrophic events such as bleaching.
120 However, several lines of evidence suggest that excess nutrients and sediments may be a
121 primary cause of coral loss and/or lack of recovery in the Caribbean. First, initial declines in
122 runoff-sensitive Acroporid coral abundance began decades before the first reported instances of
123 coral bleaching and were statistically related to human population density but not to
124 temperature stress ¹⁰. Second, centennial-scale growth rates of nearshore stress-tolerant
125 massive corals from the Mesoamerican Reef have declined more over time than offshore corals
126 with less exposure to land-based runoff ⁶⁶. Third, coral disease hotspots in the Caribbean are

127 near major sources of land-based pollution from agriculture and/or coastal development ^{6,28}.
128 Fourth, coral recruitment, abundance, diversity and health are negatively correlated with low
129 water quality and elevated local human activity ⁶⁷⁻⁷⁰. Last, abundance declines and
130 compositional changes in seagrasses which are adjacent to shallow coral reef habitats in the
131 Caribbean have also been linked to eutrophication ^{71,72}.

132 Although not tracked on a regional scale, the delivery of these land-based pollutants to
133 Caribbean reefs has likely increased dramatically over the past 50 years as a result of
134 accelerated land alteration for agricultural activities and urban, industrial, and tourism
135 development across this region ^{15,16,73-77}. Several factors have prevented a clear assessment of
136 the link between long-term declines in reef water quality and reef health in the Caribbean. First,
137 reef water quality trends have not been tracked over spatial or temporal scales commensurate
138 with the problem (watersheds and decades/centuries, respectively). Second, Caribbean reef
139 water quality is generally not monitored in a sustained or regionally coordinated manner ⁵.
140 Third, Caribbean coral loss began prior to the initiation of systematic surveys of reef ecological
141 communities ^{10,78,79}. This lack of baseline data on human and reef ecosystem dynamics has
142 hindered efforts to design integrated coastal zone management strategies in the Caribbean that
143 acknowledge the linkages and tradeoffs between land use and reef health. Last, sources of land-
144 based pollution impacting reefs may be distant and/or span national boundaries ⁷³, making it
145 difficult to link local activities on land with reef declines.

146 Fortunately, an underutilized trove of data exists that can be used to reconstruct long-term
147 change in reef water quality conditions and ecological change, enabling an assessment of
148 baseline reef water quality conditions and the role of land-based pollution in Caribbean coral

149 reef ecosystem degradation. These are historical data, in the form of: fossilized remains or
150 skeletons of reef organisms and specimens housed in natural history museum collections which
151 record water quality factors at the time of growth in their chemical compositions, historical
152 archives and notes from early scientific expeditions, archived historical satellite imagery of
153 coastal zones, and datasets from reef ecosystem monitoring programs, all of which can provide
154 decadal to centennial scale trends in reef water quality parameters directly relevant to coral
155 health. Coupled with information on reef ecosystem health and land use change from these
156 same types of historical data, it is possible to uncover the magnitude, timing, drivers, and
157 ecological consequences of Caribbean reef water quality change to motivate and inform
158 improved integrated coastal zone management.

159 Here, we focus on the Caribbean region, an enclosed sea that appears to be particularly
160 susceptible to land-based pollution impacts⁸⁰ and an area with a well-documented, relatively
161 early, and generally unidirectional history of coral reef decline. In this study, we (1) synthesize
162 the existing types of historical data that can be utilized for reconstructing change in coral reef
163 water quality to quantify the role of land-based pollution in reef declines, (2) demonstrate the
164 utility of historical data for tracking reef water quality change via an initial synthesis of historical
165 and monitoring data, (3) identify gaps in current and past reef water quality monitoring efforts,
166 and (4) call on national and regional reef management entities, academic institutions, multi-
167 lateral agencies and conservation NGOs to begin or continue ecologically-appropriate,
168 methodologically-rigorous, and sustained reef water quality monitoring efforts that are
169 standardized across the Caribbean region. This will allow for the detection of linkages between
170 water quality improvements and reef ecosystem recovery and help set ecologically meaningful

171 reef water quality targets that can support conservation and restoration efforts and promote
172 reef resilience in the face of increasing overfishing and climate change impacts.

173 **Relevant historical data**

174 Historical reef water quality can be reconstructed via a compilation of paleoecological data,
175 natural history collections, historical archives, remote sensing data, field studies, and modern
176 monitoring programs (Figure 1).

177 *Paleoecological data and natural history collections*

178 Fossils and the more recent non-fossilized remains of reef organisms can provide a record of
179 reef water quality extending several millennia. Coral cores (from individual long-lived coral
180 heads) and reef sediment cores (“reef matrix” cores) can provide a continuous record of reef
181 water quality and condition changes on millennial to centennial timescales and at decadal to
182 annual resolutions using several different approaches. The chemical signatures within reef-
183 building corals, octocorals, mollusks, algae, and seagrasses from reef sediment cores, coral
184 cores, specimens housed within natural history collections, and the taxonomic composition of
185 fossils preserved within reef sediment cores provide proxies of inputs of land-based nutrients,
186 sediments, freshwater, water clarity, and sediment oxygen levels while those organisms were
187 alive and/or those sediments were being deposited. Within coral skeletons, the abundance of
188 trace metals such as Barium (Ba), Calcium (Ca), and Yttrium (Y) provide a record of relative
189 change in land-based sedimentation^{81–83}, measures of total N and total P provide proxies of
190 relative change in total nutrient content, respectively^{84,85}, and $\delta^{15}\text{N}$ measurements indicate the
191 dominant source of nitrogen input (effluent or synthetic fertilizer)^{85–90}. Coral response to
192 changing water quality can also be assessed using the thickness and density of annual growth

193 bands in coral cores^{91,92}. Within coral and reef sediment cores, relative change in land-based
194 sediment input can be measured by measuring the weight of non-reef sediments via acid-
195 insoluble residues methods^{48,93}. Due to the known environmental tolerances of several reef
196 organisms, the composition of benthic foraminifera and bivalves within reef sediment cores can
197 provide a relative measure of change in water clarity and sediment oxygen levels^{75,94}.

198 *Historical archives*

199 Historical archives (drawings, photographs, or written records) left behind by early travelers and
200 residents of coastal regions in the Caribbean can provide information both on reef status and on
201 drivers of change extending as far back as the period of European contact (early 1500s). For
202 example, information on coral presence and extent can be derived from early observations
203 preserved in historical documents, such as nautical charts which documented reefs as a
204 navigational hazard^{95,96}, as well as historical aerial photographs of reef habitats⁹⁷. Comparisons
205 of 18th and 19th century charts to modern reef extent have documented a loss of nearshore
206 corals that may be associated with land use changes as well as dredging and filling operations
207 for development and navigation. In Florida, development of the Everglades for agriculture
208 altered freshwater inputs with widespread impact to nearshore corals in the Florida Keys^{96,98}. In
209 Brazil, increased sedimentation and siltation due to deforestation are concentrated in regions
210 where early coral loss was documented from historical charts⁹⁵. Such nautical charts exist for a
211 variety of locations in the Caribbean, including the Meso-American reef, parts of which were
212 surveyed between 1835-41⁹⁹. Early scientific expeditions also document coral community
213 composition, which can be used to track changes in diversity and dominance over time^{18,100}.

214 Historical maps, survey records, and aerial photographs are also useful for tracking changes in
215 land use that can directly impact nearby coral reefs. Colonial mapping and exploration resulted
216 in maps of valuable resources. For example, maps associated with the development of the
217 logwood trade in the late 18th century document the extent of forest prior to this impact.
218 Relevant documents include those associated with colonial exploitation, such as annual
219 handbooks prepared by colonial officers describing resources available for exploitation, as well
220 as export records that document the extent of exploitation and trade. For example, export
221 documents show that nearly 30,000 tons of logwood were shipped from Belize at the peak of
222 the industry in the late 19th century¹⁰¹. Together, this early archival information has the
223 potential to describe baseline states of coral reef-adjacent land prior to extensive deforestation
224 and development for agriculture, as well as the presence and composition of reefs.

225 *Remote sensing data*

226 Satellite imagery can provide a high temporal (daily to annual) and spatial (< 30m to kilometers)
227 resolution record of changes in reef water quality metrics from the 1970s to present. Water
228 quality proxies include measures of water clarity conditions such as photic depth (which can be
229 directly converted to Secchi depth; see next section) and turbidity as well as chlorophyll a, a
230 measure of phytoplankton productivity which is often correlated with nutrient input, and total
231 suspended sediments, a measure of land-based sedimentation^{102,103}. Satellite imagery can also
232 be used to quantify land use and land cover change (for example, change in the proportional
233 cover of unaltered to altered land within an individual watershed or broader landscape; e.g.,¹⁰⁴,
234 the main cause of increased land-based inputs to reefs^{105,106}.

235 *Field studies and monitoring programs*

236 Modern field studies and monitoring programs constitute a rich source of data for tracking
237 decadal-scale change in reef water quality since the 1970s. Numerous studies have recorded the
238 N, P, and/or $\delta^{15}\text{N}$ content of reef water samples as well as within tissues of living algae and
239 gorgonians^{93,107,108}. In water samples, N and P content are typically measured as total inorganic
240 nitrogen (DIN) and soluble reactive phosphorus (SRP), while in organisms they are typically
241 measured as total N and total P. Many of these measurements are from one-off studies that
242 were conducted at a single point in time at a given location, limiting their utility for assessing
243 change. However, several research teams working across the Caribbean have collected repeated
244 measurements, providing a decadal-scale time series of reef water quality change within a single
245 reef site or reef tract (see Table S1;^{28,38,84,85}).

246 Several reef monitoring programs have been undertaken within the Caribbean by governmental
247 agencies, academic research teams, and research consortia, although only a few have
248 implemented standardized and consistent efforts for water quality measurements related to
249 land-based inputs. A critical example is the Caribbean Coastal Marine Productivity (CARICOMP)
250 program, a monitoring effort undertaken by a network of local marine science laboratories
251 across 21 countries from 1992-2015 that measured the ecological structure and environment of
252 reefs, seagrasses, and mangroves¹⁰⁹. CARICOMP data represent the most temporally and
253 spatially extensive record of measurements for physical environmental data in the Caribbean,
254 including water temperature, salinity, and light attenuation (the latter measured via lowering a
255 “Secchi” disk into the water column and recording the depth at which it is no longer visible - i.e.,
256 the Secchi depth; Figure 1). CARICOMP data are high quality due to the standardized
257 methodologies used across study sites and adherence to sampling protocols that accounted for
258 seasonal variability by sampling physical parameters weekly throughout the year. Unfortunately,

259 CARICOMP was disbanded in 2015 due to a lack of funding, although monitoring continues at
260 select sites by local marine laboratories ¹⁰⁹.

261 More recent water quality monitoring efforts in the Caribbean utilize *in situ* or portable data
262 loggers to reduce effort in the field and allow for higher frequency sampling. Notable examples
263 include the Smithsonian Institution's Marine Global Earth Observatory (MarineGEO) Network
264 which has implemented a standardized protocol for monitoring several physical water column
265 parameters (including chlorophyll a, turbidity, salinity, and temperature) in reefs in Belize and
266 Panama since 2015 ¹¹⁰. Multiyear water quality monitoring programs are also implemented by
267 governmental agencies. However, government-led monitoring efforts in most Caribbean
268 countries have been sporadic and often utilize inconsistent and/or unreliable sampling
269 methodologies, complicating efforts to utilize these data to discern long-term or regional trends
270 ¹¹¹. A notable exception to this is the Florida International University's Southeast Environmental
271 Research Center (SERC) program, which has implemented consistent monitoring of several
272 water quality parameters from reefs in Florida since 1995 ^{112,113}. Although additional large-scale
273 programs exist for measuring the physical parameters of reef waters such as temperature,
274 salinity, and pH (e.g., the US National Oceanic Atmospheric Administration's National Coral Reef
275 Monitoring Program; ¹¹⁴), these programs do not typically measure parameters specifically
276 related to land-based pollution.

277 **METHODS**

278 **Reconstructing reef water quality change from existing historical data**

279 To better understand the local and regional causes and consequences of reef water quality
280 change on reef ecosystem health, we assessed long-term trends at two different spatial scales:

281 (1) within individual countries or reef tracts (“Case Studies”) and (2) across the Caribbean region
282 as a whole by combining data from case studies and additional locations with time series for one
283 or more water quality metric of interest. This approach allowed us to understand how the
284 differing histories of land use and human population across locations have played a role in the
285 varying trajectories of reef water quality change and ecosystem health and to detect possible
286 Caribbean-wide trends.

287 We focused on two aspects of water quality that have been most consistently collected in the
288 Caribbean over the past 50 years and that have been shown to have direct negative impacts on
289 corals: nutrients and water clarity. For nutrients, we compiled timeseries of three common
290 measurements of the abundance of nitrogen and phosphorus, the primary limiting nutrients for
291 marine algal growth: **dissolved inorganic nitrogen (the sum of nitrate, nitrite, and ammonium,
292 or DIN), soluble reactive phosphorus (orthophosphate or SRP), and $\delta^{15}\text{N}$** . We also compiled
293 timeseries of measurements in the **ratio of nitrogen to phosphorus (DIN:SRP, or N:P)**. In
294 addition, we compiled data for two commonly collected metrics of water clarity, **Secchi depth**
295 and **turbidity**. Units of measurement were micromolar concentrations (μM) for DIN and SRP,
296 meters for Secchi depth, and Nephelometric Turbidity Units (NTU) for turbidity.

297 When available, established thresholds for each water quality parameter beyond which coral
298 reef health is compromised were indicated in our analyses. Reviews of eutrophication on coral
299 reefs from locations across the Caribbean and on the Great Barrier Reef, Australia show that DIN
300 values as low as 0.5-1.0 μM and SRP values as low as 0.1 μM -0.2 μM can trigger phase-shifts
301 from dominance of reef-building corals to benthic macroalgae^{28,35,115}, while N:P values beyond

302 20:1 indicate strong P-limitation that causes metabolic stress in corals through P starvation that
303 exacerbates coral disease, bleaching, and die-off ^{26,28,30–32}.

304 Data were obtained from non peer-reviewed sources (monitoring databases, government
305 reports, and PhD and Master’s theses) as well as from peer-reviewed literature ([Table S1](#)). Data
306 sources were located via expert knowledge of working group members and their networks and
307 from searches on Google Scholar using the search terms “Caribbean coral reef water quality”,
308 “Caribbean coral reef nutrients”, “Caribbean coral reef eutrophication”, “Caribbean coral reef
309 Secchi depth”, “Caribbean coral reef stable isotopes”, and “Caribbean coral reef turbidity”.

310 Although some of the reef water quality parameters of interest could be obtained from satellite
311 data, we focused our study on data collected *in situ* due to the lower spatial and temporal
312 resolution of historical satellite data. Our synthesis therefore focused on data from coral cores,
313 natural history collections, and water samples.

314 To assess the role of water quality change in declining reef health, we also compiled available
315 published data on living coral cover, a proxy of reef-building coral abundance, ([Table S1](#)). These
316 data were compiled for the locations which also had accompanying water quality data. Coral
317 cover was determined via underwater surveys that reported the percent of surveyed substrate
318 that was covered by living reef-building corals, determined by transects or quadrats. We then
319 assessed the relationship between the above water quality metrics and coral cover via linear
320 correlations for case studies (see below) and generalized mixed effects models (GLMMs) for the
321 region as a whole. All statistical analyses were conducted using the R software package ¹¹⁶;
322 GLMMs were conducted using the lme4 package in R ¹¹⁷, and model fit was assessed using the
323 sjPlot package in R ¹¹⁸.

324 Data collected from the same research team and reef site were considered a “study”. To ensure
325 data quality and comparability across studies, data sources which satisfied the following criteria
326 were included in our database: (1) sampling methodology was consistent throughout the study
327 or the study developed reliable conversion factors that enabled comparisons across studies
328 (e.g.,^{1,119}), (2) instrumentation with appropriate detection limits for water quality parameters
329 was utilized, (3) at least two replicate samples were collected in the same location and by same
330 research team within the same year, (4) samples were collected from reef habitats not obviously
331 influenced by submarine groundwater discharge (i.e., salinity was at least 32 parts per mil), and
332 (5) the following metadata were included: reef site name, latitude and longitude, water depth of
333 sampling, reef zone, month and year of sampling, frequency and number of replicate samples,
334 and units of measurement for each water quality parameter. For each study, water quality
335 values were summarized yearly and decadal by computing averages and standard deviations
336 across replicates. For the subset of these study locations that also contained data on percent
337 living coral cover, annual and decadal averages were computed for this measure.

338 **Regional synthesis from available data**

339 To assess long-term Caribbean-wide trends in water quality and the degree of temporal and
340 spatial disparities in these trends, we synthesized all of the existing data that met the criteria
341 described above (Table S1, Figure 2). For each water quality parameter, average values were
342 computed for each year and individual study. Regional trends were then determined via
343 generalized linear mixed effects models that accounted for variation in sampling intensity over
344 space and time by estimating regional values for each water quality parameter as a function of
345 year as a fixed effect and country as a random effect¹²⁰. These regional trends were assessed for
346 the four water quality parameters for which there was sufficient temporal and spatial coverage

347 for models to converge: DIN, SRP, N:P, and Secchi depth. To assess the effect of these water
348 quality parameters on reef ecosystem health, we also modeled coral cover as a function of each
349 water quality parameter as a fixed effect and country as a random effect. For this analysis,
350 decadal averages of water quality parameters and coral cover were compared. Only sites which
351 contained at least 5 years of data for a particular water quality parameter were included in the
352 regional analyses.

