

Technical Notes and Comments

Comment on J. C. Zieman, J. W. Fourqurean, and T. A. Frankovich. 1999. Seagrass Die-off in Florida Bay: Long-term Trends in Abundance and Growth of Turtle Grass, *Thalassia testudinum*. *Estuaries* 22:460–470.

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In an issue of *Estuaries* dedicated to Florida Bay [1999 Vol. 22(2b)] Zieman et al. (1999) presented the results of long-term monitoring of seagrass abundance and productivity as well as a hypothetical model of factors leading to the seagrass die-off in Florida Bay. The causes of underlying water quality deterioration and seagrass die-off in Florida Bay have been reviewed by the Florida Bay Scientific Review Panel (Boesch et al. 1993) and more recently, the Committee on the Restoration of the Greater Everglades Ecosystem (CROGEE; National Research Council [NRC] 2002). We concur with these reviews and find no compelling evidence within the scientific literature or from our own research to support the hypothesis of Zieman et al. (1999) that hypersalinity was a significant factor leading to seagrass die-off in Florida Bay. Our comments below support the view that Zieman et al. (1999) have overstated the role of hypersalinity while categorically dismissing the role of nutrient enrichment and eutrophication in generating regional water quality degradation and seagrass die-off in Florida Bay. This issue of “getting the science right” is critical to the success of the multi-billion-dollar Comprehensive Everglades Restoration Plan (CERP) to restore natural resources in Everglades National Park and downstream waters of the Florida Keys National Marine Sanctuary (FKNMS).

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No Eutrophication in Florida Bay?

Zieman et al. (1999, p. 468) stated that “general cultural eutrophication of the water column, so often the cause of seagrass mortality around the world . . . has not been a contributing factor to the recent die-off in Florida Bay” and cited Fourqurean et al. (1993) as supporting evidence. Fourqurean et al. (1993) did not provide any data or observations of any seagrass parameters, such as density, biomass, productivity, epiphyte loads, or associated macroalgal biomass that might otherwise indicate nutrient stress in seagrass communities. Because nutrient data are not available for Florida Bay prior to the massive die-off of *Thalassia testudinum* (turtle grass) in 1987, one must rely on ecological indicators to infer the trophic status of Florida Bay’s seagrass communities. Duarte (1995) and Valiela et al. (1997) reviewed nutrient-mediated succession in seagrass ecosystems and detailed how faster-growing algal competitors, including attached epiphytes, macroalgae, and phytoplankton blooms, result from increased nutrient loads, leading to light limitation and ultimately the demise of seagrasses. The observations in 1983–1984 by Zieman and Fourqurean (1985) and Zieman et al. (1989) that “turbid conditions were common” (p. 41) and seagrass leaves were “highly epiphytized” (p. 41) in the Mainland fringe of Florida Bay were clear ecological indicators of land-based nutrient enrichment. Rudnick et al. (1999) showed increased nitrogen and phosphorus loadings into Florida Bay (see their Figs. 3 and 4) in this time-frame (1982–1985) from both Shark River Slough and Taylor Slough. These increased nutrient loads to the shallow, nitrogen-limited western and central regions of the bay (Larentyev et al. 1998; Tomas et al. 1999; Brand 2002) readily explain increasing turbidity and seagrass epiphytes. These coincidental phenomena in 1983–1984 provided the first evidence that Everglades runoff was impacting water quality and seagrass health in Florida Bay—several years prior to the massive seagrass die-off.

Although Zieman et al. (1999) presented their interpretation of the dynamics of *T. testudinum* communities in Florida Bay over the past several decades, they did not mention the ecological significance of high macroalgal biomass evident in their own data from 1983–1984 (Zieman and Fourqurean 1985; Zieman et al. 1989). A more comprehensive review that includes the role of ma-

croalgae, particularly the role of the rhodophyte *Laurencia* spp. in the eutrophication of Florida Bay seagrass communities, is presented elsewhere (Lapointe et al. 2002). Nutrient-enrichment bioassays have shown nitrogen-limited productivity of *Laurencia* in Florida Bay (Delgado and Lapointe 1995), which would be especially strong in western Florida Bay where relatively low water column N:P ratios of $\sim 20:1$ occur (Fourqurean et al. 1993). The Adaptive Environmental Assessment and Management Workshop for Florida Bay (South Florida Water Management District [SFWMD] 1995, p. 3) included observations by Florida Bay fisherman who stated “the first seagrass die-off occurred in the western Bay in 1985, when macroalgae laid so thick on the bottom that it denuded the bottom.” This report contradicts the opening statement of Zieman et al. (1999, p. 460) that “in late 1987, fishing guides reported the beginning of a large and apparently unprecedented die-off of the seagrass *T. testudinum*.”

