

## 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 ~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 ~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 ~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 Fourqurean 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 ~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  $\mu$ M, chlorophyll *a* expressed as  $\mu$ 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 (Pregall 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<sup>-2</sup> (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. CHILDRESS, 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 *Panulirus 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. LINTS. 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. CAVALETO, 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. DOTTEN, 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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**Reply to B. E. Lapointe and P. J. Barile (2004). Comment on J. C. Zieman, J. W. Fourqurean, and T. A. Frankovich. Seagrass Die-off in Florida Bay: Long-term Trends in Abundance and Growth of Turtle Grass, *Thalassia testudinum*. 1999. *Estuaries* 22: 460–470.**

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The Lapointe and Barile (2004) note claims to be a comment on our recent paper in *Estuaries* (Zieman et al. 1999), but it is really both a comment and a statement of a hypothesis. As a comment on our paper, it demonstrates a skewed reading and direct contradiction of the stated conclusions of our paper. As a statement of a new hypothesis, it relies on a very selective re-analysis of previously published work while ignoring completely the published results of the original authors. "Getting the science correct" is indeed important, owing to the large commitment of Federal and state funds to address problems of the entire south Florida ecosystem that have been caused by a century of human activities. Lapointe and Barile unfortunately have contributed no new information on the state of Florida Bay and in their comment rely on facile reinterpretation of fragments of a very robust data set that many scientists have collected over the past two decades. In this reply, we will address issues raised in roughly the same order that they appear in their comment.

Beginning in 1987, dense meadows of *Thalassia testudinum* in Florida Bay began a rapid and as yet poorly understood die-off (Robblee et al. 1991). The first contention of Lapointe and Barile is that Zieman et al. (1999, p. 467) "overstated the role

of hypersalinity" in the Florida Bay seagrass die-off. We find this curious, since in our conclusions in that paper (p. 468) we state "(w)e have presented evidence that salinity does have a negative impact on seagrass productivity, but that salinity alone is not a sufficient explanation of the die-off." Our data show a clear and significant negative relationship between growth rate of *T. testudinum* and salinity of the overlying water column (Zieman et al. 1999, Fig. 6). Our recognition that the original seagrass die-off episodes could not be fully explained by this relationship led to our outlining a conceptual model of causes and consequences of the die-off of seagrasses in Florida Bay.

It is in this conceptual model that we dismiss the importance of cultural eutrophication of the water column as the cause of the seagrass die-off in 1987. We made the statement (p. 440) 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". At this point after several years of additional study we stand behind that statement and we believe that the published literature continues to support that conclusion. We also continue to believe that hypersaline conditions are stressful for *T. testudinum*, and that sulfide toxicity and excessively high biomass with resultant high oxygen demands were also factors in the initial seagrass die-off.

Lapointe and Barile also have selectively and incompletely taken isolated fragments of the water column data generated by others and published in the refereed literature (Fourqurean et al. 1993; Boyer et al. 1997, 1999; Boyer and Jones 2002) to support their contention of anthropogenic N increase in Florida Bay while ignoring the basic finding of these papers: the benthos and water column of Florida Bay are generally P-limited, which means that excess N accumulates in the water column. Epiphyte loads on seagrasses from Florida Bay are low across most of the bay, and again are strongly linked to P availability in the water column (Frankovich and Fourqurean 1997). A claim repeated (but not supported with any data) throughout the Lapointe and Barile note is that Florida Bay showed eutrophic algal growth prior to the seagrass die-off in 1987 and that this eutrophication, driven by cultural eutrophication entering through the Everglades, was the cause of the die-off. They support this claim with statements such as "the observations in 1983–1984 by Zieman and Fourqurean (1985) and by Zieman et al. (1989) that 'turbid conditions were common' and seagrass leaves were 'highly epiphytized' in the Mainland fringe of Florida Bay were clear ecological indicators of incipient nutrient enrichment." (p. 299–301) The

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Mainland fringe is a narrow habitat band adjacent to the mainland and mangrove fringe; this mangrove fringe is a site of increased primary and secondary production in the south Florida wetland-mangrove-seagrass environment. The mangrove zone lies at the ecotone between the oligotrophic Everglades freshwater marshes and oligotrophic Florida Bay; water column nutrients are much higher in this ecotone than in the Everglades (Rudnick et al. 1999) or Florida Bay (Fourqurean et al. 1993; Boyer et al. 1997, 1999).