353 **Case studies**

354 We utilized particularly well-studied reefs as case studies to showcase the varying trajectories
355 and ecological causes and consequences of reef water quality change, focusing on reefs within
356 the following five locations: **(1) Discovery Bay, Jamaica, (2) Central and Southern Belize, (3)**
357 **Quintana Roo, Mexico, (4) Barbados, and (5) Florida Keys, USA** (Figure 2). To obtain a
358 comprehensive summary of all reliable data for a well-studied site, studies which met the
359 criteria described above and that contained at least two years of data were included. Following
360 are brief descriptions for each case study that outline reef environmental conditions that
361 influence reef exposure to land-based runoff, possible indirect atmospheric deposition (e.g., ash
362 from widespread agricultural burns) and the recent history of (a) human dynamics on land that
363 have affected land-based runoff and reef water quality change, (b) other major (chronic or
364 acute) disturbances impacting reefs, and (c) documented reef ecosystem change.

365 *Discovery Bay, Jamaica*

366 Discovery Bay on the north shore of Jamaica contains one of the most well-studied coral reefs in
367 the Caribbean and serves as the earliest example of Caribbean reef collapse⁷⁹. Shortly after
368 systematic underwater reef monitoring began in the 1970s, reefs within Discovery Bay

369 underwent a phase shift from high diversity, coral-dominated reefs to algae dominated
370 ecosystems with reduced coral cover and diversity in the 1980s⁴¹. This shift has been attributed
371 to hurricanes¹²¹, overfishing of reef herbivores¹²²⁻¹²⁴, the *Diadema antillarum* urchin die-off
372^{41,125,126}, coral disease¹²⁷, and nutrient pollution from land-based runoff^{35,128,129}. Although the
373 role of overfishing in coral declines has been hypothesized for Discovery Bay and has resulted in
374 limited fisheries management interventions¹³⁰, the lack of systematic reef water quality
375 monitoring has made it difficult to ascertain the impact of this stressor.

376 Anthropogenic impacts to reefs within Discovery Bay include the presence of a small town,
377 terrestrial runoff from agricultural and urban developments, activities of fishermen, locals and
378 tourists engaging in marine recreation, the mining of bauxite within the Discovery Bay
379 watershed, and bauxite shipping from the large marine terminal in the bay¹³⁰. Sewage collection
380 and disposal consist of individual septic tanks or soak-away pits, the number of which has
381 proliferated since the 1970s concomitant with population increases in the area^{130,131}. Although
382 no permanent rivers flow directly into Discovery Bay, groundwater enters the bay through deep
383 cracks and vents in the porous basement limestone. Groundwaters in this part of Jamaica
384 seasonally contain high levels of inorganic nitrogen but are essentially devoid of phosphates¹³²,
385 providing a significant source of nitrate to reef environments, particularly after heavy rainfall
386 events¹³³. Although it is unclear whether these nitrates are derived naturally or from
387 agricultural fertilizers and urban waste waters, an increase in macroalgae such as *Chaetomorpha*
388 and *Dictyosphaeria* spp. on reefs since the 1990s may indicate increasing nutrient input^{130, 129}
389 also found evidence of nutrient enrichment in parts of the bay.

390 *Central and Southern Belize*

391 This case study represents two well-studied offshore locations within the Belizean Barrier Reef:
392 Carrie Bow Cay located on the edge of the barrier reef 18 km from the coast of central Belize
393 and Glovers Atoll located offshore of the barrier reef and 42 km from the coast of central Belize.
394 As Carrie Bow Cay has been the location of a Smithsonian Institution field station since 1972 and
395 was part of the CARICOMP monitoring network, it contains a particularly long timeseries of
396 water quality and coral cover that extends to the present ^{134,135}. Marked declines in coral cover
397 were first observed at Carrie Bow Cay in the 1980s and have been attributed to coral disease
398 outbreaks, with declines continuing following coral bleaching and hypoxic events ¹³⁴⁻¹³⁶. These
399 coral losses have resulted in increases in benthic macroalgal abundance that have persisted to
400 the present ^{134,137}. At Glovers Reef, a comparison of coral cover surveys conducted in the 1970s
401 and 1990s suggested a shift from coral to algal domination by the 1990s attributed to coral
402 mortality from unresolved causes and possibly maintained by low levels of reef herbivory and/or
403 nutrient enrichment from land-based runoff from Honduras ^{138,139}.

404 The Belizean economy was historically centered on slash and burn and commercial agriculture
405 including sugar cane, citrus, and bananas and is now centered on tourism ¹⁴⁰⁻¹⁴². This has
406 resulted in significant land alteration, including clearing of riparian forest buffers and coastal
407 mangroves, causing nutrient enrichment, sedimentation, chemical pollution, anoxia, and heavy
408 metal pollution of terrestrial waterways ^{143,144}. Although reef water quality monitoring has been
409 sporadic within Belize, a recent study showed significant nutrient (nitrogen) enrichment of
410 nearshore reef environments from largely untreated wastewater effluent from rivers and urban
411 centers in Belize has occurred since the 1980s ^{38,143,145}. Nutrient and sediment pollution from
412 land use and land cover change and human population growth also crosses national boundaries
413 - large sediment plumes from the Ulua and Motagua Rivers in Honduras and Guatemala whose

414 watersheds have been significantly altered from industrial banana agriculture can seasonally
415 impact water quality within the Belizean Barrier Reef lagoon ^{73,104}. Recent changes in lagoonal
416 reefs within the Southern Belize Barrier Reef appear to indicate impairment due to land-based
417 runoff: they lost their architecturally important, sediment-intolerant branching *Acropora* corals
418 by the 1980s and are now dominated by weedy, more sediment-tolerant corals from the
419 *Agaricia* genus as well as macroalgae ¹³⁶.

420 CARICOMP monitoring of Secchi depth near Carrie Bow Cay began in 1993 and consists of
421 weekly readings at two habitat zones. Water clarity (“Secchi depth”) via sighting of a Secchi disk
422 is measured horizontally at 0.5 m water depth at a site just inshore from the barrier reef and
423 2km from Carrie Bow Cay (“lagoonal” site) and measured vertically on the steep forereef slope
424 on the seaward side of the barrier reef bordering Carrie Bow Cay (“offshore” site). While no
425 obvious signs of water quality declines were observed at the start of reef water quality
426 monitoring at Carrie Bow Cay, this has changed since the 1990s in tandem with accelerating land
427 use change in this region. Land development has accelerated since the 1990s from increasing
428 tourism, urbanization, and agriculture, resulting in environmentally destructive development
429 activities along rivers that are hydrologically connected to the Belize Barrier Reef lagoon and
430 offshore atolls ³⁸. Interestingly, water clarity based on satellite datasets improved during
431 lockdowns associated with the COVID-19 pandemic ¹⁴⁶.

432 Glovers Atoll was established as a marine reserve in 1993 and is part of the Belize Barrier Reef
433 Reserve System UNESCO World Heritage Site. Despite a ban on the extraction of herbivorous
434 surgeonfish and parrotfish beginning in 2009 and observed increases in the size and biomass of
435 large parrotfish at Glovers Atoll since the fishing ban, no declines in macroalgae have been

436 noted ^{147,148}. At the same time, Glovers Atoll has seen significant increases in DIN, SRP, and N:P
437 concentrations over the last three decades with values exceeding established ecological nutrient
438 thresholds ^{145,149,150}. Elevated nutrients are likely from small resorts on the atoll and poorly
439 managed watersheds on the mainland, where deforestation, unsustainable agricultural
440 practices, and sewage is transported to the remote atoll by water currents and air (i.e., ash from
441 slash and burn) ^{13,151,152}. This nutrient enrichment may explain the high cover of macroalgae that
442 has persisted for several decades in the region even in the presence of healthy herbivore
443 populations ^{67,153} and the persistently low levels of living coral within the lagoonal areas of the
444 Belizean Barrier Reef ¹⁴³. Because it is far offshore of the barrier reef and contains no permanent
445 settlements, past researchers have doubted that the reefs surrounding Glover's Atoll would be
446 noticeably impacted by land use and water quality change ¹⁵⁴. However, satellite imagery
447 showed river plumes reaching Glovers Atoll and other parts of the Mesoamerican reef after
448 Hurricane Mitch in 1998 ¹³, and subsequent work has shown this was not an isolated incident ¹⁵⁵.
449 In addition, direct measurements within Glover's lagoon, fore-reefs, and freshwater sources
450 showed elevated nutrients ¹⁴⁵.

451 *Quintana Roo, Mexico*

452 The Puerto Morelos reef system is located in the northern portion of the state of Quintana Roo
453 in the Mexican Caribbean. This is a fringing reef system that stretches parallel to the coast
454 (between 1 and 3 km) in a semi-continuous formation. This reef system has an identifiable
455 zonation with a back-reef, reef crest and fore-reef that is mostly strongly influenced by wave
456 exposure and light penetration. Historically, it had a well-developed back-reef and reef-crest
457 that were dominated by *Acropora palmata*, which contributed greatly to the structural
458 complexity of the reef; while the fore-reef was mostly low relief (limited framework

459 development), gently sloping, and colonized by sparse coral growth, and grading gradually at a
460 depth of approximately 20–25 m into an extensive sand platform. In 1998, the Puerto Morelos
461 reef system was declared a marine protected area. However, the MPA only has a marine
462 component and has not been able to regulate the rapid rates of coastal modification, which
463 likely explains the observed rates of reef degradation. Coral communities in Puerto Morelos
464 have changed rapidly over the last three decades: coral cover has declined by almost 50%,
465 driven by the significant loss of framework-building branching, foliose and digitiform coral
466 species. This has resulted in a structural and functional convergence towards the dominance of
467 low-relief species that do not contribute to reef framework accumulation ^{64,156}.

468 This reef system is adjacent to a coastline that experienced rapid coastal development during
469 the last 30–40 years. Currently, over 10 million tourists visit the north of Quintana Roo annually,
470 and the local population has grown rapidly from 88,000 in 1970 to nearly 2 million in 2020 ¹⁵⁷.
471 Consequently, coastal waters of the region have experienced eutrophication and increased
472 sedimentation levels ^{37,67,84}. Coastal dredging, construction, and marine port construction
473 contribute sedimentation and have been associated with nearby reef degradation ⁶⁷. Hotels and
474 residences are often constructed without adequate wastewater treatment facilities and due to
475 the karstic terrain, seepage is of particular concern ^{158,159}. Furthermore, loss of forest and
476 mangrove vegetation owing to hotel construction and urbanization has reduced groundwater
477 filtration, further increasing nutrient concentrations reaching the ocean ¹⁶⁰. As a result,
478 eutrophication resulting from inadequate wastewater treatment is considered a principal driver
479 of declining reef condition in the region ⁷⁰.

480 Historical water quality timeseries were synthesized for six sites within the province of Quintana
481 Roo in the Yucatan Peninsula of Mexico, from a range of sources, including measures of $\delta^{15}\text{N}$
482 analyzed from cores from the scleractinian coral *Orbicella faveolata* and museum specimens of
483 gorgonian corals, DIN, SRP, and N:P ratios from water samples, and Secchi disk measurements
484 (Table S1). A more continuous timeseries for water sample and Secchi disk measurements and
485 coral cover data were available for Puerto Morelos due to semi-consistent monitoring when it
486 was part of the CARICOMP monitoring network ¹⁰⁹.

487 *Barbados*

488 Coral reefs in Barbados have a long history of human impacts including heavy fishing and
489 nutrient runoff from urban and agricultural areas ^{119,161–163} and provides an example of the
490 interacting effects of increased eutrophication and declining herbivory (grazing) on reef
491 ecosystem functioning. Qualitative descriptions ¹⁶⁴ and quantitative surveys ¹⁶⁵ of the reefs
492 fringing the west coast of the island indicate that live coral cover began declining as early as the
493 1960s and macroalgae began increasing in the 1970s ^{166,167}. Following hurricane Allen in 1980,
494 coral was further depleted along the entire coast ¹⁶⁸. Reef surveys of water quality and coral
495 cover along the west coast of the island that occurred just prior to the widespread die-off of the
496 keystone herbivore *D. antillarum* urchin in 1983/1984 provide helpful insights into the impacts
497 of rapid land development on corals before the onset of coral bleaching and coral and urchin
498 disease outbreaks ^{166,167,169}. These surveys identified a north-south gradient of increasing
499 eutrophication and decreasing *Diadema* densities ¹⁶⁶, suggesting that (a) coral was already
500 rapidly declining before the reduction in grazing possibly due to elevated nutrient levels, and (b)
501 the still relatively high grazing rates initially controlled benthic algae abundance and
502 composition. These early surveys also suggest that by the 1980s, algal growth rates were likely

503 already near or at a maximum and corals were therefore already physiologically impaired and
504 more susceptible to storm-induced damage, disease and algal overgrowth along the entire coast
505 ^{24,28,31,128}. By the 1990s, the entire coastline was nutrient saturated, and reefs were generally
506 algae-dominated. A recent study that mapped these patterns in space and time within a multi-
507 stressor framework showed that the trajectory of benthic cover over time in Barbados can be
508 explained as a function of both eutrophication and reduced grazing ¹.

509 *Florida Keys, USA*

510 Reef water quality decline within the Florida Keys National Marine Sanctuary has been a major
511 management concern since the 1980s following the large-scale hydrological alteration and
512 development of the upstream Everglades wetlands and discharge system , significant urban and
513 tourism development of the Keys resulting in the proliferation of septic systems that have
514 leached nutrients onto reefs, and dredging for shipping and boating ^{114,170}. Although the Florida
515 Keys was historically hydrologically connected to Lake Okeechobee north of the Everglades, this
516 connection was broken in the early 20th century when lake outflows were diverted easterly and
517 westerly to provide irrigation for expanding sugarcane agriculture within the Everglades and to
518 prevent storm surges from hurricanes. To address habitat degradation within the Everglades
519 due to restricted water flow, the historical outflow of the Okeechobee southerly through the
520 Everglades began to be restored in the 1980s and peaked in the 1990s, resulting in freshwater
521 runoff enriched with N and P from fertilizers and urban stormwater flowing into Florida Bay and
522 then on to the Florida Keys since that period. In response to seagrass die-offs in Florida Bay that
523 were initially attributed to hyper-salinity, with additional releases of polluted freshwater from
524 the Everglades system also occurring in the 1990s ^{28,171}. In response to increasingly degraded
525 reef water quality, a Water Quality Protection Program for the Florida Keys National Marine

526 Sanctuary was created, resulting in a consistent and standardized reef water quality monitoring
527 program that has been conducted annually by Southeast Environmental Research Center (SERC)
528 since 1995^{112,113}. The Florida Department of Fish and Wildlife has also conducted consistent
529 monitoring of reef benthic composition (including living coral cover) since 1996 through its Coral
530 Reef Evaluation and Monitoring Project¹⁷². Although standardized reef monitoring began in the
531 1990s, much of the physical alteration of the Keys (deforestation, dredging and filling of
532 mangrove and seagrass habitat, and construction of a network of residential canals) to support
533 the growing human population occurred prior to this, during the 1950s-1970s¹⁷³. Thus, reef
534 water quality was likely already significantly degraded in the Florida Keys by the 1990s when
535 quantitative observations began.

536 Despite the designation of the Florida Keys National Marine Sanctuary and the establishment of
537 a multi-agency Water Quality Protection Program, water quality within the Keys remains greatly
538 impaired²⁸. Since the 1990s, outbreaks of coral disease and episodes of bleaching have
539 increased, resulting in coral die-offs and coral to algal phase shifts²⁸. There is much evidence to
540 support a link between coral mortality and water quality declines: during this same period, N
541 content and the N:P ratio increased on reef waters, with high $\delta^{15}\text{N}$ values indicating increased
542 sewage pollution from septic systems^{28,174}. Although ocean temperatures at some sites within
543 the Keys exceeded the coral bleaching threshold since the 1990s, a 3-decade study found that
544 mass bleaching events only occurred when N:P ratios were elevated following increased
545 Everglades runoff, highlighting the role of nutrient pollution in reduced coral resilience²⁸. In this
546 study, we synthesized changes in reef water quality and coral cover at three well-studied reef
547 sites spanning a gradient of exposure to land-based inputs: Carysfort Reef in the Upper Keys,
548 Alligator Reef in the Middle Keys, and Looe Key in the Lower Keys). Reefs in the Upper Keys are

549 least exposed to waters discharged from the Everglades via Florida Bay, reefs in the Middle Keys
550 are most exposed, and reefs in the Lower Keys have a moderate degree of exposure to runoff
551 from Florida Bay^{175,176}. Thus, Carysfort Reef, Looe Key, and Alligator Reef represent
552 lowest/moderate/greatest exposure to land-based runoff, respectively.

553 **RESULTS**

554 **Regional synthesis**

555 Our regional dataset spanned from 1972-2021 and included 30 studies, 25 reef sites, and 12
556 countries total across all four water quality metrics with sufficient coverage across space and
557 time (DIN, SRP, N:P, and Secchi depth) as well as coral cover data (Figure 2). Datasets for
558 individual water quality metrics were a subset of this full database ([Figure S1](#)). Generalized
559 linear mixed effects models revealed notable regional trends in each of these water quality
560 metrics, although the magnitude and/or direction of trends varied across countries (Figure 3).
561 Linear models provided the best fit for temporal trends in the SRP, N:P, and Secchi depth data,
562 whereas a negative binomial model provided the best fit for temporal trends in the DIN data.
563 Model-fitted annual values of DIN averaged across all reef sites increased from 1.42 to 3.90 μM
564 from 1972 to 2021, constituting a 275% increase in DIN over this 49-year time span (Figure 3a).
565 Between 1972 and 2020, model-fitted average annual values of SRP increased 208% from 0.13
566 to 0.27 μM (Figure 3b) and model-fitted average annual values of N:P increased 500% from
567 10.79 to 53.96 (Figure 3c). Secchi depth values declined within all countries except for Barbados
568 and Bermuda. Between 1992 and 2020, model-fitted average annual values of Secchi depth
569 decreased 20% from 17.13 to 13.58 meters (Figure 3d). All of these metrics indicate worsening
570 water quality for the majority of reef sites over this time period.

