MARINE CONSERVATION

Ghost reefs: Nautical charts document large spatial scale of coral reef loss over 240 years

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Massive declines in population abundances of marine animals have been documented over century-long time scales. However, analogous loss of spatial extent of habitat-forming organisms is less well known because georeferenced data are rare over long time scales, particularly in subtidal, tropical marine regions. We use high-resolution historical nautical charts to quantify changes to benthic structure over 240 years in the Florida Keys, finding an overall loss of 52% (SE, 6.4%) of the area of the seafloor occupied by corals. We find a strong spatial dimension to this decline; the spatial extent of coral in Florida Bay and nearshore declined by 87.5% (SE, 7.2%) and 68.8% (SE, 7.5%), respectively, whereas that of offshore areas of coral remained largely intact. These estimates add to finer-scale loss in live coral cover exceeding 90% in some locations in recent decades. The near-complete elimination of the spatial coverage of nearshore coral represents an underappreciated spatial component of the shifting baseline syndrome, with important lessons for other species and ecosystems. That is, modern surveys are typically designed to assess change only within the species' known, extant range. For species ranging from corals to sea turtles, this approach may overlook spatial loss over longer time frames, resulting in both overly optimistic views of their current conservation status and underestimates of their restoration potential.

INTRODUCTION

Humans have fundamentally altered coastal ecosystems over centuries, requiring a diversity of data types to describe baseline states, quantify long-term changes, and identify drivers of change (1, 2). In particular, the loss of taxa that provide biogenic habitat, such as oysters, mangroves, and coral, can result in fundamental changes to ecosystem structure and services, including the productivity of coastal fisheries, water quality, and storm protection (3–5). Historical maps have been used to estimate declines in the spatial extent of coastal habitats, such as salt marshes, over the scale of centuries (6, 7). The relative rarity of historical underwater maps has limited the ability to document long-term loss of subtidal habitats, with the notable exception of oyster reefs, whose spatial extent was often charted as part of the oyster fishery in the late 19th and early 20th centuries. Analyses of these charts have revealed that the spatial extent of oyster reefs declined by more than 50% in the Chesapeake Bay (8) and by 64% in the United States as a whole over 100 years (9). In contrast, quantifying similar changes for analogous subtidal habitats in the tropics, such as coral reefs, is difficult because the lack of economic value for these species made the incentive to map them relatively low. As a result, high-resolution, georeferenced historical data needed to describe spatial changes to coral reefs over century-long time scales are rare.

Large declines in live coral cover have been estimated over the past few decades, with an average loss of 50% documented across the Caribbean (10) and a considerably greater loss on many reefs in the Florida Keys over this same time (11, 12). Although these declines are massive, they may underestimate loss because of the limited spatial and temporal scales of analyses. Coral reef change is typically measured as percent live coral on extant reefs on the scale of square meters. In a few rare cases, landscape-scale changes over longer time scales have been documented, such as the complete loss of *Acropora palmata* reefs from Vieques Island documented with aerial photographs spanning seven decades (13). Likewise, structural losses of fringing reefs around Barbados were documented by the fortuitous discovery of aerial photographs from 1950 (14), and changes in community composition were observed over 95 years with "before and after comparisons" to early ecological surveys conducted in the Dry Tortugas (15). However, documentation of the loss of coral extent on the scale of kilometers is rare. Human impact to reefs stretches back centuries (16), with loss of reef-building corals associated with early human settlement and land-based activities, such as agriculture and deforestation (17, 18), compounded by hurricanes and sea-level rise (19, 20), but the spatial extent of this early coral loss is unknown. Therefore, temporally extended landscape-scale baselines for reefs are needed to quantify the full extent of change and to improve delineation of early drivers of change.