The oligotrophic Everglades marshes effectively remove most, if not all, of the phosphorus and much of the nitrogen that enters from human activities in the watershed; but loadings to Florida Bay and the Gulf of Mexico are proportional to rainfall (Rudnick et al. 1999). In wet years, there is increased P and N loading to the nearshore coastal system, but this loading is minor compared to other inputs. By far the greatest source of N and P for Florida Bay is water brought in via tidal exchange with the Gulf of Mexico (Fourqurean et al. 1992a, 1993; Rudnick et al. 1999). The claim made by Lapointe and Barile that the Rudnick et al. (1999) paper showed increased nutrient loadings into Florida Bay is a misinterpretation of Figs. 3 and 4 in Rudnick et al. (1999), which show loading (natural plus anthropogenic) into the headwaters of the oligotrophic Everglades, not loading into Florida Bay. There is no evidence of "increased nutrient loads to the shallow, nitrogen limited western and central regions of the bay" during 1982–1985, as claimed by Lapointe and Barile, and this statement illustrates a repeated lack of understanding of the geography and hydrology of the southern Everglades and Florida Bay on their part. We also take issue with Lapointe and Barile's selective interpretation of the literature when it comes to the relative importance of nitrogen and phosphorus in Florida Bay.

Lapointe and Barile claim that we ignore our own data on algal biomass from Florida Bay, especially data on macroalgal biomass in the bay during 1983–1984 (Zieman et al. 1989). We do not find any evidence of especially high biomass of algae in Florida Bay in 1983–1984; instead, we find that Lapointe and Barile grossly misinterpret our data. They quote our data on a "localized biomass" of *Laurencia* sp. of  $664 \text{ gm}^{-2}$ . We did report that number, but it was a localized sampling; *Laurencia* was found at only 37% of 108 survey sites, at a mean biomass of  $24.1 \text{ gm}^{-2}$  where it was present, compared to a mean of  $67 \text{ gm}^{-2}$  of green leaves of *Thalassia testudinum* (Zieman et al. 1989). Considering that *T. testudinum* has only about 10% of its biomass in green leaves (Fourqurean and Zieman 1991), this means that average *T. testudinum* bio-

mass was over  $25\times$  greater than that of *Laurencia* at sites where *Laurencia* was recorded. The biomass comparison grows when the fact that *Laurencia* was found at only 37% of our survey sites is taken into account. *Laurencia* biomass had a bay-wide average of only  $8.9 \text{ gm}^{-2}$  in 1983–1984; this is clearly and unambiguously stated in Zieman and Fourqurean (1985) and in Zieman et al. (1989). High *Laurencia* biomass occurred at a station in the southern part of Twin Key Basin, which is 15 km from the mainland Everglades coastline and in the Atlantic community, which is flushed primarily from the Atlantic and Gulf Stream, and was not due to any "predictable response to the elevated Everglades discharges" but was due to its behavior as a drift algae that is moved by the winds and currents and is blown up against lee banks or drifts in depression (Zieman et al. 1989).

The die-off of seagrasses within Florida Bay, as defined by the western boundary of Everglades National Park, was indeed first reported by fishing guides in 1987. It was at that time that we first revisited these areas for the purpose of investigating the die-off. There is anecdotal evidence of a benthic macroalgal bloom well to the north and west of Florida Bay; we suspect that this is the event referred to by Lapointe and Barile as occurring in 1985. A retrospective analysis of AVHRR images of the entire area over the period 1985–1997 did not detect seagrass loss until 1988 (Stumpf et al. 1999). One of the most striking features about the die-off of seagrasses that we (and many others) visited in 1987 and 1988 was that the plants were dying in place under a very clear water column with very low epiphyte loads. Approximately 15% of the variation of *T. testudinum* epiphyte loading in Florida Bay can be attributed to nutrient availability, particularly phosphorus (Frankovich and Fourqurean 1997). The majority of the variation is due to other factors. In seagrass ecosystems undergoing eutrophication, negative correlations of seagrass health (productivity and biomass) with epiphyte loading may be expected (Duarte 1995). As Fig. 1 illustrates, no such correlations can be made with regard to Florida Bay *T. testudinum*; the two areas of highest leaf productivity (Sprigger Bank and Tavernier Key) are coincident with the highest epiphyte loads. The epiphyte community at these sites is characterized by the encrusting coralline red algae *Hydrolithon farinosum*, which is abundant throughout most times of the year. Predominance of this epiphyte might be an indicator of oligotrophic conditions. A combination of high seagrass productivity and high epiphyte productivity may indicate positive overall seagrass ecosystem health. In the healthy subtidal *Zostera marina* meadows in Friday Harbor, Washington, simultaneous high eel-

