Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a 3-decade study

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Abstract

Increased loadings of nitrogen (N) from fertilizers, top soil, sewage, and atmospheric deposition are important drivers of eutrophication in coastal waters globally. Monitoring seawater and macroalgae can reveal long-term changes in N and phosphorus (P) availability and N:P stoichiometry that are critical to understanding the global crisis of coral reef decline. Analysis of a unique 3-decade data set for Looe Key reef, located offshore the lower Florida Keys, showed increased dissolved inorganic nitrogen (DIN), chlorophyll *a*, DIN:soluble reactive phosphorus (SRP) ratios, as well as higher tissue C:P and N:P ratios in macroalgae during the early 1990s. These data, combined with remote sensing and nutrient monitoring between the Everglades and Looe Key, indicated that the significant DIN enrichment between 1991 and 1995 at Looe Key coincided with increased Everglades runoff, which drains agricultural and urban areas extending north to Orlando, Florida. This resulted in increased P limitation of reef primary producers that can cause metabolic stress in stony corals. Outbreaks of stony coral disease, bleaching, and mortality between 1995 and 2000 followed DIN enrichment, algal blooms, and increased DIN:SRP ratios, suggesting that eutrophication interacted with other factors causing coral reef decline at Looe Key. Although water temperatures at Looe Key exceeded the 30.5 °C bleaching threshold repeatedly over the 3-decade study, the three mass bleaching events occurred only when DIN:SRP ratios increased following heavy rainfall and increased Everglades runoff. These results suggest that Everglades discharges, in conjunction with local nutrient sources, contributed to DIN enrichment, eutrophication, and increased N:P ratios at Looe Key, exacerbating P limitation, coral stress and decline. Improved management of water quality at the local and regional levels could moderate N inputs and maintain more balanced N:P stoichiometry, thereby reducing the risk of coral bleaching, disease, and mortality under the current level of temperature stress.

Introduction

Coral reefs have evolved over hundreds of millions of years and are now considered one of the most threatened ecosystems on our planet (Birkeland 1997, 2004; MEA 2005; Hughes et al. 2017). These biologically diverse ecosystems have been in decline globally since the 1970s due to a growing number of recognized stressors (Hughes et al. 2003; Wilkinson 2004). In the Caribbean basin, an estimated 40% of coral has been lost over the last 40 years (Gardner et al. 2003) and similar losses have been observed along the Great Barrier Reef, Australia (Bellwood et al. 2004; De'ath et al. 2012). Early studies focused largely on the effects of land-based nutrient pollution and eutrophication (Banner 1974; Tomascik and Sander 1987; Smith et al. 1981; Bell 1992; Lapointe and Clark 1992), which was considered a primary threat to coral reef health in the late 1980s (NOAA 1988; Ginsburg 1994). Since then, overfishing (Hughes 1994; Jackson et al. 2001), sedimentation (Rogers 1990; Fabricius 2005), increases in sea surface temperature (Goreau and Hayes 1994; Glynn 1996; Baker et al. 2008; Selig et al. 2012; Hughes et al. 2017), and ocean acidification (Kleypas et al. 2006; Hoegh-Guldberg et al. 2007; Muehllehner et al. 2016) have emerged as additional threats to coral reefs. While the potential for negative impacts (both direct and

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indirect) to coral reefs from nutrient enrichment remains a major issue (Fabricius 2005; D'Angelo and Wiedenmann 2014), the synergistic effects of anthropogenic stressors combined with climate change have the capacity to cause the greatest damage (Wilkinson 1996; Anthony et al. 2011; Zaneveld et al. 2016; Wang et al. 2018).

Nitrogen (N) enrichment, a driver of eutrophication and global change in the marine environment (Ryther and Dunstan 1971; NRC 2000; MEA 2005), has long been known as a stressor to coral reefs (Smith et al. 1981; Tomascik and Sander 1985; Bell 1992; Lapointe and Clark 1992; Fabricius 2005; Duprey et al. 2016). The issue of N enrichment to coral health is related to the paradox that highly productive coral reefs thrive under oligotrophic conditions (Darwin 1842). In their classic studies at Enewetak Atoll, Odum and Odum (1955) concluded that coral reef ecosystems have a high efficiency of phosphorus (P) cycling, which has been confirmed by subsequent studies (Pilson and Betzer 1973; Atkinson 1987). Corals are adapted to thrive at low nutrient levels typical of oligotrophic tropical waters because of tight internal nutrient cycling by endosymbiotic zooxanthellae (D'Elia and Webb 1977; Muscatine and Porter 1977; O'Neil and Capone 2008). Odum and Odum (1955) suggested that N was the limiting nutrient for coral reef communities and that N_2 fixation by cyanobacteria helped to meet the N demands necessary to sustain the high gross productivity of coral reefs. Indeed, cyanobacteria on reef flats at Enewetak Atoll fixed N_2 at high rates, helping to explain the high productivity of adjacent coral reefs (Wiebe et al. 1975). More recent studies using $\delta^{15}N$ indicated that some great star coral *Montastraea cavernosa* colonies also contain endosymbiotic cyanobacterial N_2 fixers (Lesser et al. 2007), although coral–diazotrophic interactions are complex (Rädecker et al. 2015).

Considering the contribution of N_2 fixation to the high productivity of coral reefs, this relationship could be altered by increases in external N inputs from human activities (Vitousek et al. 1997). Increased anthropogenic N loading has had major ecological consequences for coral reefs, including increased phytoplankton blooms (Caperon et al. 1976; Laws and Redalje 1979, 1982; Smith et al. 1981; Bell 1992; Yentsch et al. 2002) that reduce light and accelerate coral reef decline (Tomascik and Sander 1985; Hallock and Schlager 1986; Fabricius et al. 2016). Experimental field studies have shown myriad ecological effects of increasing N enrichment, such as enhanced growth of macroalgae (Smith et al. 1981; Lapointe 1997; Smith et al. 2007; De'ath and Fabricius 2010; Lapointe et al. 2011) and algal turfs (Hatcher and Larkum 1983; Williams and Carpenter 1988; Vermeij et al. 2010), which can inhibit coral recruitment and outcompete corals for space (Birkeland 1977; River and Edmunds 2001; Nugues et al. 2004; Vega-Thurber et al. 2012; O'Brien and Scheibling 2018; Pratte et al. 2018).

Nitrogen enrichment can also increase the prevalence of coral diseases (Bruno et al. 2003; Voss and Richardson 2006; Vega-Thurber et al. 2014; Rädecker et al. 2015; Wang et al. 2018), further accelerating coral mortality.

Altered ecological stoichiometry associated with increasing N loading from human activities (Vitousek et al. 1997; Sterner and Elser 2002; Rockström et al. 2009) can impart direct physiological effects on corals, leading to a disruption in the control of endosymbiotic zooxanthellae (Falkowski et al. 1993; Dubinsky and Stambler 1996). Dissolved inorganic nitrogen (DIN = ammonium + nitrate) enrichment controls the growth of endosymbiotic zooxanthellae (D'Elia et al. 1991; Falkowski et al. 1993; Fagoonee et al. 1999), and increased endosymbiont densities result in a greater susceptibility to coral bleaching (Cunning and Baker 2013). Elevated DIN without a balanced supply of soluble reactive phosphorus (low SRP concentrations and/or high N:P ratio) can induce P starvation in corals, effectively reducing the temperature and light thresholds for bleaching (Wooldridge 2009; Wiedenmann et al. 2013; D'Angelo and Wiedenmann 2014; Rosset et al. 2017). Much remains to be understood about how human activities on watersheds of coral reefs are altering the relative availability of N and P to coastal waters, and how these changes relate to the growing problem of mass coral bleaching, disease, and mortality.

Recognition of the paramount importance of water quality to the health of coral reefs in the Florida Keys led to its designation as an "Area of Critical State Concern" by the Florida Legislature in 1974 (Table 1). Following the first reports of coral reef decline off Key Largo in the 1970s (Dustan 1977; Dustan and Halas 1987) and the role of septic systems in contributing to nearshore eutrophication (Lapointe et al. 1990), nutrient pollution became a primary issue in the Florida Keys. In 1988, 50 coral reef experts met at a National Oceanic and Atmospheric Administration (NOAA)-sponsored workshop in Key Largo, Florida and ranked various problems affecting the coral reefs of the Florida Keys; the primary conclusion was "excessive amounts of nutrients invading the Florida Reef Tract from the Keys and from Florida Bay are a serious and widespread problem" (NOAA 1988; Table 1). Therefore, deterioration of water quality was a primary factor leading to the passage of the Florida Keys National Marine Sanctuary (FKNMS) Act in 1990, which mandated a multi-agency Water Quality Protection Program (WQPP; Table 1) consisting of NOAA, the United States Environmental Protection Agency (US EPA), and the Florida Department of Environmental Protection (FDEP). The WQPP was the first of its kind for a United States marine sanctuary (NOAA 1996; Kruczynski and McManus 2002). The boundaries of the FKNMS extended from northern Key Largo to the Dry Tortugas, encompassing an area of 7511 km^2 (NOAA 1996; Fig. 1). The FKNMS enabling

Table 1 Chronology of major management and biotic events for Florida Bay, the Florida Keys, and Looe Key Sanctuary Preservation Area (LKSPA) in the Florida Keys National Marine Sanctuary (FKNMS)

Year	Event	Reference
1972	Marine Protection, Research, and Sanctuaries Act of 1972	State of Florida (1974), Public Law 92–532
1980	Interim Action Plan and structural modifications begin to increase water deliveries to Everglades National Park and Shark River Slough	Light and Dineen (1994)
1981	Looe Key National Marine Sanctuary (LKNMS) designated at Looe Key reef	46 Federal Register 946
1981	Discolored water, algal blooms, and seagrass die-off reported by fishermen in western Florida Bay	DeMaria (1996)
1982	Heavy rainfall and water managers implementation of the "rainfall plan" increase freshwater deliveries through Shark River Slough	Cane (1983), Light and Dineen (1994), Rudnick et al. (1999)
1983	Long-spined sea urchin *Diadema antillarum* die-off in the Florida Keys and Caribbean region	Lessios et al. (1984)
1987	Mass mortality of turtlegrass *Thalassia testudinum* begins in Florida Bay	Robblee et al. (1991), Hall et al. (2016)
1987	First mass coral bleaching event observed in the Florida Keys	Jaap (1988), Causey (2008)
1988	NOAA Florida Keys Coral Reef Research and Management Workshop ranks "excessive nutrients" as a "serious and widespread problem"	NOAA (1988)
1990	Florida Keys National Marine Sanctuary and Protection Act establishes Florida Keys National Marine Sanctuary	Public Law 101-605
1990	Critical eutrophication documented in the nearshore waters of the Florida Keys	Lapointe et al. (1990), Lapointe and Clark (1992)
1990	Nitrogen enrichment linked to seagrass die-off in Florida Bay	Duarte (1990)
1991	Freshwater deliveries increased to Florida Bay and the Florida Keys through Shark River Slough and Taylor Slough	Rudnick et al. (1999), Brand (2002), Lapointe et al. (2002)
1991	Cyanobacterial bloom and sponge mortality in Florida Bay	Butler et al. (1995)
1992	Algal blooms spread from Florida Bay to offshore bank reefs of the Florida Keys	Lapointe et al. (1994), Lapointe and Matzie (1996), Lapointe et al. (2002)
1992	Congressional testimony on coral reef loss and eutrophication in the Florida Keys	Coral Reef Ecosystems Research and Protection (1992)
1992	Hypoxia observed at Looe Key Sanctuary Preservation Area (LKSPA)	Lapointe and Matzie (1996)
1992	Florida Keys Water Quality Protection Program implemented	NOAA (1996)
1994	Heavy rainfall and increased freshwater deliveries continue through Shark River Slough and Taylor Slough	Trenberth and Hoar (1996), Rudnick et al. (1999), Zhao et al. (2013)
1995	Heavy rainfall and increased freshwater deliveries continue; Plague Type II coral disease outbreak in Florida Keys	Richardson et al. (1998), Rudnick et al. (1999), Zhao et al. (2013)
1995	Historic red tide *Karenia brevis* event in Florida Keys	Klingener (1995), Steinman (1995), Caputo (1996)
1996	Unprecedented blooms of macroalgae and cyanobacteria at Looe Key reef	Lapointe et al. (2004)
1996	A 404% increase in coral disease epizootic begins in the Florida Keys	Porter et al. (2001)
1997	Second mass coral bleaching event begins in the Florida Keys	Somerfield et al. (2008), Causey (2008)
1997	Population explosion of variegated sea urchin *Lytechinus variegatus* in Florida Bay	Rose et al. (1999), Sharp (2000)
1999	Increased eutrophication indicator species (macroalgae) documented in the Florida Keys rocky intertidal zone	Smith et al. (2007)
2000	Dramatic coral loss recorded at LKSPA with decreases of 93% for elkhorn coral *Acropora palmata* and 98% for staghorn coral *A. cervicornis*	Miller et al. (2002)
2002	Black water events documented by remote sensing in the Florida Bay-Florida Keys region	Hu et al. (2003, 2004)
2002	Committee on Restoration of the Greater Everglades Ecosystem (CROGEE) report concludes hypersalinity not responsible for *T. testudinum* die-off in Florida Bay	National Research Council (2002)
2003	Hypoxia and dead zone recognized in the Florida Keys	Pew Oceans Commission (2003)
2006	*Acropora palmata* and *A. cervicornis* are listed as "threatened" under the United States Endangered Species Act (ESA)	71 Federal Register 26852
2006	Increased population densities of giant barrel sponge *Xetospongia muta* observed on reefs in the Florida Keys	McMurray et al. (2010, 2015)
2012	Black water events and water quality issues documented by remote sensing in the Florida Bay–Florida Keys region	Zhao et al. (2013)

Table 1 (continued)

Year	Event	Reference
2013	Cyanobacterial blooms and sponge mortality develop in Florida Bay following C-111 Spreader Canal Western Project and heavy rainfall	Drog (2017), Shangguan et al. (2017)
2014	Twenty additional species of coral are listed as "threatened" under the ESA	79 Federal Register 53851
2014	Third mass coral bleaching event in the Florida Keys	Eakin et al. (2016)
2015	*Thalassia testudinum* die-off documented in Florida Bay	Hall et al. (2016)

legislation recognized that nutrient enrichment from local pollution sources in the Florida Keys, as well as those outside of the FKNMS on the South Florida mainland, must be addressed through the multi-agency WQPP specifically to protect scleractinian (stony) coral cover (Table 1).

The concern about effects of runoff from the mainland was related to the greatly modified hydrology and land-use changes in South Florida over the last century. In particular, water from Lake Okeechobee, which originates to the north near Orlando, historically flowed south through the Everglades but is now partially shunted via a system of man-made canals east to the St. Lucie River and west to the Caloosahatchee River. These discharges have contributed to decreased salinity and water quality, as well as cyanobacterial blooms (*Microcystis*) in these northern estuarine systems (Lapointe et al. 2017; Kramer et al. 2018). To reduce nutrient pollution of Lake Okeechobee from the Everglades Agricultural Area and further restore southerly flow to the Everglades, water managers implemented the Interim Action Plan and structural modifications between 1980 and 1985 (Light and Dineen 1994; Table 1). Shortly thereafter in 1982, macroalgal and phytoplankton blooms expanded in western Florida Bay and downstream waters of the Florida Keys (DeMaria 1996; Table 1). Following establishment of the FKNMS in 1990, the effort to further increase freshwater flows to Florida Bay intensified (NOAA 1996). The Comprehensive Everglades Restoration Plan (CERP), authorized by Congress in 2000 (USACE and SFWMD 1999), is one of the world's largest environmental restoration projects with a goal to further increase water flows into Florida Bay and the Florida Keys region (USACE and SFWMD 1999; NRC 2002). Nonetheless, the effects of these flows on nutrient pollution and coral reef health in downstream waters of the FKNMS remain poorly understood (Ogden et al. 1994; Porter 2002).