Blooms of macroalgae are well-known indicators of eutrophication in *T. testudinum* communities and their occurrence in Florida Bay in the early 1980s was an obvious sign of water column nutrient enrichment. Den Hartog (1977, p. 100) first developed a succession model for *T. testudinum* communities and noted that “pollution leads to quite aberrant developments as the original vegetation becomes degraded and replaced by a vegetation consisting of species which are not normally involved in the succession series, or occur only as rare companion species”. Several other case studies in coastal waters of the western North Atlantic likewise describe similar nutrient mediated macroalgal blooms in *T. testudinum* communities. These case studies include sewage-impacted waters of Cancun Lagoon (Reyes and Merino 1991), the Florida Keys (Lapointe et al. 1994, 2004), and Bermuda (McGlathery 1995), as well as more localized natural enrichment from a seabird rookery at Man-O-War Cay, Belize (Lapointe et al. 1993), and a mangrove tidal creek at Norman’s Pond Cay, Exumas, Bahamas (Lapointe et al. 2003). Experimental studies have shown that growth rates of temperate and tropical macroalgae generally become nitrogen-saturated at relatively low DIN concentrations of $\sim 1.0 \mu\text{M}$ (Lapointe 1999). Table 1 presents nutrient data from a variety of tropical and subtropical settings where *T. testudinum* communities have become replaced by macroalgal blooms as mean DIN concentrations approach $\sim 1.0 \mu\text{M}$ (note the very high annual mean DIN concentrations in Florida Bay following increased freshwater inputs after 1991).

The water column nutrient and chlorophyll *a* (chl *a*) data presented by Fourqurean et al. (1993)

indicate that Florida Bay was highly nutrient enriched when the first bay-wide data were collected in 1989–1990 (Table 1). The mean and maximum bay-wide DIN concentrations were $2.68 \mu\text{M}$ and $14.37 \mu\text{M}$, respectively, well above levels known to sustain macroalgal blooms; the mean and maximum chl *a* concentrations were 1.05 and $4.86 \mu\text{g l}^{-1}$, which are also very high for tropical seagrass meadows and indicate that the nutrient-mediated succession from mixed seagrass and macroalgae to phytoplankton blooms was well underway. These data are inconsistent with the statement of Zieman et al. (1999, p. 461) that “persistent algal blooms have been present in central and western Florida Bay since 1991”. Brand (2002) has described how the chl *a* method used by Fouqurean et al. (1993) underestimated chl *a* concentrations in Florida Bay by two- to five-fold, suggesting that phytoplankton blooms were even more developed than indicated by their data.

The effects of Everglades runoff in accelerating eutrophication of Florida Bay are clear in data from the early 1990s when massive increases in fresh water flows and nitrogen loads to Florida Bay occurred (Rudnick et al. 1999; Lapointe et al. 2002). Between 1991 and 1997, increased discharges from Shark River Slough and Taylor Slough correlated significantly with decreased salinity throughout the bay and significant increases in ammonium (central bay), chl *a* (central bay, western bay), and turbidity (bay-wide, Boyer et al. 1999; Lapointe et al. 2002). Values from the South Florida Water Management District’s (SFWMD) Florida Bay water quality database in Table 1 indicate that the development of phytoplankton blooms in both the western and central bay followed the increased discharges and nitrogen loads and were most severe in central Florida Bay where the highest DIN and chl *a* concentrations occurred. Ammonium concentrations up to $120 \mu\text{M}$ (Boyer et al. 1999), several-fold higher than concentrations known to cause direct toxicity to seagrasses, were reported in this region of the bay where the massive seagrass die-off of 1987 began (Robblee et al. 1991). At concentrations as low as $25 \mu\text{M}$, ammonium is toxic to seagrasses, particularly during warm periods when its effect is cumulative over time (van Katwijk 1997; Hauxwell et al. 2001). In experimental mesocosms, nitrate enrichment to $\sim 3 \mu\text{M}$, when coupled with seasonally maximum temperatures, also caused toxicity and die-off of *Zostera marina* (Burkholder et al. 1992). Increased water column and benthic respiration and resulting hypoxia-anoxia are a widely recognized consequence of nitrogen enrichment and elevated primary productivity in many anthropogenically-altered estuaries, particularly when coupled with peak summertime tempera-

TABLE 1. Nutrient concentrations along spatial gradients in tropical *Thalassia testudinum* communities of the western North Atlantic and in Shark Bay, western Australia. Mean concentrations (\pm SE) of salinity (ppt), ammonium, nitrate + nitrite, dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), or total phosphorus (TP) as denoted by *. Nutrient concentration values expressed as μ M, chlorophyll *a* expressed as μ g/L, n = # of samples, ud = undetectable, — = no data reported. Note high DIN concentrations (mostly ammonium) in Florida Bay versus other sites.