Early nautical charts provide a unique and previously underused data source to combat the lack of spatial data over long time scales. Nautical charts from the 19th century have been used to examine the changes in mudbank locations in Florida Bay (21) and shoreline changes in the equatorial Pacific (22). However, 19th century navigational charts typically contain little ecological information compared to charts made a century earlier. In particular, 18th century British imperial mapping of overseas territories marked the first global effort to collect high-resolution spatial data on coastal areas (23); these charts often contained substantial amounts of ecological information, with coral of particular interest as a navigational hazard. The degree of biologically relevant information recorded varied by cartographer, but the best of these British maps describes the depth, shape, and color of shallow-water corals and distinguishes them from other hard structures such as rocks. As a result, these 18th century charts provide a historical baseline of the spatial extent of coral habitat, which can be used to assess large-scale changes in reef habitat over centuries. Here, we use 18th century

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British nautical charts (*24–26*) to quantify spatial changes in coral reef habitat in the Florida Keys over 240 years.

RESULTS

We identified 143 coral observations on two historical charts that span from Key Largo to the Marquesas Keys. These data represent a historical baseline of coral presence in discrete locations across the Florida Keys, distributed across five reef zones: (i) Florida Bay, (ii) nearshore patch reef, (iii) offshore patch reef, (iv) reef crest, and (v) forereef (Table 1 and table S2). Most of the observations fell into the three interior zones: the nearshore patch reef, the offshore patch reef, and the reef crest. Nineteen historical observations, all from the forereef zone, were discarded because they fell outside the range of modern benthic habitat maps.

We compared each of the locations where coral was mapped in the 1770s to modern benthic habitat data, derived from three data sets: the Millennium Coral Reef Mapping Project (*27*), the Benthic Habitats South Florida Map (*28*), and the Unified Florida Coral Reef Tract Map (*29*). In contrast to the historical data, which represent discreet observations of coral (that is, presence data), the modern maps provide information on both coral presence and absence. Therefore, our results provide an assessment of the persistence of the 143 individual coral observations mapped in the 1770s. Loss of spatial extent is defined as the number of historical coral observations that are in locations no longer represented by coral in the modern benthic habitat maps.

When we compared historical observations to benthic habitat data (figs. S1 to S3), we estimate a 52% (SE, 6.4%) loss in the occurrence of corals in the Florida Keys over 240 years. That is, just more than half of the historical coral observations are in locations where coral habitat does not exist today. Estimates of the loss of coral habitats derived independently from each of three modern data sets (Benthic Habitat, Unified Reef, and Millennium Coral) are 64% (SE, 4.9%), 68% (SE, 7.0%), and 72% (SE, 4.0%), respectively, which suggests that our estimate based on the combined data set is extremely conservative. The vast majority of historical coral observations without extant coral are now represented by seagrass and bare substrate (91 and 9% of historical mappable observations, respectively).

There was a strong spatial dimension to coral decline, with substantial loss identified in inshore areas (Fig. 1 and Table 1). We estimate that coral occurrences in Florida Bay and nearshore patch reefs declined by 87.5% (SE, 7.2%) and 68.8% (SE, 7.5%), respectively. In contrast, most of the corals mapped in the 1770s in offshore patch reefs, along the reef crest, and in the forereef are in locations characterized by coral reef habitat

today. We found 60% (SE, 11.9%), 87.9% (SE, 6.8%), and 100% (SE, 0%), respectively, of historical coral persistence across these three zones that are progressively farther from shore.

Our findings are most robust for zones 2 to 4, where the historical sample size and overlap with modern data were the highest (Table 1). Of these zones, there is a clear loss of nearshore patch reefs (zone 2), which can be seen both in channels between islands and in areas adjacent to a developed land. For example, Bahia Honda historically had extensive coral, but all inshore coral in this bay is now gone (Fig. 1D). The area around Key West demonstrates a similar pattern (Fig. 2). Historical descriptions made by 18th century surveyors support results derived from the charts (table S1). The Bahia Honda channel was described as having "a good deal of small coral," which made it ideal for anchoring, and the Key West channel had "two or three patches of Coral rocks…nearly in mid channel" (*24*). Although our sample size of historical coral observations is smaller for Florida Bay (*n* = 8), coral was encountered along the entire length of the Keys, suggesting more widespread historical prevalence. In contrast, the only remaining coral is now found in the lower Florida Bay, and reefs appear less extensive than they were 240 years ago (Fig. 1C).