Coral reefs are exposed to natural and anthropogenic stressors on temporal scales longer than the typical timeframe of ecological studies. Long-term data sets of known stressors, including nutrients, are needed to better understand the causes of coral reef degradation in the FKNMS. Patterns in climatological factors such as rainfall, as well as anthropogenic impacts, including water management and nutrient pollution, cannot be understood unless measurements are made at appropriate temporal scales (Levin 1992).

Accordingly, understanding the ecosystem change on coral reefs requires long-term monitoring to see the "invisible present" (Magnuson 1990). The lack of long-term nutrient data has limited our understanding of the effects of global N enrichment (Vitousek et al. 1997; Rockström et al. 2009) on coral reef biodiversity (Duprey et al. 2016) and alteration of N:P stoichiometry by human activities (Sterner and Elser 2002), especially in poorly studied tropical and subtropical carbonate-rich environments (Downing et al. 1999).

Because of increasing human activities and water management in South Florida, it was hypothesized that a chronic increase in N availability has increased algal blooms and altered N:P stoichiometry, which have promoted metabolic stress and decline of stony corals at Looe Key. Accordingly, the objective of this study was to fill the above knowledge gap by identifying the temporal patterns between Everglades discharges and seawater nutrient and chlorophyll *a* concentrations, C:N:P stoichiometry of reef macroalgae, temperature, and stony coral cover at Looe Key. The study used a unique long-term data set comprising 3 decades of data from Looe Key reef in the lower Florida Keys. Remote sensing imagery and monitoring of salinity and nutrient gradients between the Everglades and Looe Key in the wet and dry seasons of 2010 and 2011 were also used to better understand the effects of climate change on nutrient connectivity between the Everglades and downstream coral reefs in the FKNMS. These combined data were considered in the context of long-term patterns in water/resource management and ecosystem responses to increased nutrient loading to help inform the future effects of the CERP, climate change, and management actions that could increase the resilience of coral reefs in the FKNMS.

Materials and methods

Study site

Looe Key is a classic example of a Caribbean spur-and-groove bank reef system, located approximately 10 km south of Big Pine Key, Florida (Figs. 1, 2). The Florida Current flows to the south of Looe Key reef, and Hawk Channel flows west between the lower Florida Keys and Looe Key. The
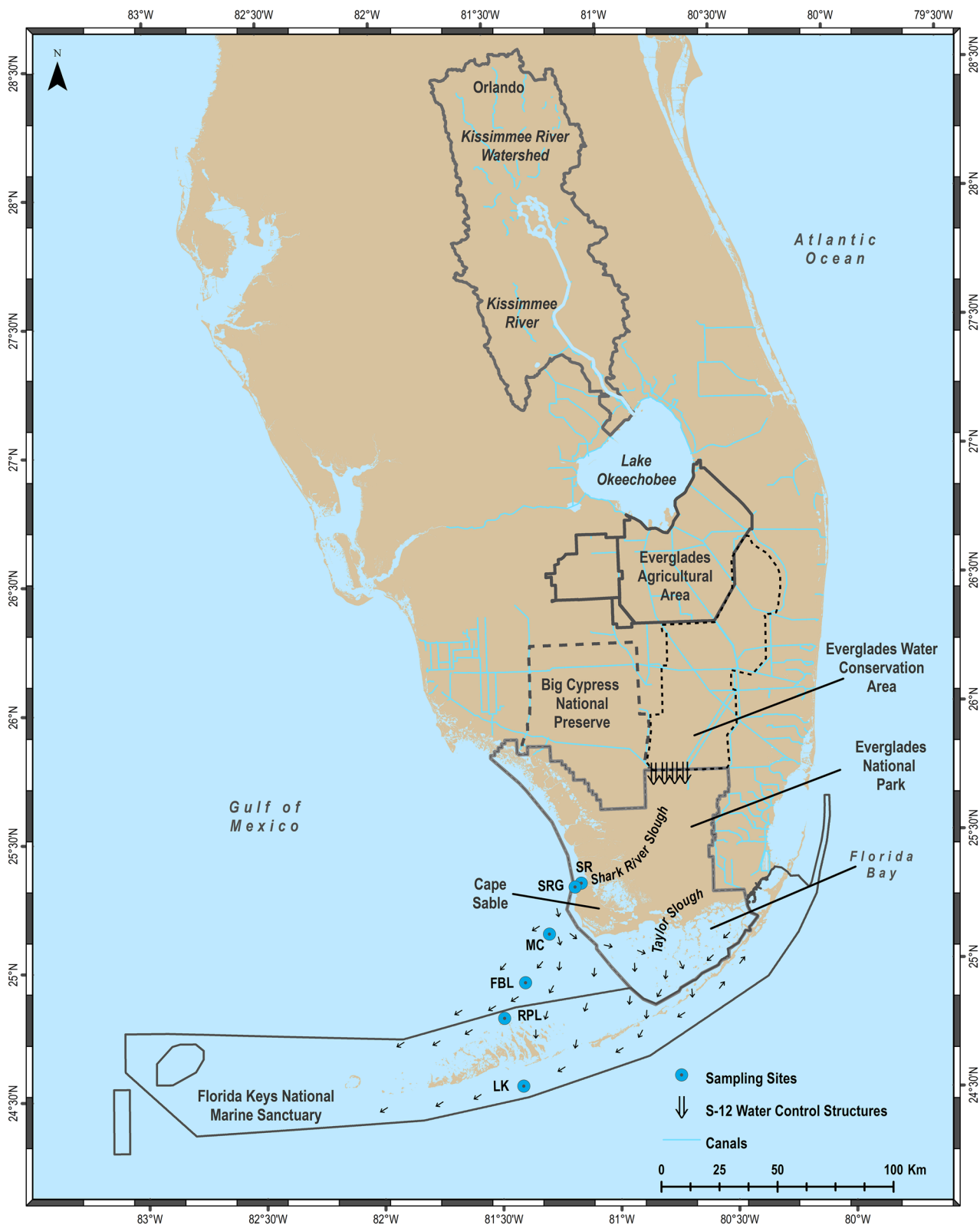
Fig. 1 South Florida, USA showing Looe Key Sanctuary Preservation Area (LK) in the Florida Keys National Marine Sanctuary and the extent of the Everglades drainage basin, extending north to Orlando, Florida. Also shown are sampling sites for the Everglades gradient transect that spanned from the mouth of Shark River (SR), to the Gulf of Mexico off of Shark River (SRG), the Middle Cape Sable (MC), Florida Bay Ledge (FBL), Rock Pile Reef (RPL), ending at LK; long-term monitoring was also conducted at the LK site. Arrows indicate the patterns of water circulation in the Florida Bay–Florida Keys region (from Klein and Orlando 1994)

Fig. 2 Aerial image of Looe Key Sanctuary Preservation Area (LKSPA), Florida Keys, USA. The view is northward, with the lower Florida Keys visible in the upper background. Photo by Brian Lapointe

spectacular reef was noted as a bank reef "par excellence" by Agassiz (1852), who described the spur-and-groove zone as "submarine elongated hillocks". Coring studies by Shinn et al. (1982) found that the well-developed spur-and-groove formation on the fore reef at Looe Key reef was a result of construction by reef building corals, especially elkhorn coral *Acropora palmata*, rather than erosion. In accordance with Title III of the Marine Protection, Research, and Sanctuaries Act, Looe Key National Marine Sanctuary (LKNMS) was established in 1981 as an 18.2 km^2 preserve, and consumptive fishing activities from the "core area" were prohibited (Table 1). In 1990, the FKNMS was designated and incorporated LKNMS, changing the name of the core area to Looe Key Sanctuary Preservation Area (LKSPA).

Early surveys at LKSPA described features of the core area, which included lush seagrass meadows (Zieman 1987), coral reefs (White and Porter 1985; Wheaton and Japp 1988), abundant fish populations (Bohnsack et al. 1987), and diverse macroalgal communities (Littler et al. 1986). Populations of grazing fishes (Scarids, Acanthurids) are especially abundant at LKSPA (Bohnsack et al. 1987; Littler et al. 1986). Local coastal waters upstream of LKSPA have sustained nutrient enrichment and eutrophication from increased sewage and stormwater runoff in the urbanized Florida Keys, as well as increased runoff from Shark River Slough into upstream coastal waters of the Gulf of Mexico, and from Taylor Slough into central Florida Bay (Fig. 1; Table 1; Lapointe et al. 2002; Boyer and Jones 2002).

Long-term monitoring at Looe Key

Long-term nutrient monitoring was conducted from 9 October 1984 to 16 November 2014 for a total of 179 sampling events. Throughout this period, seawater samples were collected in 23 years (average of 53 samples/year) on the shallow fore reef spur-and-groove zone and reef crest in the middle of LKSPA during both wet and dry seasons to capture the seasonal variability in runoff that significantly influences water quality at LKSPA (Lapointe et al. 2004). Samples included two near-bottom (0.15 m above bottom, 6 m depth) and four surface (0.5 m below the surface) water samples at each sampling event ($n = 6$). The samples were collected into clean 250 ml high density polyethylene (HDPE) bottles and held on ice in the dark until return to the Harbor Branch Oceanographic Institute at Florida Atlantic University's (HBOI-FAU) field station on Big Pine Key, where they were filtered through 0.7-μm GF/F filters and frozen at -4 °C until analysis. The samples were analyzed for NH_4^+–N, NO_3^-–N ($NO_3^- + NO_2^-$), and SRP using standard oceanographic techniques (D'Elia et al. 1997; Technicon 1973; Zimmerman et al. 1977) with low detection limits (~ 0.04 μM for NH_4^+, 0.01 μM for NO_3^-, and 0.009 μM for SRP). To assess the possible importance of vertical mixing and offshore upwelling of NO_3^-, a modified f ratio [$NO_3^-/(NO_3^- + NH_4^+)$] was used to gauge the relative importance of NO_3^- versus NH_4^+ to the DIN pool at LKSPA. Upwelled waters have high NO_3^- concentrations relative to NH_4^+, so a high f ratio indicates that NO_3^- is the dominant N species (> 0.8; McCarthy et al. 1975; Harrison et al. 1987). The methods for collection, handling, and analysis of the water samples for nutrient analysis followed a quality assurance/quality control protocol designed to prevent problems associated with sample contamination and excessive holding times to provide accurate and reliable data (D'Elia et al. 1997).

Chlorophyll *a* sampling at LKSPA began in 1987. For these samples, 100 ml of seawater was filtered through GF/F filters; filters were then frozen and extracted within 28 days. Extraction took place for 30 min with 10 ml of dimethyl sulfoxide followed by 15 ml of 90% acetone at 5 °C overnight. Samples were measured fluorometrically before and after acidification for chlorophyll *a* and phaeopigment concentrations (Burnison 1980; Parsons et al. 1984) using a Turner Designs 10-000R fluorometer equipped with an infrared-sensitive photomultiplier, calibrated using pure chlorophyll *a*.

Abundant species of benthic macroalgae (Chlorophyta, Ochrophyta, Rhodophyta) were collected during 26 sampling events between 1 June 1984 to 18 September 2014 at LKSPA to assess decadal variability in elemental composition (C:N:P). At each sampling, individual thalli of each species were collected into a nylon mesh bag and subsequently placed in a Ziploc® bag in a cooler until processing (within 8 h) at the HBOI-FAU field station on Big Pine Key. In the station, samples were gently cleaned of macroscopic epiphytes and epizoa, rinsed briefly in deionized water (< 5 s), identified (Taylor 1960; Littler and Littler 2000; Guiry and Guiry 2013) and randomly sorted into replicates ($n = 3$) for each species. Each replicate consisted of 5–10 individual thalli to ensure a representative sample. The macroalgae were dried at 65 °C to constant mass (~ 48 h) in a laboratory oven and then ground into a homogenous powder using a mortar and pestle. Samples were analyzed for elemental composition of C and N (see the following for methods http://sisbl.uga.edu/ratio.html#top and Thermo Scientific, 2007). Tissue %P was measured following the methodology of Aspila et al. (1976) and D'Elia et al. (1997).

Long-term daily maximum air temperature at Key West International Airport was used as a proxy for daily maximum air temperature at LKSPA. Variation in water temperature by year at LKSPA was examined using historical temperature data from various sources, including discreet samples collected by HBOI-FAU and the Southeast Environmental Research Center at Florida International University (SERC-FIU) during sampling events, HBOI-FAU (1984–1986) and FKNMS (1990–2003) thermograph data (Burdette 2010; Anderson, 2011), and monitoring data from CREMP (2008–2014) collected with HOBO Water Temp Pro v2 loggers (Ruzicka et al. 2017).

Live coral cover data for shallow reefs at LKSPA were acquired for scleractinian and milleporine hard corals from a pair of 9 m^2 photographic monitoring stations established on Looe Key in 1984 (see White and Porter 1985; Porter and Meier 1992 for detailed methodologies). In 1994, these photographic stations were augmented with four additional video transects covering approximately 60 m^2 each (Porter et al. 2002). Scleractinian and milleporine coral cover and macroalgal/turf algal assessments were also made in several other LKSPA survey datasets described in Lapointe et al. (2002).

Monitoring annual and seasonal variability in Everglades runoff

Shark River Slough was selected as a focal area to study effects of runoff from rainfall and water management in South Florida, as it accounts for the majority of Everglades discharges (~ 80%; Woods 2010). Shark River Slough flow data were accessed from the United States Geological Survey (http://waterdata.usgs.gov/fl/nwis/rt) and the South Florida Water Management District (http://www.sfwmd.gov/org/ema/dbhydro/index.html). Shark River Slough flow estimates were a composite of discharge data from S12A, S12B, S12C, and S12D structures located on the Tamiami Trail (see Fig. 1).

During 2010 and 2011, water samples were collected along a transect extending from Shark River in the southwestern Everglades, southward in the Gulf of Mexico along western Florida Bay, and extending offshore the lower Florida Keys to LKSPA (Fig. 1). The sampling sites along the transect included an estuarine location in Shark River (SR), the Gulf of Mexico off Shark River (SRG), Middle Cape (MC), Florida Bay Ledge (FBL), Rock Pile Reef (RPL), and LKSPA (LK; Fig. 1). Samples for dissolved nutrients and chlorophyll *a* were collected at 0.5 m depth into clean, HDPE bottles and preserved on ice in a dark cooler in the field, filtered through clean GF/F filters, and frozen below − 4 °C until analysis of the filtrate for DIN, SRP, TDN, and TDP; filters were retained for determination of chlorophyll *a* concentrations (D'Elia et al. 1997). Particulate organic matter (POM) samples were also collected along the transect to estimate the C:N ratio and δ^{15}N of phytoplankton. For these samples, triplicate 1-l samples of seawater were filtered through 200-μm nylon netting to remove macrodetritus and macrozooplankton (Savoye et al. 2003). In the laboratory, the pre-filtered samples were filtered again through 0.7-μm GF/F filters to capture the POM and dried at 65 °C in a laboratory oven. The dried filters were analyzed for stable carbon (δ^{13}C) and N (δ^{15}N) isotopes, as well as C:N ratios at the University of California, Davis, Stable Isotope Facility.