571 A comparison of decadal averages of water quality metrics and percent living coral cover
572 revealed that the N:P ratio was significantly related to coral cover, while DIN, SRP and Secchi
573 depth did not have a significant relationship with coral cover (Figure 4). Generalized linear mixed
574 effects models with country as a random effect found a negative curvilinear effect of the N:P
575 ratio on coral cover, with this model finding that N:P explains 12% of the variation in decadal
576 values in coral cover across sites (Figure 4c). A second-degree polynomial model provided the
577 best fit for this relationship.

578 **Case studies**

579 *Discovery Bay, Jamaica*

580 The available reef water quality data for Discovery Bay indicates that the water quality record is
581 too sparse and recent to conclusively assess the role of this factor in documented coral declines.
582 Trends in nutrients from 1980-2010 indicate that DIN, SRP, and N:P values were already
583 exceeding the thresholds for negative impacts to corals by 1980. Although DIN and SRP declined
584 throughout this time period, SRP declined below threshold levels more rapidly than DIN (Figure
585 5A). These differential rates of change resulted in N:P ratios exceeding threshold values in 1980,
586 1987, 2002, and 2010 but not in 1998 (Figure 5B).

587 Although the Secchi depth record does not begin until 1992, it indicates a clear decline in reef
588 water clarity within the bay from 28.2 to 19.8 m between 1992 and 2000 and a leveling off from
589 2000 to 2002 (Figure 5C). The monitoring of reef benthos began in 1972, prior to water quality
590 studies, and indicates a clear decline in coral cover prior to the 1980s (Figure 5D; ⁵. These early
591 declines may be attributed to longstanding overfishing that removed reef herbivores ¹²⁴ and/or
592 early water quality declines that occurred prior to water quality monitoring and have not been

593 documented. Annual coral cover values were not linearly correlated with annual values of DIN,
594 SRP, N:P, or Secchi (comparison of coral cover and Secchi shown in Figure 5E). Discovery Bay
595 represents a site where substantial local human stressors predate water quality monitoring, and
596 thus where data from paleoecological material or natural history collections are necessary for an
597 adequate assessment of the role of land-based pollution in observed reef degradation.

598 *Carrie Bow Cay and Glovers Reef, Belize*

599 Carrie Bow Cay contains the longest continuous timeseries of *in situ* measurements of water
600 quality change in the Caribbean. Consistent (generally weekly) Secchi depth measurements have
601 been collected at two reef sites described above (lagoon and offshore site, Figure 6A). This
602 timeseries reveals that water clarity declined by 18% between 1993 and 2019 within both reef
603 zones, from 12.8 to 10.5 m in the lagoon site and 23.8 to 19.4 m in the offshore site. At the
604 lagoon site, these water quality declines were accompanied by a 40% decline in living coral,
605 from 27 to 16% between 1994 and 2019 (Figure 6B; coral cover was not monitored at the
606 offshore site). There is a significant positive relationship between Secchi depth and living coral
607 cover at the lagoon site, indicating a clear relationship between declining water clarity and
608 declining coral cover (Figure 6C).

609 A comparison of nutrient measurements from water samples at Glovers Reef in 1990, 2005, and
610 2018 show a peak in DIN and SRP in 2005 which exceeded the DIN threshold value affecting
611 coral health (Figure 6D). During this same time period, the N:P ratio steadily increased, reaching
612 just below the threshold value affecting coral health in 2018 (Figure 6E). Measurements of coral
613 cover at this same location in 1970, 1996, and 2017 show a marked and steady decline in coral
614 cover from 81% to 12% across this ~50 year time period. Together, these results show that (1)

615 offshore reef sites have also been significantly affected by water quality declines in terms of
616 water clarity and nutrient content and (2) coral declines occurred contemporaneously with
617 water quality declines.

618 However, land alteration in the region began long before water quality measurements began in
619 1990; expansion of coffee plantations began in 1880, bananas in 1900, and road building and
620 deforestation in the 1930s¹⁶. Long annually resolved coral cores can be used to extend records
621 of water quality change back in time prior to direct measurements. Indeed, *Orbicella* spp. coral
622 cores from two other sites in Belize, Turneffe Atoll in the north and Sapodilla Cayes in the south,
623 also showed evidence for increasing influence of land-based runoff from the start of the cores in
624 1890 and 1900 (respectively) to 2000, with Sapodilla Cayes more affected due to proximity to
625 major sources of runoff from Honduras and Guatemala¹⁶. While long-term coral growth rates
626 did not slow down in response to increasing runoff, as originally expected,¹⁷⁷ found that
627 increased land-based runoff reduced the thermal tolerance threshold of *Orbicella* spp. corals,
628 driving mass coral bleaching in 1998 despite lower heat stress than earlier in the century, and
629 that corals at the Sapodilla Cayes exposed to more land-based runoff struggled to recover after
630 bleaching compared to those at Turneffe Atoll¹⁵.

631 *Quintana Roo, Mexico*

632 DIN and SRP values consistently exceeded thresholds for eutrophication since the 1980s (Figure
633 7a,b) while the N:P ratio exceeded the threshold for maintaining coral health from 1980-2010
634 (Figure 7c). Longer timeseries of $\delta^{15}\text{N}$ values from reef-building and soft corals reliably tracked
635 sewage inputs from tourism development. $\delta^{15}\text{N}$ values increased at Puerto Morelos between
636 1970 and 2010 (indicating increased sewage inputs) and were found to be positively correlated

637 with population growth from tourism development⁹⁰. $\delta^{15}\text{N}$ of gorgonian corals dipped between
638 2006 and 2009 during a period of decreased tourist visitations and once again increased from
639 2009 to 2011 when tourist visitations again increased at the more developed site of Akumal,
640 while $\delta^{15}\text{N}$ declined between 2005-2011 at the less developed site of Mahahual (Figure 7d;⁸⁴. At
641 Puerto Morelos, Secchi values declined slightly between 1992 and 2005 (averaging 21.4m in the
642 1990s and 21.1m in the 2000s; Figure 7e), while coral cover declined drastically between 1978
643 and 2016 from 35% to 18% (Figure 7f). Coral cover was nearly-significantly negatively correlated
644 with $\delta^{15}\text{N}$ values at Puerto Morelos, suggesting a relationship between sewage-derived nutrient
645 inputs and coral abundance at this nearshore site (Figure 7g). This case study highlights the
646 utility of using chemical records such as stable isotope analyses of paleontological and modern
647 specimens of corals for tracking land-based eutrophication trends, extending these records into
648 the period prior to consistent and reliable water quality monitoring.

649 *Barbados*

650 DIN thresholds beyond which coral health is compromised were already exceeded at some sites
651 by 1972, with the mean value exceeding this threshold in 1981, 1992, and 1993 (Figure 8a). In
652 contrast, SRP values remained below values negatively impacting coral health at all sites and
653 time periods except for one site in 1981 (Figure 8b). The mean N:P ratio was at or near the
654 threshold value in 1972 and 1981 and exceeded threshold values in 1992 and 1993 (Figure 8c).
655 Although only recorded at one site in 1972, coral cover declined notably at that site from 37% in
656 1972 to 11% in 1981 and continued to decline to 6% in 1993 (Figure 8d). Mean coral cover
657 across all sites declined from 9% in 1981 to 6% in 1993 (Figure 8d). Although coral cover had a
658 negative relationship with DIN, SRP, and N:P, these relationships were not statistically
659 significant, possibly due to the small number of time periods from which to detect a trend.

660 *Florida Keys*

661 At all three focal reef sites, DIN increased from 1983 until the mid-2000s, after which it declined
662 until 2021 (Figure 9a). DIN exceeded the threshold value beyond which coral health is
663 compromised at multiple time points (Figure 9a). SRP fluctuated at each site from 1983-2021,
664 with maxima occurring in the 1990s at Looe Key and in the 2000s at Alligator Reef and Carysfort
665 Reef. SRP remained below the threshold value for coral health throughout the time series
666 (Figure 9b). At all three reef sites, the N:P ratio exceeded the threshold value for coral health in
667 the mid-1990s, mid 2000s, and late 2010s (Figure 9c). At all three reef sites, turbidity was
668 generally more variable and higher between the mid-1990s to 2010 and lower between 2011
669 and 2021 (Figure 9d). At the two reef sites for which there is coral cover data for the 1980s
670 (Carysfort Reef and Looe Key), coral cover was halved between the 1980s and 1990s, and coral
671 cover continued to decline at all three reef sites from the 1990s to 2021 (Figure 9e). At the reef
672 site level, coral cover was not correlated with any water quality metrics, possibly due to coral
673 cover declines occurring prior to the availability of the water quality data.

674 Records of $\delta^{15}\text{N}$ spanning the 1970s to early 2000s from Florida Keys gorgonian skeletons
675 showed similar evidence of increases in nutrient input ¹⁷⁸. Other studies using coral skeletal
676 geochemistry found evidence for both elevated coastal runoff and recirculation of this land-
677 based runoff in the Florida Keys in the 1970s ¹⁷⁹, and evidence of restrictions in waterflow
678 between Florida Bay and the Florida Keys after construction of the Miami to Key West railway in
679 the early 1900s ¹⁸⁰. Nutrient runoff from “managed” Everglades freshwater discharges in Florida
680 Bay has led to algal blooms that have caused mortality of benthic organisms, including a
681 sustained bloom from 2005 to 2008 ⁶⁷.

682 **DISCUSSION**

683 **Status and trends in Caribbean coral reef water quality and impacts on reef health**

684 Our synthesis of historical and modern reef water quality confirms that there has been a notable
685 increase in nutrient levels and a decrease in water clarity between 1970 and 2021 on a regional
686 scale across the Caribbean (Figure 3). A comparison of these water quality metrics with a key
687 metric of reef health, coral cover, found a negative correlation between the N:P ratio and coral
688 cover, but no correlation between coral cover and DIN, SRP, or Secchi depth (Figure 4). This
689 result supports previous findings that the balance between nitrogen and phosphorus (N:P ratio)
690 has a greater impact on coral health than the absolute value of N or P alone^{25,28,30,31}. The power
691 to detect stronger relationships between water quality metrics and coral cover at a regional
692 scale was likely hindered by the limited length of individual timeseries, the fact that major land
693 use and reef water quality changes pre-date our water quality timeseries at many locations, and
694 the uneven distribution of water quality samples across space and time.

695 Our analysis of more well-studied reef sites (“case studies”) provides several insights into the
696 relationship between reef water quality and ecosystem health that can inform improved reef
697 and coastal zone management. For example, at Discovery Bay, Jamaica, N, P, and N:P ratio levels
698 exceeded threshold levels for coral health prior to the die-off of the *Diadema* urchin which has
699 been cited as the driver of the coral to algal phase shift on these reefs⁴¹. At Carrie Bow Cay,
700 Belize, reef water quality monitoring began early enough to capture some effects from large-
701 scale land development activities, enabling us to detect a significant correlation between
702 declines in water clarity and declines in coral cover (Figure 6c). Similarly, at Puerto Morelos,
703 Mexico, $\delta^{15}\text{N}$ from coral cores provided a timeseries of this proxy of N inputs from sewage
704 pollution that extended far enough back in time (1970s) to detect a negative trend in this water

705 quality metric which was correlated with declines in coral cover (Figure 7g). Even the limited
706 sampling across a long time series at Glovers atoll, Belize indicates that even isolated, offshore
707 reefs are affected by nutrient enrichment (Figure 6d). Together, these results confirm that land-
708 based pollution has played an under-appreciated role in reef health in the Caribbean that was
709 initiated by 1970 or earlier.

710 The relative dearth of attention paid to the role of land-based pollution on reef health and
711 resilience has stymied more effective reef management interventions in many Caribbean
712 locations. In Discovery Bay, coral declines observed in the 1980s were attributed solely to the
713 loss of herbivory, precluding more holistic management efforts to address a combination of
714 overfishing and nutrient stress. Results from the Florida Keys highlight that “water
715 management” policy for one connected ecosystem (Everglades) can have drastic consequences
716 for another (lower Florida reef tract), emphasizing the need for a holistic approach that better
717 considers land-sea connections (i.e., integrated coastal zone management) ¹⁸¹.

718 However, poor water quality is increasingly recognized as a threat to ecological and human
719 health by reef managers across the Caribbean. At one of our case study locations, the Florida
720 Keys, nutrient levels and water clarity have generally remained stable or improved in tandem
721 with recent improvements in wastewater management ¹⁸², although sedimentation levels
722 remain high ¹⁸³. Unfortunately, reef water quality has declined since the 1970s at the remaining
723 case study locations. In addition, live hard coral cover has not recovered at any case study site
724 included in this study, likely due to the synergistic effects of climate change, overfishing, and
725 land-based runoff on coral reefs in the Caribbean, which can together exacerbate the impacts of

726 individual stressors ^{1,15,177,184}, and the increasingly chronic nature of thermal stress events from
727 climate change ¹⁸⁵.

728 Water quality timeseries from our case studies confirm a recent revelation that land-based
729 nutrient pollution is a pervasive problem within Marine Protected Areas (MPAs) that threatens
730 their conservation goals¹⁸⁶. Some case study sites (Belize, Barbados, Puerto Morelos) are within
731 MPAs and/or are in locations where the harvest of reef herbivores is prohibited (Florida Keys,
732 Belize, Quintana Roo, Mexico) but have nevertheless experienced declines in water quality,
733 increases in macroalgal cover compared to historical estimates, and declines in coral cover. For
734 example, the Belize Barrier Reef has a comprehensive system of MPAs and a nation-wide ban on
735 the take of herbivorous fishes such as parrotfish since 2009, which has led to a successful
736 increase in these fish stocks followed by a gradual decrease in fleshy macroalgae from 24% in
737 2014 to 17% in 2023 (although turf algae increased during this period; ¹⁸⁷). However, coral cover
738 continues to decline along the majority of the Belize Barrier Reef ¹⁸⁷. Thus, while the protection
739 of reef herbivores may help slow the algal overgrowth of reefs, it cannot shield reefs from
740 increasingly stressful environmental conditions driven by climate change and declining water
741 quality, including nutrient enrichment from a variety of land-based sources which must also be
742 mitigated ^{147,188}. This highlights the urgent need for integrated coastal zone management plans
743 that provide effective regulation of land-based activities adding nutrient pollution into coastal
744 ecosystems, up to 100km away. Land management strategies should include targeted efforts to
745 reduce runoff and associated air-borne pollution (i.e., ash) to protect reef ecosystem health ¹⁸⁸
746 and the setting and enforcement of minimum water quality targets to support coral health and
747 persistence (such as Mexico's NORM001 of 2021 which increased the standards of all

748 wastewater effluents to meet the Cartagena Convention standards for Class I waters adjacent to
749 coral reefs or seagrasses).

750 **Declining water quality and the future of reefs**

751 Regional assessments of land-based sources of coastal pollution in the Caribbean indicate that
752 sewage is a major concern in some areas due to the widespread lack of proper wastewater
753 treatment and rapid growth in population and tourism since the 1980s^{76,187,189}. The causal link
754 between sewage and associated nutrients and phytoplankton blooms has been well-
755 documented for freshwater, temperate, and tropical coastal marine systems including coral
756 reefs^{34,40,93,190-193}. Sewage inputs to coral reefs and adjacent seagrass beds due to tourism
757 development has been particularly well-documented in the Mexican Caribbean^{85,194-197}.

758 In addition to sewage impacts, many Caribbean reef locations suffer from increased
759 sedimentation due to changes in land use, with negative impacts to corals^{63,189,198-200}. Central
760 and South America have experienced the greatest loss in forest cover of any region globally
761 since 1990, linked to rapid increases in agricultural expansion and intensification that have
762 occurred since 1970^{74,201}. Even distant but large-scale land use change appears to have
763 measurable negative consequences on Caribbean corals^{16,188,202}. While much focus has been
764 placed on the decimation of reef-building corals caused by mass bleaching events and the
765 importance of addressing climate change to ensure coral survival, water quality has been and
766 will continue to be an important driver of coral loss and will prevent recovery if not addressed.
767 Importantly, the regulation of activities contributing to nutrient pollution are within the
768 legislative framework of coral reef-bearing states, unlike global climate change which is almost

769 always beyond the potential control of reef-bearing states that have an insignificant
770 contribution to greenhouse gas emissions.

771 While some coral reefs have developed in locations with naturally challenging water quality
772 conditions ^{203,204} and some work has suggested that such turbid water reefs may act as refugia
773 during marine heatwaves ^{205,206}, declines in water quality can also make corals more susceptible
774 to bleaching and disease and impair their recovery following disturbance ^{24,31,53,177}. Nutrient
775 pollution can also stimulate algal blooms and macroalgal growth that can directly smother corals
776 or drive microbialization that also kills corals ⁴²; indeed, some nearshore sites in the Florida Keys
777 with elevated nutrients have 0% living coral cover ²⁰⁷. Terrigenous sedimentation from land-use
778 change also poses a great risk to coral health and can lead to tissue necrosis ²⁰⁸. Importantly,
779 reefs with low water quality due to anthropogenic land-based runoff have distinct
780 environmental conditions from naturally turbid reefs. Naturally turbid reefs are not typically
781 subjected to the chronic multiple stressors that anthropogenically impaired water quality reefs
782 are (nutrient loading, sedimentation, and land-based pollutants) and typically have lower
783 suspended sediment loads due to more intact watersheds ²⁰⁸. While corals in naturally turbid
784 environments are adapted to these conditions, in the Caribbean it appears that the majority of
785 hard corals in naturally oligotrophic environments are not, as indicated by their early losses
786 prior to disease and bleaching outbreaks ^{10,75}.