In contrast, the vast majority of mapped historical coral occurrences in the offshore patch reef (zone 3) and reef crest (zone 4) are in areas with existing coral habitat (Fig. 1C). The historical coral data along the reef crest (zone 4) and forereef (zone 5) demonstrate both the persistence of coral in these zones and the robust nature of the early nautical charts. The alignment of historical and modern coral is nearly exact in some locations (fig. S1), suggesting a little change to the overall reef structure. This overlap also demonstrates a high level of precision in historical mapping. Nineteen of the 22 observations in the forereef were discarded because they fell outside the depth range of the modern surveys, which reports coral cover only within the depth limit for satellite sensing of approximately 20 m (*30*). Conversely, sounding lead lines were able to report benthic substrate type from depths of up to 60 m (*31*). It is notable that early manual sampling methods were able to provide some observations in the mesophotic depths, which remain the least explored parts of the coral reef today (*32*).

DISCUSSION

Our analysis of long-term change to corals in the Florida Keys adds a larger-scale spatial component to previous estimates of coral loss and provides an essential missing dimension of ecosystem change. We found a distinct spatial pattern of loss, with complete or nearly complete inshore loss of coral. In particular, small-patch reefs in the

Table 1. Characteristics of the five reef zones, number of historical coral observations, mean depth of historical coral observations, and mean percent loss across zones. Percent loss represents the number of discrete historical observations in each zone that are represented by modern coral on modern benthic habitat maps. Values are mean estimates of change using three threshold distances (0.25, 0.5, and 0.75 km). na, not applicable.

Zone	Name	Depth range of corals (m)	Historical coral observations	Mean percent loss (SE, range)
1	Florida Bay	2.1–11.4	8	87.5 (7.2, 75–100)
2	Nearshore patch reef	0.6–9.1	31	68.8 (7.5, 61.3–83.9)
3	Offshore patch reef	0.6–12.3	35	40.0 (11.9, 22.9–62.9)
4	Reef crest	1.2–14.6	47	12.1 (6.8, 4.3–25.5)
5	Forereef	12.8–58.5	22	0 (0, na)

southern regions of Florida Bay, in channels, and in the nearshore have been disproportionately degraded. In contrast, we found complete or nearly complete survival of historical coral habitat on the reef crest and forereef; these areas have experienced massive losses in live coral cover but are still broadly classified as reef habitat (11, 12). This is important because estimates of changes to coral cover are typically based on observations in areas with extant coral cover, with areas lacking coral undersampled by the very design of modern surveys. For example, in the Florida Keys, monitoring efforts in nearshore areas were eliminated in 2001 because of consistently low coral cover (33). Although this may make sense from a monitoring perspective, it ultimately underestimates long-term loss. Our analysis demonstrates that entire sections of the reef that were present before