Satellite remote sensing

Satellite remote sensing can provide a synoptic and long-term view of water quality, including changes in algal blooms, turbidity, and water clarity. Algorithm development to derive accurate water quality data products in optically shallow waters, such as the Florida Keys and Florida Bay, is still active research (Barnes et al. 2014, 2018). Therefore, multi-sensor satellite images from the Landsat Thematic Mapper (TM), Advanced Very High Resolution Radiometer (AVHRR), Sea-viewing Wide Field-of-view Sensor (Sea-WiFS), Moderate Resolution Imaging Spectroradiometer (MODIS), and Visible Infrared Imaging Radiometer Suite

(VIIRS) satellite measurements were used to inspect the spatial patterns to assess connectivity between Shark River Slough, Taylor Slough, and the Florida Keys. These data were obtained from USGS, NASA, and NOAA. For earlier sensors, true color (i.e., Red–Green–Blue composite) images or surface reflectance images were used. For more recent sensors, chlorophyll *a* anomaly images were used. Here chlorophyll *a* anomaly is defined as the difference between current chlorophyll *a* and a 2-month average 2 weeks prior, following the approach of Stumpf et al. (2003). The anomaly of > 1 mg/m^3 shows new blooms referenced against mean conditions 2 weeks previously. For VIIRS, chlorophyll *a* anomaly images were obtained from the NOAA OCView (Mikelsons and Wang 2018).

Statistical analyses

Surface and bottom seawater samples were combined to calculate daily, annual, and decadal means with standard error for dissolved nutrients. Undetectable nutrient species were excluded from mean or ratio calculations. If either NH_4^+ or NO_3^- was undetectable, the value for the other inorganic N species was considered to be the total measurable DIN for the sample. The *f* ratio and DIN:SRP were only calculated when both components of the ratio were above detection limits.

Due to the long-term nature of the dataset, a variety of statistical methods were used to analyze the data at different intervals. All analyses were conducted in RStudio for Mac V.1.2.1335 and statistical significance was considered at $P \leq 0.05$. Polynomial regression analysis (fifth order) was used to model the temporal relationships of raw data for NH_4^+, NO_3^-, DIN, SRP, chlorophyll *a*, DIN:SRP, and maximum air temperature at Key West airport over the study period (1984–2014). Regressions were plotted with R package "ggplot2" (Wickham 2009) and "ggpubr" (Kassambara 2018). Extreme outliers were identified with box plots and removed prior to daily regression analyses.

Spearman rank correlations were calculated for environmental variables on annual averages to determine the relatedness of variables using R package "Hmisc" (Harrell 2019). A correlation matrix was constructed showing relationships of nutrient concentrations, population size of Monroe County, precipitation (annual average of Clewiston, Orlando, West Palm Beach, and Flamingo, Florida, USA), Shark River flow rate, maximum water temperature, and coral cover. Annual periodicity was chosen so that yearly estimates of percent living coral cover could be considered in analyses.

Stepwise regression analyses were performed on annual averages to model the variation in biological response variables (living coral cover and chlorophyll *a* concentrations) attributable to other environmental variables (maximum

water temperature, flow, precipitation, population, NH_4^+, NO_3^-, DIN, *f* ratio, SRP, and DIN:SRP). Regression models were constructed based on both the Akaike information criterion (AIC) and *P* values using the "olsrr" package in R (Hebbali 2018). Highly correlated variables, such as NH_4^+ and NO_3^- with DIN, were not included together in model building to avoid consideration of redundant information. Variance inflation factors (VIFs) were checked to avoid effects of multicollinearity; VIFs > 4 were closely examined and VIFs > 10 were removed. Coral cover and chlorophyll *a* were naturally log transformed to meet linear model assumptions. Simple linear regressions were also performed on response variables using significant environmental variables from the stepwise regressions.

Changes in the elemental composition (C:N:P) of macroalgal tissue were assessed at the decadal level due to a coarser resolution in the available dataset. Further, decadal periods (1980s, 1990s, 2000s, and post 2010) represent different management actions, rainfall patterns, and temperature, and provide insight to the effects of water management, climate change, and cumulative effects on long-term changes at LKSPA. Thus, macroalgal elemental composition, dissolved nutrients, chlorophyll *a*, and macroalgal C:N:P data were all compared by decade with Kruskal–Wallis tests followed by Dunn–Sidak pairwise tests on the individual pairs to account for multiple comparisons with R package "FSA" (Ogle 2019). Nutrient and chlorophyll *a* data from the 2010 and 2011 Shark River–LKSPA transect sampling were compared by year and season (wet/dry) with Kruskal–Wallis tests followed by Dunn–Sidak pairwise tests.

Results

Long-term monitoring at Looe Key

Datasets were assessed for dissolved nutrients ($n = 1378$), chlorophyll *a* ($n = 598$), macroalgal tissue C:N:P ($n = 250$), and temperature from LKSPA over 3 decades (1984–2014). Significant linear relationships were observed between many of the environmental variables as a function of year; however, non-linear models yielded a better fit to the data. Outliers in the daily averages dataset were removed prior to polynomial regression analyses, including $NH_4^+ > 3$ (1 day), DIN > 3 (3 days), SRP > 0.5 (1 day), DIN:SRP > 100 (1 day), and chlorophyll $a > 1.25$ (2 days). NH_4^+ increased in the early 1990s, then leveled off in the 2000s (polynomial regression, $r^2 = 0.05$, $F_{3,162} = 3.56$, $P = 0.016$; Fig. 3a). NO_3^- increased sharply in the early 1990s and remained elevated through 2014 (polynomial regression, $r^2 = 0.15$, $F_{3,165} = 11.1$, $P < 0.001$; Fig. 3b). As such, there was a statistically significant positive relationship of DIN concentrations over time (polynomial regression, $r^2 = 0.26$,
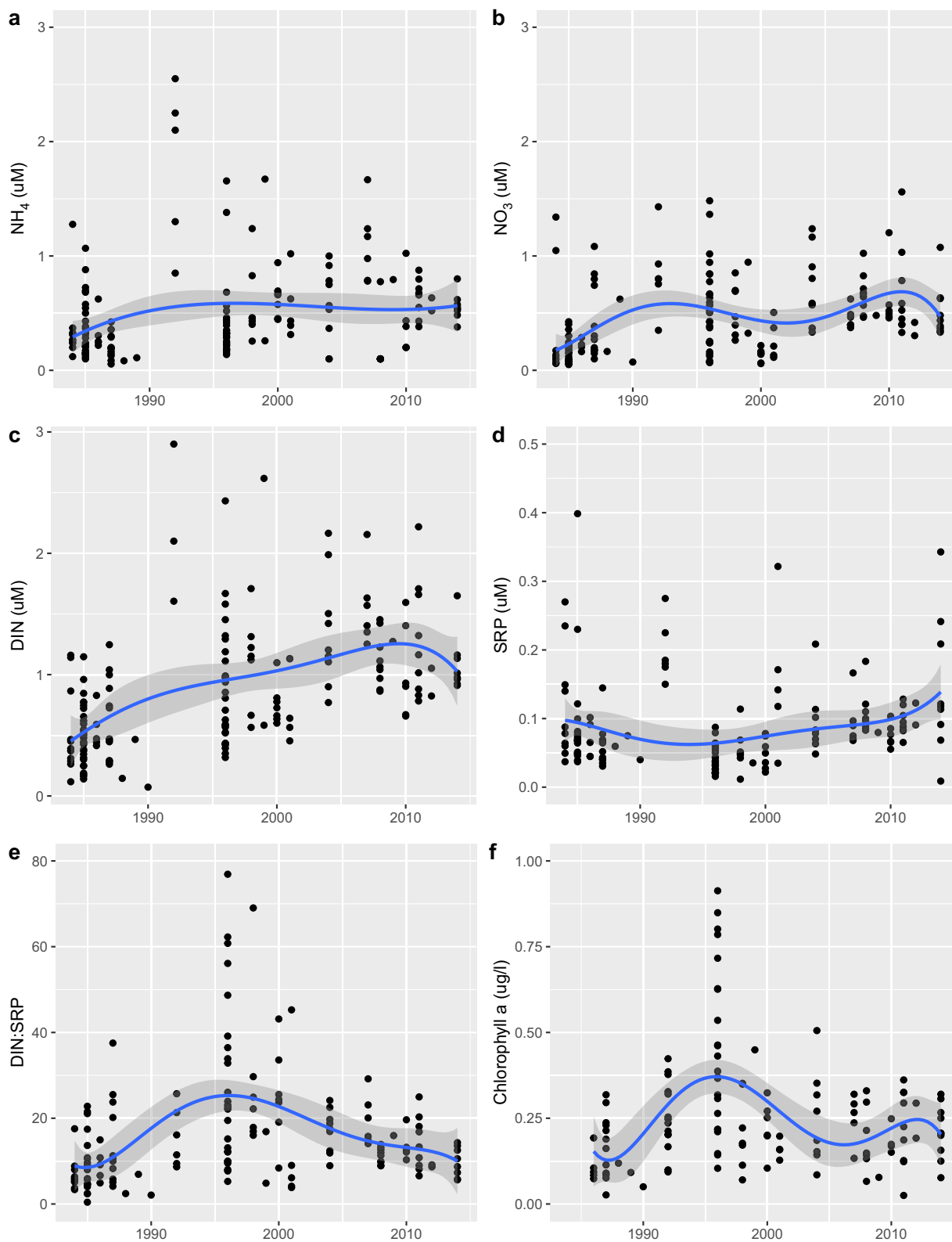
Fig. 3 Temporal relationships of **a** ammonium (NH$_4^+$), **b** nitrate (NO$_3^-$), **c** dissolved inorganic nitrogen (DIN), **d** soluble reactive phosphorus (SRP), **e** DIN:SRP, and **f** chlorophyll a (Chl a) at Looe Key reef from 1984 to 2014 modeled with polynomial regressions (blue line) showing 95% confidence intervals in gray

Fig. 4 Spearman correlation matrix of annual Looe Key data (maximum water temperature, Shark River Slough flow, precipitation, Monroe County population, chlorophyll a, NH_4^+, NO_3^-, DIN, f ratio, SRP, and percent coral cover) showing correlation coefficient (top) and P values (bottom, italicized); red shading indicates significant positive correlations, blue shading represents significant negative correlations, and gray shading represents marginal significance ($P > 0.05$ and ≤ 0.10); significance considered at ≤ 0.05

	Temp	Flow	Precip	Pop	Chla	NH4+	NO3-	DIN	f-ratio	SRP	Coral
Flow	-0.34 *0.075*										
Precip	-0.46 *0.011*	0.64 *< 0.001*									
Pop	-0.39 *0.037*	0.39 *0.021*	0.29 *0.095*								
Chla	0.00 *0.997*	0.48 *0.039*	0.13 *0.611*	0.31 *0.204*							
NH4+	-0.27 *0.273*	0.23 *0.326*	0.08 *0.738*	0.36 *0.121*	0.47 *0.052*						
NO3-	-0.24 *0.310*	0.46 *0.038*	0.41 *0.066*	0.29 *0.207*	0.47 *0.044*	0.25 *0.283*					
DIN	-0.31 *0.184*	0.46 *0.036*	0.39 *0.078*	0.30 *0.184*	0.64 *0.003*	0.81 *< 0.001*	0.70 *< 0.001*				
f-ratio	-0.25 *0.297*	0.05 *0.840*	0.25 *0.295*	0.14 *0.544*	-0.21 *0.399*	-0.55 *0.011*	0.46 *0.043*	-0.14 *0.569*			
SRP	-0.16 *0.510*	0.38 *0.091*	0.41 *0.064*	-0.11 *0.634*	0.34 *0.161*	0.33 *0.158*	0.33 *0.149*	0.45 *0.043*	-0.38 *0.097*		
Coral	0.24 *0.318*	-0.06 *0.822*	0.16 *0.507*	0.02 *0.935*	0.19 *0.574*	-0.39 *0.188*	-0.46 *0.112*	-0.64 *0.018*	-0.30 *0.325*	-0.02 *0.957*	
DIN:SRP	-0.05 *0.830*	0.19 *0.404*	0.01 *0.955*	0.41 *0.066*	0.50 *0.029*	0.55 *0.012*	0.34 *0.127*	0.62 *0.003*	-0.13 *0.574*	-0.10 *0.670*	-0.35 *0.239*

$F_{3,162} = 20.5$, $P < 0.001$; Fig. 3c). The relationship of SRP over the study period was not as strong as DIN, but the relationship over time was significant (polynomial regression, $r^2 = 0.06$, $F_{3,150} = 4.37$, $P = 0.005$; Fig. 3d). SRP concentrations displayed an inverse relationship to DIN in the 1990s, whereby it initially decreased and then gradually increased in the 2010s (Fig. 3d). DIN:SRP increased from relatively low values in the 1980s and peaked in 1996, decreasing in the 2010s (polynomial regression, $r^2 = 0.22$, $F_{3,150} = 15.1$, $P < 0.001$; Fig. 3e). The change in chlorophyll a over the study period was also statistically significant with a pattern that included a peak in 1996 followed by a decrease and another increase in 2014 (polynomial regression, $r^2 = 0.15$, $F_{3,123} = 8.28$, $P < 0.001$; Fig. 3f).

Many of the environmental variables were significantly correlated during the 3 decades of water sampling at Looe Key. Temperature was negatively correlated with precipitation (Spearman rank correlation, $r_s = -0.46$, $n = 29$, $P = 0.011$; Fig. 4). Shark River Slough flow was positively correlated with a number of variables, including precipitation (Spearman rank correlation, $r_s = 0.64$, $n = 35$, $P < 0.001$), population (Spearman rank correlation, $r_s = 0.39$, $n = 35$, $P = 0.021$), chlorophyll a (Spearman rank correlation, $r_s = 0.48$, $n = 19$, $P = 0.039$), NO_3^- (Spearman rank correlation, $r_s = 0.46$, $n = 21$, $P = 0.038$), and DIN (Spearman rank correlation, $r_s = 0.46$, $n = 21$, $P = 0.036$; Fig. 4). Chlorophyll a had a significant positive correlation with NO_3^- (Spearman rank correlation, $r_s = 0.47$, $n = 19$, $P = 0.044$), DIN (Spearman rank correlation, $r_s = 0.64$, $n = 19$, $P = 0.003$), and DIN:SRP (Spearman rank correlation, $r_s = 0.50$, $n = 19$, $P = 0.029$; Fig. 4). NH_4^+ was positively correlated with DIN (Spearman rank correlation,

$r_s = 0.81$, $n = 20$, $P < 0.001$) and DIN:SRP (Spearman rank correlation, $r_s = 0.55$, $n = 20$, $P = 0.012$, but negatively correlated with f ratio (Spearman rank correlation, $r_s = -0.55$, $n = 20$, $P = 0.011$; Fig. 4). Similarly, NO_3^- was positively correlated with DIN (Spearman rank correlation, $r_s = 0.70$, $n = 21$, $P < 0.001$) and f ratio (Spearman rank correlation, $r_s = 0.46$, $n = 20$, $P = 0.043$; Fig. 4). DIN was positively correlated with SRP (Spearman rank correlation, $r_s = 0.45$, $n = 21$, $P = 0.043$) and DIN:SRP (Spearman rank correlation, $r_s = 0.62$, $n = 21$, $P = 0.003$), but negatively correlated with coral cover (Spearman rank correlation, $r_s = -0.64$, $n = 13$, $P = 0.018$; Fig. 4).

