Consumers Rule: Predator Primacy in Shallow Benthic Ecosystems

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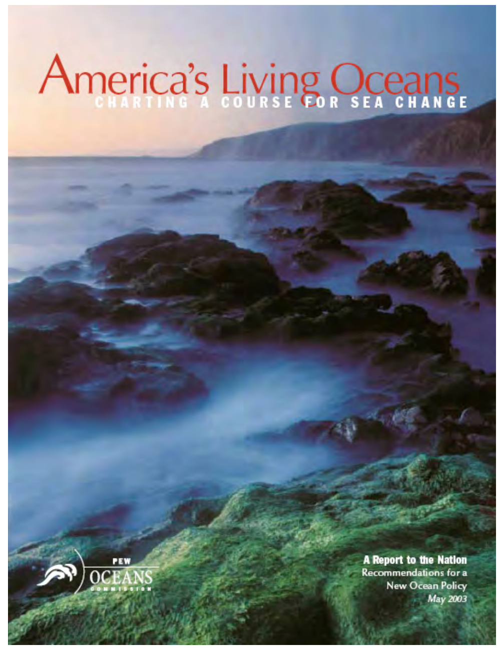
High-Profile Publications Linking Nutrient Pollution to Negative Coastal Impacts

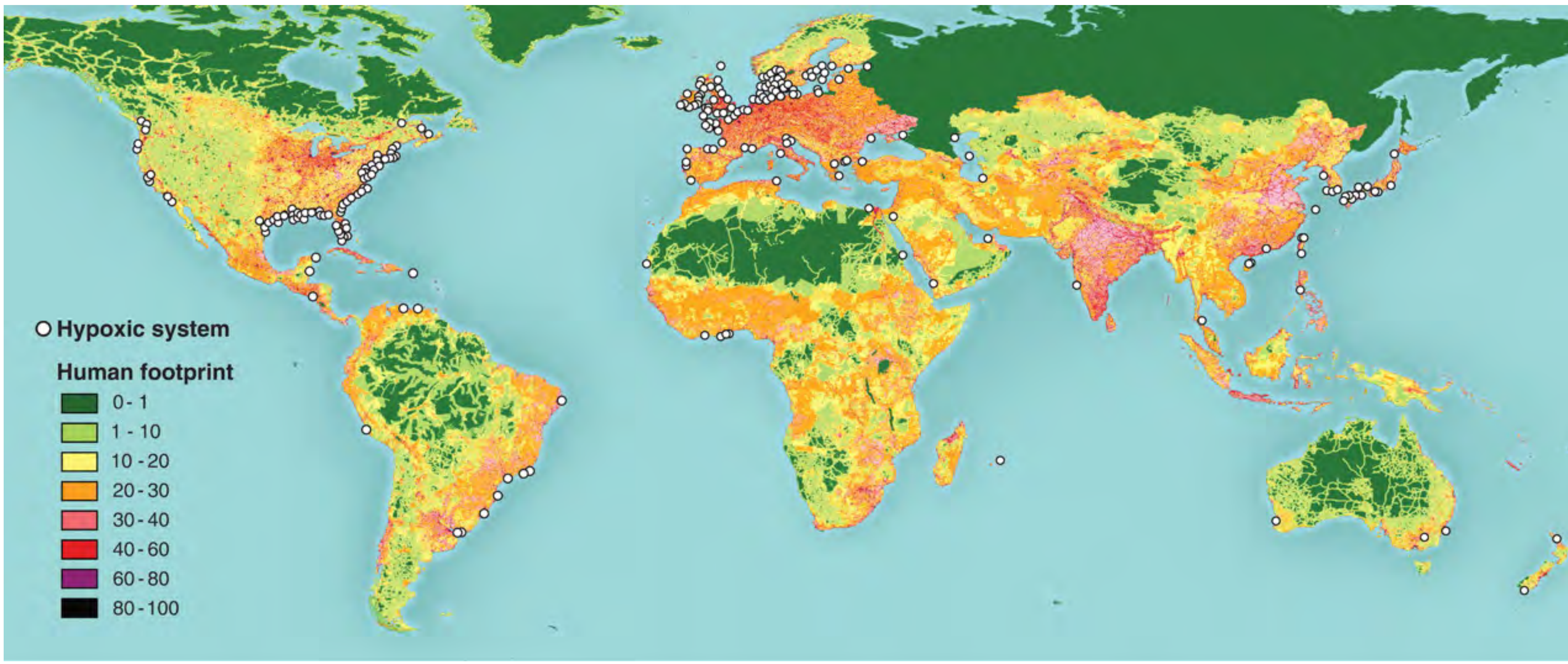


"…nutrient pollution is the most pervasive and troubling pollution problem currently facing U.S. coastal waters" National Research Council, 2000