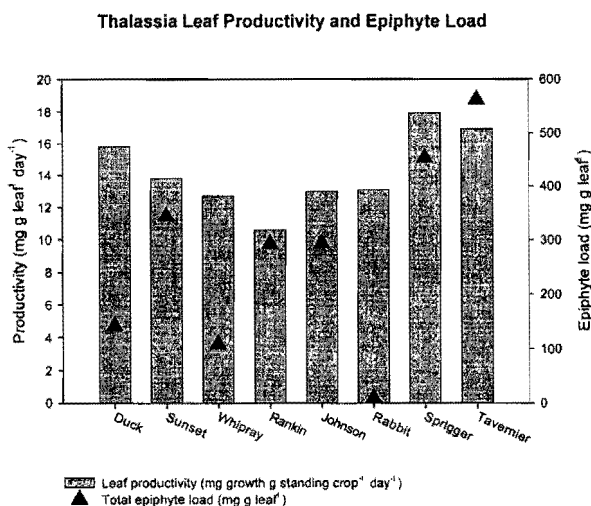


Fig. 1. Seagrass growth rates with epiphyte loads from 8 long-term monitoring sites in Florida Bay (1991–1992). Note that the highest seagrass growth rates were at the sites with the highest epiphyte loads.

grass productivity and epiphyte productivity was also observed (Nelson and Waaland 1997). The spatial and temporal distributions of Florida Bay epiphyte loads are disjunct from that of seagrass die-off. Florida Bay epiphyte loads are highest during winter and early spring and are greatest at sites experiencing greater marine influence (Frankovich and Zieman 1994; Frankovich 1996). In contrast, primary seagrass die-off is most prominent during the fall and has occurred at western interior sites. Under the present low nutrient regime in Florida Bay, seagrass biomass and productivity are not negatively correlated with epiphyte loading. These were not and are not the symptoms of seagrass loss caused by eutrophication of the water column.

We agree that pollution can lead “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” (Den Hartog 1977, p. 100); however, that did not happen in Florida Bay and certainly not, as implied, in 1983–1984. All of the abundant macroalgal species listed in Zieman et al. (1989) are normal members of the greater seagrass community of south Florida, and none are in eutrophic abundance. We did not make a linkage between eutrophication and the loss of *T. testudinum* in Florida Bay as there is none.

While there is a place for generalities, they can also be used to deflect a point even when specific information is available. In the marine environment, dissolved inorganic nitrogen (DIN) concentrations are the most frequently “limiting” nutri-

ent (Ryther and Dunstan 1971; Nixon 1995). The assumption of N-limitation of Florida Bay ignores the documentation of the widespread P-limitation of the Florida Bay benthos and water column. Numerous works have shown many seagrass meadows in south Florida and the Caribbean to be specifically phosphorus limited (Short et al. 1985, 1990; Williams 1987, 1990; Powell et al. 1989, 1991; Fourqurean et al. 1992a,b, 1993; Frankovich and Fourqurean 1997). We submit that such specific research references are more pertinent than broad-scope review papers.

Lapointe and Barile state Florida Bay is obviously eutrophic based solely on water column nitrogen numbers. They then cite our work (Fourqurean et al. 1993) to indicate “that Florida Bay was highly nutrient enriched when the first Bay-wide data were collected in 1989–1990.” (Lapointe and Barile 2004, p. 158). We completely reject this overly simplistic statement that continues to ignore the phosphorus limitation within most of Florida Bay. While it is true that some phytoplankton bioassay experiments have shown that N is a limiting factor for phytoplankton biomass at some times in western Florida Bay (Lavrentyev et al. 1998; Tomas et al. 1999; Cotner et al. 2000), stoichiometric evidence suggests that, in the benthos, there is an abundance of N with respect to P. N:P ratios in the water column and in *T. testudinum* leaves are indeed about 20:1 on the extreme western margin of Florida Bay, but in many of the areas of initial seagrass die-off, both water column and seagrass N:P ratios are in excess of 80:1—surely this is not consistent with N limitation of the entire ecosystem, as proposed by Lapointe and Barile. Relying on water column nutrient ratios to make these arguments, as Lapointe and Barile do, is tenuous at best. Wear et al. (1999), in a study of epiphyte enrichment on seagrasses in northern Florida noted on p. 210 that “water column nutrients, however, can be a poor indicator of the extent of eutrophication in aquatic systems because soluble nutrients are rapidly removed”, citing Suttle and Harrison (1988), Suttle et al. (1990), and Tomasko and Lapointe (1991). Similar conclusions were reached by Smith et al. (1981), Borum (1985), and Valiela et al. (1990).