Biological responses (% coral cover and chlorophyll a concentration) were modeled against potential drivers. Stepwise multiple regressions on coral cover against temperature, Shark River Slough flow, population, chlorophyll a, DIN, SRP, DIN:SRP, and f ratio using P values as selection criteria showed that annual coral cover was best predicted by DIN concentrations (linear regression, $r^2 = 0.60$, $F_{1,11} = 16.4$, $P = 0.002$; Fig. 5a); no other environmental variables entered the model. These results matched those obtained in a simple linear regression of coral cover and DIN (Fig. 5a). When an alternate stepwise regression was performed exchanging NH_4^+ and NO_3^- for DIN, f ratio was excluded from the model based on a VIF of 29.3. The final model included NO_3^- and water temperature (linear regression, $r^2 = 0.41$, $F_{2,10} = 5.16$, $P = 0.028$), but the coefficients of the models were not significant (NO_3^- $P = 0.075$ and water temperature $P = 0.092$).

Stepwise multiple regression analysis on chlorophyll a concentration against temperature, Shark River Slough flow, population, DIN, SRP, DIN:SRP, and f ratio showed
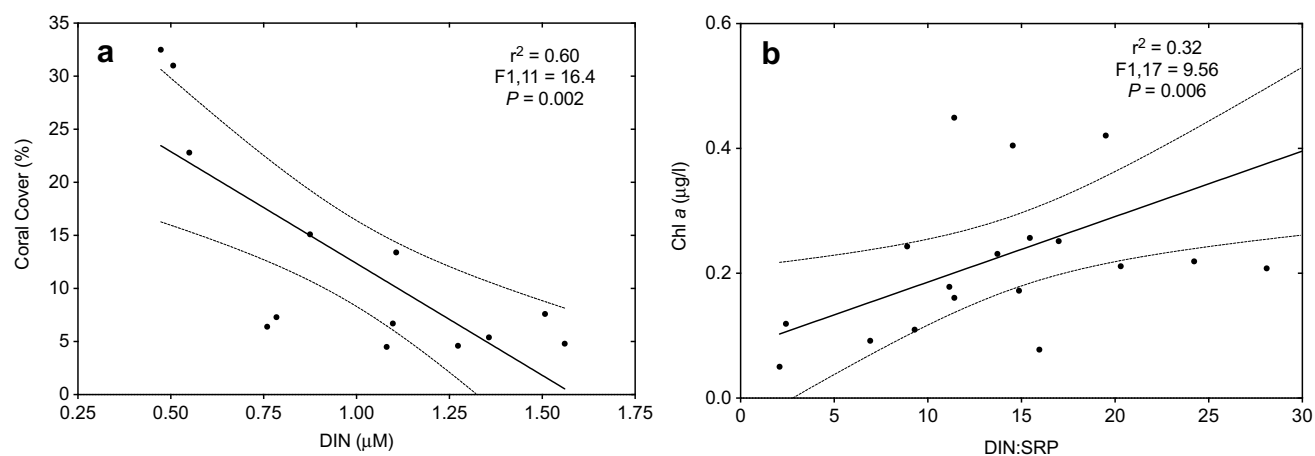
Fig. 5 Driving factors of biological changes at Looe Key reef, showing modeled relationships between **a** percent cover of living coral and DIN concentrations, as well as **b** chlorophyll *a* concentrations and DIN:SRP

that chlorophyll *a* concentrations were best predicted by DIN:SRP and Shark River Slough flow (linear regression, $r^2 = 0.45$, $F_{2,16} = 8.33$, $P = 0.003$). DIN:SRP alone was also a significant predictor of chlorophyll *a* concentrations (linear regression, $r^2 = 0.32$, $F_{1,17} = 9.56$, $P = 0.006$; Fig. 5b), but the model fit (r^2) improved when flow was also considered. When the stepwise regression was conducted exchanging NH_4^+ and NO_3^- for DIN, no additional variables entered the model.

Decadal analysis of nutrient data from LKSPA revealed significant enrichment of NH_4^+ (Kruskal–Wallis test, $H_3 = 141$, $P < 0.001$), NO_3^- (Kruskal–Wallis test, $H_3 = 325$, $P < 0.001$), and DIN (Kruskal–Wallis test, $H_3 = 397$, $P < 0.001$) in the 1990s, which continued through the 2000s and 2010s (Table 2; Fig. 6a). In the 1980s, average concentrations of NH_4^+ (0.36 ± 0.01 μM), NO_3^- (0.20 ± 0.01 μM), and DIN (0.51 ± 0.02 μM) were relatively low compared to subsequent decades (Table 2). Concurrent with increased rainfall and water deliveries to Shark River Slough between 1991 and 1993 (Fig. 6e), concentrations of both NH_4^+ and NO_3^- increased, contributing to significant DIN enrichment, which remained elevated through 2014 (Fig. 6a). The *f* ratio significantly increased in the 1990s (Kruskal–Wallis test, $H_3 = 57.0$, $P < 0.001$) to 0.49, indicating that NH_4^+ and NO_3^- contributed similarly to the DIN pool (Table 2). Despite a spike similar to DIN in 1992 (Fig. 6), SRP subsequently decreased and then increased more gradually over the study period, with an overall significant (Kruskal–Wallis test, $H_3 = 130$, $P < 0.001$) difference between each decade (Table 2; Fig. 6b). This temporal trend in DIN and SRP resulted in a significant (Kruskal–Wallis test, $H_3 = 147$, $P < 0.001$) decadal increase in the DIN:SRP ratio from 9.48 in the 1980s to 26.5 in the 1990s, 16.3 in the 2000s, and 14.9 in the 2010s (Fig. 6c). During the 1980s, DIN:SRP ratios

increased, peaking in 1987 at an annual average of 15:1 with the highest values (25–57) observed from January to August. In the 1990s, the annual average DIN:SRP ratio peaked in 1996 at the highest observed annual average of 31:1. Following a decreasing trend in the 2000s, the DIN:SRP ratio increased again in 2014 to 20:1 (Fig. 6c). Overall, decadal averages of nutrient concentrations at LKSPA were significantly higher for all analytes, except SRP, between the 1980s and subsequent decades; SRP concentrations were significantly higher in the 2000s and 2010s than prior decades (Table 2).

Like DIN, chlorophyll *a* concentrations also increased significantly (Kruskal–Wallis test, $H_3 = 89.9$, $P < 0.001$) in the early 1990s, and remained elevated through the 2000s and 2010s (Fig. 6d). Chlorophyll *a* averaged 0.14 μg/l in the 1980s and increased to an annual maximum value of 0.60 μg/l in 1996 following 5 years of increased water deliveries from Shark River Slough and heavy rainfall in 1994/1995 (Table 2; Fig. 6d, e). Since 1999, chlorophyll *a* decreased with reduced flows from Shark River Slough, averaging 0.25 μg/l (Table 2; Fig. 6d, e). Subsequent analyses revealed a significant linear relationship between chlorophyll *a* at LKSPA and Shark River Slough flows (linear regression, $r^2 = 0.25$, $F_{1,17} = 5.67$, $P = 0.029$; Fig. 7).

Living coral cover at LKSPA declined from ~33% in 1984 to ~6% in 2008 (Fig. 6f). The annual rate of coral decline was variable over the period of study, but increased from 1985 to 1987 and 1997 to 1999 (Fig. 6f). Between 1984 and 1985, the annual rate of coral decline was 1.5%, then increased from 1985 to 1986 to 8.2% (Fig. 6f), largely as a result of mortality of the *A. palmata* that historically dominated the shallow reef at LKSPA. The rate of coral decline from 1991 to 1996 was 2.7%/year, which increased to 7.5%/year between 1997 and 1999 as a result of additional rapid loss of the remaining *A. palmata*. Between 2000 and 2010,

Table 2 Descriptive statistics by decade for ammonium (NH_4^+), nitrate + nitrite (NO_3^-), DIN ($NH_4^+ + NO_3^-$), soluble reactive phosphorus (SRP), chlorophyll a (Chl a), f ratio, and DIN:SRP at Looe Key

Variable	Kruskal–Wallis test	Parameter	1980s	1990s	2000s	2010s
Ammonium (µM)	($H_3 = 141, P < 0.001$)	n	585	152	217	194
		Min	0.05	0.06	0.13	0.18
		Max	2.68	4.42	2.3	4.62
		Median	0.26	0.37	0.50	0.50
		Avg ± SE	0.36 ± 0.01	0.61 ± 0.05	0.57 ± 0.04	0.57 ± 0.04
		Pairwise	a	b	b	c
Nitrate + Nitrite (µM)	($H_3 = 325, P < 0.001$)	n	621	167	209	194
		Min	0.01	0.02	0.03	0.08
		Max	2.44	1.82	1.88	6.92
		Median	0.11	0.47	0.44	0.45
		Avg ± SE	0.20 ± 0.01	0.55 ± 0.03	0.49 ± 0.02	0.55 ± 0.05
		Pairwise	a	b	b	b
Dissolved inorganic nitrogen (µM)	($H_3 = 397, P < 0.001$)	n	659	172	217	194
		Min	0.02	0.05	0.3	0.39
		Max	2.68	5.72	2.87	7.28
		Median	0.41	0.86	1.02	0.97
		Avg ± SE	0.51 ± 0.02	1.07 ± 0.08	1.13 ± 0.08	1.21 ± 0.08
		Pairwise	a	b	c	c
Soluble reactive phosphorus (µM)	($H_3 = 130, P < 0.001$)	n	309	146	208	194
		Min	0.03	0.01	0.01	0.01
		Max	0.58	0.66	0.55	0.64
		Median	0.07	0.04	0.08	0.09
		Avg ± SE	0.09 ± < 0.01	0.08 ± 0.01	0.10 ± 0.01	0.11 ± 0.01
		Pairwise	a	b	c	d
Chlorophyll a (µg/l)	($H_3 = 89.9\ P < 0.001$)	n	70	166	176	186
		Min	0.02	0.03	0.04	0.02
		Max	0.37	2.5	1.75	1.18
		Median	0.11	0.30	0.20	0.21
		Avg ± SE	0.14 ± 0.02	0.41 ± 0.03	0.25 ± 0.02	0.25 ± 0.02
		Pairwise	a	b	c	c
f ratio	($H_3 = 57.0, P < 0.001$)	n	540	147	209	194
		Min	0.02	0.01	0.03	0.06
		Max	0.93	0.93	0.8	0.95
		Median	0.30	0.51	0.43	0.46
		Avg ± SE	0.34 ± 0.01	0.49 ± 0.04	0.41 ± 0.03	0.47 ± 0.03
		Pairwise	a	b	c	b
DIN:SRP	($H_3 = 147, P < 0.001$)	n	305	146	208	194
		Min	0.1	1.25	0.79	1.45
		Max	56.7	205	90.8	165
		Median	7.24	19.06	13.70	11.07
		Avg ± SE	9.53 ± 0.55	26.5 ± 2.20	16.3 ± 1.13	14.9 ± 1.08
		Pairwise	a	b	c	d

Kruskal–Wallis test results and post hoc pairwise comparisons shown by decade; letters indicate significant differences ($P < 0.05$)

living coral cover on the shallow reefs at LKSPA reef was ~6% and decreased at an annual rate of < 1%/year (Fig. 6f).

Maximum monthly air temperature observed at Key West International Airport did not increase significantly over the study period, as indicated by a slope not different from zero (linear regression, $r^2 < 0.001$, $F_{1,1732} = 0.017$, $P = 0.90$). Maximum water temperature at LKSPA had an overall range of 14.7 °C during the study period with the
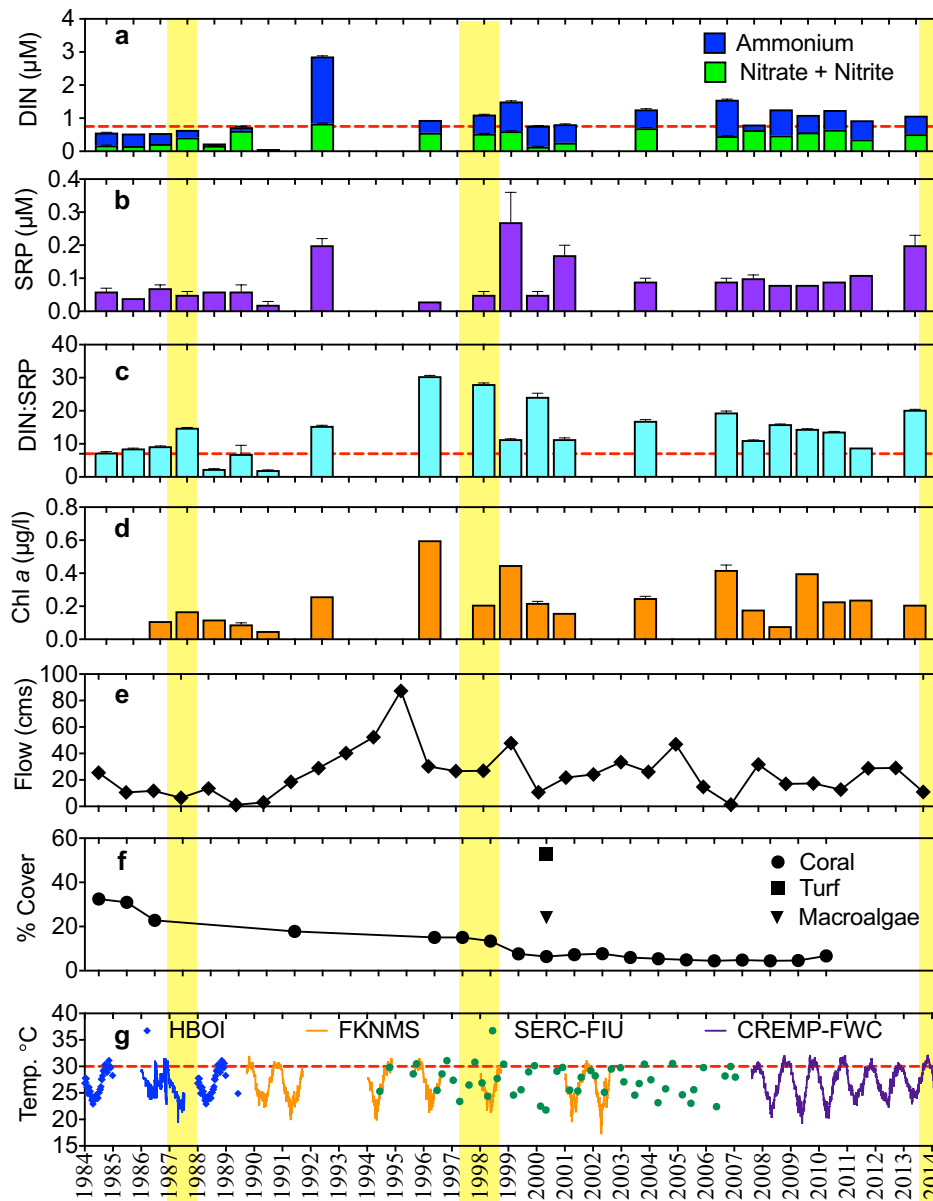
Fig. 6 Long-term monitoring data from Looe Key reef, showing the three mass bleaching events (1987, 1997/1998, 2014) in yellow in relation to annual averages (±SE) of **a** dissolved inorganic nitrogen (DIN) concentrations with a red dashed line representing the US EPA strategic target for coral reef ecosystems in the FKNMS at 0.75 μM, **b** soluble reactive phosphorus (SRP), **c** DIN:SRP ratio with a red dashed line indicating reported ratios for healthy coral reefs (Smith et al. 1981; Crossland et al. 1984; Furnas et al. 1995), **d** chlorophyll *a* (Chl *a*), and **e** flow rate of Everglades discharges through Shark River Slough from the combined S-12 structures (cms). Also showing, **f** percent coral cover; note the high percent cover of turf algae and macroalgae observed in 2000 (Lapointe et al. 2002). Water tempera-

ture (°C) is presented **g** as discreet samples (points) or the daily maximum of continuous measurements (lines) at (FKNMS) from 1984 to 2014 with data compiled from Harbor Branch Oceanographic Institute-Florida Atlantic University (HBOI-FAU), Florida Keys National Marine Sanctuary Looe Key buoy (FKNMS-Buoy), FKNMS-Water Quality Monitoring Program (FKNMS-WQMP) collected by Southeast Environmental Research Center-Florida International University (SERC-FIU), and temperature logger data from Coral Reef Evaluation and Monitoring Project via Florida Fish and Wildlife Commission (CREMP-FWC); the red dashed line shows the Florida Keys coral bleaching threshold of 30.5 °C proposed by Manzello et al. (2007)

lowest water temperature (17.2 °C) recorded in 2003 and the highest (31.9 °C) in 1990. The bleaching threshold of 30.5 °C (Manzello et al. 2007) was exceeded in at least 15