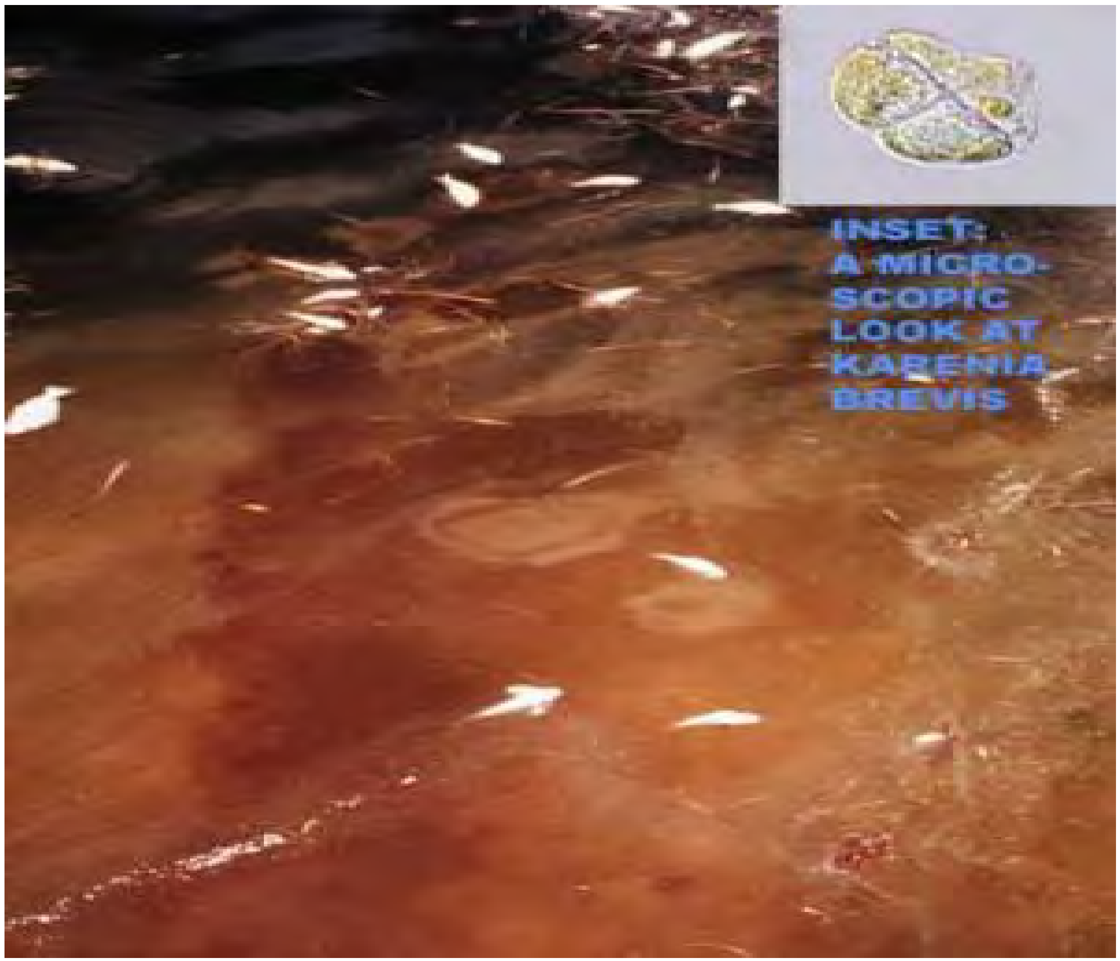
"Today, pollution from the nutrients N and P represents the largest source of degradation in coastal waters…" Issues in Ecology, 2000

Systems with eutrophication-associated dead zones

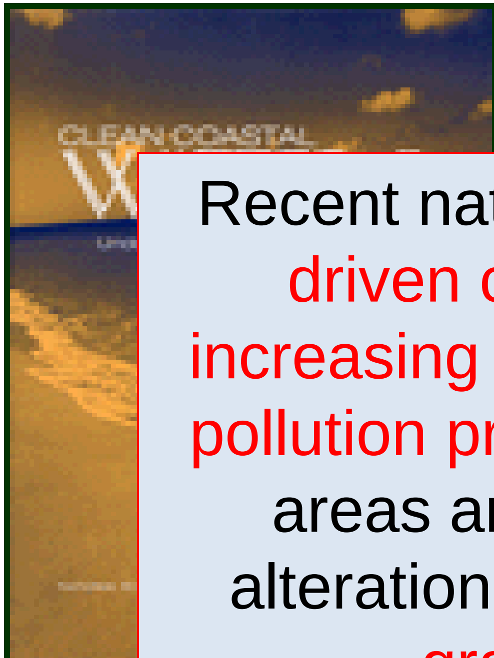
Source: Diaz and Rosenberg 2008, Science 321



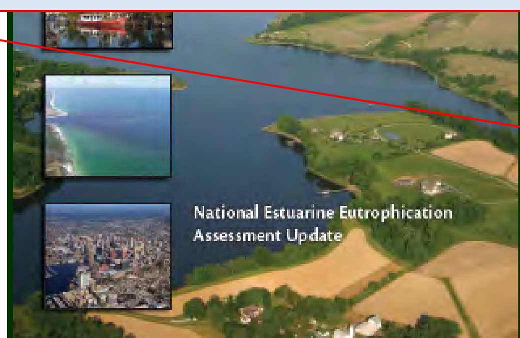
Harmful Algal Blooms (Red Tide)

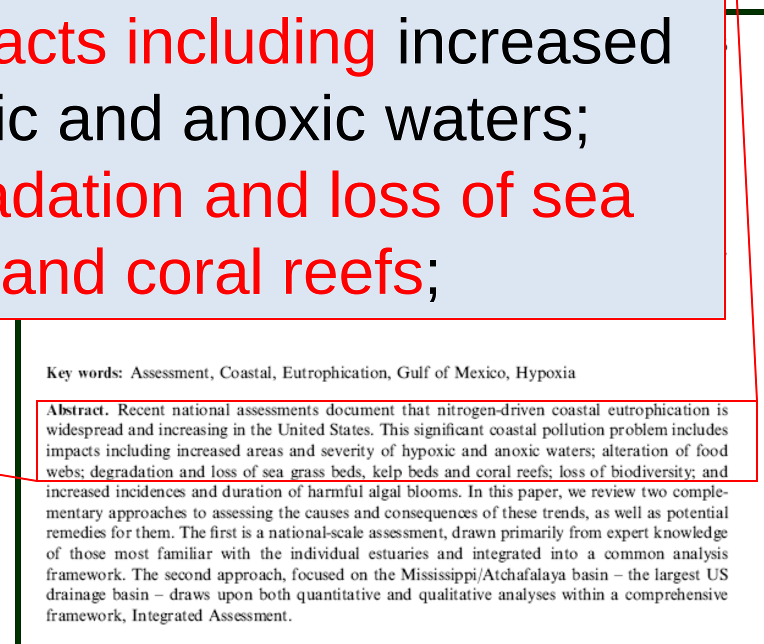


Publications Linking Eutrophication to Loss of Seagrass, Kelp and Coral via Algal Overgrowth



Recent national assessments document that nitrogen-driven coastal eutrophication is widespread and increasing in the United States. This significant coastal pollution problem includes impacts including increased areas and severity of hypoxic and anoxic waters; alteration of food webs; degradation and loss of sea grass beds, kelp beds and coral reefs;