787 To combat coral loss, there is an increased focus on restoring coral reefs through a range of
788 methods including coral gardening and outplanting and assisted reproduction ²⁰⁹. Current
789 restoration efforts include those focused on breeding and introducing a limited range of coral
790 genotypes that are resistant to thermal stress, but efforts are lacking to address the impacts of

791 water quality declines on coral health. Additional strategies may be required, including efforts to
792 improve reef water quality and informed selection of sites where water quality is conducive to
793 restoration success. To maximize chances of successful restoration outcomes, reef water quality
794 should be assessed prior to site selection for restoration projects and tracked as part of project
795 monitoring. Efforts to improve or maintain water quality should be a required component of
796 coral restoration initiatives, potentially funded by the polluters which are often indirect
797 beneficiaries of the coral restoration (e.g. coastal resorts). Ideally, this will prevent selection of
798 sites with poor water quality that will hinder long-term success and help identify causes of
799 failures to improve restoration outcomes. In the case of the threatened staghorn coral *Acropora*
800 *cervicornis*, an experiment showed that no genotypes used for restoration projects were
801 resistant to both eutrophication (in the form of elevated DIN levels) and disease and that the
802 combined exposure to both stressors can lead to a loss of disease resistance ¹². Thus, water
803 quality considerations should be better integrated into coral restoration theory and practice.

804 On a positive note, improving coastal water quality can facilitate Caribbean reef management
805 goals. Water quality improvements may make herbivore protection efforts more effective:
806 adequate controls on nutrient enrichment may allow herbivorous fishes to control macroalgal
807 abundance on reefs, which can promote the maintenance or recovery of coral dominance
808 ^{35,128,148}. As reef restoration science begins to explore the possibility of restoring herbivorous
809 fishes and invertebrates to assist in coral recovery, improved water quality may also play a
810 critical role in the success of these efforts ²¹⁰. The mitigation of land-based inputs such as
811 nutrients and sediments can also buffer losses and increase rates of coral recovery following
812 thermal stress events and hurricanes ^{184,211}.

813 **Understanding and improving Caribbean reef water quality**

814 This synthesis of available water quality data demonstrates that Caribbean coral reefs have
815 experienced long-term declines in water quality that are related to widely documented declines
816 in reef health. This study also reveals that temporal and spatial gaps in available water quality
817 data have hindered a rigorous assessment of the role of water quality declines in coral loss and
818 provides examples for the use of existing and additional historical records to help fill in data
819 gaps and better understand these links. By linking water quality and reef health metrics through
820 time at individual sites, appropriate water quality management targets can be defined more
821 broadly and applied where data and times series are limited or absent. In addition, links
822 between water quality observations and drivers such as urban development, tourism, and
823 agriculture (whether from direct observations via monitoring programs, satellite image analysis
824 or reconstructions from historical data sources; Figure 1) can help identify the major factors
825 affecting water quality, informing management decisions and avoiding lower-impact efforts
826 targeting factors of less importance. Targeted measures such as $\delta^{15}\text{N}$ can quantitatively discern
827 between different nitrogen sources - a necessary step in formulating solutions.

828 Historical datasets can provide important baseline information about water quality conditions at
829 a given site prior to degradation, information that is critical for setting targets and determining
830 when water quality has been restored to site-appropriate conditions. For example, it would be
831 unreasonable to expect that water clarity at reef sites within semi enclosed lagoons (such as
832 nearshore sites in southern Belize and the semi-enclosed lagoonal system in Bocas del Toro,
833 Panama) that have always been affected by some level of riverine input should ever reach the
834 same low nutrient levels measured in an offshore carbonate atoll like Glover's Reef. Setting

835 realistic targets appropriate to a given reef area is important to ensure that success is possible,
836 and to know when it has been achieved.

837 **Recommendations**

838 This study demonstrates that monitoring water quality on coral reefs is critical for identifying
839 pollution impacts on reef ecosystem health and resilience and for developing effective
840 management strategies that address this stressor. We therefore advocate for sustained and
841 standardized reef water quality monitoring programs to be implemented across the Caribbean
842 as part of reef management. The following recommendations are the minimum requirements to
843 ensure reef water quality monitoring programs can guide improved management of pollution
844 impacts:

- 845 • *Management bodies should provide sustained funding for the development and*
846 *implementation of a standardized reef water quality monitoring protocol.* Depending on the
847 availability of resources and analytical facilities, a water quality program could range from
848 collecting the minimum and most low-cost measurement of water quality (water visibility
849 via Secchi disk) to chemical parameters related to nutrient inputs (DIN, SRP, $\delta^{15}\text{N}$) if water
850 samples are collected and processed following best practices²¹². A common issue in the
851 chemical analysis of reef water samples is the lack of nearby laboratories with appropriate
852 instrumentation. This common barrier could be alleviated by conducting *in-situ* water
853 quality measurements via a multisensor sonde¹¹⁰.
- 854 • *Water quality data should be shared openly with the scientific and management*
855 *communities and the public.* To support education and outreach of stakeholders on the state
856 of reef water quality, data should be summarized and deposited in an open-access online

857 data portal that can be integrated with existing portals of coral reef community
858 compositional change.

- 859 • *Reef water quality trends should be considered when assessing reef health and resilience.*

860 This would allow for the designation of ecologically appropriate water quality thresholds, for
861 a quantitative assessment of the role of water quality change in observed reef ecosystem
862 declines, and for a much-needed assessment of the interaction between water quality
863 conditions and susceptibility to disease outbreaks and coral bleaching.

- 864 • *Historical reef water quality data should be considered in monitoring efforts when feasible.*

865 Existing and untapped sources of historical data such as those highlighted in this paper
866 should be utilized to create a “retrospective monitoring program” for reef sites which lack
867 modern water quality monitoring. Existing data sources include coral and mollusk samples
868 from geological and natural history collections, historical satellite data, and historical
869 archives, whereas untapped data sources could include the collecting of new coral cores.

- 870 • *Restoration efforts and other management interventions should explicitly consider reef
871 water quality in their designs.* Given the rate of declining water quality on Caribbean reefs,
872 any restoration activity should consider not only the current condition of the system to be
873 restored, but also how it has changed in both ecological and environmental terms. There are
874 many instances in which the first action in a restoration program should be to restore water
875 quality rather than to physically manipulate organisms or engineer new reef communities.

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888 **References**

- 889 1. Bieg, C., Vallès, H., Tewfik, A., Lapointe, B. E. & McCann, K. S. Toward a Multi-stressor
890 Theory for Coral Reefs in a Changing World. *Ecosystems* **27**, 310–328 (2024).
- 891 2. Halpern, B. S. *et al.* Recent pace of change in human impact on the world’s ocean. *Sci.*
892 *Rep.* **9**, 11609 (2019).
- 893 3. Harborne, A. R., Rogers, A., Bozec, Y.-M. & Mumby, P. J. Multiple Stressors and the
894 Functioning of Coral Reefs. *Annu. Rev. Mar. Sci.* **9**, 445–468 (2017).
- 895 4. Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A. & Watkinson, A. R. Long-Term Region-
896 Wide Declines in Caribbean Corals. *Science* **301**, 958–960 (2003).
- 897 5. Jackson, E. J., Donovan, M., Cramer, K. & Lam, V. *STATUS AND TRENDS OF CARIBBEAN*
898 *CORAL REEFS: 1970-2012*. (2014).
- 899 6. Alvarez-Filip, L., González-Barrios, F. J., Pérez-Cervantes, E., Molina-Hernández, A. &
900 Estrada-Saldívar, N. Stony coral tissue loss disease decimated Caribbean coral
901 populations and reshaped reef functionality. *Commun. Biol.* **5**, 440 (2022).
- 902 7. Bruckner, A. & Hill, R. Ten years of change to coral communities off Mona and Desecheo
903 Islands, Puerto Rico, from disease and bleaching. *Dis. Aquat. Organ.* **87**, 19–31 (2009).
- 904 8. McField, M. D. Influence of disturbance on coral reef community structure in Belize.
905 *Proc. Ninth Int. Coral Reef Symp.* **1**, 63–68 (2000).
- 906 9. Miller, J. *et al.* Coral disease following massive bleaching in 2005 causes 60% decline in
907 coral cover on reefs in the US Virgin Islands. *Coral Reefs* **28**, 925–937 (2009).
- 908 10. Cramer, K. L. *et al.* Widespread loss of Caribbean acroporid corals was underway before
909 coral bleaching and disease outbreaks. *Sci. Adv.* **6**, eaax9395 (2020).
- 910 11. Díaz-Ortega, G. & Hernández-Delgado, E. A. Unsustainable Land-Based Source Pollution
911 in a Climate of Change: A Roadblock to the Conservation and Recovery of Elkhorn Coral
912 & Acropora palmata (Lamarck 1816). *Nat. Resour.* **05**, 561–581 (2014).
- 913 12. Palacio-Castro, A. M., Dennison, C. E., Rosales, S. M. & Baker, A. C. Variation in
914 susceptibility among three Caribbean coral species and their algal symbionts indicates

- 915 the threatened staghorn coral, *Acropora cervicornis*, is particularly susceptible to
 916 elevated nutrients and heat stress. *Coral Reefs* **40**, 1601–1613 (2021).
- 917 13. Andréfouët, S., Mumby, P., McField, M., Hu, C. & Muller-Karger, F. Revisiting coral reef
 918 connectivity. *Coral Reefs* **21**, 43–48 (2002).
- 919 14. Maliao, R. J., Turingan, R. G. & Lin, J. Phase-shift in coral reef communities in the Florida
 920 Keys National Marine Sanctuary (FKNMS), USA. *Mar. Biol.* **154**, 841–853 (2008).
- 921 15. Carilli, J. E., Norris, R. D., Black, B., Walsh, S. M. & McFIELD, M. Century-scale records of
 922 coral growth rates indicate that local stressors reduce coral thermal tolerance threshold.
 923 *Glob. Change Biol.* **16**, 1247–1257 (2010).
- 924 16. Carilli, J. E., Prouty, N. G., Hughen, K. A. & Norris, R. D. Century-scale records of land-
 925 based activities recorded in Mesoamerican coral cores. *Mar. Pollut. Bull.* **58**, 1835–1842
 926 (2009).
- 927 17. Aronson, R. B., Macintyre, I. G., Wapnick, C. M. & O’Neill, M. W. PHASE SHIFTS,
 928 ALTERNATIVE STATES, AND THE UNPRECEDENTED CONVERGENCE OF TWO REEF
 929 SYSTEMS. *Ecology* **85**, 1876–1891 (2004).
- 930 18. Cramer, K. L. *et al.* The transformation of Caribbean coral communities since humans.
 931 *Ecol. Evol.* **11**, 10098–10118 (2021).
- 932 19. Toth, L. T. *et al.* The unprecedented loss of Florida’s reef-building corals and the
 933 emergence of a novel coral-reef assemblage. *Ecology* **100**, e02781 (2019).
- 934 20. Falkowski, P. G., Dubinsky, Z., Muscatine, L. & McCloskey, L. Population Control in
 935 Symbiotic Corals. *BioScience* **43**, 606–611 (1993).
- 936 21. Hoegh-Guldberg, O. Population dynamics of symbiotic zooxanthellae in the coral
 937 *Pocillopora damicornis* exposed to elevated ammonium [(NH₄)₂ SO₄] concentrations.
 938 *Pac Sci* **48**, 263–272 (1994).
- 939 22. Hoegh-Guldberg, O. & Smith, G. Influence of the population density of zooxanthellae
 940 and supply of ammonium on the biomass and metabolic characteristics of the reef
 941 corals *Seriatopora hystrix* and *Stylophora pistillata*. *Mar. Ecol. Prog. Ser.* **57**, 173–186
 942 (1989).
- 943 23. Muscatine, L., Porter, J. W. & Kaplan, I. R. Resource partitioning by reef corals as
 944 determined from stable isotope composition: I. ¹³C of zooxanthellae and animal tissue
 945 vs depth. *Mar. Biol.* **100**, 185–193 (1989).
- 946 24. Bruno, J. F., Petes, L. E., Drew Harvell, C. & Hettinger, A. Nutrient enrichment can
 947 increase the severity of coral diseases. *Ecol. Lett.* **6**, 1056–1061 (2003).
- 948 25. Buckingham, M. C. *et al.* Impact of nitrogen (N) and phosphorus (P) enrichment and
 949 skewed N:P stoichiometry on the skeletal formation and microstructure of symbiotic
 950 reef corals. *Coral Reefs* **41**, 1147–1159 (2022).
- 951 26. D’Angelo, C. & Wiedenmann, J. Impacts of nutrient enrichment on coral reefs: new
 952 perspectives and implications for coastal management and reef survival. *Curr. Opin.*
 953 *Environ. Sustain.* **7**, 82–93 (2014).
- 954 27. Dubinsky, Z. & Stambler, N. Marine pollution and coral reefs. *Glob. Change Biol.* **2**, 511–
 955 526 (1996).
- 956 28. Lapointe, B. E., Brewton, R. A., Herren, L. W., Porter, J. W. & Hu, C. Nitrogen enrichment,
 957 altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a 3-decade
 958 study. *Mar. Biol.* **166**, 108 (2019).

- 959 29. Muller-Parker, G., McCloskey, L. R. L., Hoegh-Guldberg, O. & McAuley, P. Effect of
960 Ammonium Enrichment on Animal and Algal Biomass of the Coral *Pocillopora*
961 *damicornis*. *Pac. Sci.* **48**, 273–283.
- 962 30. Rosset, S., Wiedenmann, J., Reed, A. J. & D'Angelo, C. Phosphate deficiency promotes
963 coral bleaching and is reflected by the ultrastructure of symbiotic dinoflagellates. *Mar.*
964 *Pollut. Bull.* **118**, 180–187 (2017).
- 965 31. Wiedenmann, J. *et al.* Nutrient enrichment can increase the susceptibility of reef corals
966 to bleaching. *Nat. Clim. Change* **3**, 160–164 (2013).
- 967 32. Wooldridge, S. A. Water quality and coral bleaching thresholds: Formalising the linkage
968 for the inshore reefs of the Great Barrier Reef, Australia. *Mar. Pollut. Bull.* **58**, 745–751
969 (2009).
- 970 33. Lesser, M. P. Eutrophication on Coral Reefs: What Is the Evidence for Phase Shifts,
971 Nutrient Limitation and Coral Bleaching. *BioScience* **71**, 1216–1233 (2021).
- 972 34. Lapointe, B. E., Thacker, K., Hanson, C. & Getten, L. Sewage pollution in Negril, Jamaica:
973 effects on nutrition and ecology of coral reef macroalgae. *Chin. J. Oceanol. Limnol.* **29**,
974 775–789 (2011).
- 975 35. Lapointe, B. E., Littler, M. M. & Littler, D. S. Macroalgal overgrowth of fringing coral reefs
976 at Discovery Bay, Jamaica: bottom-up versus top-down control.
977 <http://repository.si.edu/xmlui/handle/10088/2590> (1997).
- 978 36. Hernández-Terrones, L. *et al.* Groundwater Pollution in a Karstic Region (NE Yucatan):
979 Baseline Nutrient Content and Flux to Coastal Ecosystems. *Water. Air. Soil Pollut.* **218**,
980 517–528 (2011).
- 981 37. Velázquez-Ochoa, R. & Enríquez, S. Environmental degradation of the Mexican
982 Caribbean reef lagoons. *Mar. Pollut. Bull.* **191**, 114947 (2023).
- 983 38. Lapointe, B. E., Tewfik, A. & Phillips, M. Macroalgae reveal nitrogen enrichment and
984 elevated N:P ratios on the Belize Barrier Reef. *Mar. Pollut. Bull.* **171**, 112686 (2021).
- 985 39. Vermeij, M. J. A. *et al.* The Effects of Nutrient Enrichment and Herbivore Abundance on
986 the Ability of Turf Algae to Overgrow Coral in the Caribbean. *PLoS ONE* **5**, e14312 (2010).
- 987 40. Walker, D. I. & Ormond, R. F. G. Coral death from sewage and phosphate pollution at
988 Aqaba, Red Sea. *Mar. Pollut. Bull.* **13**, 21–25 (1982).
- 989 41. Hughes, T. P. Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean
990 Coral Reef. *Science* **265**, 1547–1551 (1994).
- 991 42. Haas, A. F. *et al.* Global microbialization of coral reefs. *Nat. Microbiol.* **1**, 16042 (2016).
- 992 43. Kline, D., Kuntz, N., Breitbart, M., Knowlton, N. & Rohwer, F. Role of elevated organic
993 carbon levels and microbial activity in coral mortality. *Mar. Ecol. Prog. Ser.* **314**, 119–125
994 (2006).
- 995 44. Smith, J. E. *et al.* Indirect effects of algae on coral: algae-mediated, microbe-induced
996 coral mortality. *Ecol. Lett.* **9**, 835–845 (2006).
- 997 45. Junjie, R. K., Browne, N. K., Erftemeijer, P. L. A. & Todd, P. A. Impacts of Sediments on
998 Coral Energetics: Partitioning the Effects of Turbidity and Settling Particles. *PLoS ONE* **9**,
999 e107195 (2014).
- 1000 46. López-Londoño, T. *et al.* Sobrevivencia y respuestas fisiológicas de corales expuestos a
1001 elevada turbidez en el arrecife Varadero, Caribe colombiano. *Bol. Investig. Mar. Costeras*
1002 **52**, 135–158 (2023).
- 1003 47. López-Londoño, T. *et al.* Physiological and ecological consequences of the water optical
1004 properties degradation on reef corals. *Coral Reefs* **40**, 1243–1256 (2021).