European settlement are now largely gone—much like the early disappearance of *Acropora* reefs around Barbados in the first half of the 20th century (14, 34). This spatial pattern underscores an important large-scale change that is easily undetected in shorter time-frame studies: the loss of inshore coral. This change in baseline perceptions has the potential to reduce expectations for spatial extent, cover, and ecological interactions on reefs, as well as for their restoration (17, 35). In addition, our analysis demonstrates the untapped value of early nautical charts for describing long-term ecological changes for biogenic habitats, such as coral, that otherwise lack written historical records over the scale of centuries. In particular, nautical charts produced for other heavily trafficked colonial regions—including Jamaica's Kingston Harbor and Hong Kong Harbor—have the potential to provide a more
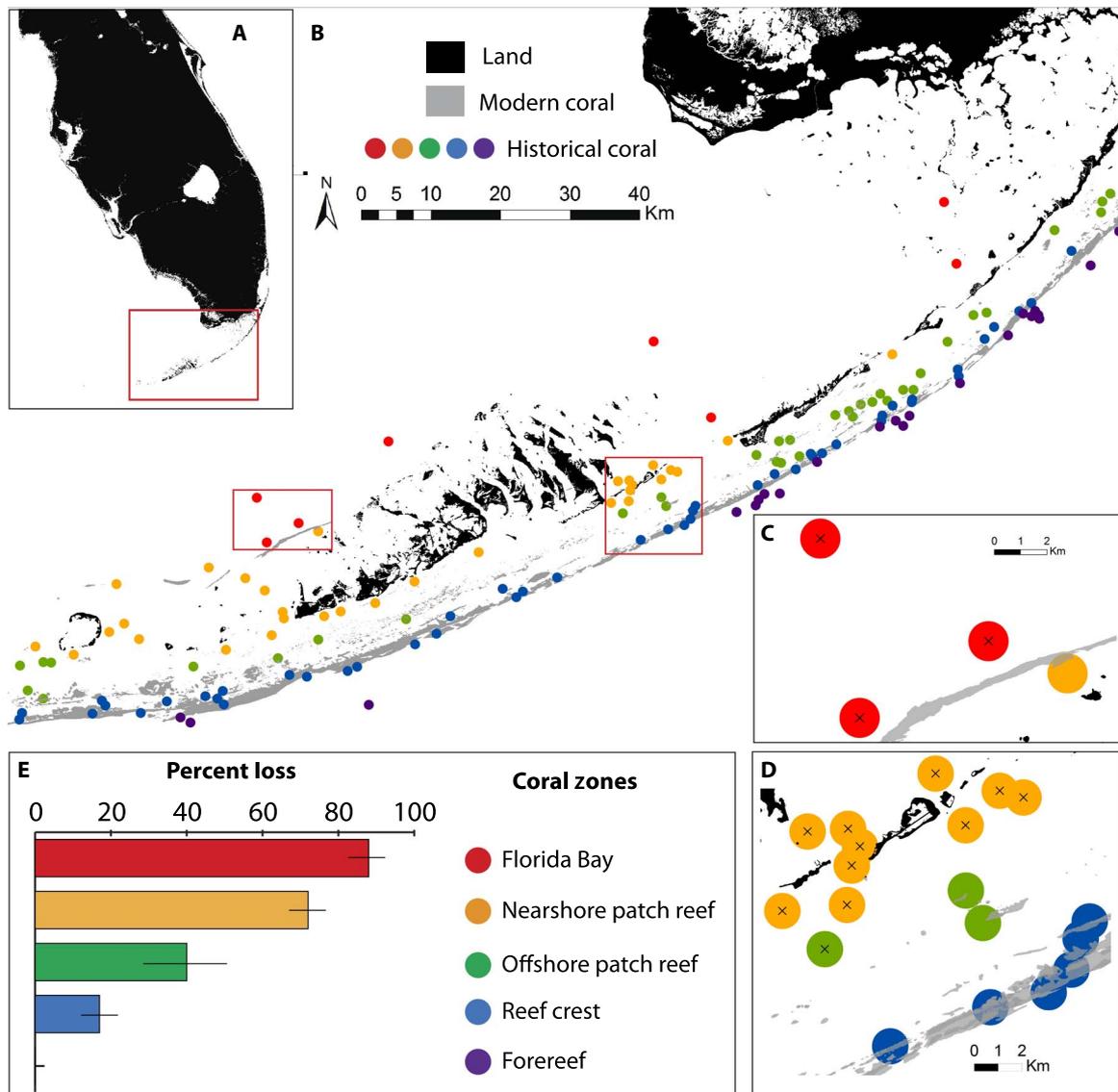

Fig. 1. A strong spatial gradient to coral loss in the Florida Keys. (**A**) Study area. (**B**). Modern and historical coral occurrences in the Florida Keys. The color of dots corresponds with the five delineated coral zones. (**C**) Enlarged area demonstrates the loss of coral from Florida Bay (red). (**D**) Enlarged area (Bahia Honda) demonstrates the loss of the nearshore patch reef (yellow) and the persistence of coral in the reef crest zone (blue). For (C) and (D), corals that no longer remain are indicated with an X. (**E**) Percent loss by zone. Bars represent the mean estimate of loss derived from three distance thresholds diameters (0.25, 0.5, and 0.75 km). Error bars represent the SEs across those three estimates.

complete measure of decline of coral reef systems since European contact.