Site	Year	N	Salinity	Ammonium	Nitrite + Nitrate	DIN	SRP/TP	Chl- <i>a</i>	Reference
Florida Bay									
(bay-wide)	1989–1990	187	41.4 \pm 0.4	1.89 \pm 0.15	0.72 \pm 0.07	2.68 \pm 0.21	0.03 \pm 0.01	1.05 \pm 0.07	Fourqurean et al. 1993
(central bay)	1991	76	42.7 \pm 1.3	7.56 \pm 1.81	0.32 \pm 0.06	7.87 \pm 0.87	0.91 \pm 0.15*	1.81 \pm 0.17	SFWMD
(central bay)	1992	51	31.5 \pm 1.3	31.86 \pm 16.16	1.70 \pm 1.42	33.56 \pm 17.58	1.96 \pm 0.80*	2.45 \pm 0.23	SFWMD
(central bay)	1993	49	36.1 \pm 1.1	4.56 \pm 1.65	1.76 \pm 1.45	6.30 \pm 3.09	1.53 \pm 0.65*	3.91 \pm 0.32	SFWMD
(central bay)	1994	52	34.6 \pm 1.2	9.26 \pm 1.95	1.86 \pm 1.34	11.13 \pm 3.31	1.47 \pm 0.61*	4.55 \pm 0.39	SFWMD
(central bay)	1995	45	26.6 \pm 0.56	15.99 \pm 2.36	2.53 \pm 1.77	18.52 \pm 4.13	1.45 \pm 0.71*	2.79 \pm 0.35	SFWMD
(western bay)	1991	59	40.2 \pm 0.5	1.70 \pm 0.18	0.54 \pm 0.10	2.24 \pm 0.28	0.61 \pm 0.05*	1.38 \pm 0.09	SFWMD
(western bay)	1992	76	34.6 \pm 0.7	4.89 \pm 1.90	1.34 \pm 0.95	6.23 \pm 2.85	1.15 \pm 0.47*	1.74 \pm 0.10	SFWMD
(western bay)	1993	73	35.5 \pm 0.6	3.79 \pm 0.98	1.47 \pm 0.98	5.27 \pm 1.96	0.95 \pm 0.45*	2.45 \pm 0.18	SFWMD
(western bay)	1994	78	35.0 \pm 0.4	4.64 \pm 0.96	1.52 \pm 0.93	6.15 \pm 1.88	0.95 \pm 0.41*	2.36 \pm 0.23	SFWMD
(western bay)	1995	59	29.8 \pm 0.3	4.58 \pm 1.29	1.64 \pm 1.21	6.22 \pm 2.49	1.02 \pm 0.48*	1.93 \pm 0.23	SFWMD
Florida Keys									
Big Pine Key	1996	102	36.5	1.48 \pm 0.04	0.52 \pm 0.12	2.10 \pm 0.18	0.06 \pm 0.04	1.86 \pm 2.11	Lapointe et al. 2004
Little Palm Island	1996	102	36.5	0.50 \pm 0.07	0.64 \pm 0.04	1.18 \pm 0.11	0.04 \pm 0.03	0.55 \pm 0.77	Lapointe et al. 2004
Looe Key	1996	99	36.4	0.39 \pm 0.06	0.51 \pm 0.04	0.87 \pm 0.09	0.03 \pm 0.03	0.59 \pm 0.46	Lapointe et al. 2004
Bermuda									
Bailey's Bay-inner	1990	18	—	0.23 \pm 0.04	1.35 \pm 0.08	1.59 \pm 0.12	—	—	McGlathery 1995
Bailey's Bay-outer	1990	18	—	0.17 \pm 0.04	0.88 \pm 0.06	1.02 \pm 0.12	—	—	McGlathery 1995
Bahamas									
Norman's Pond Cay	1997–1999	8	37.2	0.69 \pm 0.33	0.43 \pm 0.15	1.12 \pm 0.46	0.04 \pm 0.04	—	Lapointe et al. 2003
(NPC)-waterfall									
NPC-algal halo	1997–1999	8	36	0.54 \pm 0.05	0.15 \pm 0.22	0.71 \pm 0.66	0.03 \pm 0.03	—	Lapointe et al. 2003
Belize									
Man-O-War Cay	1988–1990	16	36	1.21 \pm 0.26	3.63 \pm 1.31	4.84 \pm 0.49	1.56 \pm 0.48	—	Lapointe et al. 1993
Twin Cays	1988–1990	16	36	0.41 \pm 0.10	0.36 \pm 0.02	0.77 \pm 0.12	0.14 \pm 0.03	—	Lapointe et al. 1993
Curlew Reef	1988–1990	16	36	0.09 \pm 0.04	ud	0.09 \pm 0.12	ud	—	Lapointe et al. 1993
Australia									
Shark Bay	1981–1983	—	55.0	—	—	0.35	0.03	—	Atkinson 1987

tures (D'Avanzo and Kremer 1994; Valiela et al. 1997). Extended periods of anoxia (in both diurnal and seasonal time scales) in Florida Bay seagrass communities may have caused accumulation of toxic concentrations of hydrogen sulfide as a result of increased anaerobic respiration in the benthos (Goodman et al. 1995), and alteration of redox conditions necessary for uptake of ammonium in interstitial waters by root systems (Pregnall et al. 1984). These conditions may have been directly involved with widespread seagrass decline starting in the summer of 1987 (Carlson et al. 1994), following several years of accelerated external loading of nitrogen and build-up of organic matter. Lapointe and Matzie (1996) also observed die-off of *T. testudinum* in canal systems of the lower Florida Keys coincident with anoxia during summer of 1992 following years of organic build-up from sewage pollution.