- 1005 48. Cortés, J. & Risk, M. A reef under siltation stress: Cahuita, Costa Rica. *Bull. Mar. Sci.* **36**,
1006 339–356 (1985).
- 1007 49. Erftemeijer, P. L. A., Riegl, B., Hoeksema, B. W. & Todd, P. A. Environmental impacts of
1008 dredging and other sediment disturbances on corals: A review. *Mar. Pollut. Bull.* **64**,
1009 1737–1765 (2012).
- 1010 50. Fabricius, K. E. Effects of terrestrial runoff on the ecology of corals and coral reefs:
1011 review and synthesis. *Mar. Pollut. Bull.* **50**, 125–146 (2005).
- 1012 51. Rogers, C. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol.*
1013 *Prog. Ser.* **62**, 185–202 (1990).
- 1014 52. Wear, S. L. & Thurber, R. V. Sewage pollution: mitigation is key for coral reef
1015 stewardship. *Ann. N. Y. Acad. Sci.* **1355**, 15–30 (2015).
- 1016 53. Vega Thurber, R. L. *et al.* Chronic nutrient enrichment increases prevalence and severity
1017 of coral disease and bleaching. *Glob. Change Biol.* **20**, 544–554 (2014).
- 1018 54. Voss, J. D. & Richardson, L. L. Nutrient enrichment enhances black band disease
1019 progression in corals. *Coral Reefs* **25**, 569–576 (2006).
- 1020 55. Fuess, L. E., Palacio-Castro, A. M., Butler, C. C., Baker, A. C. & Mydlarz, L. D. Increased
1021 Algal Symbiont Density Reduces Host Immunity in a Threatened Caribbean Coral
1022 Species, *Orbicella faveolata*. *Front. Ecol. Evol.* **8**, (2020).
- 1023 56. Bourne, D. G., Morrow, K. M. & Webster, N. S. Insights into the Coral Microbiome:
1024 Underpinning the Health and Resilience of Reef Ecosystems. *Annu. Rev. Microbiol.* **70**,
1025 317–340 (2016).
- 1026 57. Klinges, G., Maher, R. L., Vega Thurber, R. L. & Muller, E. M. Parasitic ‘*Candidatus*
1027 *Aquarickettsia rohweri*’ is a marker of disease susceptibility in *ACROPORA CERVICORNIS* but
1028 is lost during thermal stress. *Environ. Microbiol.* **22**, 5341–5355 (2020).
- 1029 58. Klinges, J. G., Patel, S. H., Duke, W. C., Muller, E. M. & Vega Thurber, R. L. Phosphate
1030 enrichment induces increased dominance of the parasite *Aquarickettsia* in the coral
1031 *Acropora cervicornis*. *FEMS Microbiol. Ecol.* **98**, fiac013 (2022).
- 1032 59. Harrison, P. & Ward, S. Elevated levels of nitrogen and phosphorus reduce fertilisation
1033 success of gametes from scleractinian reef corals. *Mar. Biol.* **139**, 1057–1068 (2001).
- 1034 60. Hunte, W. & Wittenberg, M. Effects of eutrophication and sedimentation on juvenile
1035 corals: II. Settlement. *Mar. Biol.* **114**, 625–631 (1992).
- 1036 61. Koop, K. *et al.* ENCORE: The Effect of Nutrient Enrichment on Coral Reefs. Synthesis of
1037 Results and Conclusions. *Mar. Pollut. Bull.* **42**, 91–120 (2001).
- 1038 62. Zaneveld, J. R. *et al.* Overfishing and nutrient pollution interact with temperature to
1039 disrupt coral reefs down to microbial scales. *Nat. Commun.* **7**, 11833 (2016).
- 1040 63. Oliver, L. M., Fisher, W. S., Fore, L., Smith, A. & Bradley, P. Assessing land use,
1041 sedimentation, and water quality stressors as predictors of coral reef condition in St.
1042 Thomas, U.S. Virgin Islands. *Environ. Monit. Assess.* **190**, 213 (2018).
- 1043 64. Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M. & Watkinson, A. R. Flattening of
1044 Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B*
1045 *Biol. Sci.* **276**, 3019–3025 (2009).
- 1046 65. Loya, Y. Effects of Water Turbidity and Sedimentation on the Community Structure of
1047 Puerto Rican Corals. *Bull. Mar. Sci.* **26**, 450–466 (1976).
- 1048 66. Baumann, J. H. *et al.* Nearshore coral growth declining on the Mesoamerican Barrier
1049 Reef System. *Glob. Change Biol.* **25**, 3932–3945 (2019).

- 1050 67. Arias-González, J. E. *et al.* A coral-algal phase shift in Mesoamerica not driven by
1051 changes in herbivorous fish abundance. *PLOS ONE* **12**, e0174855 (2017).
- 1052 68. Ennis, R. S., Brandt, M. E., Wilson Grimes, K. R. & Smith, T. B. Coral reef health response
1053 to chronic and acute changes in water quality in St. Thomas, United States Virgin Islands.
1054 *Mar. Pollut. Bull.* **111**, 418–427 (2016).
- 1055 69. Fabricius, K. E. Factors Determining the Resilience of Coral Reefs to Eutrophication: A
1056 Review and Conceptual Model. in *Coral Reefs: An Ecosystem in Transition* (eds Dubinsky,
1057 Z. & Stambler, N.) 493–505 (Springer Netherlands, Dordrecht, 2011). doi:10.1007/978-
1058 94-007-0114-4_28.
- 1059 70. Suchley, A. & Alvarez-Filip, L. Local human activities limit marine protection efficacy on
1060 Caribbean coral reefs. *Conserv. Lett.* **11**, e12571 (2018).
- 1061 71. Govers, L. L., Lamers, L. P. M., Bouma, T. J., De Brouwer, J. H. F. & Van Katwijk, M. M.
1062 Eutrophication threatens Caribbean seagrasses – An example from Curaçao and Bonaire.
1063 *Mar. Pollut. Bull.* **89**, 481–486 (2014).
- 1064 72. Orth, R. J. *et al.* A Global Crisis for Seagrass Ecosystems. *BioScience* **56**, 987 (2006).
- 1065 73. Berger, M., Canty, S. W. J., Tuholske, C. & Halpern, B. S. Sources and discharge of
1066 nitrogen pollution from agriculture and wastewater in the Mesoamerican Reef region.
1067 *Ocean Coast. Manag.* **227**, 106269 (2022).
- 1068 74. Carr, D. L., Lopez, A. C. & Bilsborrow, R. E. The population, agriculture, and environment
1069 nexus in Latin America: country-level evidence from the latter half of the twentieth
1070 century. *Popul. Environ.* **30**, 222–246 (2009).
- 1071 75. Cramer, K. L., O’Dea, A., Leonard-Pingel, J. S. & Norris, R. D. Millennial-scale change in
1072 the structure of a Caribbean reef ecosystem and the role of human and natural
1073 disturbance. *Ecography* **43**, 283–293 (2020).
- 1074 76. DeGeorges, A., Goreau, T. J. & Reilly, B. Land-Sourced Pollution with an Emphasis on
1075 Domestic Sewage: Lessons from the Caribbean and Implications for Coastal
1076 Development on Indian Ocean and Pacific Coral Reefs. *Sustainability* **2**, 2919–2949
1077 (2010).
- 1078 77. Ruiz-Fernández, A. C. *et al.* 210Pb-derived sediment accumulation rates across the
1079 Wider Caribbean Region. *J. Environ. Radioact.* **223–224**, 106366 (2020).
- 1080 78. Cramer, K. L., Jackson, J. B. C., Angioletti, C. V., Leonard-Pingel, J. & Guilderson, T. P.
1081 Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and
1082 bleaching. *Ecol. Lett.* **15**, 561–567 (2012).
- 1083 79. Jackson, J. B. C. *et al.* Historical Overfishing and the Recent Collapse of Coastal
1084 Ecosystems. *Science* **293**, 629–637 (2001).
- 1085 80. Roff, G. & Mumby, P. J. Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.*
1086 **27**, 404–413 (2012).
- 1087 81. Carriquiry, J. D. & Horta-Puga, G. The Ba/Ca record of corals from the Southern Gulf of
1088 Mexico: Contributions from land-use changes, fluvial discharge and oil-drilling muds.
1089 *Mar. Pollut. Bull.* **60**, 1625–1630 (2010).
- 1090 82. D’Olivo, J. P. & McCulloch, M. Impact of European settlement and land use changes on
1091 Great Barrier Reef river catchments reconstructed from long-term coral Ba/Ca records.
1092 *Sci. Total Environ.* **830**, 154461 (2022).
- 1093 83. Prouty, N. G., Hughen, K. A. & Carilli, J. Geochemical signature of land-based activities in
1094 Caribbean coral surface samples. *Coral Reefs* **27**, 727–742 (2008).

- 1095 84. Baker, D. M., Rodríguez-Martínez, R. E. & Fogel, M. L. Tourism's nitrogen footprint on a
1096 Mesoamerican coral reef. *Coral Reefs* **32**, 691–699 (2013).
- 1097 85. Baker, D. M., Jordán-Dahlgren, E., Maldonado, M. A. & Harvell, C. D. Sea fan corals
1098 provide a stable isotope baseline for assessing sewage pollution in the Mexican
1099 Caribbean. *Limnol. Oceanogr.* **55**, 2139–2149 (2010).
- 1100 86. Baker, D., MacAvoy, S. & Kim, K. Relationship between water quality, $\delta^{15}\text{N}$, and
1101 aspergillosis of Caribbean sea fan corals. *Mar. Ecol. Prog. Ser.* **343**, 123–130 (2007).
- 1102 87. Duprey, N. N. *et al.* Megacity development and the demise of coastal coral communities:
1103 Evidence from coral skeleton $\delta^{15}\text{N}$ records in the Pearl River estuary. *Glob. Change Biol.*
1104 **26**, 1338–1353 (2020).
- 1105 88. Marion, G. S., Jupiter, S. D., Radice, V. Z., Albert, S. & Hoegh-Guldberg, O. Linking
1106 isotopic signatures of nitrogen in nearshore coral skeletons with sources in catchment
1107 runoff. *Mar. Pollut. Bull.* **173**, 113054 (2021).
- 1108 89. Marion, G. S. *et al.* Coral skeletal $\delta^{15}\text{N}$ reveals isotopic traces of an agricultural
1109 revolution. *Mar. Pollut. Bull.* **50**, 931–944 (2005).
- 1110 90. Rico-Esenaro, S. D., De Jesús Adolfo Tortolero-Langarica, J., Iglesias-Prieto, R. &
1111 Carricart-Ganivet, J. P. The $\delta^{15}\text{N}$ in *Orbicella faveolata* organic matter reveals
1112 anthropogenic impact by sewage inputs in a Mexican Caribbean coral reef lagoon.
1113 *Environ. Sci. Pollut. Res.* **30**, 118872–118880 (2023).
- 1114 91. Castillo, K. D., Ries, J. B. & Weiss, J. M. Declining Coral Skeletal Extension for Forereef
1115 Colonies of *Siderastrea siderea* on the Mesoamerican Barrier Reef System, Southern
1116 Belize. *PLoS ONE* **6**, e14615 (2011).
- 1117 92. Guzman, H. M., Cipriani, R. & Jackson, J. B. C. Historical Decline in Coral Reef Growth
1118 after the Panama Canal. *AMBIO J. Hum. Environ.* **37**, 342–346 (2008).
- 1119 93. Risk, M. J., Lapointe, B. E., Sherwood, O. A. & Bedford, B. J. The use of $\delta^{15}\text{N}$ in assessing
1120 sewage stress on coral reefs. *Mar. Pollut. Bull.* **58**, 793–802 (2009).
- 1121 94. Reymond, C. E., Roff, G., Chivas, A. R., Zhao, J. & Pandolfi, J. M. Millennium-scale records
1122 of benthic foraminiferal communities from the central Great Barrier Reef reveal spatial
1123 differences and temporal consistency. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **374**,
1124 52–61 (2013).
- 1125 95. Fogliarini, C. O., Longo, G. O., Francini-Filho, R. B., McClenachan, L. & Bender, M. G.
1126 Sailing into the past: Nautical charts reveal changes over 160 years in the largest reef
1127 complex in the South Atlantic Ocean. *Perspect. Ecol. Conserv.* **20**, 231–239 (2022).
- 1128 96. McClenachan, L., O'Connor, G., Neal, B. P., Pandolfi, J. M. & Jackson, J. B. C. Ghost reefs:
1129 Nautical charts document large spatial scale of coral reef loss over 240 years. *Sci. Adv.* **3**,
1130 e1603155 (2017).
- 1131 97. Lewis, J. Evidence from aerial photography of structural loss of coral reefs at Barbados,
1132 West Indies. *Coral Reefs* **21**, 49–56 (2002).
- 1133 98. Wingard, G. L., Bernhardt, C. E. & Wachnicka, A. H. The Role of Paleoecology in
1134 Restoration and Resource Management—The Past As a Guide to Future Decision-
1135 Making: Review and Example from the Greater Everglades Ecosystem, U.S.A. *Front. Ecol.*
1136 *Evol.* **5**, (2017).
- 1137 99. Allen, B. Sketch of the Eastern Coast of Central America, Compiled from Notes of
1138 Captain Richard Owen and the Officers of Her Majesty's Ship Thunder, and Schooner
1139 Lark. *J. R. Geogr. Soc. Lond.* **11**, 76 (1841).

- 1140 100. Fogliarini, C. O., Abbad, E. L., Bleuel, J., Longo, G. O. & Bender, M. G. Revisiting 150 years
1141 of coral studies to assess changes in species records, distribution, and functional
1142 structure of corals in the Brazilian Province. *Ocean Coast. Manag.* **257**, 107340 (2024).
- 1143 101. Camille, M. & Espejo-Saavedra, R. Historical Geography of the Belizean Logwood Trade.
1144 in *Yearbook* vol. 22 77–85 (1996).
- 1145 102. Callejas, I. A. *et al.* A GEE toolkit for water quality monitoring from 2002 to 2022 in
1146 support of SDG 14 and coral health in marine protected areas in Belize. *Front. Remote*
1147 *Sens.* **3**, 1020184 (2022).
- 1148 103. Fabricius, K. E., Logan, M., Weeks, S. J., Lewis, S. E. & Brodie, J. Changes in water clarity
1149 in response to river discharges on the Great Barrier Reef continental shelf: 2002–2013.
1150 *Estuar. Coast. Shelf Sci.* **173**, A1–A15 (2016).
- 1151 104. Burke, L. & Sugg, Z. *Hydrologic Modeling of Watersheds Discharging Adjacent to the*
1152 *Mesoamerican Reef.* (2006).
- 1153 105. Carlson, R. R., Foo, S. A. & Asner, G. P. Land Use Impacts on Coral Reef Health: A Ridge-
1154 to-Reef Perspective. *Front. Mar. Sci.* **6**, 562 (2019).
- 1155 106. Valderrama, L. *et al.* Evaluation of Mangrove Cover Changes in Mexico During the 1970–
1156 2005 Period. *Wetlands* **34**, 747–758 (2014).
- 1157 107. Adam, T. C. *et al.* Landscape-scale patterns of nutrient enrichment in a coral reef
1158 ecosystem: implications for coral to algae phase shifts. *Ecol. Appl.* **31**, e2227 (2021).
- 1159 108. Schaffelke, B., Carleton, J., Skuza, M., Zagorskis, I. & Furnas, M. J. Water quality in the
1160 inshore Great Barrier Reef lagoon: Implications for long-term monitoring and
1161 management. *Mar. Pollut. Bull.* **65**, 249–260 (2012).
- 1162 109. Cortés, J. *et al.* The CARICOMP Network of Caribbean Marine Laboratories (1985–2007):
1163 History, Key Findings, and Lessons Learned. *Front. Mar. Sci.* **5**, (2019).
- 1164 110. Harper, L., MarineGEO, & Tennenbaum Marine Observatories Network. MarineGEO
1165 Sampling Event & Environmental Monitoring Protocol. Preprint at
1166 <https://doi.org/10.25573/SERC.14555511.V3> (2022).
- 1167 111. Boles, E. *Stocktake and Mapping of Water Quality Monitoring Programs and Protocols*
1168 *within Belize— A Preliminary Step in the Standardization Process.* (2018).
- 1169 112. Environmental Protection Agency. *Water Quality Protection Program for the Florida*
1170 *Keys National Marine Sanctuary: Phase III Report.* (1995).
- 1171 113. Krusczyński, W. *Water Quality Concerns in the Florida Keys: Sources, Effects and*
1172 *Solutions.* (1999).
- 1173 114. NOAA Coral Program.
1174 https://repository.library.noaa.gov/view/noaa/32748/noaa_32748_DS1.pdf (2001).
- 1175 115. Bell, P. R. F. Eutrophication and coral reefs—some examples in the Great Barrier Reef
1176 lagoon. *Water Res.* **26**, 553–568 (1992).
- 1177 116. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation
1178 for Statistical Computing. (2024).
- 1179 117. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using
1180 lme4. *J. Stat. Softw.* **67**, (2015).
- 1181 118. Lüdtke, D. sjPlot: Data Visualization for Statistics in Social Science. R package version
1182 2.8.17. (2024).
- 1183 119. Allard, P. Changes in coral community structure in Barbados: effects of eutrophication
1184 and reduced grazing pressure. (McGill University, 1994).