Although they extend the baseline spatially and temporally, these historical data are not without limitations, in particular, the inability to know precisely how "coral" was defined by the chart makers. Representation of coral on the charts suggests two complementary methods of benthic habitat classification. The first has been described as the use of a weighted line with a tallow, which was also used to record depth (21, 31). Coral sampled in this way is represented by the word coral along a horizontal transect of depth readings. The use of a weighted line allowed early British map makers to probe deeper depths than typical modern surveys and benthic habitat maps, which are typically based on satellite images. However, like more recent satellite mapping efforts, 18th century maps of deep-water corals had limited precision because they inferred the location of reefs by the presence of coral on the seabed. The second method of historical mapping—observation from the surface—is implied by the

two-dimensional contours drawn to represent larger coral outcroppings and the written descriptions accompanying them. For example, a series of approximately 10 shallow (1 to 2 m) reef structures in the Lower Keys are described on the chart as "brown coral banks" in "only one or two feet of water," which almost certainly describe stands of A. palmata. One potential issue with charting from surface observations is either the risk of mischaracterizing other large biogenic structures (such as sponges) as corals or, alternatively, classifying all hard structures posing an obstruction to navigation as coral. However, the detailed written descriptions that accompany the charts, and the fact that "rocks" are distinguished from coral on the chart, make both of these scenarios unlikely. One real limitation of the historical data is not knowing whether chart makers had the ability or interest to distinguish between live and dead coral. Dead coral would have very different coloration so it could be distinguished from the surface in shallow water, but this would have been impossible to discern at deeper depths. Although this limits the comparison to modern metrics of change, the goal of our
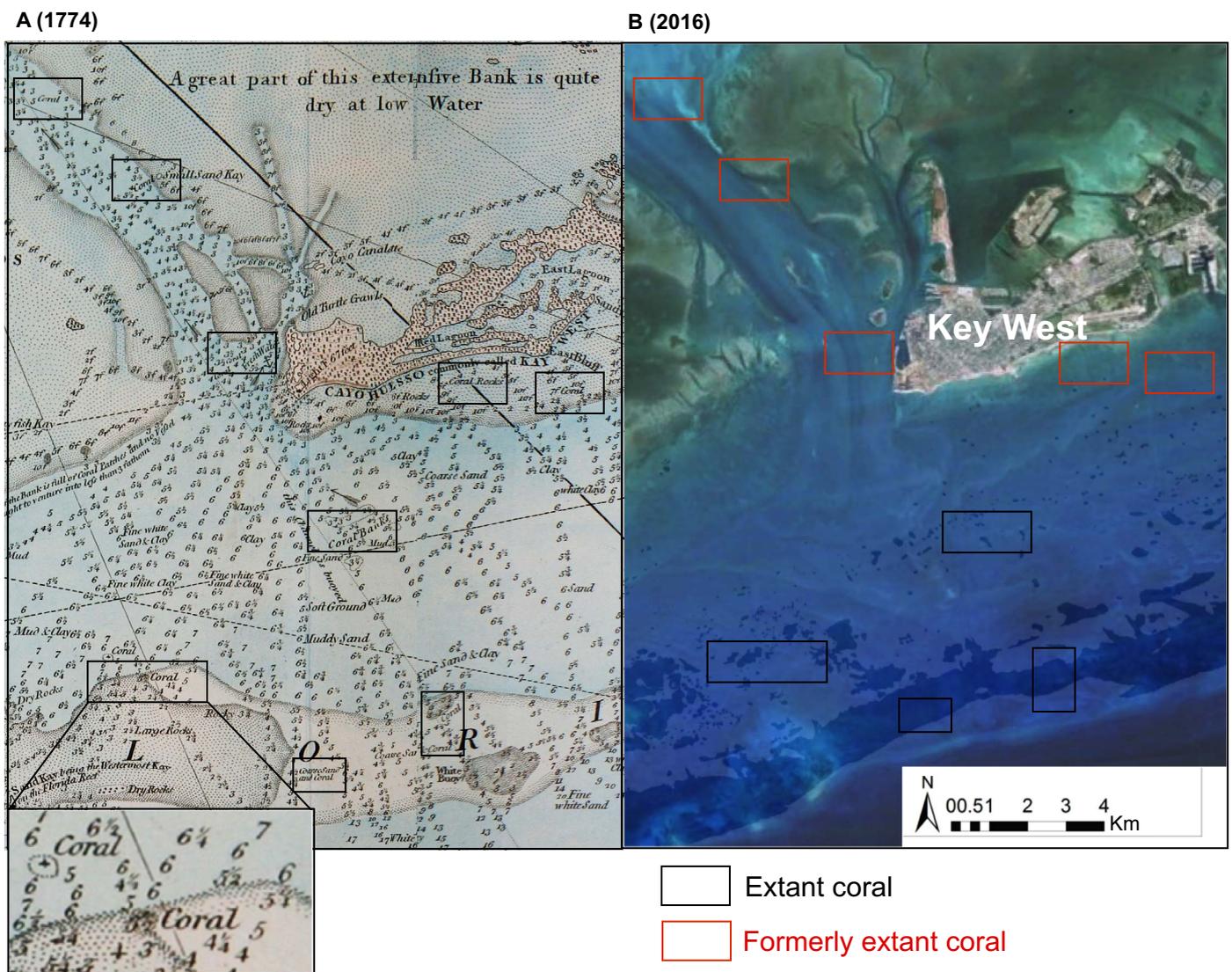