The importance of nitrogen enrichment from the Everglades watersheds to algal blooms in Florida Bay were reported over a decade ago (Lapointe and Clark 1992). The Florida Bay Science Program Management Committee (Boesch et al. 1993, p. 12) concluded that algal blooms in the western bay "predated the seagrass die-off" and "could result from increased nutrient loading in the Shark River Slough discharge" and that "the western bay blooms may be characteristic of a troublesome and growing trend of coastal eutrophication". A recent National Oceanic and Atmospheric Administration National Estuarine Eutrophication Assessment ranked Florida Bay as having a high level of expression of eutrophic conditions, an index based on chl *a*, macroalgal abundance problems, epiphyte abundance problems, low dissolved oxygen, nuisance and toxic algal blooms, and loss of submerged aquatic vegetation (Bricker et al. 1999). Considering the massive human alteration of water quality and nutrient loading from agricultural and urban sources on South Florida's watersheds, the conclusion of Zieman et al. (1999) that cultural eutrophication has not been a factor in the seagrass die-off in Florida Bay would seem untenable.

Thalassia testudinum: A "Stenohaline" Marine Plant?

Zieman et al. (1999, p. 461) stated in their introduction that "*T. testudinum* . . . thrives in a fairly narrow salinity range" and later in the discussion that "*T. testudinum* is a stenohaline marine plant", citing the work of McMillan and Moseley (1967) as supporting evidence. Their statements are not supported by the work of McMillan and Moseley (1967) who grew four species of seagrasses in Texas over 55 d at salinities up to 74 ppt and reported growth of *T. testudinum* up to 60 ppt; this apparent

upper salinity tolerance exceeds the mean salinity reported for Rankin Lake (40 ppt) and Rabbit Key Basin (36–38 ppt) in 1987 where *T. testudinum* began its die-off in Florida Bay (Zieman et al. 1999). This experimental work conducted over thirty years ago does not support the statement by Zieman et al. (1999) that "a series of stresses . . . including salinity stress . . . caused the die-off of . . . *T. testudinum* beds". Zieman et al. (1999, p. 468) relied heavily on the early observations and anecdotes of Tabb et al. (1962) for the potential role of hypersalinity on seagrass mortality in Florida Bay, but Tabb et al. (1962, p. 38) concluded that *T. testudinum* thrives under hypersaline conditions in Florida Bay by stating "with marked reduction in salinity beginning in the winter of 1957 and ending in 1960, the *Thalassia* underwent decline in size and abundance . . . they did not return in abundance until the drought of 1961–1962, reaching peak growth and coverage in the spring of 1962. Thus it appears that long periods of near or slightly above normal salinities are a requirement for maximum growth of *Thalassia*". Regarding the potential impact of hypersalinity on fish populations in Florida Bay, Tabb and Roessler (1989, p. 31) more recently concluded "hypersalinity . . . an assumption that exists today, but which has yet to be proven by convincing quantitative study, either in field or laboratory".

Contrary to the interpretation of Zieman et al. (1999), there is substantial scientific evidence that *T. testudinum* grows well over a broad range of salinities. As a result of various morphological (Jagels 1973, 1983) and physiological (Puhlich 1986) characteristics, *T. testudinum* grows in portions of Laguna Madre where salinities range between 45–50 ppt (Conover 1964) and in areas of the Bahamas where salinities range up to 46.5 ppt (Jagels 1983). DeFelice and Lynts (1978) reported finding *T. testudinum* in portions of Florida Bay that were regularly hypersaline. A sibling species, *T. hemprichii*, is normally found in the hypersaline areas of the northern Red Sea (Price et al. 1988). In both Antigua (Tomasko et al. 1999) and Bermuda (Smith 1995), density, biomass, and productivity of *T. testudinum* was apparently unaffected by discharges of hypersaline brine from reverse osmosis desalination facilities. In Charlotte Harbor, Florida, Tomasko and Hall (1999) found that *T. testudinum* was able to persist in locations where salinity varied from <5 to >30 ppt, although biomass and productivity declined when salinities were below 20 ppt for extended periods of time. The contention of Zieman et al. (1999) that *T. testudinum* is a stenohaline marine plant is not supported by the scientific literature.

The water quality and seagrass data from Florida

Bay over the past two decades indicates that the recent trend towards decreasing salinity between 1991 and 1997 have been much more damaging to the bay than any prior effects of hypersalinity. Water managers increased fresh water flows beginning in 1991 via both Shark River Slough and Taylor Slough to reduce salinity bay-wide (McIvor et al. 1994). Between 1990 and 1995, salinity decreased dramatically throughout Florida Bay (from ~41 ppt to 23 ppt bay-wide, SFWMD) with corresponding increases in nitrate, ammonium, chl *a*, and turbidity, especially in central and western Florida Bay (Boyer et al. 1999; Lapointe et al. 2002, Table 1). In the Interior, Mainland, and Gulf portions of Florida Bay, Hall et al. (1999) showed significant declines in shoot density between 1984 and 1994 for *T. testudinum*. For *Halodule wrightii* and *Syringodium filiforme*, biomass was lower in 1994 than in 1984. Hall et al. (1999, p. 458) stated that “. . . recent observations (Durako and Hall unpublished data) indicate continued dramatic losses of *T. testudinum* in western Florida Bay”, an area of the bay that is not affected by hypersalinity. As the data of Zieman et al. (1999) also show, standing crop, short shoot density, and areal productivity all decreased dramatically in both their die-off and control sites between 1989–1990 and 1995 (their Figs. 3 and 4) as the bay-wide salinity decreased. A loss of seagrass cover also followed the reduction of salinity in Laguna Madre, Texas, a result of associated increases in turbidity from maintenance dredging and eutrophication (Quammen and Onuf 1993).