Key words: Assessment, Coastal, Eutrophication, Gulf of Mexico, Hypoxia

Abstract. Recent national assessments document that nitrogen-driven coastal eutrophication is widespread and increasing in the United States. This significant coastal pollution problem includes impacts including increased areas and severity of hypoxic and anoxic waters; alteration of food webs; degradation and loss of sea grass beds, kelp beds and coral reefs; loss of biodiversity; and increased incidences and duration of harmful algal blooms. In this paper, we review two complementary approaches to assessing the causes and consequences of these trends, as well as potential remedies for them. The first is a national-scale assessment, drawn primarily from expert knowledge of those most familiar with the individual estuaries and integrated into a common analysis framework. The second approach, focused on the Mississippi/Atchafalaya basin – the largest US drainage basin – draws upon both quantitative and qualitative analyses within a comprehensive framework, Integrated Assessment.

The Seagrass Example: Bottom - Up Control

As Nutrients Increase

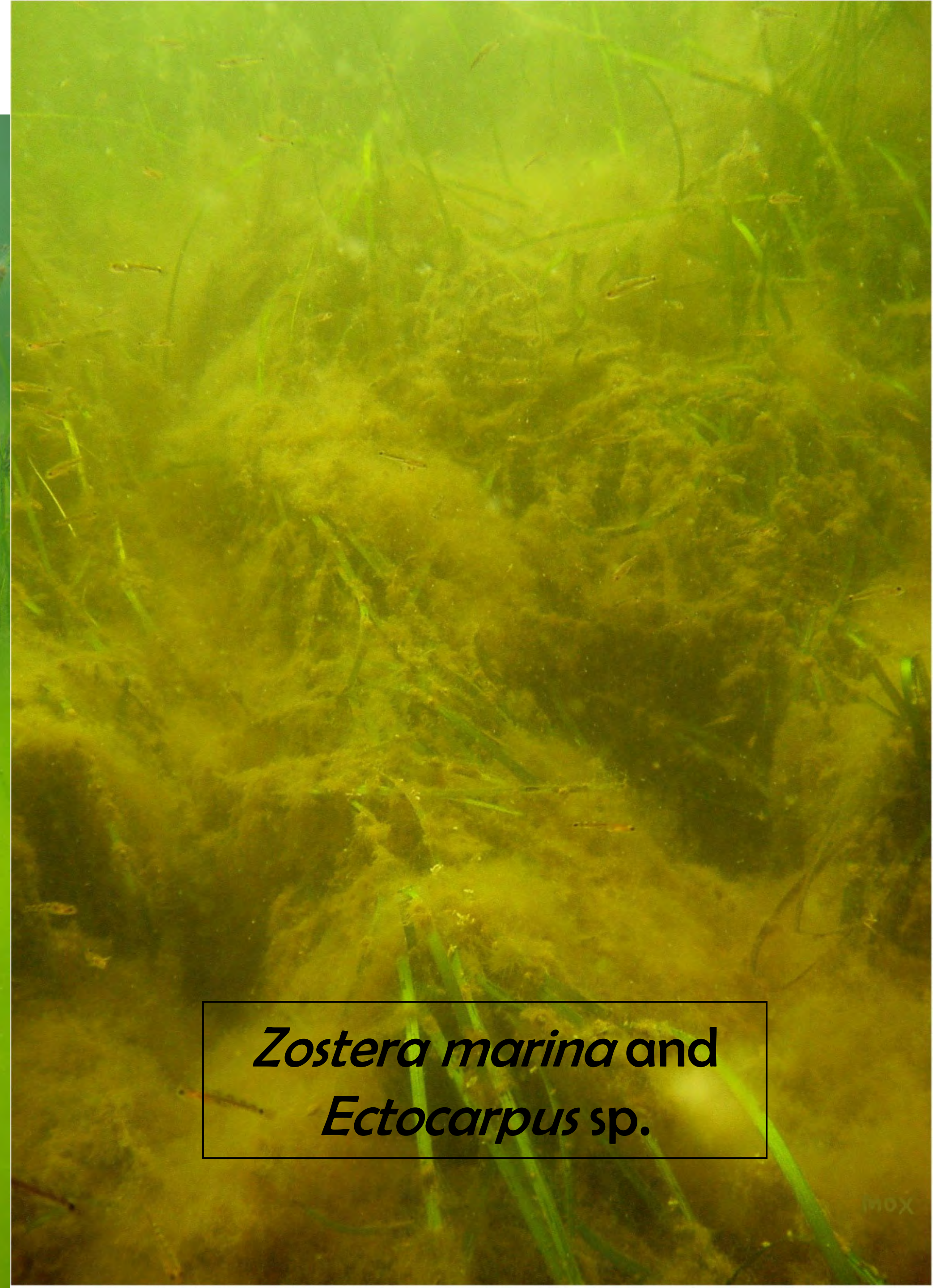
↓

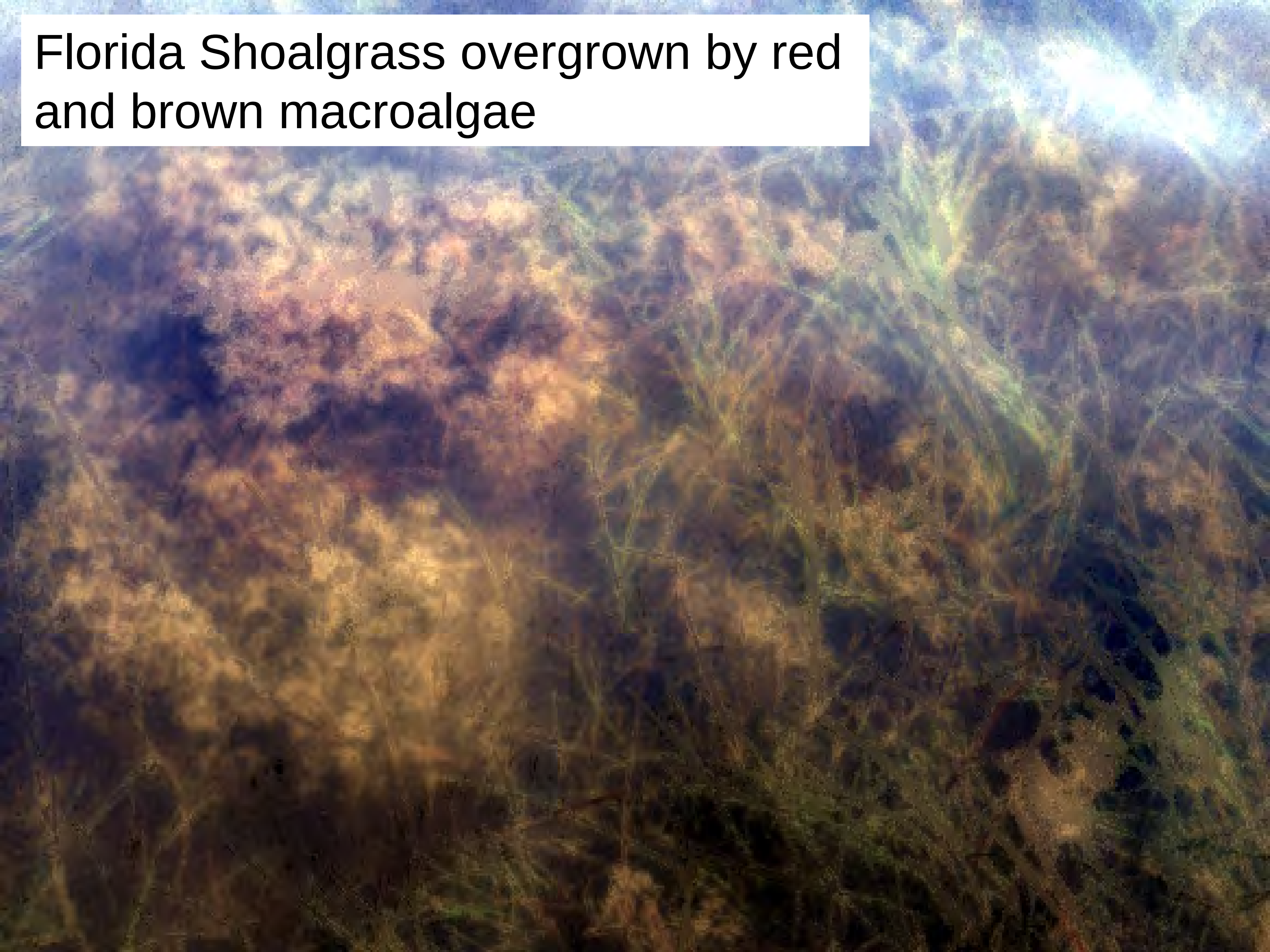
Algal Epiphytes Increase and

↓

Seagrass Loss Occurs

Swedish West coast

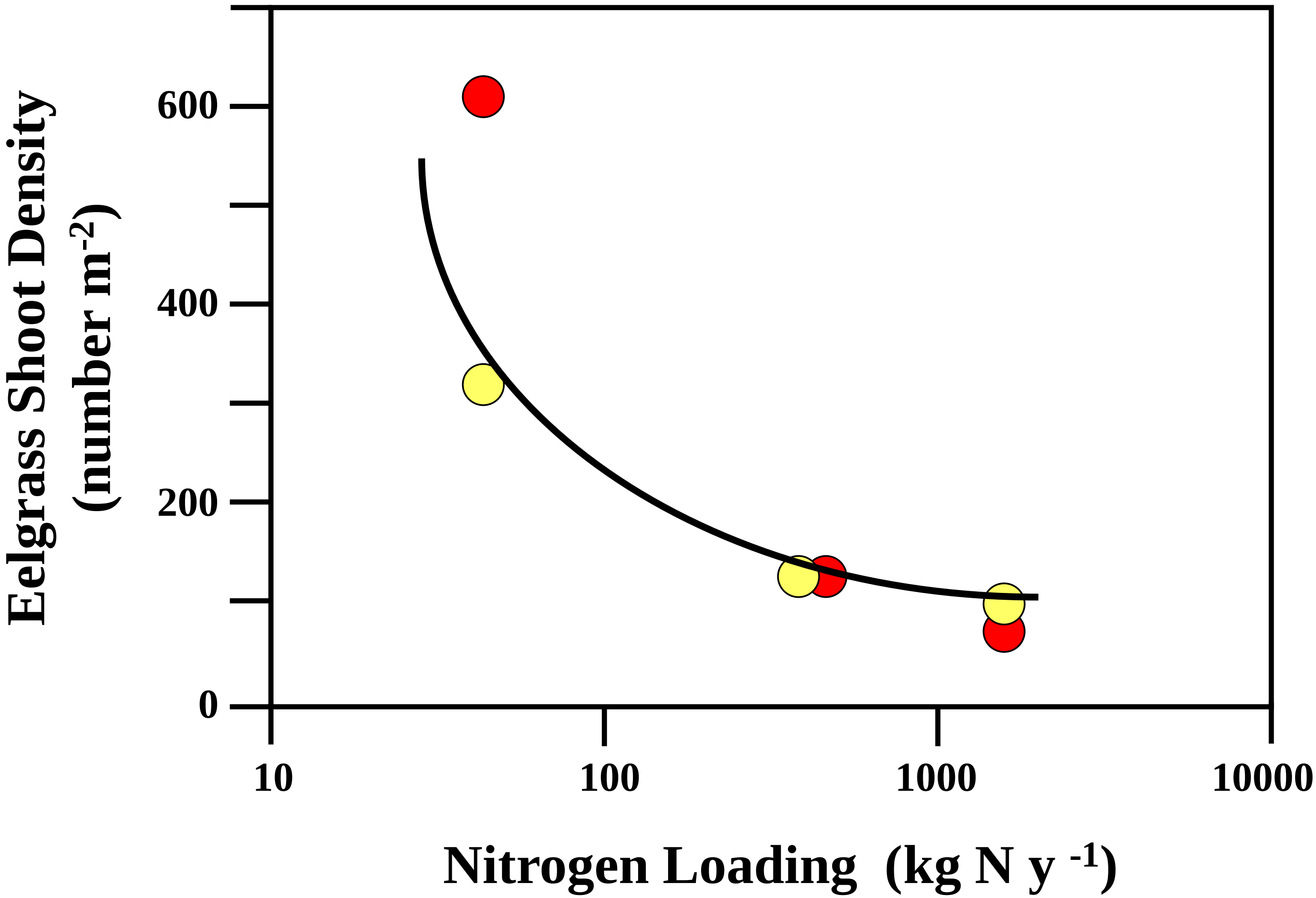




Florida Shoalgrass overgrown by red and brown macroalgae

Frequently Cited Studies that Ascribe Seagrass Loss to Nutrient Enrichment

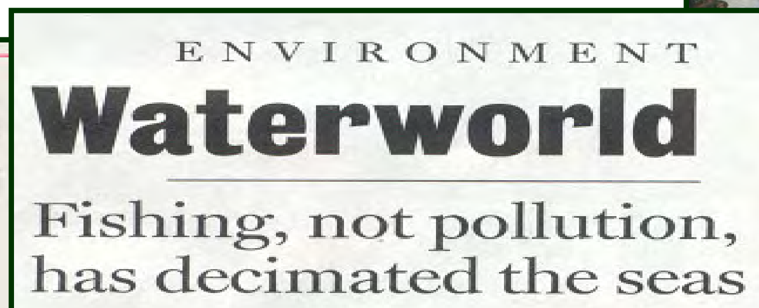