(249 recorded data points) of the 30 years during this study (Fig. 6g).

The taxonomic composition of macroalgal collections varied during the long-term study, but the common
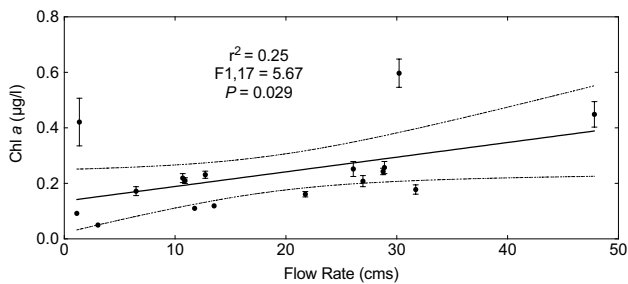
Fig. 7 Linear regression analysis showing the significant relationship between annual average ($\pm$ SE) chlorophyll a (Chl a) concentrations at Looe Key reef and annual average flow rate of Shark River Slough with 95% confidence intervals

ochrophyta *Dictyota* spp. and rhodophyta *Laurencia poiteaui* were collected repeatedly over the 3-decade study. A total of 250 macroalgae samples were analyzed for molar C:N:P ratios (1980s $=$ 17, 1990s $=$ 22, 2000s $=$ 54, and 2010s $=$ 158; Table 3). The C:N ratio did not vary significantly during the study (Kruskal–Wallis test, $H_3 = 4.83$, $P = 0.185$; Fig. 8a), averaging 22.2 in the 1980s, 23.8 in the 1990s, 25.2 in the 2000s, and 28.1 in the 2010s (Table 3). The C:P ratio increased significantly (Kruskal–Wallis test, $H_3 = 51.4$ $P < 0.001$) from 579 in the 1980s to 1643 in the 1990s, 1473 in the 2000s, and 1943 in the 2010s (Fig. 8b). This increasing trend for the C:P ratio was mirrored by parallel increases in the N:P ratio, which increased significantly (Kruskal–Wallis test, $H_3 = 51.7$, $P < 0.001$) from 26.8 in the 1980s to 69.4 in the 1990s, 59.2 in the 2000s, and 71.3 in the 2010s (Table 3; Fig. 8c).

Annual and seasonal variability in Everglades runoff

Seawater sampling along the Shark River–LKSPA transect (Fig. 1) showed seasonal and year-to-year variability in salinity, DIN, and DIN:SRP ratios. Salinity along the transect averaged 34.9 ± 0.6 in the dry seasons, compared to 30.0 ± 1.6 in the wet seasons. In the relatively dry year of 2010, DIN concentrations were significantly higher in the wet versus dry season, with concentrations in the wet season $> 0.75 \mu M$ along the entire transect to LKSPA. High DIN concentrations, up to $8 \mu M$, occurred in the Shark River estuary during the 2011 wet season, again with concentrations $\sim 0.75 \mu M$ or more along the entire transect to LKSPA (Fig. 9a). In contrast to DIN, SRP concentrations in 2011 were higher in the dry season and decreased from $> 0.2 \mu M$ in Shark River to $\sim 0.07 \mu M$ at LKSPA (Fig. 9b). Accordingly, the DIN:SRP ratio was significantly higher (Kruskal–Wallis test, $H_1 = 26.65$, $P < 0.001$) in the wet versus dry seasons and highest (60–80) in the 2011 wet season at Shark River (Fig. 9c). The TDN:TDP was also significantly higher in the wet season (Kruskal–Wallis

test, $H_1 = 15.44$, $P < 0.001$) and showed a similar pattern to DIN:SRP, with generally higher values in the wet versus dry seasons and the highest values (~ 150) at Shark River during the 2011 wet season (Fig. 9d).

Relatively low C:N ratios of $\sim 6{:}1$ in POM were associated with high chlorophyll a concentrations of ~ 4–6 $\mu g/l$ along the Shark River–LKSPA transect in the wet season of 2010 (Fig. 9e, f). In contrast, higher C:N ratios of 13:1–18:1 were associated with lower chlorophyll a values $< 2 \mu g/l$ along the transect in the dry season of 2010 (Fig. 9e, f). Similarly, higher chlorophyll a occurred in the wet versus dry season of 2011. Average chlorophyll a concentrations ranged from ~ 2 to 6 $\mu g/l$ between Shark River and the Rock Pile Reef north of the lower Florida Keys, with lower values of $\sim 0.3 \mu g/l$ at offshore LKSPA (Fig. 9e).

The $\delta^{15}N$ values of the POM between Shark River and LKSPA ranged from $\sim + 1$ to $+ 5\%$ in 2010, with more enriched values ($+ 2$ to $+ 5\%$) occurring at sites downstream of Shark River along western Florida Bay and more depleted values at LKSPA (Fig. 9g). A different pattern occurred in 2011 with more enriched values ($+ 4$–5%) along most of the sites downstream of Shark River, including LKSPA ($\sim + 5\%$; Fig. 9g).

Satellite remote sensing

The connectivity of water discharges from the South Florida mainland with the coastal waters of the lower Florida Keys is evident in remote sensing imagery. For example, the spatial pattern of discharges from Shark River Slough can be seen in various satellite remote sensing imagery over the period of study between 1984 and 2014 (Fig. 10). After the 1989–1990 drought and following major water releases from Shark River Slough and Taylor Slough in 1991, highly turbid water was apparent in western Florida Bay in a true color Landsat image on 29 May 1992; discolored water was also apparent in central Florida Bay and this extended southward to the lower Florida Keys (Fig. 10a). In South Florida, "black water" refers to the phenomenon of water discoloration due to high concentrations of phytoplankton (either dinoflagellates or diatoms) and/or colored dissolved organic matter (CDOM), where the Everglades is known to be a large source of CDOM (Hu et al. 2002). After several years of increased water deliveries and heavy rainfall in 1994–1995, extensive turbid water downstream of Shark River Slough in the upstream "backcountry" of the Florida Keys was apparent in an AVHRR image on 12 March 1996 (Fig. 10b). Black water events associated with Shark River Slough discharges were visible in many SeaWiFS images (Zhao et al. 2013). More recently, VIIRS chlorophyll a anomaly images on 24 November 2013 and 27 January 2014 showed bloom features from the Shark River Slough and Taylor Slough to the lower Florida Keys (Fig. 10c, d).

Table 3 Molar carbon:nitrogen (C:N), carbon:phosphorus (C:P), and nitrogen:phosphorus (N:P) ratios of macroalgae collected from Looe Key in the 1980s, 1990s, 2000s, and 2010s; values represent averages ± SE, division totals are italicized, and bold values represent decadal averages

Decade	Division	Species	n	C:N	C:P	N:P
1980s			**17**	**22.2 ± 30.1**	**579 ± 33**	**26.8 ± 1**
	Ochrophyta		*10*	*21.6 ± 1.3*	*597 ± 59*	*27.7 ± 2.1*
		Dictyota divaricata	6	18.5 ± 0.7	536 ± 57	28.8 ± 3
		Padina jamaicensis	2	25.3 ± 0.6	571 ± 32	22.6 ± 0.7
		Stypopodium zonale	2	27 ± 0.8	804 ± 180	29.6 ± 5.7
	Rhodophyta		*7*	*23.2 ± 4.1*	*554 ± 70*	*25.6 ± 1.7*
		Chondria sp.	1	12.2	374	30.8
		Laurencia poiteaui	2	12 ± 0.4	361 ± 5.2	30.2 ± 1.5
		Liagora sp.	2	30.2 ± 0.3	676 ± 6	22.5 ± 0
		Meristiella gelidium	2	33.1 ± 3.6	713 ± 96	21.5 ± 0.6
1990s			**22**	**23.8 ± 25.2**	**1643 ± 121**	**69.4 ± 2.2**
	Chlorophyta		*11*	*25 ± 0.7*	*1696 ± 204*	*67.6 ± 7.4*
		Cladophora fuliginosa	9	24.5 ± 0.8	1865 ± 208	75.1 ± 6.7
		Cladosiphon occidentalis	1	25.2	755	30
		Codium isthmocladum	1	29.3	1116	38.2
	Ochrophyta		*2*	*26.7 ± 0.3*	*2309 ± 581*	*86.4 ± 21*
		Dictyota dichotoma	1	26.4	1729	65.6
		Dictyota divaricata	1	27	2890	107
	Rhodophyta		*9*	*21.7 ± 1.5*	*1429 ± 129*	*67.8 ± 8.1*
		Laurencia papillosa	1	25.7	1591	62.1
		Laurencia poiteaui	8	21.1 ± 1.6	1409 ± 144	68.5 ± 9.1
2000s			**54**	**25.2 ± 56.5**	**1473 ± 67**	**59.2 ± 1.7**
	Chlorophyta		*24*	*29.7 ± 1.3*	*1936 ± 71*	*67.7 ± 3.2*
		Cladophoropsis membranacea	3	29.7 ± 1.6	1320 ± 69	44.7 ± 2.3
		Halimeda goreaui	12	32.5 ± 0.7	2154 ± 64.1	66.8 ± 2.1
		Halimeda opuntia	9	26 ± 2.8	1852 ± 76	76.7 ± 6.3
	Ochrophyta		*18*	*23.9 ± 1.3*	*1153 ± 56*	*48.9 ± 1.4*
		Dictyota menstrualis	9	20.2 ± 0.5	1035 ± 43	51.4 ± 2
		Dictyota sp.	6	23.8 ± 0.7	1127 ± 50.2	47.4 ± 1.8
		Lobophora variegata	3	35 ± 0.3	1555 ± 142	44.6 ± 4.4
	Rhodophyta		*12*	*18 ± 0.9*	*1025 ± 37*	*57.8 ± 2.3*
		Hypnea spinella	3	22 ± 0.2	1148 ± 11.1	52.2 ± 0.9
		Laurencia chondroides	3	14.8 ± 0.3	1008 ± 43.5	68.4 ± 3.8
		Laurencia poiteaui	6	17.7 ± 1.1	971 ± 58.8	55.3 ± 2.2
2010s			**158**	**28.1 ± 82.1**	**1943 ± 89.3**	**71.3 ± 2.3**
	Chlorophyta		*56*	*37.3 ± 1.7*	*2470 ± 101*	*68.5 ± 2.1*
		Caulerpa prolifera	2	18.8 ± 0.9	1522 ± 126	80.9 ± 3
		Cladophora catenata	9	27 ± 1	1940 ± 177	71.3 ± 5
		Halimeda goreaui	36	42.7 ± 2	2737 ± 125	66 ± 2.7
		Halimeda opuntia	9	30 ± 1.5	2142 ± 134	73.1 ± 5.5
	Ochrophyta		*59*	*22.8 ± 0.8*	*1458 ± 59*	*64.3 ± 1.7*
		Dictyota cervicornis	6	32.7 ± 0.2	2013 ± 193	61.7 ± 5.7
		Dictyota crispata	6	28.7 ± 2.6	1791 ± 212	61.9 ± 2.3
		Dictyota menstrualis	27	19.9 ± 0.3	1189 ± 36.2	60.3 ± 2.1
		Dictyota sp.	9	20.4 ± 0.3	1274 ± 58	62.4 ± 2.1
		Dictyota spp.	5	16.4 ± 0.8	1281 ± 68	79.3 ± 7.6
		Stypopodium zonale	6	29 ± 2.2	2205 ± 50	78.1 ± 5.5
	Rhodophyta		*43*	*23.4 ± 1.3*	*1923 ± 129*	*84.4 ± 4.5*
		Acanthophora spicifera	3	24.5 ± 1.3	3297 ± 496	133 ± 13
		Chondria capillaris	3	28.3 ± 0.4	1553 ± 59	55 ± 2.8
		Eucheuma isiforme	3	37.4 ± 2.2	3301 ± 225	88.5 ± 2
		Ganonema farinosum	3	35.4 ± 0.3	2368 ± 182	67.2 ± 5.6
		Haloplegma duperreyi	3	15.3 ± 0.2	746 ± 65	48.7 ± 4.3
		Laurencia poiteaui	24	18.2 ± 0.7	1597 ± 105	88 ± 4.6

Table 3 (continued)

Decade	Division	Species	n	C:N	C:P	N:P
		Liagora ceranoides	3	41.8 ± 0.3	2389 ± 46	57.3 ± 0.7
		Red Turf *	7	19.5 ± 0.3	2832 ± 211	293 ± 31