In describing how hypersalinity contributed to the massive seagrass die-off in 1987, Zieman et al. (1999) stated that “these dense beds became overcrowded and unstable”. The hypothesis that lush meadows are unstable is also unsupported by the scientific literature. Zieman et al. (1999) claimed that *T. testudinum* meadows with biomass higher than 50 to 100 g dry wt m⁻² (see their Fig. 7) are overcrowded, even though *T. testudinum* meadows often have biomass values in excess of these values in the Florida Keys and Belize (Tomasko and Lapointe 1991), Charlotte Harbor (Tomasko and Hall 1999), Sarasota Bay (Tomasko et al. 1996), and Tampa Bay (Dixon and Leverone 1995).

Despite the substantial evidence linking declines in biomass, density, and productivity of *T. testudinum*, *H. wrightii*, and *S. filiforme* with decreasing salinity and associated increases in DIN (mostly ammonium), chl *a*, and turbidity since 1991, Zieman et al. (1999, p. 467) concluded that “an increase in the mass-specific productivity of *T. testudinum* in Florida Bay . . . suggests the stresses on seagrasses have lessened over the monitoring period . . . despite a decrease in water clarity” and that “the less-

ening of stress is a direct consequence of the loss of seagrass biomass from Florida Bay”. We cannot understand this logic, which equates seagrass die-off with seagrass recovery. The term biomass specific productivity is a result of leaf turnover rate multiplied by a factor of 10. In Tampa Bay (Dixon and Leverone 1995), Sarasota Bay (Tomasko et al. 1996), and Charlotte Harbor (Tomasko and Hall 1999), leaf turnover rates have shown variation due to season, but not location; in these studies, shoot densities, areal blade biomass, and areal blade productivity values varied significantly between locations with different nutrient loads, water clarity, and salinity regimes. If biomass specific productivity is a good indicator of seagrass health, why hasn't the increase in turnover rates seen after 1992 (Fig. 4b) led to increased density, standing crop, and areal productivity for the years 1993–1995 (Figs. 3a, 3b, and 4c, respectively)? This disconnect between their data and interpretation is difficult to reconcile in context with their conclusion (Zieman et al. 1999, p. 469) that “our observations and . . . conceptual model predict the losses of seagrasses from Florida Bay may be slowing and that the ecosystem may be reaching a new equilibrium”.

Restoring seagrass communities in Florida Bay by reducing salinity is a primary management goal of the Comprehensive Everglades Restoration Plan (CERP) and is supported by the FKNMS whose mission is to provide long-term protection to the coral reef resources of the Florida Keys. As stated in the Water Quality Protection Program for the FKNMS developed by U.S. EPA (1996, p. 11): “most scientists believe that recent ecological problems in Florida Bay are the result of long-term reduction in freshwater flow from the Everglades to the Bay. The mechanism has not been documented, but high salinities and a long-term change from an estuarine to a marine system are believed to be contributing factors”. Scientific evidence to support these assumptions does not exist. The recent National Academy of Sciences CROGEE report (NRC 2002, p. 2 of Executive Summary) states:

“An important assumption often made by scientists and managers associated with the CERP, and by the public, is that the increased flows of water deemed necessary to restore habitats in the Everglades also will contribute to the restoration and enhancement of Florida Bay . . . For a number of reasons, these assumptions may not be correct. First, the evidence linking turtle grass die-off to hypersalinity is equivocal and there is little agreement within the Florida Bay research community that this was the causative factor of the die-off. In addition to the uncertainties concerning the amount of fresh surface and groundwater that may enter Florida Bay

because of the CERP, it is possible that an increase in water would also bring an increase in nutrient inputs.”

We believe that a body of scientific evidence supports the view that increased water deliveries to Florida Bay between 1991 and 1997 has already resulted in significant nutrient enrichment that caused severe and irreparable damage not only to the bay, but also to downstream waters of the FKNMS. The ecological effects of these nutrient inputs followed, with few exceptions, the predictable responses of a shallow, subtropical seagrass and coral reef ecosystem to escalating nutrient loads. The damage included a sponge die-off (Butler et al. 1995), loss of macroalgal biodiversity (Dawes et al. 1999), increased algal blooms and turbidity (Brand 2002; Lapointe et al. 2002), and a 38% loss of coral cover throughout the FKNMS between 1996 and 1999 (Harvell et al. 1999; Porter et al. 2002). CERP water management policies (as promulgated by the U.S. Army Corp of Engineers and SFWMD) for restoration of Florida Bay (see Redfield 2000) are based on the spurious hypotheses (see review of Gunderson and Walters 2002) in Zieman et al. (1999) and supporting literature from the issue of *Estuaries* [1999 Vol. 22(2)] dedicated to Florida Bay. Nutrient pollution associated with discharges of Everglades runoff into Florida Bay and the FKNMS is a case study of excessive nitrogen enrichment (Vitousek et al. 1997) that is widely affecting U.S. coastal waters (Bricker et al. 1999; Howarth et al. 2000; NRC 2000). This alternative interpretation of the factors causing seagrass die-off in Florida Bay will be critical to the success of efforts to restore the linked ecosystems of the Everglades, Florida Bay, and the Florida Reef Tract.