Study	Species	Method	Grazers Included
Twilley et al. 1985	*Potamogeton perfoliatus* *Ruppia maritima*	Pond Experiment	No
Cambridge et al. 1986	*Posidonia spp.*	Field Observation	No
Burkholder et al. 1992	*Zostera marina*	Lab Experiment	No
Valiela et al. 1992	*Zostera marina*	Field Observation	No
Taylor et al 1995	*Zostera marina*	Lab Experiment	No
Hauxwell et al. 2001	*Zostera marina*	Field Observation	No
Hauxwell et al. 2003	*Zostera marina*	Field Observation	No

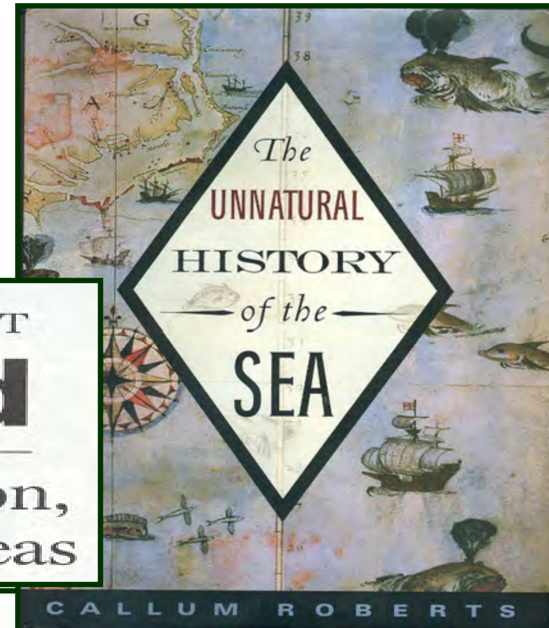


Source: Deegan, 2002. *Estuaries* 25(4b):727-742

Effects of Overfishing on Marine Ecosystems (Top Down Control)

Historical Overfishing and the Recent Collapse of Coastal Ecosystems -
Jackson et al., 2001. *Science 293:629-638*