[a]Red turf algae were not included in the 2010 averages
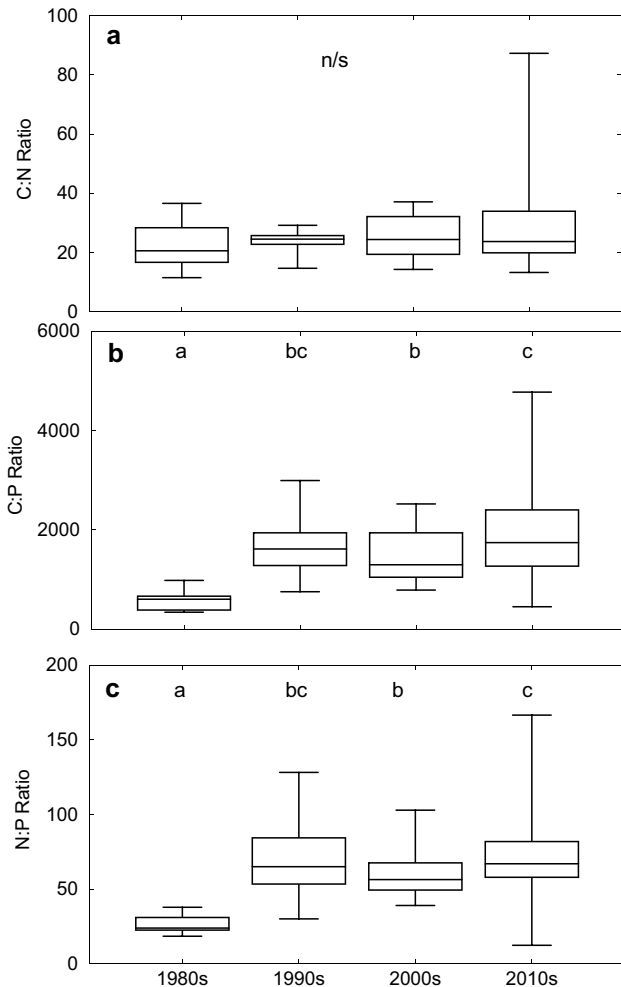
Fig. 8 Decadal distributions of molar C:N:P ratios for macroalgae collected at Looe Key reef from 1984 to 2014 ($n = 250$), including **a** C:N, **b** C:P, and **c** N:P; significant differences (Kruskal–Wallis, $P < 0.001$) denoted by letters

Discussion

The significant long-term changes in DIN availability, N:P stoichiometry, and eutrophication at LKSPA provide compelling evidence that land-based N loading should be considered a major contributing factor to the coral reef degradation at LKSPA. Notably, DIN and chlorophyll *a* concentrations at LKSPA increased significantly between 1992 and 1996 and

remained elevated (above 1980s baseline values) through 2014. The DIN concentrations at LKSPA averaged over 1.0 μM since the early 1990s, a value considered as an ecological nutrient threshold concentration for degradation of coral reefs from eutrophication (Smith et al. 1981; Bell 1992; Lapointe et al. 1993; Lapointe 1997). From 2012 to 2016, 62–72% of the water quality monitoring samples in the FKNMS fell below the 1995–2005 baseline value for meeting compliance with the US EPA strategic target DIN value of 0.75 μM (Briceno and Boyer 2018). Similar to DIN, chlorophyll *a* concentrations, which peaked in 1996 at ~0.6 μg/l, have averaged 0.25 μg/l since 2000, a value almost twofold higher than the baseline average value of 0.14 μg/l in the 1980s. For comparison, the US EPA strategic target for reefs in the FKNMS is 0.2 μg/l (Briceno and Boyer 2018) and the numeric nutrient criteria (NNC) for chlorophyll *a* in the lower Florida Keys is 0.3 μg/l (FAC, 62–302.532).

A DIN and chlorophyll *a* "breakpoint" in the long-term data record at LKSPA occurred between 1992 and 1996 during a period of increased Everglades discharges from both Shark River Slough and Taylor Slough (Rudnick et al. 1999). During this time, salinity decreased throughout Florida Bay, while DIN increased from threefold to sixfold in the central bay, chlorophyll *a* increased fivefold in the central bay and threefold in the western bay, and turbidity some fourfold to twentyfold in the central and western bay, respectively (Boyer et al. 1999). This period of increased freshwater flows and N loading was followed by a 404% increase in coral diseases throughout the downstream waters of the FKNMS (Porter et al. 2001; Table 1). The highest disease incidence was reported for LKSPA with 43% of coral colonies diseased (Santavy et al. 2006). The increase in coral diseases and mortality affected 82% of the CRMP reef sites throughout the FKNMS between 1996 and 2000, where 12 different coral diseases were identified (Porter et al. 2001). Plague Type II disease, which was first observed in June 1995, affected 17 of the 43 species of stony corals in the FKNMS and caused 38% mortality in *Dichocoenia stokesii* by October 1995 (Richardson et al. 1998). The dramatic epizootic between 1996–2000 was a major agent of coral mortality not only at LKSPA, but also throughout the FKNMS where 38% loss of living coral cover occurred (Porter et al. 2002).

Although the long-term monitoring data presented here elucidates only a temporal relationship between nutrient

Fig. 9 Seasonal transects from Shark River to Looe Key reef, showing average concentrations of **a** dissolved inorganic nitrogen (DIN) with a red dashed line representing the US EPA strategic target for coral reef ecosystems in the FKNMS at 0.75 µM, **b** soluble reactive phosphorus (SRP), **c** DIN:SRP ratio showing values reported for healthy coral reefs as a red dashed line (Smith et al. 1981; Crossland et al. 1984; Furnas et al. 1995), **d** total dissolved nitrogen:total dissolved phosphorus ratio (TDN:TDP), **e** chlorophyll *a* concentrations with a red dashed line showing the US EPA strategic target at 0.2 µg/l, **f** molar carbon:nitrogen ratios of particulate organic matter (POM) showing the Redfield ratio as a black dotted line, and **g** δ15N values of POM at Shark River (SR), Shark River Gulf (SRG), Mid Cape (MC), Florida Bay Ledge (FBL), Rock Pile (RPL), and Looe Key Sanctuary Preservation Area (LK) in the 2010 and 2011 wet and dry seasons; values represent mean ± SE (*n* = 3/site/event)
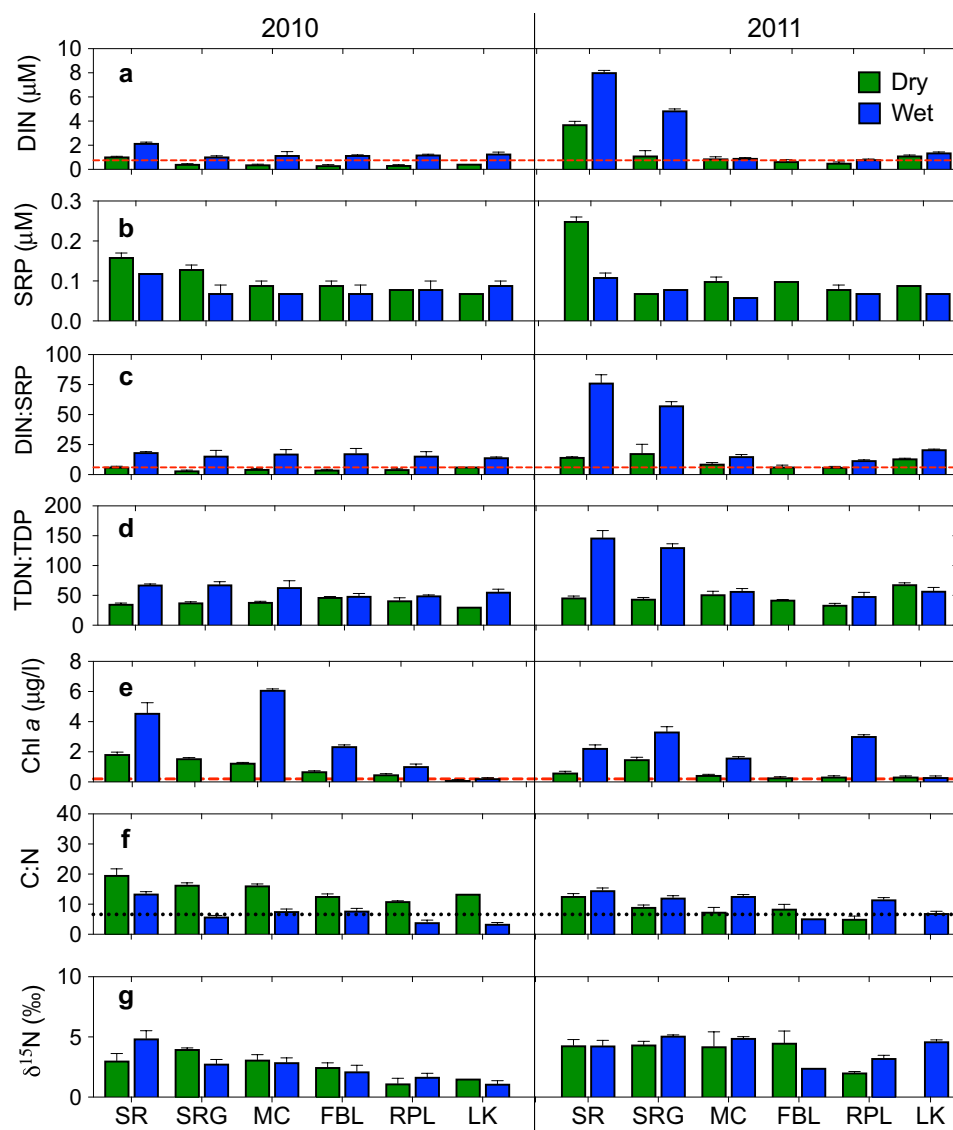
enrichment, algal blooms, and coral diseases, supporting experimental research provides cause and effect mechanisms. Experimental nutrient enrichment studies with the red seaweed *Gracilaria tikvahiae* near Big Pine Key in the lower Florida Keys indicated that while both N and P limited the growth during the dry winter months, only P limited the growth in the wet summer months when DIN concentrations increased twofold (1.14–2.42 µM) and N:P ratios increased from 8.1 to 30.1 (Lapointe 1987). Field and laboratory experiments also showed that NO_3^- enrichment up to 3 µM increased the progression of black band disease (Voss and Richardson 2006). Further, experimental field studies on reefs offshore Key Largo in the upper Florida Keys showed a twofold increased response in prevalence of disease from nutrient-enriched treatments relative to controls (Vega-Thurber et al. 2014), thus indicating a causal relationship between DIN enrichment and coral disease. The

combination of experimental evidence and the correlation of the increased Everglades discharges between 1991 and 1996 with DIN enrichment, algal blooms, and coral disease outbreak in the FKNMS strongly points to nutrient pollution as the common thread linking these ecological phenomena (NRC 2000).

DIN enrichment, P limitation, and coral resistance to thermal stress

Over the 3-decade study, DIN:SRP ratios were much higher at LKSPA compared to lower values between 4.3:1 and 7.2:1 for healthy coral reefs (Smith et al. 1981; Crossland et al. 1984; Furnas et al. 1995), and showed three prominent annual spikes coinciding with the three mass bleaching events on offshore reefs of the FKNMS in 1987 (Fig. 11a), 1997/1998 (Fig. 11b–d), and 2014 (Fig. 11e, f). Whereas
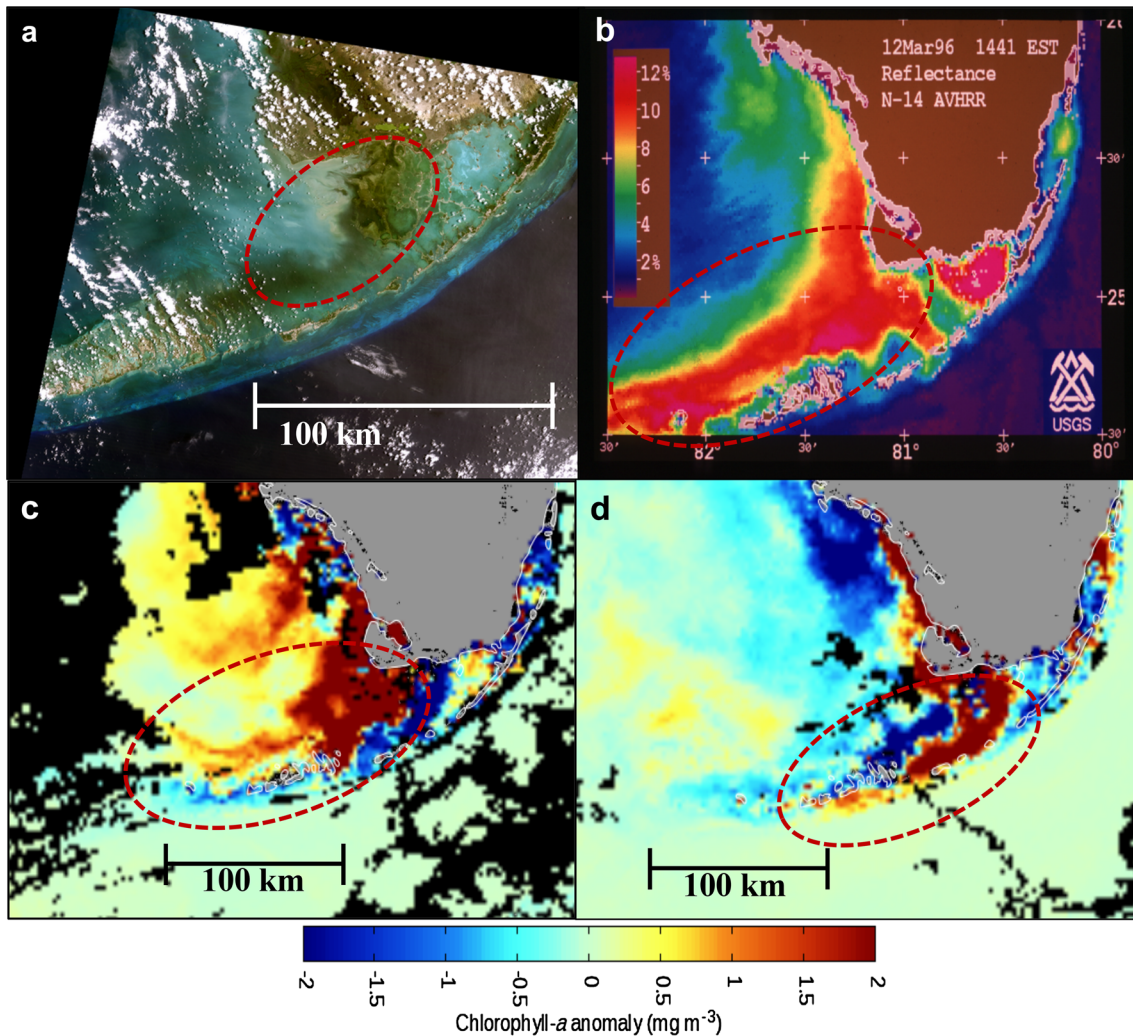
Fig. 10 Remote sensing imagery of discolored water and algal blooms in the Florida Bay and the Florida Keys region between 1992 and 2013 showing connectivity of the mainland and the lower Florida Keys, all outlined in red. **a** Landsat true color image on 29 May 1992 shows turbid water in western Florida Bay and discolored, black water in central Florida Bay that extends southward to the lower Florida Keys; **b** AVHRR reflectance image on 12 March 1996 shows high turbidity from the Shark River Slough plume extending beyond the lower Florida Keys towards Dry Tortugas; **c, d** VIIRS chlorophyll *a* anomaly images show phytoplankton blooms off Shark River Slough reaching the lower Florida Keys that were partially composed of the cyanobacterium, *Synechococcus*, on **c** 24 November 2013 and **d** 27 January 2014