- 1185 120. Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models*
1186 *and Extensions in Ecology with R*. (Springer New York, New York, NY, 2009).
1187 doi:10.1007/978-0-387-87458-6.
- 1188 121. Woodley, J. D. *et al.* Hurricane Allen's Impact on Jamaican Coral Reefs. *Science* **214**, 749–
1189 755 (1981).
- 1190 122. Jackson, J. B. C. Reefs since Columbus. *Coral Reefs* **16**, S23–S32 (1997).
- 1191 123. Munro, J. *Caribbean Coral Reef Fishery Resources. Vol. 7. WorldFish, 1983. vol. 7*
1192 (WorldFish, 1983).
- 1193 124. Woodley, J. The effects of trap-fishing on reef communities in Jamaica. in *13th Meeting*
1194 *of the Association of Island Marine Laboratories of the Caribbean* vol. 13 27 (1979).
- 1195 125. Liddell, W. & Ohlhorst, S. Patterns of reef community structure, north Jamaica. *Bull.*
1196 *Mar. Sci.* **4**, 311–329 (1987).
- 1197 126. Liddell, W. D. & Ohlhorst, S. L. Changes in benthic community composition following the
1198 mass mortality of *Diadema* at Jamaica. *J. Exp. Mar. Biol. Ecol.* **95**, 271–278 (1986).
- 1199 127. Aronson, R. B. & Precht, W. F. White-band disease and the changing face of Caribbean
1200 coral reefs. in *The Ecology and Etiology of Newly Emerging Marine Diseases* (ed. Porter,
1201 J. W.) 25–38 (Springer Netherlands, Dordrecht, 2001). doi:10.1007/978-94-017-3284-
1202 0_2.
- 1203 128. Lapointe, B. E. Simultaneous top-down and bottom-up forces control macroalgal blooms
1204 on coral reefs (Reply to the comment by Hughes *et al.*). *Limnol. Oceanogr.* **44**, 1586–
1205 1592 (1999).
- 1206 129. Webber, M., Edwards-Myers, E., Campbell, C. & Webber, D. Phytoplankton and
1207 zooplankton as indicators of water quality in Discovery Bay, Jamaica. *Hydrobiologia* **545**,
1208 177–193 (2005).
- 1209 130. Gayle, P. & Woodley, J. *Discovery Bay, Jamaica. CARICOMP-Caribbean Coral Reef,*
1210 *Seagrass and Mangroves Sites.* 17–33
1211 <https://www.vliz.be/imisdocs/publications/ocrd/270170.pdf#page=31> (1988).
- 1212 131. Statistical Institute of Jamaica. *Population Census 1982: Parish of St. Ann.* (1993).
- 1213 132. D'Elia, C., Webb, K. & Porter, J. Nitrate-Rich Groundwater Inputs To Discovery Bay,
1214 Jamaica - A Significant Source Of N To Local Coral Reefs. *Bull. Mar. Sci.* **31**, 903–910
1215 (1981).
- 1216 133. Greenaway, A. M. & Gordon-Smith, D.-A. The effects of rainfall on the distribution of
1217 inorganic nitrogen and phosphorus in Discovery Bay, Jamaica. *Limnol. Oceanogr.* **51**,
1218 2206–2220 (2006).
- 1219 134. Koltes, K., Tschirky, J. & Feller, I. *Carrie Bow Cay, Belize. CARICOMP-Caribbean Coral*
1220 *Reef, Seagrass and Mangrove Sites. Coastal Region and Small Island Papers. 1998;3:79-*
1221 *94. 79–94* (1998).
- 1222 135. Koltes, K. H. & Opishinski, T. B. Patterns of Water Quality and Movement in the Vicinity
1223 of Carrie Bow Cay, Belize. (2009).
- 1224 136. Aronson, R. B., Macintyre, I. G., Precht, W. F., Murdoch, T. J. T. & Wapnick, C. M. THE
1225 EXPANDING SCALE OF SPECIES TURNOVER EVENTS ON CORAL REEFS IN BELIZE. *Ecol.*
1226 *Monogr.* **72**, 233–249 (2002).
- 1227 137. Alves, C. *et al.* Twenty years of change in benthic communities across the Belizean
1228 Barrier Reef. *PLOS ONE* **17**, e0249155 (2022).

- 1229 138. McClanahan, T. & Karnauskas, M. Relationships between benthic cover, current
1230 strength, herbivory, and a fisheries closure in Glovers Reef Atoll, Belize. *Coral Reefs* **30**,
1231 9–19 (2011).
- 1232 139. Schaffelke, B., Carleton, J., Skuza, M., Zagorskis, I. & Furnas, M. J. Water quality in the
1233 inshore Great Barrier Reef lagoon: Implications for long-term monitoring and
1234 management. *Mar. Pollut. Bull.* **65**, 249–260 (2012).
- 1235 140. Garcia-Saqui, J., Saqui, P. & Chicas, S. *Identification of Deforestation and Forest*
1236 *Degradation Drivers in Belize. Program for the Reduction of Emissions from*
1237 *Deforestation and Forest Degradation in Central America and the Dominican Republic.*
1238 *Final Report. 2011.* (2011).
- 1239 141. King, R., Pratt, J., Warner, M. & Zisman, S. *Agricultural Development Prospects in Belize.*
1240 159 (1993).
- 1241 142. Murray, R. A governance analysis of three MPAs in Belize: Conservation objectives
1242 compromised by tourism development priorities? *Mar. Policy* **127**, 104243 (2021).
- 1243 143. Healthy Reefs Initiative (HRI). *2022 Mesoamerican Reef Report Card.*
1244 [https://www.healthyreefs.org/cms/wp-content/uploads/2022/12/2022-Report-Card-](https://www.healthyreefs.org/cms/wp-content/uploads/2022/12/2022-Report-Card-MAR.pdf)
1245 [MAR.pdf](https://www.healthyreefs.org/cms/wp-content/uploads/2022/12/2022-Report-Card-MAR.pdf) (2022).
- 1246 144. McField, M., Wells, S. & Gibson, J. *State of the Coastal Zone Report, Belize, 1995.* 31
1247 (1996).
- 1248 145. Lapointe, B. & Tewfik, A. Nutrient enrichment as a factor driving macroalgal blooms on
1249 the Belize Barrier Reef Complex. in *Proceedings of the Gulf and Caribbean Fisheries*
1250 *Institute* vol. 71 280–281 (2019).
- 1251 146. Callejas, I. A. *et al.* Effect of COVID-19 Anthropause on Water Clarity in the Belize Coastal
1252 Lagoon. *Front. Mar. Sci.* **8**, 648522 (2021).
- 1253 147. McClanahan, T. & Muthiga, N. Change in fish and benthic communities in Belizean patch
1254 reefs in and outside of a marine reserve, across a parrotfish capture ban. *Mar. Ecol.*
1255 *Prog. Ser.* **645**, 25–40 (2020).
- 1256 148. Tewfik, A., Burns-Perez, V. & Alamina, V. *Glover’s Reef Marine Reserve Long-Term Atoll*
1257 *Monitoring Program II, 2017.* 19 pp. (2018).
- 1258 149. Anton, A. *Nutrient Assessment at Glovers Reef Marine Reserve (Belize).* (2006).
- 1259 150. Tomasko, D. & Lapointe, B. Productivity and biomass of *Thalassia testudinum* as related
1260 to water column nutrient availability and epiphyte levels: field observations and
1261 experimental studies. *Mar. Ecol. Prog. Ser.* **75**, 9–17 (1991).
- 1262 151. Cherrington, E. *et al.* *Forest Cover and Deforestation in Belize: 1980-2010.* 1–42 (2010).
- 1263 152. Sundarambal, P., Tkalich, P. & Balasubramanian, R. Impact of biomass burning on ocean
1264 water quality in Southeast Asia through atmospheric deposition: eutrophication
1265 modeling. *Atmospheric Chem. Phys.* **10**, 11337–11357 (2010).
- 1266 153. Suchley, A., McField, M. D. & Alvarez-Filip, L. Rapidly increasing macroalgal cover not
1267 related to herbivorous fishes on Mesoamerican reefs. *PeerJ* **4**, e2084 (2016).
- 1268 154. McClanahan, T. R. & Muthiga, N. A. An ecological shift in a remote coral atoll of Belize
1269 over 25 years. *Environ. Conserv.* **25**, 122–130 (1998).
- 1270 155. Paris, C. B. & Chérubin, L. M. River-reef connectivity in the Meso-American Region. *Coral*
1271 *Reefs* **27**, 773–781 (2008).
- 1272 156. Estrada-Saldívar, N., Jordán-Dalhgren, E., Rodríguez-Martínez, R. E., Perry, C. & Alvarez-
1273 Filip, L. Functional consequences of the long-term decline of reef-building corals in the

- 1274 Caribbean: evidence of across-reef functional convergence. *R. Soc. Open Sci.* **6**, 190298
 1275 (2019).
- 1276 157. INEGI. *Anuario Estadístico y Geográfico de Quintana Roo, 2017*. 405 (2017).
- 1277 158. Bauer-Gottwein, P. *et al.* Review: The Yucatán Peninsula karst aquifer, Mexico.
 1278 *Hydrogeol. J.* **19**, 507–524 (2011).
- 1279 159. Murray, G. Constructing Paradise: The Impacts of Big Tourism in the Mexican Coastal
 1280 Zone. *Coast. Manag.* **35**, 339–355 (2007).
- 1281 160. Ellis, E. A., Hernandez Gomez, U. & Romero-Montero, J. A. Los procesos y causas del
 1282 cambio en la cobertura forestal de la Península Yucatán, México. *Ecosistemas* **26**, 101–
 1283 111 (2017).
- 1284 161. Bell, P., Tomascik, T. & Ginsburg, R. The demise of the fringing coral reefs of Barbados
 1285 and in regions in the Great Barrier Reef (GBR) lagoon—impacts of eutrophication. in
 1286 *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and*
 1287 *History* 319–325 (Miami, 1994).
- 1288 162. Gill, D. A., Oxenford, H. A., Turner, R. A. & Schuhmann, P. W. Making the most of data-
 1289 poor fisheries: Low cost mapping of small island fisheries to inform policy. *Mar. Policy*
 1290 **101**, 198–207 (2019).
- 1291 163. Tosic, M., Bonnell, R. B., Dutilleul, P. & Oxenford, H. A. Runoff Water Quality, Landuse
 1292 and Environmental Impacts on the Bellairs Fringing Reef, Barbados. in *Remote Sensing*
 1293 *and Geospatial Technologies for Coastal Ecosystem Assessment and Management* (ed.
 1294 Yang, X.) 521–553 (Springer Berlin Heidelberg, Berlin, Heidelberg, 2009).
 1295 doi:10.1007/978-3-540-88183-4_22.
- 1296 164. Lewis, J. B. THE CORAL REEFS AND CORAL COMMUNITIES OF BARBADOS, W.I. *Can. J.*
 1297 *Zool.* **38**, 1133–1145 (1960).
- 1298 165. Stearn, C. W., Scoffin, T. P. & Martindale, W. Calcium Carbonate Budget of a Fringing
 1299 Reef on the West Coast of BarbadosPart I—Zonation and Productivity. *Bull. Mar. Sci.* **27**,
 1300 479–510 (1977).
- 1301 166. Tomascik, T. & Sander, F. Effects of eutrophication on reef-building corals: II. Structure
 1302 of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar. Biol.*
 1303 **94**, 53–75 (1987).
- 1304 167. Tomascik, T. & Sander, F. Effects of eutrophication on reef-building corals. *Mar. Biol.* **87**,
 1305 143–155 (1985).
- 1306 168. Mah, A. J. & Stearn, C. W. The effect of Hurricane Allen on the Bellairs fringing reef,
 1307 Barbados. *Coral Reefs* **4**, 169–176 (1986).
- 1308 169. Tomascik, T. & Sander, F. Effects of eutrophication on reef-building corals: III.
 1309 Reproduction of the reef-building coral *Porites porites*. *Mar. Biol.* **94**, 77–94 (1987).
- 1310 170. Lapointe, B. E. & Clark, M. W. Nutrient Inputs from the Watershed and Coastal
 1311 Eutrophication in the Florida Keys. *Estuaries* **15**, 465 (1992).
- 1312 171. Hall, M., Furman, B., Merello, M. & Durako, M. Recurrence of *Thalassia testudinum*
 1313 seagrass die-off in Florida Bay, USA: initial observations. *Mar. Ecol. Prog. Ser.* **560**, 243–
 1314 249 (2016).
- 1315 172. Ruzicka, R. *et al.* *CREMP 2009 Final Report*. (2010).
- 1316 173. Florida Department of Environmental Regulation. *Florida Keys Monitoring Study: Water*
 1317 *Quality Assessment of Five Selected Pollutant Sources in Marathon, Florida*. 187 (1987).

- 1318 174. Lapointe, B. E., Barile, P. J. & Matzie, W. R. Anthropogenic nutrient enrichment of
 1319 seagrass and coral reef communities in the Lower Florida Keys: discrimination of local
 1320 versus regional nitrogen sources. *J. Exp. Mar. Biol. Ecol.* **308**, 23–58 (2004).
 1321 175. Lidz, B. & Shinn, E. Paleoshorelines, Reefs, and a Rising Sea: South Florida, U.S.A. *J.*
 1322 *Coast. Res.* **7**, 203–229 (1991).
 1323 176. Shinn, E. A. *et al.* *Reefs of Florida and the Dry Tortugas: Miami to Key West, Florida July*
 1324 *2–7, 1989.* (American Geophysical Union, Washington, D. C., 1989). doi:10.1029/FT176.
 1325 177. Carilli, J. E., Norris, R. D., Black, B. A., Walsh, S. M. & McField, M. Local Stressors Reduce
 1326 Coral Resilience to Bleaching. *PLoS ONE* **4**, e6324 (2009).
 1327 178. Ward-Paige, C., Risk, M. & Sherwood, O. Reconstruction of nitrogen sources on coral
 1328 reefs: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in gorgonians from Florida Reef Tract. *Mar. Ecol. Prog. Ser.* **296**,
 1329 155–163 (2005).
 1330 179. Purdy, C. B., Druffel, E. R. M. & Hugh D., L. Anomalous levels of ^{90}Sr and $^{239,240}\text{Pu}$ in
 1331 Florida corals: Evidence of coastal processes. *Geochim. Cosmochim. Acta* **53**, 1401–1410
 1332 (1989).
 1333 180. Swart, P. K. *et al.* The stable oxygen and carbon isotopic record from a coral growing in
 1334 Florida Bay: a 160 year record of climatic and anthropogenic influence. *Palaeogeogr.*
 1335 *Palaeoclimatol. Palaeoecol.* **123**, 219–237 (1996).
 1336 181. Loiseau, C., Thiault, L., Devillers, R. & Claudet, J. Cumulative impact assessments
 1337 highlight the benefits of integrating land-based management with marine spatial
 1338 planning. *Sci. Total Environ.* **787**, 147339 (2021).
 1339 182. Kelly, E., Gidley, M., Sinigalliano, C., Kumar, N. & Solo-Gabriele, H. M. Impact of
 1340 wastewater infrastructure improvements on beach water fecal indicator bacteria levels
 1341 in Monroe County, Florida. *Sci. Total Environ.* **763**, 143024 (2021).
 1342 183. Duran, A. *et al.* Long sediment-laden algal turf likely impairs coral recovery on Florida’s
 1343 coral reefs. *Coral Reefs* **43**, 1109–1120 (2024).
 1344 184. Gove, J. M. *et al.* Coral reefs benefit from reduced land–sea impacts under ocean
 1345 warming. *Nature* **621**, 536–542 (2023).
 1346 185. Bove, C. B., Mudge, L. & Bruno, J. F. A century of warming on Caribbean reefs. *PLOS*
 1347 *Clim.* **1**, e0000002 (2022).
 1348 186. Carrasco Rivera, D. E. & Wenger, A. S. Wastewater pollution undermines coastal marine
 1349 protection: Implications for 30x30 and effective conservation. *Ocean Coast. Manag.*
 1350 **276**, 108150 (2026).
 1351 187. McField, M. *et al.* *2024 Mesoamerican Reef Report Card. Healthy Reefs for Healthy*
 1352 *People.* www.healthyreefs.org (2024).
 1353 188. Delevaux, J. M. S. *et al.* Social–ecological benefits of land–sea planning at multiple scales
 1354 in Mesoamerica. *Nat. Sustain.* **7**, 545–557 (2024).
 1355 189. UNEP. *Regional Overview of Land-Based Sources of Pollution in the Wider Caribbean*
 1356 *Region. CEP Technical Report No. 33. UNEP Caribbean Environment Programme,*
 1357 *Kingston.* (1994).
 1358 190. deBruyn, A. M. H., Marcogliese, D. J. & Rasmussen, J. B. The role of sewage in a large
 1359 river food web. *Can. J. Fish. Aquat. Sci.* **60**, 1332–1344 (2003).
 1360 191. Lapointe, B. E. & Bedford, B. J. Stormwater nutrient inputs favor growth of non-native
 1361 macroalgae (Rhodophyta) on O’ahu, Hawaiian Islands. *Harmful Algae* **10**, 310–318
 1362 (2011).