Fig. 2. Example of nearshore coral loss near Key West, Florida. (**A**) Excerpt of Guald's 1774 nautical chart, with locations of coral indicated with black rectangles. The inset shows an enlarged image of two adjacent historical coral references. (**B**) Same area today, represented by Google Earth imagery overlaid on the compiled modern benthic habitat map. Black rectangles indicate areas of coral persistence; gray rectangles indicate coral loss.

study was to identify broad-scale changes in the distribution of coral reef habitats. Therefore, our results provide a complementary analysis to more recent finer-scale assessments of loss in live coral cover.

Because of these differences in metrics of change, our estimate of 52% loss are in addition to, not contradictory of, previous estimates of decline in coral cover estimated over the scale of decades, such as the 50% loss across the Caribbean basin (10) or the 75 to 80% decline in the Keys (10, 11). These estimates are based on field measurements of live coral since the 1970s on areas of known reef habitat, such as those at Key Largo Dry Rocks, where stony coral declined from 57 to 14% between 1974 and 2000 (11), and at Carysfort Reef, where living coral cover declined by 92% between 1974 and 1999 (12). Although coral cover has markedly declined throughout the Keys, these areas are still broadly classified as reef habitat. In contrast, our data describe a larger-scale loss in the spatial extent of reef habitat that is no longer described as such. The areas of loss are largely nonoverlapping; for example, neither of the two studies mentioned above are in the nearshore zone (zone 2), where we found the largest change. Similarly, of the 19 sites used in a meta-analysis of change in coral reef cover (36) that overlap geographically with our study, only 3 sites are from this nearshore zone. Therefore, our results expand the spatial baseline to include not only the loss in percent cover of live reef on extant reefs but also the loss of whole reefs. As a result, the declines of >50% in the extent of coral reefs over large spatial scales that we identify, together with subsequent finer-scale losses in live coral cover of 75 to 80% over the past three decades, suggest a massive cumulative loss of reef coral in the Florida Keys since the American Revolution.