peak summer temperatures exceeded the coral bleaching threshold of 30.5 °C (Manzello et al. 2007; Manzello 2015) in many years during the 3-decade study, the three mass bleaching events on offshore bank reefs only occurred in years following major land-based runoff when the DIN:SRP ratios were elevated. The 1987 bleaching event was preceded by increased water deliveries to the Everglades and heavy El Niño rainfall (Table 1). This resulted in DIN enrichment and increasing DIN:SRP ratios up to 57:1 in summer of 1987 at LKSPA, with an annual average of 15:1 for 1987. A higher annual DIN:SRP spike to 31:1 occurred 1 decade later in 1996 following major increases in water deliveries and heavy rainfall in 1994/1995 prior to the mass bleaching in

fall of 1997 (Fig. 11b; Table 2). Lastly, a DIN:SRP spike to 19:1 and mass bleaching occurred in 2014 following heavy rainfall in 2013, increased water deliveries associated with the C-111 Spreader Canal Western Project as part of the CERP, and phytoplankton blooms in central Florida Bay that extended south to the lower Florida Keys (Shangguan et al. 2017; Fig. 10d; Table 1). Increases in DIN:SRP ratios result in a lowered resistance of corals to light and temperature-induced bleaching from enlarged (suboptimal) zooxanthellae densities that disrupt the autotrophic energy relations of the coral–algae symbiosis, leading to P starvation (Wiedenmann et al. 2013; D'Angelo and Wiedenmann 2014; Rosset et al.
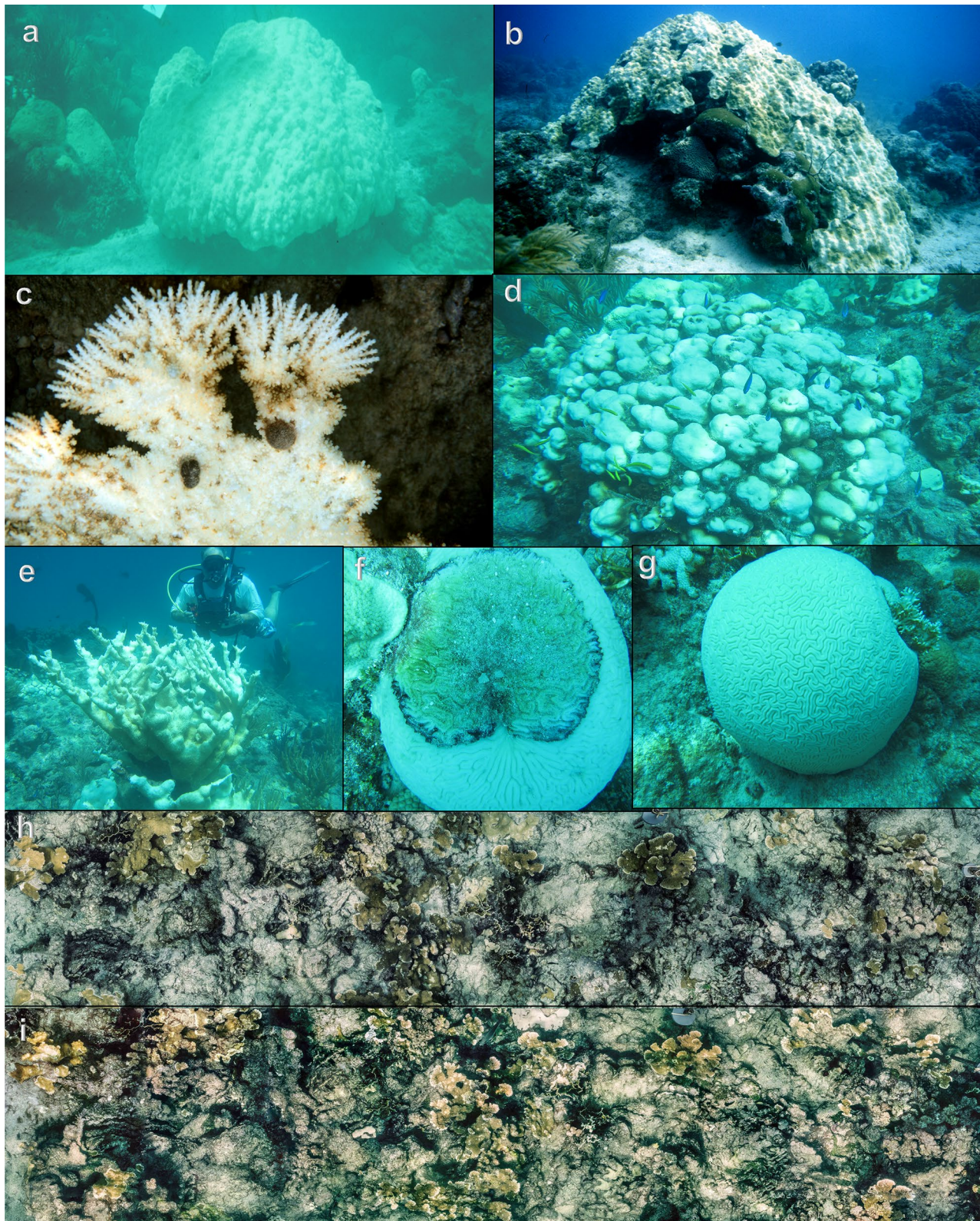
Fig. 11 Coral in the lower Florida Keys, showing three mass bleaching events including: **a** September 1987, **b** November 1997, **c** February 1998, and **d–g** September 2014, as well as **h** a healthy reef in June 1997 and **i** a severely diseased, but unbleached, reef at the same location (Eastern Dry Rocks) in September 1997; photo credits **a**, **d–g** Brian Lapointe, **b**, **c** Craig Quirolo and **h**, **i** James Porter

2017) and reduction of the coral photosynthesis to respiration (P:R) ratio (Wooldridge 2014).

Some suggest that increased sea surface temperatures during the 1997/1998 El Niño led to one of the worst mass coral bleaching and mortality events in Florida Keys history (Manzello et al. 2007). Interestingly, this mass bleaching event began during cooler temperatures in October 1997 (Fig. 11b) and continued through the winter of 1998 (Fig. 11c, d). This followed several years of turbid, nutrient-enriched green water flowing out of Florida Bay that coincided with elevated seawater DIN:SRP ratios (22–32 between 1996 and 1998). Temperatures were not elevated at LKSPA until late 1998 (see NOAA degree heating week data products at https://www.ospo.noaa.gov/Products/ocean/cb/dhw/index.html). Further, while bleaching might have contributed to the coral mortality after summer 1998, bleaching did not initiate mortality in the summer of 1997 (see Porter et al. 2002; Fig. 11h, i). The high coral mortality during this period was caused primarily by coral diseases that began expanding in 1994, and nutrients correlated spatially with the virulence of diseases (Kim and Harvell 2004). Because coral disease and bleaching can often be confused, coral loss may be attributed to bleaching when it is actually due to disease. For example, several massive colonies of *Montastraea annularis* became infected with white plague in 1996 and died prior to the July 1998 census (Porter et al. 2001). Had it not been for careful monitoring of this colony, its complete loss, recorded in 1998, would almost certainly have been attributed to the worldwide coral bleaching event which occurred in late summer of that year. These visual observations are confirmed by the quantitative analysis on the reduction in abundance of *M. annularis* for this station, which occurred prior to the Keys-wide bleaching event (Porter et al. 2001).

The temporal pattern of increasing DIN, DIN:SRP ratios, and chlorophyll *a* at LKSPA in the 1990s suggests that this period would also have reduced resistance of stony corals to thermal stress and coral bleaching. These findings are consistent with research on the Great Barrier Reef, where high chlorophyll concentrations were associated with DIN enrichment at reef locations characterized by low resistance to thermal stress and coral bleaching (Wooldridge 2009; Wooldridge and Done 2009). Recent research has elucidated the physiological mechanisms through which elevated DIN and DIN:SRP ratios result in P starvation, increasing susceptibility of corals to heat- and light-induced bleaching (Wiedenmann et al. 2013; D'Angelo and Wiedenmann 2014) and death (Rosset et al. 2017). The seawater DIN:SRP ratios at LKSPA associated with bleaching events (15:1, 31:1, and 19:1) greatly exceeded the ratios reported for healthy coral reefs (4.3:1–7.2:1; Smith et al. 1981; Crossland et al. 1984; Furnas et al. 1995). In addition, the SRP concentrations at LKSPA were in a range (0.05–0.12 μM) found to

be detrimental to corals in laboratory experiments which demonstrated that P starvation can become critically limiting at concentrations < 0.18 μM, if N:P ratios exceed 22:1 (Rosset et al. 2017). In fact, in the present study, the SRP values were considerably lower than those reported in the Rosset et al. (2017) experiments, suggesting that negative effects of DIN enrichment occur at the relatively low ambient SRP concentrations measured at Looe Key.

Other experimental field studies and monitoring in the FKNMS further support a linkage between DIN enrichment, P limitation, and coral bleaching. Cook et al. (2002) provided evidence that corals were P limited during the bleaching event in 1997, when the mountainous star coral *Montastraea faveolata* had very high N:P ratios (29:1–34:1) and C:P ratios (195:1–221:1), indicative of P starvation (N:P > 22:1; Rosset et al. 2017). Although a major Caribbean-wide bleaching event occurred in 2005, DIN:SRP ratios at LKSPA were decreasing at that time and only minor to patchy bleaching occurred in the FKNMS that year (Causey 2008). While some have suggested that bleaching caused coral mortality that year (Manzello et al. 2007), Ruzicka et al. (2013) demonstrated with high statistical confidence that there was no significant coral loss anywhere in the Florida Keys in 2005. Other studies of the patchy coral bleaching in the FKNMS in 2005, 2006, and 2007 indicated that shallow water coral colonies at locations with high concentrations of chlorophyll *a* and DIN showed higher prevalence of bleaching (Wagner et al. 2010). Experimental studies on reefs offshore Key Largo in the upper Florida Keys showed an over threefold increase in coral bleaching frequency in nutrient-enriched treatments relative to controls (Vega-Thurber et al. 2014), providing evidence that links nutrient enrichment to coral bleaching.

Alterations in N:P stoichiometry of reef macroalgae

The significant increase in the C:P and N:P ratios of macroalgae at LKSPA, which would be expected to have profound ecological effects, provides additional evidence of increasing P limitation at LKSPA during this study. This finding is most apparent in the significant increases in C:P and N:P ratios of the ochrophyte *Dictyota* spp. and the rhodophyte *Laurencia poiteaui* in the 1990s, which were at least twofold higher in these ratios compared to the 1980s. These data support research showing how human activities are increasing N enrichment of the biosphere at a much greater rate than P (NRC 2000; Rockström et al. 2009). This altered N:P stoichiometry could be driving some ecosystems, like coral reefs in the Florida Keys, to higher levels of P limitation, which would be expected to have profound effects on structure and function of aquatic ecosystems (Downing et al. 1999; Sterner and Elser 2002). Studies of the effects of increased C:P and N:P ratios on algae–grazer interactions

are needed to address the fundamental question as to how this stoichiometric shift affects the ecological dynamics of coral reef food webs.

The increased C:P and N:P ratios that developed at LKSPA since the 1990s are much higher than other values reported for macroalgae. The high C:P (1643:1–1943:1) and N:P (59:1–71:1) ratios from the 1990s to present at LKSPA are well above the mean values reported for macroalgae globally (700:1 and 35:1, respectively; Atkinson and Smith 1983), as well as those from P limited carbonate-rich coral reefs (976:1 and 43.4, respectively) in the Caribbean region (Lapointe et al. 1992). Furthermore, turf algae, which now dominate the benthic cover of former coral-dominated reefs at LKSPA, had even higher C:P (2832 ± 211) and N:P (293 ± 31) ratios than those of the reef macroalgae when collected simultaneously in 2012 at LKSPA (Table 3). Experimental studies have shown that N enrichment supports expansion of algal turfs, which now dominate cover on Caribbean coral reefs (Vermeij et al. 2010). The results of this study suggest that turf algae are responding strongly to the increased DIN at LKSPA.

The C:P and N:P ratios of reef macroalgae at the offshore LKSPA are now skewed so high (1943 and 71.3, respectively) that they resemble the values reported for macroalgae on N-enriched Jamaican fringing reefs. Early studies by D'Elia et al. (1981) at Discovery Bay, Jamaica, brought attention to the importance of widespread NO_3^--enriched groundwater discharges that contained low SRP concentrations and high N:P ratios, suggesting P limitation on surrounding reefs. Strong P limitation of reef macroalgae at Discovery Bay was subsequently demonstrated by nutrient enrichment bioassays, alkaline phosphatase assays, seawater DIN:SRP ratios, and macroalgae C:N:P (Lapointe 1997). The seawater ratios ranged from 103:1 in groundwater-fed grottos to 41:1 on the fore reef, and tissue N:P ratios of macroalgae ranged from 57:1 in the grottos to 39:1 on the fore reef. More recent studies of reef macroalgae in the Negril Marine Park, a highly urbanized tourist destination on the north coast of Jamaica similar to the carbonate-rich Florida Keys, indicated even higher C:P and N:P ratios, averaging 1580:1 and 62:1, respectively (Lapointe et al. 2011). Such values are very similar to the values in macroalgae at LKSPA since the 1990s. The high N:P ratios in Jamaican coastal waters help to explain the first incidence of coral bleaching in the Caribbean that was reported at Kingston, Jamaica, following heavy runoff from Hurricane Flora in 1963 (Goreau 1964). Although the bleaching was initially attributed to reduced salinity, more recent research suggests that Hurricane Flora's high N:P stormwater runoff was a likely factor increasing coral stress and a lowered tolerance to light- and temperature-induced bleaching (Wiedenmann et al. 2013; Rosset et al. 2017).

Local versus regional sources of N enrichment

The increased seawater DIN, chlorophyll a, and macroalgal N:P ratios reflect the cumulative effects of land-based and atmospheric N loads from a variety of local and regional sources. Land-based sources of nutrient pollution impacting the Florida Keys have long been a major concern to planners (State of Florida 1974), scientists (NOAA 1988), and resource managers (Continental Shelf Associates 1991; NOAA 1996; Kruczynski and McManus 2002). Geologists have noted the preferential distribution of coral reefs in the Florida Keys, which are absent or poorly developed in offshore areas lacking major islands but where large tidal passes allow "inimical waters" of Florida Bay and the Gulf of Mexico to stress reef growth from hot or cold water, elevated turbidity, and nutrients (Ginsburg and Shinn 1993; Boyer and Jones 2002; Toth et al. 2018). Although frontal eddies on the northern/western sides of the Florida Current (Lee et al. 1995; Kourafalou and Kang 2012) and episodic upwelling/internal tidal bores have been noted as potential sources of natural NO_3^- and SRP enrichment on offshore bank reefs (Lapointe and Smith 1987; Szmant and Forrester 1996; Leichter et al. 2003), the relatively low f ratios (~ 0.5) at LKSPA, generally warm temperatures, and increased chlorophyll a during our long-term study indicate nutrient transport from upstream nutrient sources in the Florida Keys, Florida Bay, and Gulf of Mexico along southwest Florida (Smith 1994; Smith and Pitts 2002; Boyer and Jones 2002; Lapointe et al. 2004; Rudnick et al. 1999). The relatively low rates of nitrification/denitrification in carbonate-rich subtropical ecosystems allow for cumulative enrichment of both NH_4^+ and NO_3^- in coastal waters (Rivera-Monroy and Twilley 1996; Downing et al. 1999), which was evident in this long-term study.