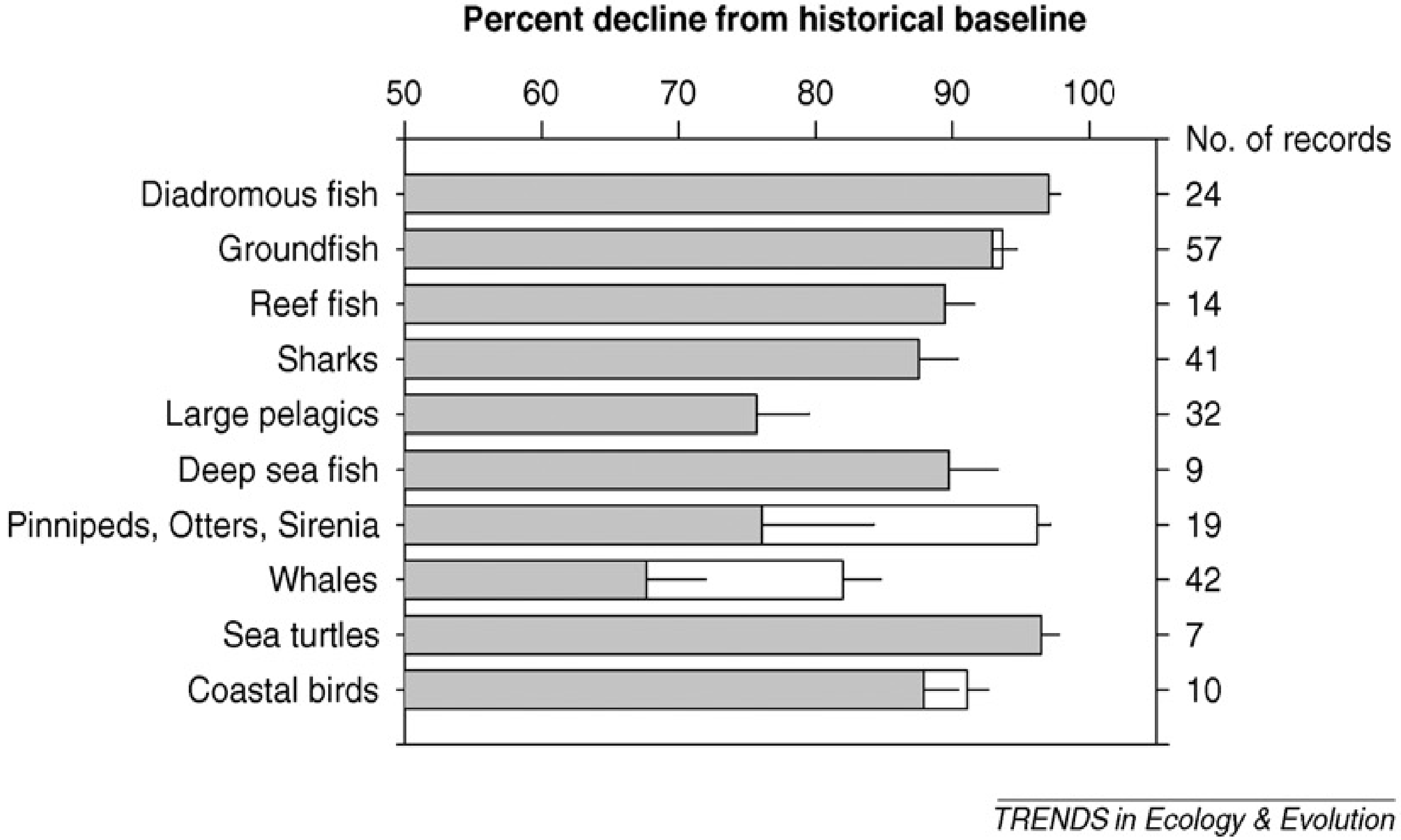




SHIFTING BASELINES

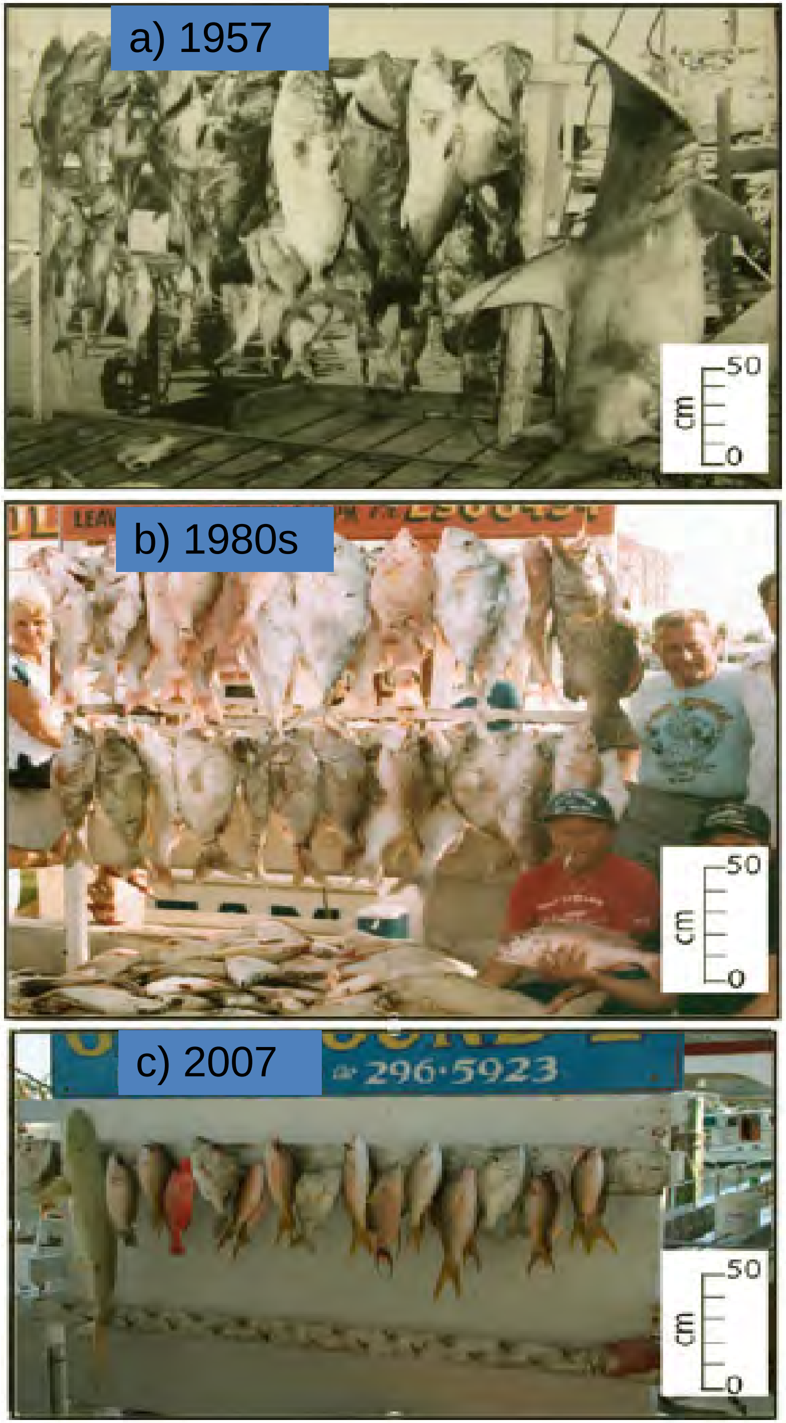
www.shiftingbaselines.org

Changes of large marine animals relative to historical baselines



The graph shows the average decline and standard error for each species group to the low point in abundance (white bars) and to the most recent point in the data series (gray bars; in many cases the same as the low point).