It is also curious that Lapointe and Barile have extracted data from a funding agency data base (their Table 1, Florida Bay numbers attributed to SFWMD) instead of citing the refereed, published analyses of these data (Fourqurean et al. 1993; Boyer et al. 1997, 1999; Boyer and Jones 2002). Were they to consult the papers, they would see clearly that chlorophyll *a* (chl *a*) concentrations in the water column of Florida Bay have not behaved in a manner completely consistent with their model.

Chlorophyll concentrations have significantly increased in western Florida Bay, but in central Florida Bay, a sharp rise over the period 1989–1994 was followed by just as sharp a fall during the period 1994–1998, while eastern Florida Bay, the region closest to land-derived nutrients sources, there has been a significant decline in water column chlorophyll over the period 1989–1997 (Boyer et al. 1999). Lapointe and Barile have resorted to casting doubt on published chl *a* data to try to strengthen their case by citing an unsupported and factually incorrect pronouncement made by Brand (2002). It is not correct that there are systematic methodological errors in the chl *a* data (Boyer personal communication). Caution must also be taken when making facile comparisons of time series, as Lapointe and Barile make when they claim that a decrease in salinity in Florida Bay correlates with freshwater discharges in Shark Slough and Taylor Slough. Such correlations prove little. Freshwater runoff and rainfall are highly correlated in south Florida, and at this time runoff contributes very little to the freshwater budget of Florida Bay (Nuttall et al. 2000). The major contributor to interannual salinity variability is the balance between precipitation and evaporation directly over Florida Bay. During years with relatively high rainfall, salinity is lowered in Florida Bay and freshwater discharge increases—both of these are a direct response to rain, but the freshening of the bay currently has little to do with stream discharge (Nuttall et al. 2000).

We agree with Lapointe and Barile that ammonium concentrations in Florida Bay are indeed high—and we and others have reported on this fact many times (e.g., Fourqurean et al. 1993; Boyer et al. 1997, 1999). Our interpretation of the causes are different than Lapointe and Barile's. The high ammonium concentrations in Florida Bay are coincident with the most strongly P-limited regions of the bay. We have hypothesized that this ammonium is the result of lack of utilization of this N by severely P-limited primary producers; and anaerobic decomposition of organic matter and some interference in the nitrification and denitrification of that DIN.

What should be made of the rating of Florida Bay as highly eutrophic in the NOAA Eutrophication Assessment (Bricker et al. 1999)? The answer is complex. This assessment was based on a survey of a few scientists' opinions, and was not based on an analysis of data. Why would some scientists report that Florida Bay was, in their opinion, eutrophic? The answer lies in the change in water clarity that followed the seagrass die-off. As can be clearly seen in the time series data on water quality of Florida Bay presented in Boyer et al. (1999), tur-

bidity increased markedly beginning in late 1991–early 1992, a full 4 yr after the major episodes of seagrass die-off in 1987–1988. The switch from a clear water column to a very turbid one was obvious to all observers of Florida Bay. The most likely causes of this turbidity increase is an increase in suspended sediment and phytoplankton that occurred as a consequence of the loss of seagrasses in 1987–1988, not as a cause. It appears that internal loading of nutrients as a consequence of decomposition and sediment resuspension, led to increases in phytoplankton biomass. The loss of seagrass during the die-off not only caused an increase in the internal nutrient loadings, but, simultaneously, a very important nutrient sink was lost (i.e., the *T. testudinum* plants themselves). Using estimates of *T. testudinum* TP and TN nutrient uptake rates of 2.25 mg P<sup>-2</sup> day<sup>-1</sup> and 16.28 mg N<sup>-2</sup> day<sup>-1</sup> (Madden et al. 2003), the loss of 4,000 hectares of *T. testudinum* resulted in an estimated annual addition of 240 metric tons of TN and 33 metric tons of TP, which then became available for uptake by phytoplankton and macroalgae. These nutrient amounts are approximately 97 times larger than the annual TP loading and 8.9 times larger than the annual TN loading into Florida Bay through Taylor Creek (0.34 and 26.8 metric tons, respectively; Rudnick et al. 1999).

Increased turbidity and phytoplankton biomass did indeed cause light availability problems for Florida Bay seagrasses. The response to decreased light was a thinning of the *T. testudinum* biomass and an initial sharp decrease in the biomass of *Halodule wrightii* and *Syringodium filiforme* (Hall et al. 1999). It is interesting that the distribution of *T. testudinum* was largely unaffected by these events (Hall et al. 1999). *Halophila* species have recently begun to show up in Florida Bay (Durako et al. 2002). This species has a very low light requirement for a seagrass, and is often found in deep or turbid waters. Epiphyte accumulation rates are 1–2 orders of magnitude lower than those observed in the Patuxent River estuary of Chesapeake Bay using identical techniques (Table 1).