- 1363 192. Laws, E. & Redalje, D. Effect of sewage enrichment on the phytoplankton population of
1364 a subtropical estuary. *Pac. Sci.* **33**, 129–144 (1979).
- 1365 193. Savage, C., Elmgren, R. & Larsson, U. Effects of sewage-derived nutrients on an estuarine
1366 macrobenthic community. *Mar. Ecol. Prog. Ser.* **243**, 67–82 (2002).
- 1367 194. Camacho-Cruz, K. *et al.* Changes in the enrichment of dissolved inorganic nutrients in
1368 the coastal waters of the Mexican Caribbean, influenced by submarine groundwater
1369 discharges 2016–2019. *Mar. Pollut. Bull.* **185**, 114308 (2022).
- 1370 195. Camacho-Cruz, K. A., Ortiz-Hernández, Ma. C., Sánchez, A., Carrillo, L. & De Jesús
1371 Navarrete, A. Water quality in the eastern karst region of the Yucatan Peninsula:
1372 nutrients and stable nitrogen isotopes in turtle grass, *Thalassia testudinum*. *Environ. Sci.*
1373 *Pollut. Res.* **27**, 15967–15983 (2020).
- 1374 196. Metcalfe, C. D. *et al.* Contaminants in the coastal karst aquifer system along the
1375 Caribbean coast of the Yucatan Peninsula, Mexico. *Environ. Pollut.* **159**, 991–997 (2011).
- 1376 197. Sánchez, A., Ortiz-Hernández, Ma. C., Talavera-Sáenz, A. & Aguíñiga-García, S. Stable
1377 nitrogen isotopes in the turtle grass *Thalassia testudinum* from the Mexican Caribbean:
1378 Implications of anthropogenic development. *Estuar. Coast. Shelf Sci.* **135**, 86–93 (2013).
- 1379 198. Bégin, C. *et al.* Increased sediment loads over coral reefs in Saint Lucia in relation to land
1380 use change in contributing watersheds. *Ocean Coast. Manag.* **95**, 35–45 (2014).
- 1381 199. Duran, A. *et al.* Long sediment-laden algal turf likely impairs coral recovery on Florida’s
1382 coral reefs. *Coral Reefs* **43**, 1109–1120 (2024).
- 1383 200. Roberts, M., Hanley, N., Williams, S. & Cresswell, W. Terrestrial degradation impacts on
1384 coral reef health: Evidence from the Caribbean. *Ocean Coast. Manag.* **149**, 52–68
1385 (2017).
- 1386 201. Uriarte, M., Yackulic, C. B., Lim, Y. & Arce-Nazario, J. A. Influence of land use on water
1387 quality in a tropical landscape: a multi-scale analysis. *Landsc. Ecol.* **26**, 1151–1164
1388 (2011).
- 1389 202. Wynne, S. Observational evidence of regional eutrophication in the Caribbean Sea and
1390 potential impacts on coral reef ecosystems and their management in Anguilla, BWI.
1391 *Anguilla Fish. Mar. Resour. Res. Bull.* **8**, 1–22 (2017).
- 1392 203. Morgan, K. M., Perry, C. T., Smithers, S. G., Johnson, J. A. & Daniell, J. J. Evidence of
1393 extensive reef development and high coral cover in nearshore environments:
1394 implications for understanding coral adaptation in turbid settings. *Sci. Rep.* **6**, 29616
1395 (2016).
- 1396 204. Santana, E. F. C. *et al.* Turbidity shapes shallow Southwestern Atlantic benthic reef
1397 communities. *Mar. Environ. Res.* **183**, 105807 (2023).
- 1398 205. Cacciapaglia, C. & Van Woesik, R. Climate-change refugia: shading reef corals by
1399 turbidity. *Glob. Change Biol.* **22**, 1145–1154 (2016).
- 1400 206. Sully, S. & Van Woesik, R. Turbid reefs moderate coral bleaching under climate-related
1401 temperature stress. *Glob. Change Biol.* **26**, 1367–1373 (2020).
- 1402 207. Thanopoulou, Z., Patus, J. & Sealey, K. S. Water quality negatively impacts coral
1403 occurrence in eutrophic nearshore environments of the Florida Keys. *Front. Mar. Sci.* **9**,
1404 1005036 (2022).
- 1405 208. Zweifler (Zvifler), A., O’Leary, M., Morgan, K. & Browne, N. K. Turbid Coral Reefs: Past,
1406 Present and Future—A Review. *Diversity* **13**, 251 (2021).
- 1407 209. Boström-Einarsson, L. *et al.* Coral restoration – A systematic review of current methods,
1408 successes, failures and future directions. *PLOS ONE* **15**, e0226631 (2020).

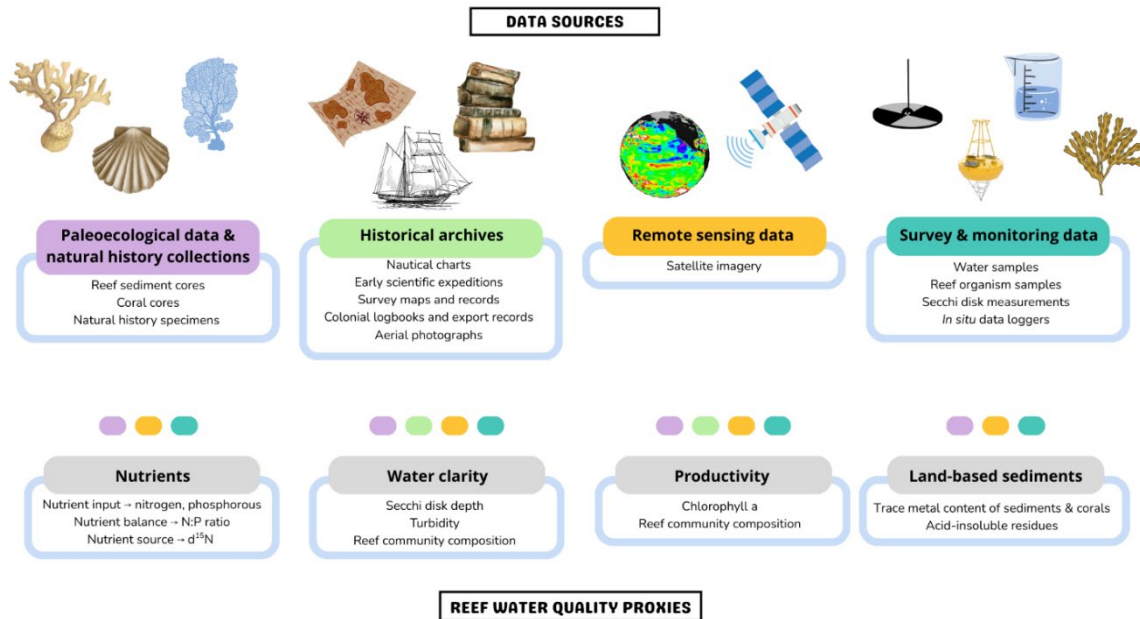
- 1409 210. Butler, M. J. *et al.* Restoration of herbivory on Caribbean coral reefs: are fishes, urchins,
 1410 or crabs the solution? *Front. Mar. Sci.* **11**, 1329028 (2024).
 1411 211. Edwards, H. J. *et al.* How much time can herbivore protection buy for coral reefs under
 1412 realistic regimes of hurricanes and coral bleaching?: CORAL AND CLIMATE CHANGE.
 1413 *Glob. Change Biol.* **17**, 2033–2048 (2011).
 1414 212. Wenger, A. S. *et al.* *Water Pollution Toolkit*. [https://library.wcs.org/en-us/Scientific-](https://library.wcs.org/en-us/Scientific-Research/Research-Publications/Publications-Library/ctl/view/mid/40093/pubid/DMX5)
 1415 [Research/Research-Publications/Publications-Library/ctl/view/mid/40093/pubid/DMX5](https://library.wcs.org/en-us/Scientific-Research/Research-Publications/Publications-Library/ctl/view/mid/40093/pubid/DMX5)

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1417 **Figures**

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1422 **Figure 1.** Historical data useful for tracking trends in various aspects of reef water quality. The

1423 data sources that can provide information for a specific water quality proxy are indicated by

1424 colored ovals. Earth image from <https://images.nasa.gov/>

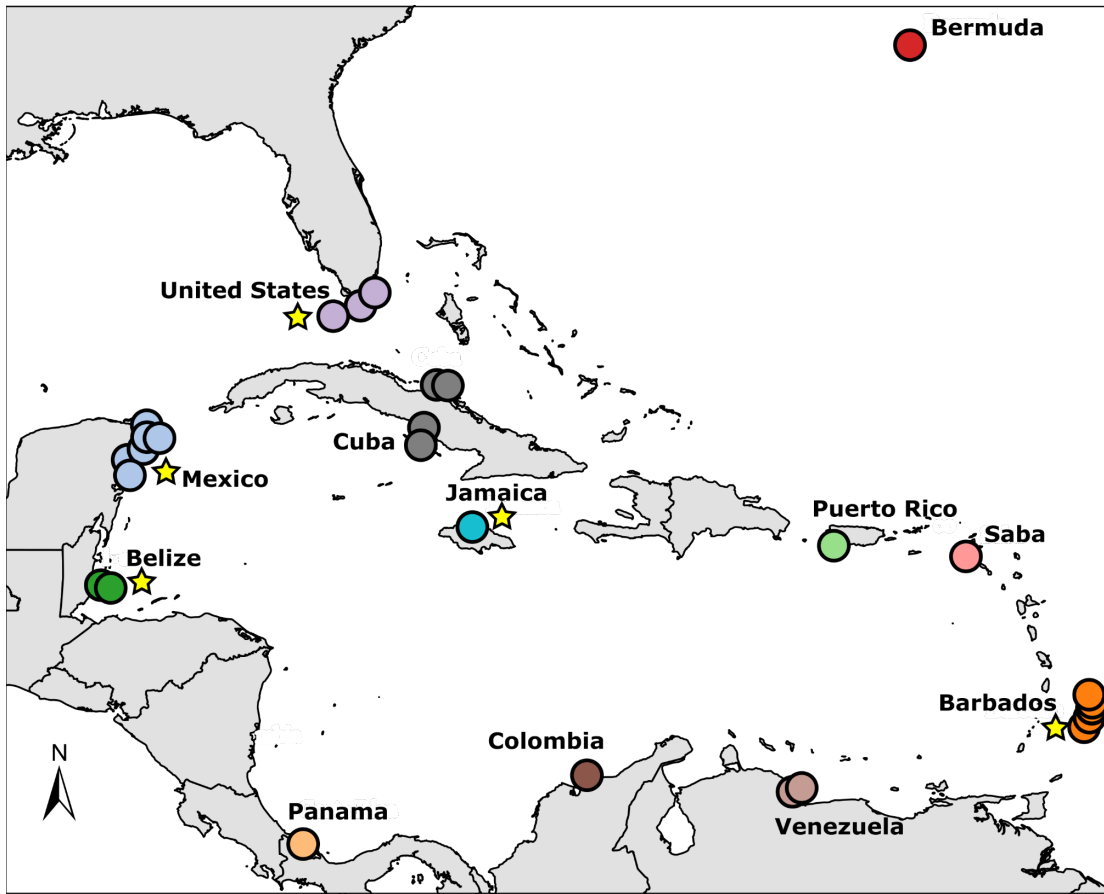
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1432 **Figure 2.** Location of studies from which trends in reef water quality were assessed. Where data
1433 were available, coral cover trends were compared with water quality trends. Stars indicate case
1434 study locations; all other locations included in regional analyses only.

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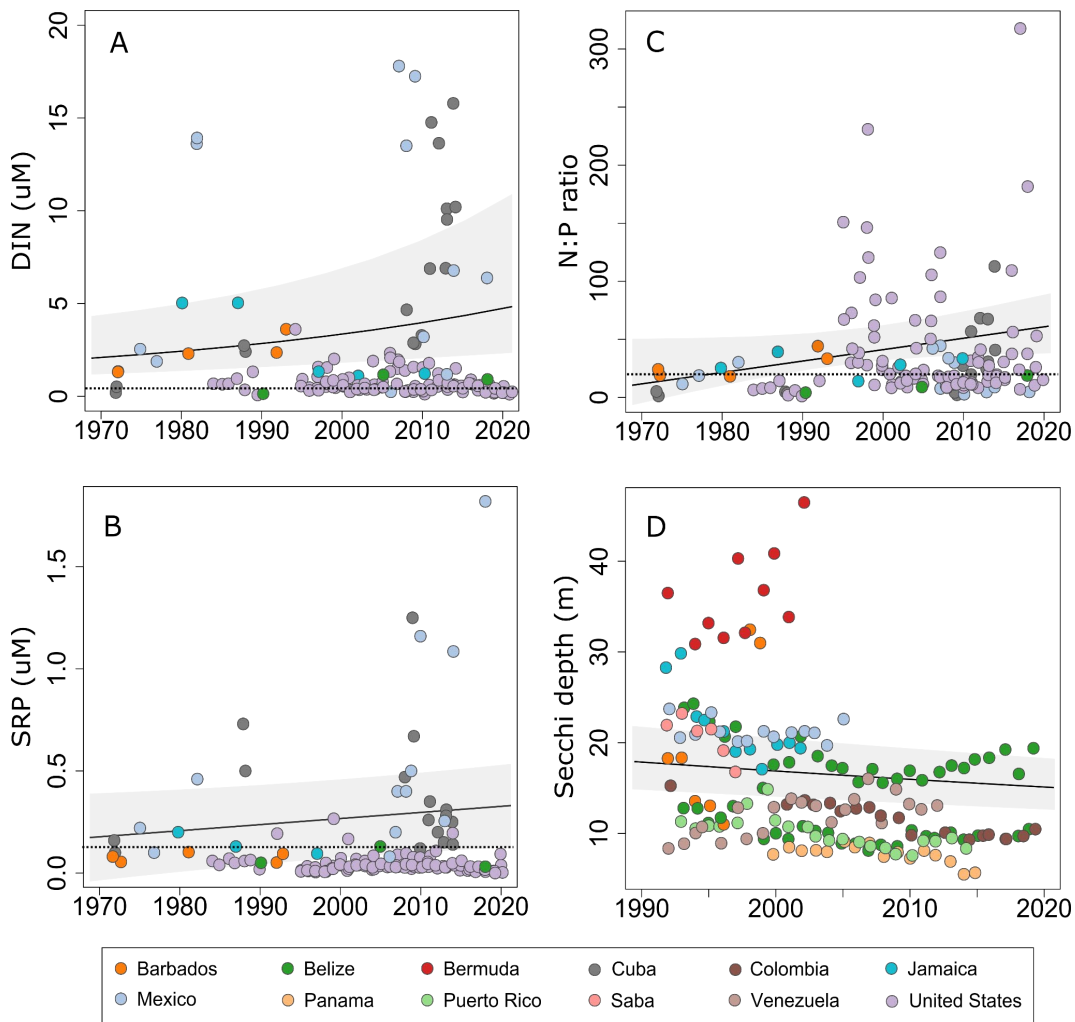
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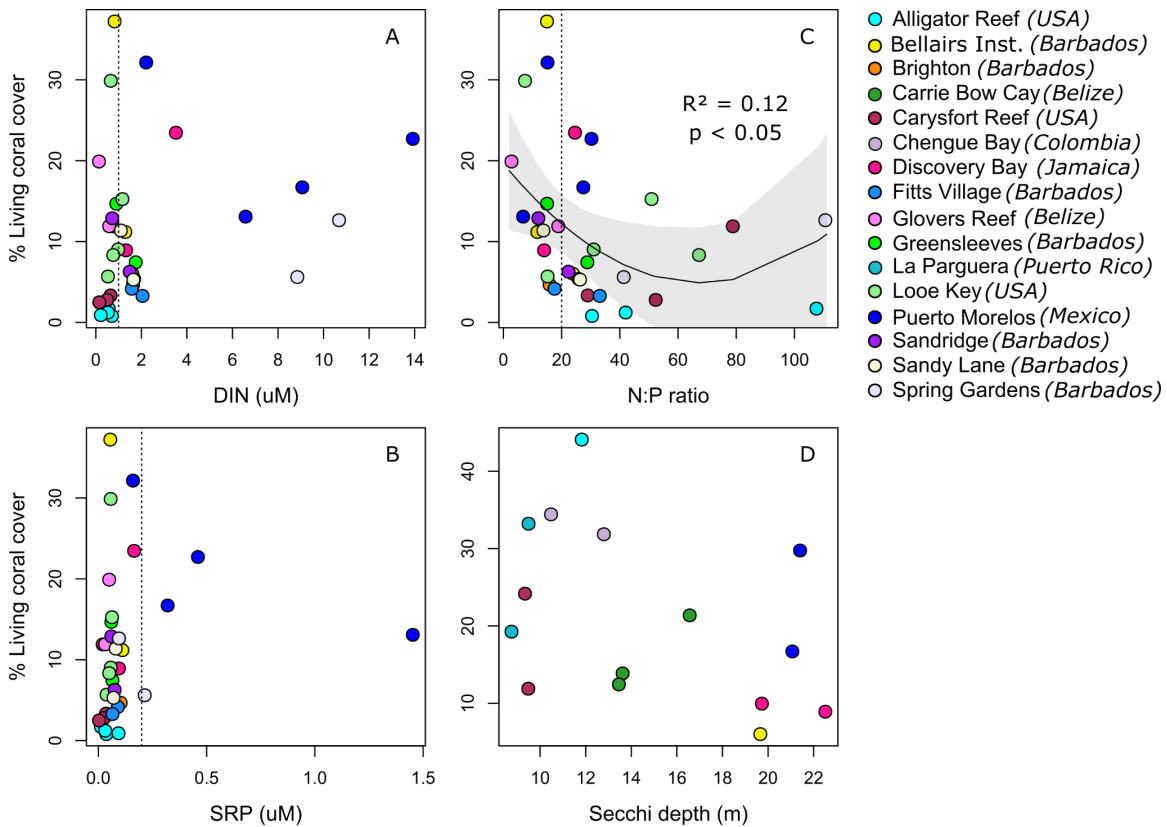
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1444 **Figure 3.** Regional trends in water quality parameters with sufficient temporal and spatial
1445 coverage. Points are annual averages of replicate measurements within an individual reef site.
1446 Dotted black lines are threshold values for nutrients beyond which coral health is compromised.
1447 Solid black line is modeled fit from generalized linear mixed effects models with country as a
1448 random effect or generalized linear models; shaded area includes 95% confidence interval of
1449 model fit. One anomalously high N:P value for 2018 from the Florida Keys (N:P = 606) was
1450 excluded from figure 3C to improve visual interpretation of trend. The two sets of dark green
1451 points in figure 3D represent the offshore (higher Secchi depth values) and lagoonal (lower
1452 Secchi depth values) monitoring sites near Carrie Bow Cay, Belize.