Source: Lotze & Worm 2009. TREE



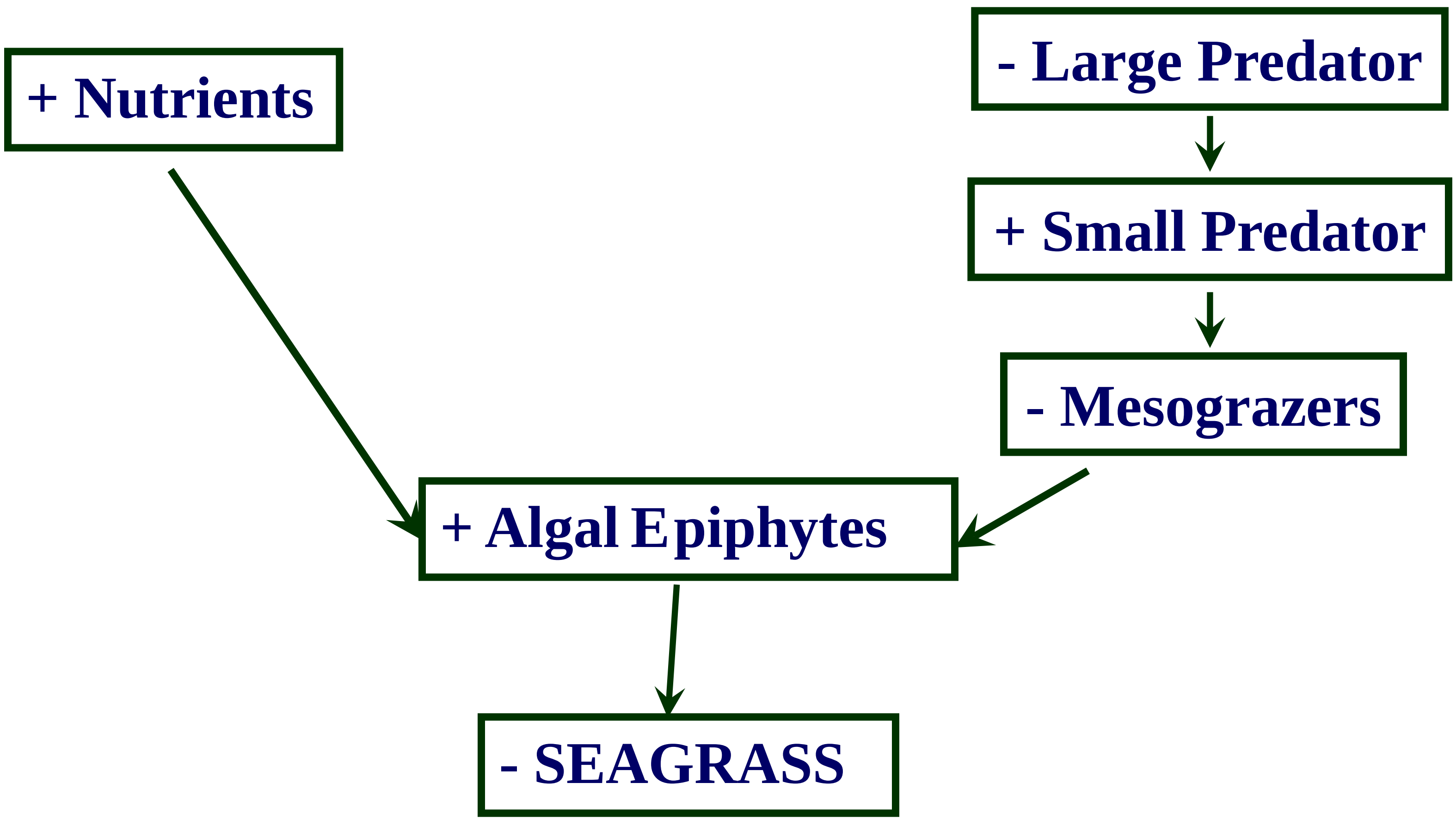
Trophy fish caught on Key West charter boats (a) 1957, (b) early 1980s, and (c) 2007

Source: McClenachan 2008, Conservation Biology

Alternative Causes of Seagrass Die-Off

Eutrophication (Bottom Up)

Overfishing (Top Down-Trophic Cascade)



Goals for Today

- **To synthesize the results of experiments, and meta-analyses of experiments, that compare the relative importance of top-down and bottom-up factors on seagrass meadows and coral reefs**
- **To discuss the implications of this synthesis**
- **To consider some unanswered questions about the operation of top-down and bottom up factors in coastal waters, and suggest some opportunities for future research**

Data Sources

- **Data from seagrass meadows are emphasized, because I know them best and there is much information about them, but we will also consider results from coral reefs and rocky shores**

- **Only data from manipulative experiments are considered, as I believe this is the only conclusive way of evaluating the magnitude of indirect food web effects**