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LITERATURE CITED

- ATKINSON, M. J. 1987. Low phosphorus sediments in a hypersaline marine bay. *Estuarine, Coastal and Shelf Science* 24:335–347.
- BOESCH, D. F., N. E. ARMSTRONG, C. F. D'ELIA, N. G. MAYNARD, H. W. PAERL, AND S. L. WILLIAMS. 1993. Deterioration of the Florida Bay ecosystem: An evaluation of the scientific evidence. FWS/PMC. Florida Bay Research Program, Miami, Florida.
- BOYER, J. N., J. W. FOURQUREAN, AND R. D. JONES. 1999. Seasonal and long-term trends in the water quality of Florida Bay (1989–1997). *Estuaries* 22:412–430.
- BRAND, L. 2002. The transport of terrestrial nutrients to south Florida coastal waters, p. 361–413. In J. W. Porter and K. G. Porter (eds.), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, Florida.
- BRICKER, S. B., C. C. CLEMENT, D. E. PIRHALLA, S. P. ORLANDO, AND D. R. G. FARROW. 1999. National Estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries. National Oceans Studies Special Projects Office, National Oceanic and Atmospheric Administration, Silver Springs, Maryland.
- BURKHOLDER, J. M., K. M. MASON, AND H. B. GLASGOW, JR. 1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina*: Evidence from seasonal mesocosm experiments. *Marine Ecology Progress Series* 81:163–178.
- BUTLER, M. J., J. K. HUNT, W. F. HERRINKIND, M. J. CHILDRRESS, R. BERTELSEN, W. SHARP, T. MATTHEWS, J. M. FIELD, AND H. G. MARSHALL. 1995. Cascading disturbances in Florida Bay, USA: Cyanobacterial blooms, sponge mortality, and implications for juvenile spiny lobsters *Panularis argus*. *Marine Ecology Progress Series* 129:119–125.
- CARLSON, P. R., L. A. YARBRO, AND T. R. BARBER. 1994. Relationship of sediment sulfide to mortality of *Thalassia testudinum* in Florida Bay. *Bulletin of Marine Science* 54:733–746.
- CONOVER, J. T. 1964. The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. *Botanica Marina* 7:4–41.
- D'AVANZO, C. AND J. N. KREMER. 1994. Diel oxygen dynamics and anoxic events in an eutrophic estuary of Waquoit Bay, Massachusetts. *Estuaries* 17:131–139.
- DAWES, C. J., C. URANOWSKI, J. ANDORFER, AND B. TEASDALE. 1999. Changes in the macroalga taxa and zonation at the Content Keys, Florida. *Bulletin of Marine Science* 64:95–102.
- DEFELICE, D. R. AND G. W. LYNTS. 1978. Benthic marine diatom associations: Upper Florida Bay (Florida) and associated sounds. *Journal of Phycology* 14:25–33.
- DELGADO, O. AND B. E. LAPOINTE. 1995. Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. *Coral Reefs* 13:151–159.
- DEN HARTOG, C. 1977. Structure, function, and classification in seagrass communities, p. 89–119. In C. P. McRoy and C. Helfferich (eds.), *Seagrass Ecosystems: A Scientific Perspective*. Marcel Dekker, Inc., New York.
- DIXON, L. K. AND J. R. LEVERONE. 1995. Light requirements of *Thalassia testudinum* in Tampa Bay, FL. Final report. Southwest Florida Water Management District, Tampa, Florida.
- DUARTE, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41:87–112.
- FOURQUREAN, J. W., R. D. JONES, AND J. C. ZIEMAN. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. *Estuarine, Coastal and Shelf Science* 36:295–314.
- GOODMAN, J. L., K. A. MOORE, AND W. C. DENNISON. 1995. Photosynthetic responses of eelgrass (*Zostera marina*) to light and sediment sulfide in a shallow barrier island lagoon. *Aquatic Botany* 50:37–47.
- GUNDERSON, L. H. AND C. J. WALTERS. 2002. Resilience in wet landscapes of southern Florida, p. 165–182. In L. H. Gunderson and L. Pritchard (eds.), *Resilience and the behavior of large-scale systems*. Island Press, Washington, D.C.
- HALL, M. O., M. J. DURAKO, J. W. FOURQUREAN, AND J. C. ZIEMAN. 1999. Decadal-scale changes in seagrass distribution and abundance in Florida Bay. *Estuaries* 22:445–459.
- HARVELL, C. D., K. KIM, J. M. BURKHOLDER, R. R. COLWELL, P. R. EPSTEIN, D. J. GRIMES, E. E. HOFMANN, E. K. LIPP, A. D. M.