Of all the points raised by Lapointe and Barile, one we wish we had stated more clearly is on the general salinity response of *T. testudinum* to salinity. A more precise statement than "*T. testudinum* is a stenohaline marine plant" (on p. 467) would be that it is capable of surviving in a broad range of salinities, but that it thrives in a fairly narrow salinity range. The data presented in Zieman et al. (1999) clearly demonstrate reduced growth rates in hypersaline conditions. There is also literature support of this finding. Lapointe and Barile noted our citation of McMillan and Moseley (1967) and we recognize that the overall design of this pio-

TABLE 1. Mean Epiphyte Accumulation Rates. The Florida Bay rates are from T. Frankovich, March–April 2001, 7–11 d accumulation. The Patuxent River rates are from Stankelis et al. (1999; seasonal means estimated from graph, pages 102–103), 6–8 d accumulation.

|                        | Total Epiphyte<br>( $\mu\text{g cm}^{-2} \text{ day}^{-1}$ ) | Epiphyte<br>Chlorophyll <i>a</i><br>( $\mu\text{g cm}^{-2} \text{ day}^{-1}$ ) |
|------------------------|--------------------------------------------------------------|--------------------------------------------------------------------------------|
| Florida Bay            |                                                              |                                                                                |
| Duck Key               | 19                                                           | 4                                                                              |
| Bob Allen              | 13                                                           | 15                                                                             |
| Sprigger               | 52                                                           | 18                                                                             |
| Patuxent River estuary | 60–520                                                       | 100–500                                                                        |

neering work is not perfect. However, they overlooked our citation of Zieman (1975), where a field study of nearly 200 productivity measurements over a two-year period showed highest productivities near 30 psu. Zieman (1975) stated on p. 108 that “*Thalassia* showed a salinity optimum in these studies of 30 ppt, with decreased productivity above and below this.” *T. testudinum* can tolerate salinities as low as 3.5–5 ppt (Sculthorpe 1967) or as high as 60 ppt (McMillan and Moseley 1967) for short periods of time, but usually undergoes defoliation.

Lapointe and Barile misrepresent the citations of Tabb et al. (1962) that we used. Tabb et al. (1962, p. 42) do indeed state that “with marked reduction in salinity . . . the *Thalassia* underwent decline in size and abundance” and we also believe that to be true. Tabb et al. (1962, p. 43) state that it appears “that long periods of near or *slightly above normal salinities* (our emphasis) are a requirement for maximum growth of *Thalassia*.” That statement is in agreement with our work but gives no basis for the misleading statement of Lapointe and Barile (2004, p. xx) that “Tabb et al. (1962) concluded that *T. testudinum* thrives (our emphasis) under hypersaline conditions.” Tabb et al. (1962) did not conclude that hyper salinity caused *T. testudinum* to “thrive” as stated by Lapointe and Barile (2004, p. 160). This occurred at Salinities at or just above “normal salinities” (Tabb et al. 1962; p. 43). Tabb et al. (p. 74–75) later stated that “under hypersaline conditions (above 40–50‰) the turtle grass *Thalassia testudinum* is adversely affected. The blades of the “grass” die back and expose the bottom muds. This was actually the first description of a small-scale seagrass die off in Florida Bay.

Lapointe and Barile misrepresent the conceptual model presented in Zieman et al. (1999) time and again. It is not true that the conceptual model concludes that hypersalinity caused the seagrass die-off. We state that hypersalinity is but one stress on seagrasses in Florida Bay. Just as important in our conceptual model is the observation that sea-