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1455 **Figure 4.** Relationship between water quality parameters and coral cover on a regional scale.

1456 Points are decadal averages of replicate measurements within an individual reef site. Black line is

1457 modeled fit from generalized linear mixed effects models with country as a random effect; shaded

1458 area includes 95% confidence interval of model fit. Model fit shown in Figure 4C is statistically

1459 significant; models explored to describe the relationship for other water quality parameters and

1460 coral cover were not statistically significant. Vertical lines are threshold nutrient values beyond

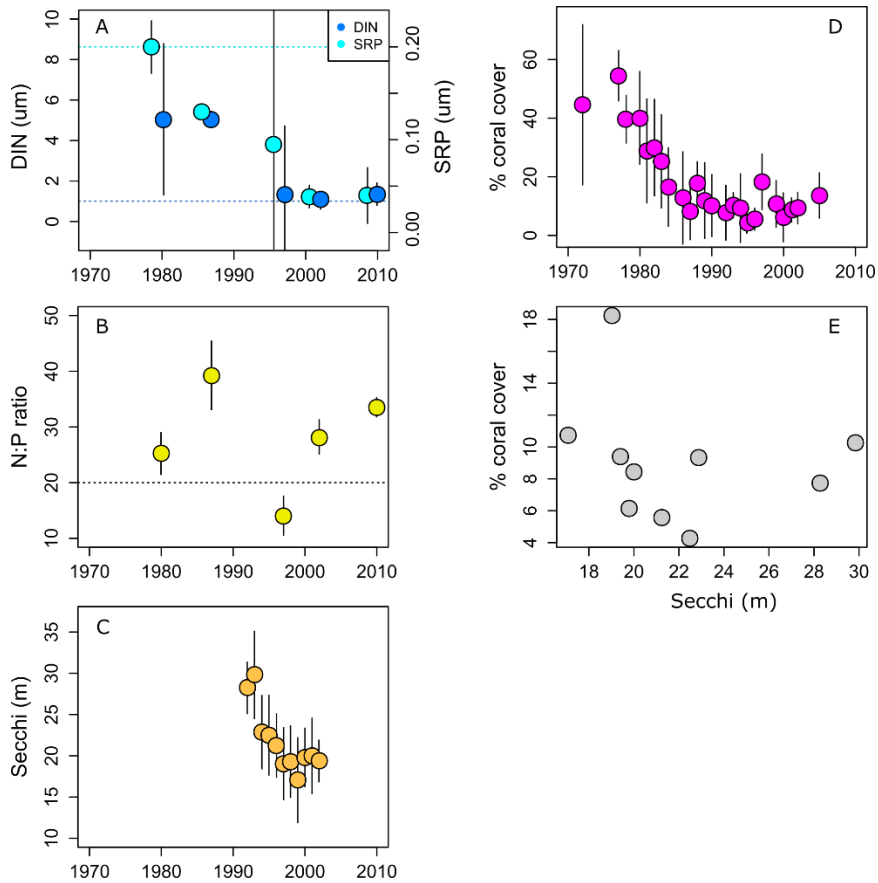
1461 which coral health has been shown to be compromised.

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1467 **Figure 5.** Synthesis of existing water quality and coral cover data for Discovery Bay, Jamaica.

1468 Horizontal lines indicate threshold values beyond which coral health is compromised.

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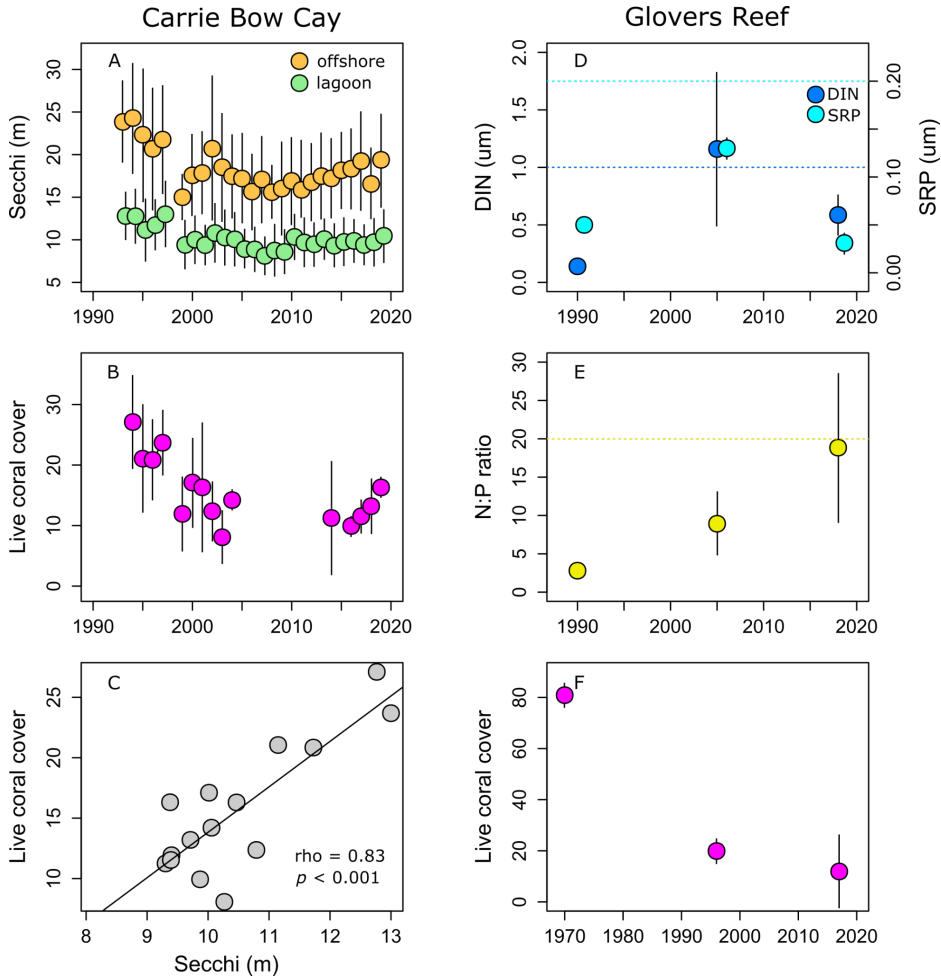
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1481 **Figure 6.** Synthesis of existing water quality and coral cover data for Carrie Bow Cay and Glovers

1482 Reef, Belize. Vertical lines are standard deviations; horizontal lines indicate threshold values

1483 beyond which coral health is compromised. Trendline indicates significant linear correlation

1484 between Secchi depth and coral cover for the lagoonal site near Carrie Bow Cay.

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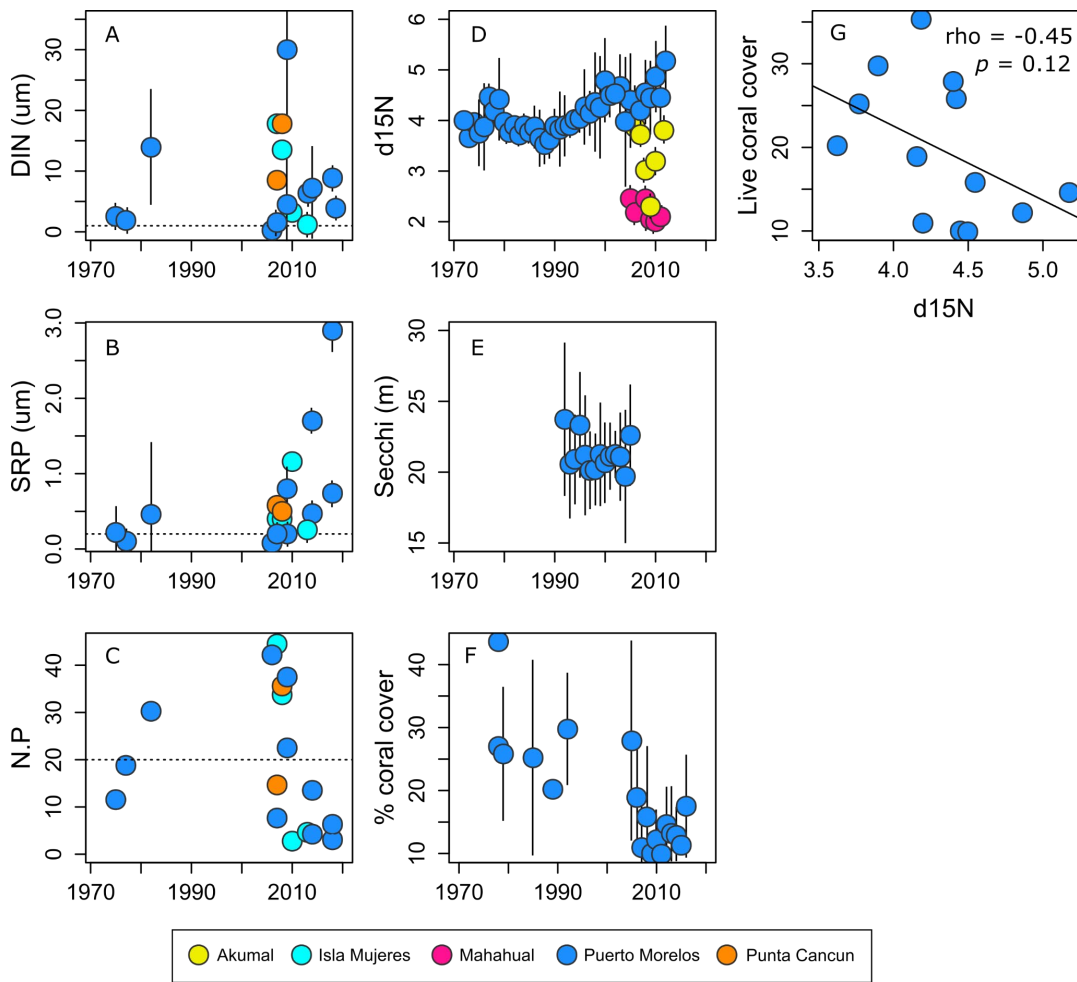
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1494 **Figure 7.** Synthesis of existing water quality and coral cover data for reef sites within Quintana

1495 Roo, Mexico. Horizontal lines indicate threshold values beyond which coral health is

1496 compromised.

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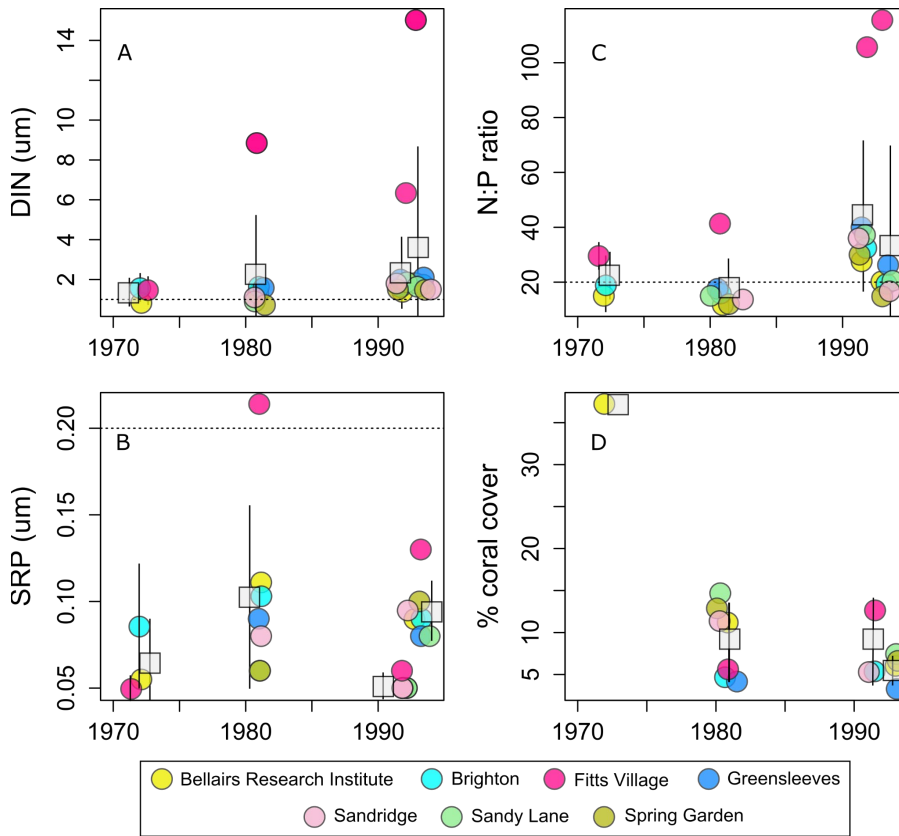
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1506 **Figure 8.** Synthesis of existing water quality and coral cover data for reef sights in Barbados.

1507 Vertical lines are standard deviations; squares are annual averages across all reef sites;

1508 horizontal lines indicate threshold values beyond which coral health is compromised.

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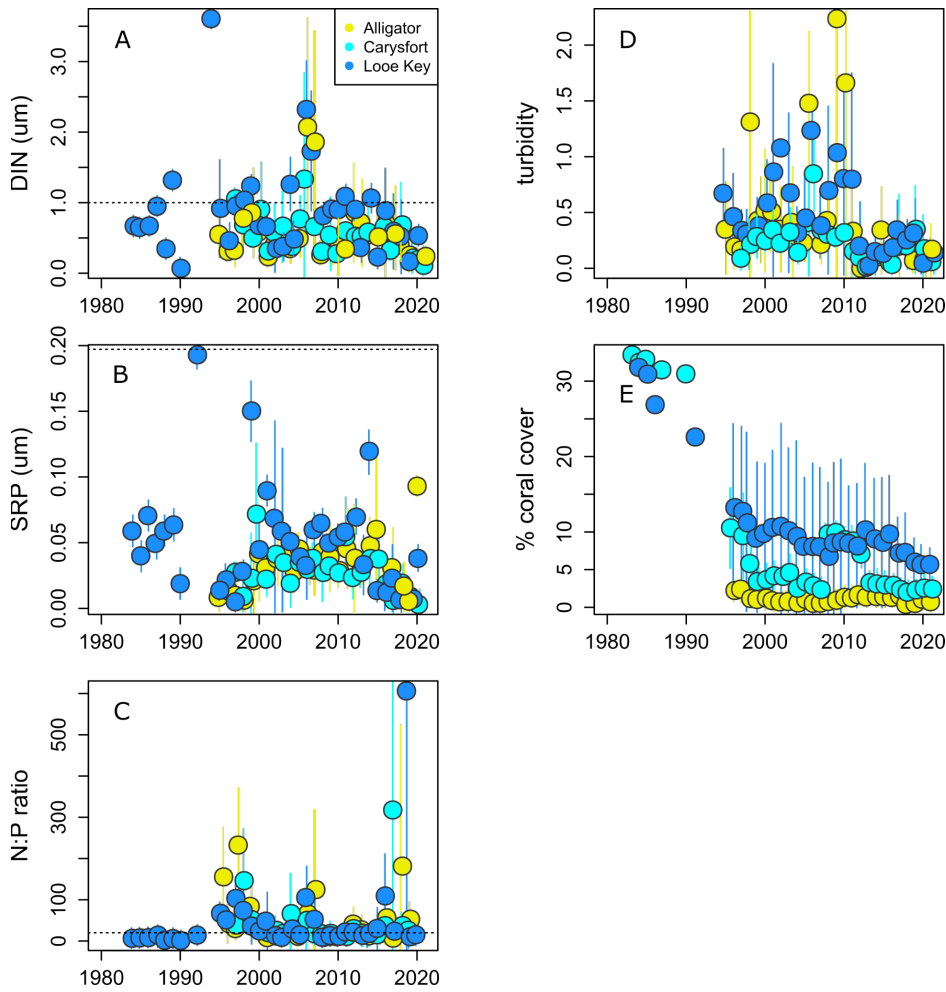
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1520 **Figure 9.** Synthesis of existing water quality and coral cover data for three reef sights in the
1521 Florida Keys. Vertical lines are standard deviations; horizontal lines indicate threshold values
1522 beyond which coral health is compromised. Trendline indicates significant linear correlation.
1523 Alligator Reef is in the Middle Keys and represents the highest exposure to land-based runoff,
1524 Carysfort Reef is in the Upper Keys and represents the lowest exposure to land-based runoff, and
1525 Looe Key is in the Lower Keys and represents moderate exposure to land-based runoff.

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