This large spatial scale of decline in coral reef habitat highlights the effects of early disturbance mechanisms that are different from the dominant drivers of modern coral reef degradation (37, 38). Our results dovetail with those derived from paleoecological analyses that implicate terrestrial development and hydrological changes with coral death in the early 20th century (17, 18, 39), by suggesting that these early drivers had widespread nearshore impact. Chronologies reconstructed from coral and sediment cores in Florida Bay demonstrate abrupt changes in the first decades of the 20th century, coincident with the construction of a railway between 1906 and 1914, which linked the islands and restricted ecological and physical exchange between the Bay and the reef tract, as well as changes to the hydrography of Florida Bay associated with large-scale drainage and land conversion in the Everglades between 1900 and 1930 (40). For example, isotopic analyses of Florida Bay corals show an increase in salinity and accumulation of the products of the oxidation of organic carbon between 1907 and 1910, whereas historical coral core fluorescence patterns suggest a decline in freshwater input by as much as 59% between 1912 and 1931 (41, 42).

One limitation of the data derived from coral cores is their restricted spatial distribution. Our result that 88% of Florida Bay corals have been lost suggests that the ecological changes documented in discrete coral skeleton samples may have had widespread impacts. Similar increases in organic carbon in Florida Bay have also occurred in response to rapid sea-level rise and destruction of mangroves by hurricanes. Analysis of aerial photographs from the 1930s and 1950s demonstrated the collapse of coastal wetlands in Southwest Florida, coincident with increases in relative sea level since 1930. Hurricanes have also affected nearshore environments; analysis of aerial photographs following a major 1935 storm shows that 100 m of mangrove coastline was eroded and mangroves adjacent to the channels were destroyed far inland. The collapse of both coastal wetlands and mangroves has led to the release of organic-rich sediments

into Florida Bay and the Florida Reef Tract, with negative effects on nearshore corals (20). Likewise, the development and dredging in the Keys (40) are likely associated with the loss of nearshore corals documented here.

The loss of nearshore reef has ecological implications and suggests large-scale shifts in the marine ecosystems of the Florida Keys. Reductions in nearshore reefs would have resulted in simultaneous reductions in the habitat of particular organisms or life stages of organisms, such as the many reef fish that use inshore reef habitats at different life stages (43). Therefore, the nearshore patch reefs present in the 18th century likely supported higher fish biomass for these species while also increasing the connectivity among similar habitats throughout the Florida Keys and southern portions of Florida Bay. At the same time, increases in salinity in the early 20th century have been associated with an increase in seagrass habitats in Florida Bay (44). Seagrasses support a different suite of marine fauna than do patch reefs, including pink shrimp (*Farfantepenaeus duorarum*), which was, until recently, one of the largest commercial harvests in Florida (41). Our results suggest that the seagrass ecosystems that have characterized this region throughout the 20th century may have been less abundant 200 years ago, with implications for baselines and restoration (45, 46).

Finally, our results highlight the broad need to take a landscape-scale approach when assessing long-term ecological change in the ocean. In particular, for species whose populations are spatially structured, a strong need exists to consider long-term spatial change in assessing long-term change and designing conservation assessments and to include alternative data sources to obtain a full assessment of overall loss. For example, failing to account for long-term spatial loss of breeding populations is problematic for green turtles (*Chelonia mydas*), a species for which localized increases have masked a longer-term history of loss of entire nesting populations (47, 48). Assessments of change focusing only on the species' extant range run the risk of overlooking larger-scale loss over longer time frames. As a result, they provide overly optimistic views of the species' current conservation status and underestimate their restoration potential.