- E. OSTERHAUS, R. M. OVERSTREET, J. M. PORTER, G. W. SMITH, AND G. R. VASTA. 1999. Emerging marine diseases—Climate links and anthropogenic factors. *Science* 285:1505–1510.
- HAUXWELL, J., J. CEBRIAN, C. FURLONG, AND I. VALIELA. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82:1007–1022.
- HOWARTH, R., D. ANDERSON, J. CLOERN, C. ELFRING, C. HOPKINSON, B. LAPOINTE, T. MALONE, N. MARCUS, K. MCGLATHERY, A. SHARPLEY, AND D. WALKER. 2000. Nutrient pollution of coastal rivers, bays, and seas. Issues in Ecology, Number 7. Ecological Society of America, Washington, D.C.
- JAGELS, R. 1973. Studies of a marine grass *Thalassia testudinum* I. Ultrastructure of the osmoregulatory leaf cells. *American Journal of Botany* 60:1003–1009.
- JAGELS, R. 1983. Further evidence for osmoregulation in epidermal leaf cells of seagrasses. *American Journal of Botany* 70:327–333.
- LAPOINTE, B. E. 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. Reply to the comment of Hughes et al. *Limnology and Oceanography* 44:1586–1592.
- LAPOINTE, B. E., P. J. BARILE, C. S. YENTSCH, M. M. LITTLER, D. S. LITTLER, AND B. KAKUK. 2003. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exuma Cays, Bahamas: A "natural" experiment. *Journal of Experimental Marine Biology and Ecology* in press.
- LAPOINTE, B. E. AND M. W. CLARK. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. *Estuaries* 15:465–476.
- LAPOINTE, B. E., M. M. LITTLER, AND D. S. LITTLER. 1993. Modification of benthic community structure by cultural eutrophication: The Belize Barrier Reef. *Proceedings from the 7th International Coral Reef Symposium* 1:323–333.
- LAPOINTE, B. E. AND W. R. MATZIE. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. *Estuaries* 19:422–435.
- LAPOINTE, B. E., W. R. MATZIE, AND P. J. BARILE. 2002. Biotic phase-shifts in Florida Bay and fore reef communities of the Florida Keys: Linkages with historical freshwater flows and nitrogen from Everglades runoff, p. 629–648. In J. W. Porter and K. G. Porter (eds.), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, Florida.
- LAPOINTE, B. E., W. R. MATZIE, AND P. J. BARILE. 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: Discrimination of local versus regional nitrogen sources. *Journal of Experimental Marine Biology and Ecology* in press.
- LAPOINTE, B. E., D. A. TOMASKO, AND W. R. MATZIE. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* 54:696–717.
- LARENTYEV, P. J., H. A. BOOTSMA, T. H. JOHNGEN, J. F. CAVALETTI, AND W. S. GARDNER. 1998. Microbial plankton resource limitation: Insights from community structure and seston stoichiometry in Florida Bay, USA. *Marine Ecology Progress Series* 165:43–57.
- MCGLATHERY, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* 122:239–252.
- MCIVOR, C. C., J. A. LEY, AND R. D. BJORK. 1994. Changes in freshwater inflow from the Everglades to Florida Bay, including the effects on biota and biotic responses, p. 117–146. In S. Davis and J. C. Ogden (eds.), *The Everglades: The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, Florida.
- MCMILLAN, C. AND F. N. MOSELEY. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. *Ecology* 48:503–506.
- NATIONAL RESEARCH COUNCIL (NRC). 2000. Clean coastal waters: Understanding and reducing the effects of nutrient pollution. Ocean Studies Board, Water Science and Technology Board, Washington, D.C.
- NATIONAL RESEARCH COUNCIL (NRC). 2002. Florida Bay research programs and their relation to the Comprehensive Everglades Restoration Plan. Committee on Restoration of the Greater Everglades Ecosystem, Water Science and Technology Board, Board on Environmental Studies and Toxicology, Washington, D.C.
- PORTER, J. W., V. KOSMYNIN, K. L. PATTERSON, K. G. PORTER, W. C. JAPP, J. L. WHEATON, K. HACKETT, M. LYBOLT, C. P. TSOKOS, G. YANEV, D. M. MARCINEK, J. DOTTE, D. EAKEN, M. PATTERSON, O. W. MEIER, M. BRILL, AND P. DUSTAN. 2002. Detection of coral reef change by the Florida keys coral reef monitoring project, p. 749–769. In J. W. Porter and K. G. Porter (eds.), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, Florida.
- PREGNALL, A. M., R. D. SMITH, T. A. KURSAR, AND R. S. ALBERTE. 1984. Metabolic adaptation of *Zostera marina* (eelgrass) to diurnal periods of root anoxia. *Marine Biology* 83:141–147.
- PRICE, A. G. R., C. J. CROSSLAND, A. R. DAWSON-SHEPARD, R. J. McDOWALL, P. A. H. MEDLEY, M. STAFFORD-SMITH, R. F. G. ORMOND, AND T. J. WRATHALL. 1988. Aspects of seagrass ecology along the eastern coast of the Red Sea. *Botanica Marina* 31:83–92.
- PUBLICH, W. M. 1986. Variations in leaf soluble amino acids and ammonium content in subtropical seagrasses related to salinity stress. *Plant Physiology* 80:283–286.
- QUAMMEN, M. L. AND C. ONUF. 1993. Laguna Madre: Seagrass changes continue decades after salinity reduction. *Estuaries* 16:302–310.
- REDFIELD, G. W. 2000. Ecological research for aquatic science and environmental restoration in south Florida. *Ecological Applications* 10:990–1005.
- REYES, E. AND M. MERINO. 1991. Diel dissolved oxygen dynamics and eutrophication in a shallow well-mixed tropical lagoon (Cancun, Mexico). *Estuaries* 14:372–381.
- ROBBLEE, M. B., T. R. BARBER, P. R. CARLSON, M. J. DURAKO, J. W. FOURQUREAN, L. K. MUEHLSTEIN, D. PORTER, L. A. YARBRO, R. T. ZIEMAN, AND J. C. ZIEMAN. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay. *Marine Ecology Progress Series* 71:297–299.
- RUDNICK, D. T., Z. CHEN, D. L. CHILDERS, J. N. BOYER, AND T. D. FONTAINE. 1999. Phosphorus and nitrogen inputs to Florida Bay: The importance of the Everglades watershed. *Estuaries* 22:398–416.
- SMITH, S. R. 1995. Final report on the marine environmental impact of the Wellington Water Works reverse osmosis plant. Bermuda Biological Station for Research, Inc., Ferry Reach, Bermuda.
- SOUTH FLORIDA WATER MANAGEMENT DISTRICT (SFWMD). 1995. Florida Bay adaptive environmental assessment and management workshop, July 11–13. Duck Key, Florida.
- TABB, D. C., D. L. DUBROW, AND R. B. MANNING. 1962. The ecology of northern Florida Bay and adjacent estuaries. State of Florida Board of Conservation, Technical series No. 39. The Marine Laboratory, University of Miami, Miami, Florida.
- TABB, D. C. AND M. A. ROESSLER. 1989. History of studies on juvenile fishes of coastal waters of Everglades National Park. *Bulletin of Marine Science* 44:23–34.
- TOMAS, C. R., B. BENDIS, AND K. JOHNS. 1999. Role of nutrients in regulating plankton blooms in Florida Bay, p. 323–327. In H. Kumpf, K. Steidinger, and K. Sherman (eds.), *The Gulf of Mexico Large Marine Ecosystem: Assessment, Sustainability, and Management*. Blackwell Sciences, Malden, Massachusetts.