grass die-off in 1987–1988 was confined to only the very densest seagrass beds in Florida Bay. Surely, some result of the dense seagrass community caused a stress on seagrasses that led to their demise. In our conceptual model, we stated on p. 468 that “these dense beds became overcrowded and unstable,” but we nowhere state that “meadows with biomass higher than 50 to 100 g dry wt<sup>-2</sup> are overcrowded.” (2003, p. 468) Our model hypothesizes that as Florida Bay became more marine, *T. testudinum* both expanded its coverage, often at the expense of the more euryhaline *H. wrightii*, and increased greatly in biomass. This is supported by the changes in seagrass distribution between the map of Schmidt (1979) and our map in 1983–1984 (Zieman et al. 1989), by Fig. 7 in Zieman et al. (1999), and by the observations of numerous observations of fishing guides as reported by Michael Collins, then president of the Islamorada Guides Association and currently a member of the governing board of the South Florida Water Management District. The seagrass beds that succumbed to the initial die-off of *T. testudinum* in 1987 were indeed unusually dense. At the beginning of our sampling of the die-off, 8 mo after it began, average standing crop at die-off stations was 200 g m<sup>-2</sup>. Lapointe and Barile claim that such densities are common, but there is no support for this in the literature. Tomasko and Lapointe (1991) report densities at 17 locations from Florida and the Caribbean, and a maximum leaf biomass of 150 g m<sup>-2</sup>, but an average of only 48 g m<sup>-2</sup>. Based on a comprehensive monitoring program in south Florida seagrass beds, a typical *T. testudinum* meadow has a leaf density of 40–50 g m<sup>-2</sup>, and they rarely exceed 80 g m<sup>-2</sup> (Fourqurean et al. 2001).

We find that there is no “substantial evidence” as stated by Lapointe and Barile (p. 161) linking declines in biomass, density, and productivity of *T. testudinum*, *H. wrightii*, and *S. filiforme* with decreasing salinity.” Declines before 1991 were definitely not associated with increases in nutrients, chl *a*, and turbidity, as the bay remained generally clear except at the immediate die-off basins. Figure 2 shows an aerial view of Rankin Lake in the summer of 1988, early in the die-off. The clear water column and dense seagrass with coalescing patches of bare sediment were the symptom of the die-off in this basin and are not characteristic of eutrophication events. Figure 3 shows an underwater close-up of the same area. Note the clean water, clean green leaves with few epiphytes, and brown to black lesions on the leaves caused by the slime mold *Labyrinthula*. This photo of seagrasses as they were dying is clearly not consistent with eutrophication-induced loss of seagrass.

There is no “disconnect between their data and



Fig. 2. The water column overlying seagrasses in Rankin Lake. Prior to the original episodes of seagrass die-off in 1989 remained optically clear as can be seen in this low-level oblique photograph taken on Rankin Lake in central Florida Bay ( $25^{\circ}6.3'N$ ,  $81^{\circ}47.5'W$ ).

interpretation" in our discussion of the time series of seagrass growth rates in Zieman et al. (1999), as stated by Lapointe and Barile on p. 161. Although mass-specific productivity increased total standing crop continued to decrease because of a reduction in density of short shoots and accelerated leaf loss. We attributed "this increase in mass-specific productivity to a thinning of the seagrass canopy and the subsequent decrease in light attenuation within the plant canopy." (p. 467) This is consistent with earlier work where Zieman et al. (1984) showed *T. testudinum* to increase its turnover rate by as much as 30% in response to canopy thinning by green sea turtles.

The restoration of historic fresh water flow to the southern Everglades and Florida Bay is a major driving force of the Everglades restoration plan. Lapointe and Barile rely on selective citation to overstate the support for their ideas about the cause of change in Florida Bay, while continuing to ignore the published interpretations of the data that they selectively use to create their "just so" story. The local, state, and Federal resource management agencies and policy makers responsible for the stewardship of Florida Bay were not at all confused by various hypotheses pertaining to the demise of Florida Bay. We believe that these policy makers have been influenced by a progression of papers and a body of knowledge that has built up over the past decade that have shown that the restoration of historic waterflows to the lower Everglades and Florida Bay is the key to the restoration of the whole ecosystem.

### Summary

While cultural eutrophication of the coastal ocean is widespread and has negatively impacted



Fig. 3. An actively dying seagrass meadow in Rankin Lake in 1989. Note the clear water and absence of notable epiphyte load or macroalgae.

many ecosystems, it was clearly not the cause of the 1987–1988 Florida Bay seagrass die-off. The published literature paints a clear picture. Lapointe and Barile (2004) have ignored much of this literature, and have instead presented a superficial re-analysis of very selective subsets of published works and gray literature. Proper environmental stewardship should be based on a careful analysis of ecological data from the system at hand. The analyses presented by Lapointe and Barile can simply not withstand scrutiny, and their direct criticisms of our paper (Zieman et al. 1999) are largely without support.