Particular concern has centered on local nutrient and bacterial pollution associated with sewage pollution from a growing residential and tourist population in the Florida Keys that could contribute to declining coral reef health (Kruczynski and McManus 2002). The residential population of the Florida Keys increased from 68,730 in 1984 to 74,044 in 2014, and tourism (overnight stays, not including day trippers) also increased in this period, reaching 3.6 million in 2014. Several studies have demonstrated the couplings between nutrient enrichment from local sewage pollution in the Florida Keys (septic systems result in high N:P ratios of $\sim 100:1$ in groundwaters; Lapointe et al. 1990) and algal blooms and hypoxia (Lapointe and Clark 1992; Lapointe et al. 2004), including the offshore LKSPA (Lapointe and Matzie 1996). Ward-Paige et al. (2005) reported increased growth of the fecal bioindicator and boring sponge *Cliona delitrix*, which has caused bioerosion of reef frameworks over broad areas of the FKNMS. On reefs offshore Key Largo, barrel sponges increased by

33–46% between 2000 and 2006 (McMurray et al. 2010), which could reflect increasing eutrophication and nutrient subsidies in POM. The white pox disease that contributed to widespread mortality of *A. palmata* at LKSPA and other bank reefs of the FKNMS during this study was identified as *Serratia marcescens*, an opportunistic fecal bacterium (Sutherland et al. 2011). This bacterium exhibits significant seasonal variability, increasing during the summer wet season (Patterson et al. 2002; Joyner et al. 2015) in similar periodicity to blooms of benthic macroalgae, phytoplankton, and seagrass epiphytes that also correspond with seasonally higher DIN concentrations at LKSPA during the summer months (Lapointe et al. 2004).

In comparison to local nutrient sources from the Florida Keys, relatively little attention has focused on how Everglades runoff affects the health of downstream waters in the FKNMS. In a review of sources of nutrient pollution in the FKNMS, no mention was made on contributions of river discharges from the Everglades (Kruczynski and McManus 2002), even though rivers are generally known to be a major stressor to coral reef growth (Hubbard 1996). On the Great Barrier Reef, Australia, research and management have long centered on the role of river discharges in nutrient loading, eutrophication, and declining coral reef health that can extend for hundreds of kilometers from river mouths (Bell 1992; Van Woesik et al. 1999; Devlin and Brodie 2005; Brodie et al. 2007; De'ath and Fabricius 2010; Fabricius et al. 2016). Shark River Slough is the primary conduit for freshwater flow (~80%) from the central Everglades basin (Fig. 1) and provides water to five rivers: North River, Shark River, Harney River, Broad River, and Lostman's River. The N:P ratio of water in Shark River Slough is very high (260:1; Rudnick et al. 1999) and reflects selective uptake of P relative to N as water flows south through the Everglades wetlands (Urban et al. 1993; Rudnick et al. 1999). The annual flows from these rivers are highly variable and largely dependent on rainfall and water management, with an estimated range from <5 to >140 m^3/s (Zhao et al. 2013). In the early 1980s, implementation of the "rainfall plan" brought increased water deliveries to the Everglades (Table 1), which together with heavy rainfall in 1982, 1983, 1986, and 1987, resulted in 1500 to 2000 tons/year of TN discharged from the S-12 structures into Shark River Slough (Rudnick et al. 1999). Following the FKNMS Act of 1990 and requests for more freshwater to decrease salinity in Florida Bay (McIvor et al. 1994), increased water deliveries combined with heavy rainfall between 1991 and 1995 resulted in extremely high flows and TN inputs to Shark River Slough, ranging from 1500 to ~3000 tons/year between 1992 and 1996 (Rudnick et al. 1999). Other than rainfall in the Everglades, the water in Shark River Slough can include runoff from both agricultural and urban land uses extending north to Orlando, Florida (Fig. 1). Examples from satellite remote sensing illustrate how freshwater runoff from the Everglades results in black water events and phytoplankton blooms that are transported by coastal currents through the FKNMS, where they are harmful to coral reef health (Fig. 10; Hu et al. 2003, 2004; Zhao et al. 2013).

Critical examination of the temporal decline in coral cover during our study at LKSPA revealed two distinct periods of rapid coral loss that followed increased Everglades runoff. Rapid coral loss first occurred in 1985–1987 (8.2%/year), and again in 1996–1999 (7.5%/year) when annual rates of coral mortality were much higher than the average 1.4%/year for Caribbean reefs in the same period (Gardner et al. 2003). This high rate of coral loss at LKSPA largely reflects the mortality of *A. palmata* on shallow reefs and cannot be attributed to hurricane impacts that might otherwise have explained such high losses (Porter and Meier 1992). The rapid coral loss at LKSPA between 1996 and 2000 followed water management actions to increase freshwater deliveries from the Everglades over concern that high bay-wide salinities in 1989/1990 (41 psu) were the cause of extensive cyanobacterial blooms and seagrass die-off in Florida Bay. These blooms were thought to have been supported by nutrients released from large-scale seagrass die-off that occurred in summer 1987 (McIvor et al. 1994; Table 1). The effects of this discharge were exacerbated by heavy rainfall in 1983 and again in 1994/1995 (Lapointe et al. 2002; Woods 2010).

The Shark River–LKSPA transect data support previous studies which have shown that N loading from increased Shark River Slough discharges enhances phytoplankton blooms in lower salinity downstream waters along the western side of Florida Bay (Lapointe et al. 2002; Brand 2002; Nelson et al. 2017). The C:N ratios in particulate organic matter (POM) along the transect were 12:1–20:1 in the 2010 dry season but decreased to 6:1–18:1 in 2011, when greater rainfall resulted in lower salinity levels. The dry season C:N values were relatively high and characteristic of N-limited phytoplankton growth, as molar C:N ratios for phytoplankton generally range between 6 and 10 (Redfield 1958; Brzezinski 1985; Montagnes et al. 1994; Savoye et al. 2003). The δ^{15}N values of POM in Shark River and downstream sites were relatively low in 2010 (+1 to +4‰) as compared to 2011 (+4 to +5‰). The higher 2011 values suggest greater contributions from more enriched N sources, such as urban wastewater runoff or cattle farms (+3 to +10‰) as compared to atmospheric deposition, N$_2$ fixation, peat oxidation, and agricultural fertilizers that have more depleted values ($<+2$‰; Heaton 1986; Kendall et al. 2007). Seasonal and annual changes in δ^{15}N values in macroalgae at LKSPA from low values of +2‰ to enriched values of +4 to 5‰ were also reported in previous studies in response to annual and seasonal variability in rainfall and Everglades flows (Lapointe et al. 2004).

The 2010–2011 Shark River–LKSPA transect data illustrated the nutrient connectivity (DIN enrichment, increased DIN:SRP ratios, and chlorophyll *a*) in the wet season that extends from the Gulf of Mexico to offshore coral reefs at LKSPA. This finding is consistent with previous observations that phytoplankton blooms in coastal waters of southwest Florida and western Florida Bay are enhanced by reduced salinity and N enrichment associated with Everglades runoff (Brand 2002; Heil et al. 2007; Boyer et al. 1999; Boyer et al. 2009; Zhao et al. 2013; Nelson et al. 2017). The elevated DIN and chlorophyll *a* in Gulf of Mexico waters downstream from the Everglades are advected southwards via coastal currents and into waters of the FKNMS (Smith 1994; Smith and Pitts 2002; Fig. 1), where they can contribute to eutrophication and degradation of coral reef communities (Yentsch et al. 2002; Lapointe et al. 2004; Hu et al. 2004; Zhao et al. 2013). This nutrient connectivity is strongest in the summer–fall wet season when salinity values of 33 psu or lower occur at LKSPA (Lapointe and Matzie 1996; Porter 2002). This connectivity explains why annual chlorophyll *a* concentrations at LKSPA increased from < 0.14 µg/l in the 1980s to 0.60 µg/l in 1996 following peak Everglades discharges from both Shark River Slough and Taylor Slough in 1995 (McIvor et al. 1994; Rudnick et al. 1999). The importance of the Everglades N contributions is evidenced by the significant positive relationship between annual Shark River Slough flows and chlorophyll *a* at LKSPA (Fig. 7), as well as the higher rate of coral decline (7–8%/year) following years of heavy rainfall and/or increased water deliveries in the 1980s and 1990s compared to lower rates of coral loss (~ 1%/year) in drier periods.

Management implications for increasing N on a warming planet

This long-term record of increased DIN, chlorophyll *a,* N:P ratios, and P limitation at LKSPA, combined with various remote sensing products, provides compelling evidence for an important role of land-based N enrichment in driving widespread algal blooms, P depletion of surface waters, and coral reef decline. The altered N:P stoichiometry can cause P starvation in corals and exacerbate the effects of high temperature on coral bleaching, disease, and reef degradation. Climate cooling has been hypothesized to have caused the shutdown of reef growth in the Florida Keys over the past 3000–6000 years (Toth et al. 2018). Now, modern climate change and other anthropogenic disturbances, including N enrichment and altered N:P stoichiometry, appear to be pushing reefs past a critical threshold and into the current novel state dominated by turf algae, macroalgae, sponges, and soft corals.

This analysis indicates that anthropogenic nutrient loading from local sources in the Florida Keys and regionally from the greater Everglades ecosystem is interacting with a changing climate to create conditions unfavorable for living coral at LKSPA. Local sewage and stormwater discharges from residential development have increasingly impacted nearshore waters of the Florida Keys for decades (Lapointe et al. 1990; Lapointe and Clark 1992; Kruczynski and McManus 2002; Ward-Paige et al. 2005), and contributed to the long-term DIN enrichment and increased N:P ratios at Looe Key during this study (Lapointe et al. 2004). Following Florida legislation between 1996 and 1999 that mandated nutrient reduction from cesspits, septic systems, and wastewater treatment plants in Monroe County, a Wastewater Master Plan was developed to achieve advanced wastewater treatment (AWT) standards for all treated wastewater effluent (3 mg/l TN; 1 mg/l TP). Almost 20 years later, centralized wastewater collection systems now serve most (~ 66%) of the current residential population of ~ 76,000 people and an estimated 3.8 million tourists annually and includes deep well injection (~ 1000 m) of treated effluent in Key Largo, the lower Keys, and Key West. This $1.0 billion wastewater infrastructure upgrade will reduce the nutrient and bacterial contributions from local wastewater sources in the Florida Keys in the future.

Unfortunately, the policy of increasing freshwater flows from the Everglades to reduce salinity in Florida Bay has been a priority of the FKNMS since the early 1990s (Continental Shelf Associates 1991; NOAA 1996; Table 1) and continues today as a major goal of the CERP. The policy of sending more water south has been controversial (Stevens 1997) because of long-standing disagreement on this subject within the scientific community since establishment of the FKNMS in 1990 (Porter 2002; NRC 2002). Nevertheless, political decisions were made to increase freshwater flows in the early 1990s, which led to a worsening of algal blooms and turbidity in Florida Bay (Brand 2002; Lapointe et al. 2002; Lapointe et al. 2004; Butler and Dolan 2017; Nelson et al. 2017), rather than improved water quality as desired and originally predicted (NOAA 1996). This policy was based largely on the assumption that drought-induced hypersalinity preceded and initiated the seagrass die-off in 1987 (Kruczynski and McManus 2002). The drought actually occurred in 1989–1990 (Trimble et al. 1990), 2 years following the seagrass mortality event (Hall et al. 2016) (see flow data in Fig. 3e; Table 2). The algal blooms that developed in Florida Bay between 1991 and 1995 were associated with increased water deliveries from both Shark River and Taylor Slough, as well as heavy rainfall, which lowered bay-wide salinity but increased N loading, chlorophyll *a*, and turbidity (Rudnick et al. 1999; Boyer et al. 1999; Brand 2002; Lapointe et al. 2002; Nelson et al. 2017; Table 1).

In their review of the CERP on Florida Bay (NRC 2002), the Committee on Restoration of the Greater Everglades Ecosystem (CROGEE) concluded that "the assumption that

increased flows of water deemed necessary for the Everglades also will contribute to the restoration and enhancement of Florida Bay, for a number of reasons, may not be correct". They noted that "the evidence linking hypersalinity to seagrass die-off is equivocal and there is little agreement within the Florida Bay research community that this was the causative factor of the die-off. Florida Bay phytoplankton blooms appear to develop where nitrogen-enriched water from the eastern bay and land drainage mixes with relatively phosphorus-rich water of the central/western bay. Thus, the increasing freshwater fluxes through Shark River Slough could potentially increase the frequency, intensity, and duration of phytoplankton blooms in regions of the Bay and may be carried through the Keys to the coral reefs". The long-term data presented in this study support the conclusions of the CROGEE, notably how increasing contributions of Everglades discharges between 1991 and 1995 were not restricted to triggering algal blooms only in western Florida Bay, but also more widespread blooms in sensitive downstream waters of the FKNMS (Hu et al. 2003, 2004; Lapointe et al. 2004; Zhao et al. 2013). Ocean-related activities associated with coral reefs add more than $8.5 billion/ year and 70,400 jobs to the local economy in southeast Florida (https://floridakeys.noaa.gov/corals/economy.html), so the future health of the FKNMS is essential for sustaining the tourist-based economy (Going with the flow 2002). Without coupled policies to reduce anthropogenic impacts, the designation of a Marine Protected Area, such as the FKNMS, is not enough to protect coral reefs from the effects of land-based nutrient pollution (Risk 1999) or climate change (Selig et al. 2012).

Finally, this study broadens the discussion of how the combination of local and regional management efforts can more effectively mitigate nutrient pollution (Wolff et al. 2018) and mass bleaching events on coral reefs (Manfrino et al. 2013). These data make clear that this is not an either (temperature) or (nutrients) situation, but rather a "both/and" combination of multiple stressors (Zaneveld et al. 2016; Wang et al. 2018). Aggressive management is especially important as new threats to coral health continue to emerge, such as the recent "Stony Coral Tissue Loss Disease". These findings indicate that implementation of regional N management strategies (Howarth and Paerl 2008; Conley et al. 2009) is critical for CERP if, as identified, the goals include recovery of downstream coral reefs and other economically important marine habitats, such as sponges (Butler and Dolan 2017) and seagrasses in Florida Bay (Duarte 1990). Synergism between N enrichment and high temperatures has also been noted for degradation of the seagrass *Zostera marina* (Burkholder et al. 2007), suggesting the possibility of even more widespread ecosystem effects on seagrass meadows in the FKNMS. This issue is especially important considering that N loading is predicted to increase by 19% globally as a result of changes in precipitation due to climate change (Sinha et al. 2017), a finding that argues for urgency to prevent further degradation (Rabalais et al. 2009). The future success of CERP will rely on recognizing the hydrological and nutrient linkages between the Everglades, Florida Bay, and the Florida Keys (Porter 2002) and that N must be better managed in upland watersheds (Howarth and Paerl 2008; Conley et al. 2009). Regional N reduction strategies in the Everglades basin, combined with ongoing local wastewater improvements in the Florida Keys, should be expected to enhance coral reef resilience and survival in the FKNMS under current levels of thermal stress.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement This article does not contain any studies with human participants or animals performed by any of the authors.

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