- TOMASKO, D. A., N. J. BLAKE, C. W. DYE, AND M. A. HAMMOND. 1999. Effects of the disposal of reverse osmosis seawater desalination discharges on a seagrass meadow (*Thalassia testudinum*) offshore of Antigua, West Indies, p. 99–112. In S. Bortone (ed.), *Seagrasses: Monitoring, Ecology, Physiology, and Management*. CRC Press, Boca Raton, Florida.
- TOMASKO, D. A., C. J. DAWES, AND M. O. HALL. 1996. The effects of anthropogenic nutrient enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19:448–456.
- TOMASKO, D. A. AND M. O. HALL. 1999. Productivity and biomass of the seagrass *Thalassia testudinum* along a gradient of freshwater influence in Charlotte Harbor, Florida (USA). *Estuaries* 22:592–602.
- TOMASKO, D. A. AND B. E. LAPOINTE. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. *Marine Ecology Progress Series* 75:9–17.
- U.S. ENVIRONMENTAL PROTECTION AGENCY (EPA). 1996. Water Quality Protection Program for the Florida Keys National Marine Sanctuary, First Biennial Report to Congress. EPA, Washington, D.C.
- VALIELA, I., J. MCCLELLAND, J. HAUXWELL, P. J. BEHR, D. HERSH, AND K. FOREMAN. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 42:1105–1118.
- VAN KATWIJK, M. M., L. H. T. VERGEER, G. H. W. SCHMITZ, AND J. G. M. ROELOFS. 1997. Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 157:159–173.
- VITOUSEK, P. M., J. D. ABER, R. W. HOWARTH, G. E. LIKENS, P. A. MATSON, D. W. SCHINDLER, W. H. SCHLESINGER, AND D. G. TILMAN. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737–752.
- ZIEMAN, J. C. AND J. W. FOURQUREAN. 1985. The distribution and abundance of benthic vegetation in Florida Bay, Everglades National Park. Final report contract # CX5280-2-2204. South Florida Research Center, National Park Service, Homestead, Florida.
- ZIEMAN, J. C., J. W. FOURQUREAN, AND T. A. FRANKOVICH. 1999. Seagrass die-off in Florida Bay: Long-term trends in abundance and growth of turtle grass *Thalassia testudinum*. *Estuaries* 22:460–470.
- ZIEMAN, J. C., J. W. FOURQUREAN, AND L. IVERSON. 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292–311.

SOURCES OF UNPUBLISHED MATERIAL

- DURAKO, M. J., Unpublished Data. University of North Carolina at Wilmington, Center for Marine Research, 7205 Wrightsville Avenue, Wilmington, North Carolina 28403
- HALL, M., Unpublished Data. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, 100 Eighth Avenue, Southeast, St. Petersburg, Florida 33701

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