We are most concerned with the restoration of the historic Florida Bay, and this means the Florida Bay prior to the upstream water modifications. What we do not want is a return to a highly restricted system that created the conditions of the 1980s. The bay communities of the 1980s were aesthetically pleasing, but much of the bay was more like a back-reef seagrass community than an estu-

arine community. As Fourqurean and Robblee (1999, p. 355) stated as a summary to the collected works published in the special issue of *Estuaries* on long-term changes in Florida Bay, "... the natural state of the Florida Bay ecosystem is one of variability and change. For this reason, a clear causal link between recent changes in the ecosystem and human activities in the ecosystem eludes detection. To their credit, governments and resource managers have adopted a precautionary approach and are proceeding in recognition of the possible ecological consequences of their actions. Indeed, long-term plans for the renovation of the water management infrastructure have ecosystem restoration as a principal goal. But, restoration to what state? The insight to be drawn from this volume [1999, *Estuaries*, 22(2B)] is that the objectives for a restored Florida Bay must take account its inherently variable nature. To manage the bay as a static system would alter the nature of Florida Bay far more than may have already occurred."

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#### LITERATURE CITED

- BORUM, J. 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology* 87:211-218.
- BOYER, J. N., J. W. FOURQUREAN, AND R. D. JONES. 1997. Spatial characterization of water quality in Florida Bay and White-water Bay by multivariate analyses: Zones of similar influence. *Estuaries* 20:743-758.
- 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* 2:412-430.
- BOYER, J. N. AND R. D. JONES. 2002. View from the bridge: External and internal forces affecting the ambient water quality of the Florida Keys national marine sanctuary, p. 609-628. In J. W. Porter and K. G. Porter (eds.), *The Everglades, Florida Bay, and the Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, Florida.
- 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 the Coral Reefs of the Florida Keys*. 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.
- COTNER, J. B., R. H. SADA, H. BOOTSMA, T. JOHNGEN, J. F. CAVALETTO, AND W. S. GARDNER. 2000. Nutrient limitation of heterotrophic bacteria in Florida Bay. *Estuaries* 23:611-620.
- DEN HARTOG, C. 1977. Structure, function, and declassification in seagrass communities, p. 89-119. In C. P. McRoy and C. Helfferich (eds.), *Seagrass Communities: A Scientific Perspective*. Marcel Dekker, Inc., New York.
- DUARTE, C. J. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41:87-112.
- DURAKO, M. J., M. O. HALL, AND M. MERELLO. 2002. Patterns of change in the seagrass dominated Florida Bay hydroscape, p. 523-538. In J. W. Porter and K. G. Porter (eds.), *The Everglades, Florida Bay, and the Coral Reefs of the Florida Keys*. CRC Press, Boca Raton, Florida.
- FOURQUREAN, J. W., R. D. JONES, AND J. C. ZIEMAN. 1993. Processes influencing water column nutrient characteristics and phosphorous limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distribution. *Estuarine, Coastal and Shelf Science* 36:295-314.
- FOURQUREAN, J. W., G. V. N. POWELL, AND J. C. ZIEMAN. 1992a. Phosphorus limitation of primary production in Florida Bay: Evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* 37:162-171.
- FOURQUREAN, J. W. AND M. B. ROBBLEE. 1999. Florida Bay: A history of recent ecological changes. *Estuaries* 22:344-357.
- FOURQUREAN, J. W., A. W. WILLISIE, C. D. ROSE, AND L. M. RUTTEN. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* 138:341-354.
- FOURQUREAN, J. W. AND J. C. ZIEMAN. 1991. Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 69:161-170.
- FOURQUREAN, J. W., J. C. ZIEMAN, AND G. V. N. POWELL. 1992b. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology* 114:57-65.
- FRANKOVICH, T. A. 1996. Epiphyte loads and production on the seagrass *Thalassia testudinum*. M.S. Thesis, University of Virginia, Charlottesville, Virginia.
- FRANKOVICH, T. A. AND J. W. FOURQUREAN. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159:37-50.
- FRANKOVICH, T. A. AND J. C. ZIEMAN. 1994. Total epiphyte and epiphytic carbonate production on *Thalassia testudinum* across Florida Bay. *Bulletin of Marine Science* 54:679-695.
- 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.
- LAPORTE, B. E., AND P. J. BARILE. 2004. Comment on J. C. Ziemann, 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.
- LAVRENTYEV, B. E., H. A. BOOTSMA, T. H. JOHNGEN, J. F. CAVALETTO, 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.
- MADDEN, C. J., A. McDONALD, S. KELLY, M. KOCH, AND W. M. KEMP. 2003. Use of a dynamic, mechanistic simulation model to assess ecology and restoration of the Florida Bay seagrass community. Joint Conference on the Science and Restoration of the Greater Everglades and Florida Bay Ecosystem, April 13-18. Palm Harbor, Florida.
- MCMILLAN, C. AND F. N. MOSELEY. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. *Ecology* 48:503-506.
- NELSON, T. A. AND J. R. WAALAND. 1997. Seasonality of eelgrass, epiphyte, and grazer biomass and productivity in subtidal eelgrass meadows subjected to moderate tidal amplitude. *Aquatic Botany* 56:51-74.
- NIXON, S. W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* 41:199-219.
- NUTTLE, W. K., J. W. FOURQUREAN, B. J. COSBY, J. C. ZIEMAN, AND