METHODS

Imperial nautical charts as a historical ecological data source

The Florida Keys were charted by the British Admiralty between 1773 and 1775 (24–26). We obtained high-resolution reproductions of British nautical charts from the Admiralty Library and Archive of the UK Hydrographic Office (fig. S2). These charts contain notations of benthic composition, including sand, coral, shells, rocks, gravel, mud, clay, and seagrass, which were surveyed both visually and through the use of weighted lead lines with tallow or wax pockets to obtain a substrate sample (31). Descriptive ecological information accompanies the nautical charts, both recorded directly as text on the chart (fig. S2) and published separately as sailing directions, which provided more details about locations of interest (24) (table S1). Together, these sources contain information, including specific reference points, hazards, and water depths that contextualize data extracted from the charts.

Quantifying coral change

We identified all observations of coral recorded on the historical charts and compared each to three modern sources of information on the spatial distribution of coral in the Florida Keys: the Millennium Coral Reef Mapping Project (27), the Benthic Habitats South Florida Map (28), and the Unified Florida Coral Reef Tract Map (29).

These three maps used are largely derived from satellite imagery, with classification of benthic habitats based on spectral characteristics. Similar data sets have been used to detect changes over time in Florida's reefs (49–51); groundtruthing exercises have placed the accuracy of this method at 80 to 90% for coral (52), but this can be less if water column turbidity is high (49). This lack of accuracy in some locations is evident in the inconsistencies among the three maps (fig. S3). Because of this lack of agreement in modern coral cover (fig. S3), we chose to use all three maps to ensure the greatest possible cover. This method is certain to have resulted in an overestimate of modern coral extent. We chose this approach to ensure that our estimates of loss were as conservative as possible but also estimate loss using each data set independently. Finally, because they are largely derived from satellite imagery, the modern data are of relatively low spatial resolution. In some locations, maps include more highly resolved sonar and Lidar data, but the resolution is typically between 600 and 900 m^2. To compensate for this lack of fine-scale resolution in the modern data, we chose relatively large threshold distances for the historical data (up to 0.75 km), which correspond to the level of resolution present in the modern maps.

To quantify historical coral persistence, we compared each historical coral observation on the hydrological chart to the nearest recorded coral in any of the three modern data sources, which allows for the greatest chance of encountering modern coral and therefore produces the most conservative estimate of change. Our results therefore represent the persistence of coral habitat observed in the 1770s. We define the loss of spatial extent as the number of historical observations in locations that are not represented by coral in the modern benthic habitat maps.

We aligned the maps in ArcGIS by georeferencing the historical maps to a shapefile of modern land area in the Florida Keys using fixed reference points that would not be expected to change, such as deep channels. To confirm the alignment for coral, the depth of each historical coral observation was compared to modern bathymetric reference points. To account for any remaining error in the alignment of the maps and the lack of fine-scale resolution in the modern data described above, we used distance thresholds of 0.25, 0.5, and 0.75 km from each historical coral observation to determine the persistence of modern coral; if modern coral existed in any direction within the specified distance, then it was considered present. We then derived average persistence from the three threshold distances (fig. S1). For each point where coral was absent, we determined current benthic cover from the habitats identified by the Unified Florida Coral Reef Tract Map. In the rare cases where a historical data point fell outside the range of the modern maps, it was discarded.

Finally, to assess spatial change, we divided the historical maps into five reef zones: (i) Florida Bay, (ii) nearshore patch and fringing reef, (iii) offshore patch reef, (iv) reef crest, and (v) forereef (Table 1 and fig. S2). These zones were based on reef contours delineated on the historical maps, which align with current bathymetric zones and depth gradients.

SUPPLEMENTARY MATERIALS
Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/9/e1603155/DC1

fig. S1. Example of method used to estimate coral persistence.
fig. S2. Historical coral maps and zones and all historical coral observations (see table S2 for the additional data on each coral observation).
fig. S3. The three modern coral data layers showing the differences and overlaps among them.
table S1. Descriptive data from Gauld (1790) and the text box on the chart (fig. S1).

table S2. All historical data, with coral observation number, map (Lower Keys versus Upper Keys), depth in meters, reef zone, and distance to nearest modern coral.

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