- M. B. ROBBLEE. 2000. Influence of net freshwater supply on salinity in Florida Bay. *Water Resources Research* 36:1805-1822.
- POWELL, G. V. N., J. W. FOURQUREAN, W. J. KENWORTHY, AND J. C. ZIEMAN. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: Observational and experimental evidence. *Estuarine, Coastal and Shelf Science* 32:567-579.
- POWELL, G. V. N., W. J. KENWORTHY, AND J. W. FOURQUREAN. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Sciences* 44:324-340.
- 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.
- RYTHER, J. H. AND W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science* 171:1008-1013.
- SCHMIDT, T. W. 1979. Ecological study of fishes and the water quality characteristics of Florida Bay, Everglades National Park, Florida. Final project report RSP-EVER-36. South Florida Research Center, Everglades National Park, Homestead, Florida.
- SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. Arnold Publishing, London, U.K.
- SHORT, F. T., W. M. DAVIS, R. A. GIBSON, AND C. F. ZIMMERMAN. 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine, Coastal and Shelf Science* 20:419-430.
- SHORT, F. T., W. C. DENNISON, AND D. G. CAPONE. 1990. Phosphorus-limited growth of the tropical seagrasses *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series* 62:169-174.
- SMITH, S. V., W. J. KIMMERER, E. A. LAWS, R. E. BROCK, AND T. W. WALSH. 1981. Kaneohe Bay sewage diversion experiment perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35:278-396.
- STANKELIS, R. M., W. R. BOYNTON, AND J. M. FRANK. 1999. Submerged aquatic vegetation (SAV) habitat evaluation, p. 77-117. In W. R. Boynton and F. M. Rohland (eds.), Ecosystems Process Component Level 1. Interpretive report no. 16. Chesapeake Biological Laboratory, Solomons, Maryland.
- STUMPF, R. P., M. L. FRAYER, M. J. DURAKO, AND J. C. BROCK. 1999. Variations in water clarity and bottom albedo in Florida Bay from 1985-1997. *Estuaries* 22:431-444.
- SUTTLE, C. A. AND P. J. HARRISON. 1988. Ammonium and phosphate uptake kinetics of size-fractionated plankton from an oligotrophic freshwater lake. *Journal of Plankton Research* 10:133-149.
- SUTTLE, C. A., J. A. FUHRMAN, AND D. G. CAPONE. 1990. Rapid ammonium cycling and concentration-dependent partitioning of ammonium and phosphate: Implications for carbon transfer in plankton communities. *Limnology and Oceanography* 35:424-433.
- 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.
- TOMAS, C. R., B. BENDIS, AND K. JOHNS. 1999. Role of nutrients in regulating plankton blooms in Florida Bay, p. 323-337. In H. Kumpf, K. Steidinger, and K. Sherman (eds.), The Gulf of Mexico Large Marine Ecosystem. Blackwell Science, Malden, Massachusetts.
- 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.
- VALIELA, I., J. COASTA, K. FORMAN, J. M. TEAL, B. HOWER, AND D. AUBREY. 1990. Transport of groundwater-borne nutrients from watersheds and their effects on coastal waters. *Biogeochemistry* 10:177-197.
- WEAR, D. J., M. J. SULLIVAN, A. D. MOORE, AND D. F. MILLIE. 1999. Effects of water-column enrichment on the production dynamics of three seagrass species and their epiphytic algae. *Marine Ecology Progress Series* 179:201-213.
- WILLIAMS, S. L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series* 35:91-98.
- WILLIAMS, S. L. 1990. Experimental studies of Caribbean seagrass development. *Ecological Monographs* 60:449-469.
- ZIEMAN, J. C. 1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. *Estuarine Research* 1: 541-561.
- 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 R. L. IVERSON. 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292-311.
- ZIEMAN, J. C., R. L. IVERSON, AND J. C. OGDEN. 1984. Herbivory effects on *Thalassia testudinum* leaf growth and nitrogen content. *Marine Ecology Progress Series* 15:151-158.

#### SOURCE OF UNPUBLISHED MATERIALS

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