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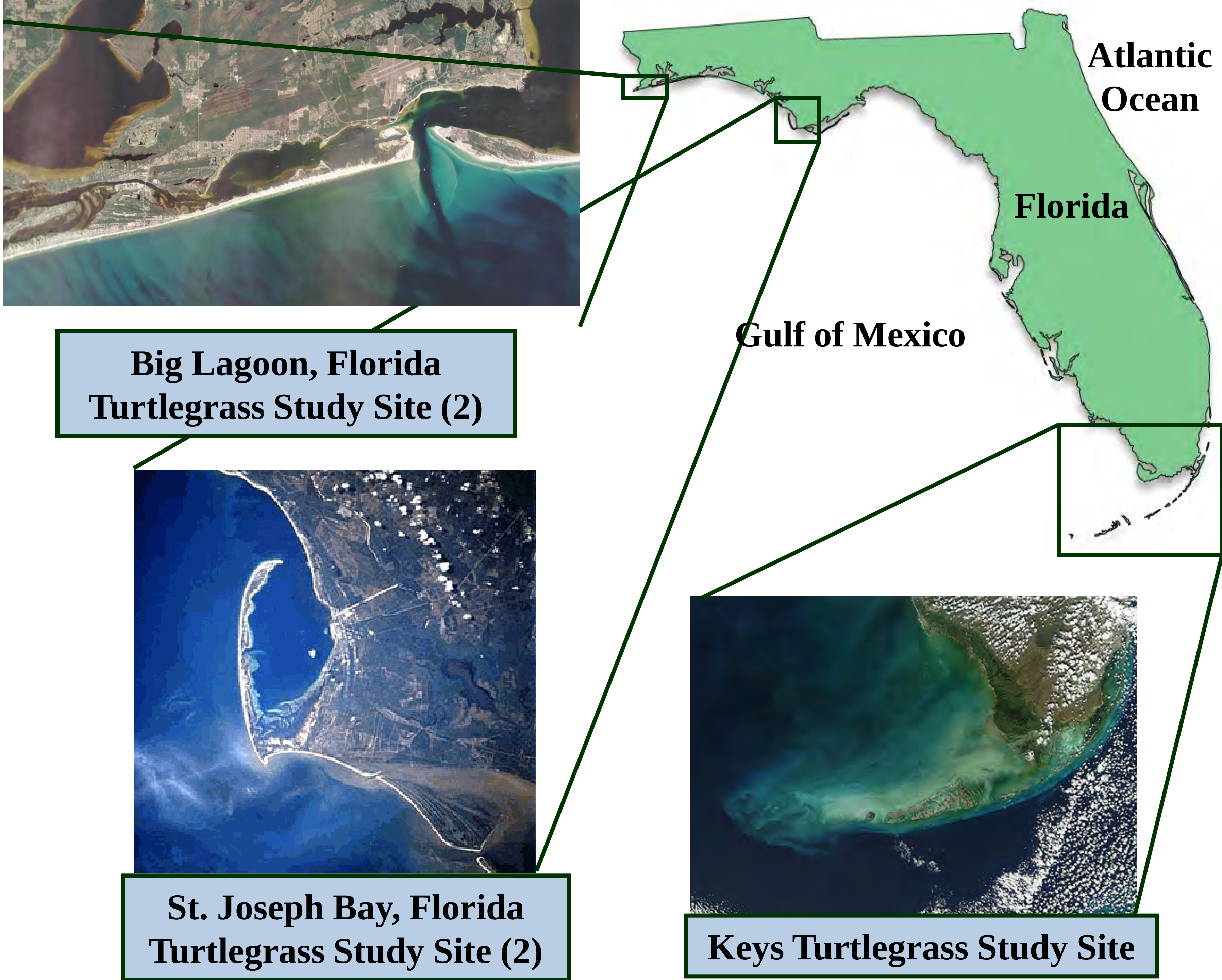
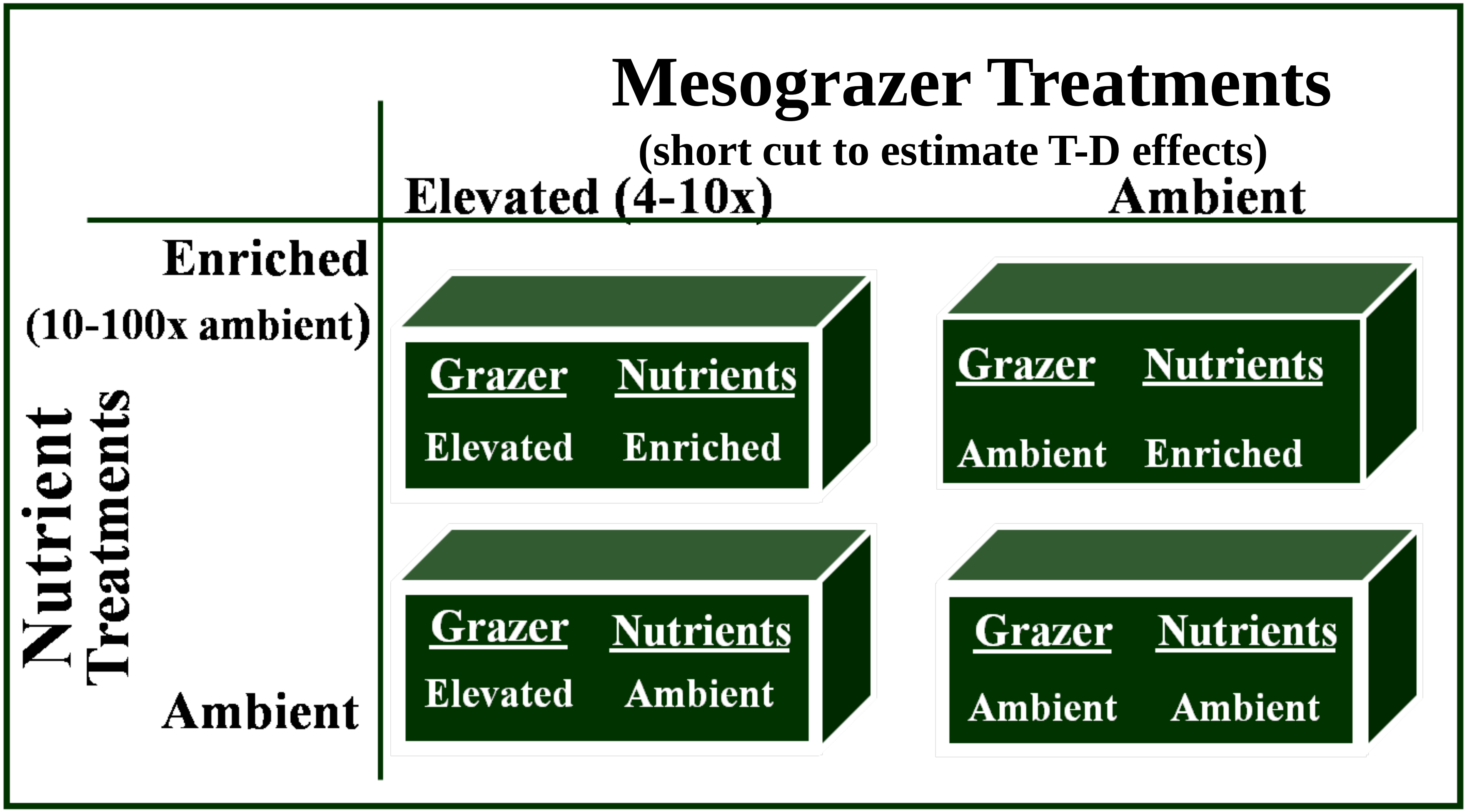

Atlantic Ocean
Florida
Gulf of Mexico
Big Lagoon, Florida
Turtlegrass Study Site (2)
St. Joseph Bay, Florida
Turtlegrass Study Site (2)
Keys Turtlegrass Study Site

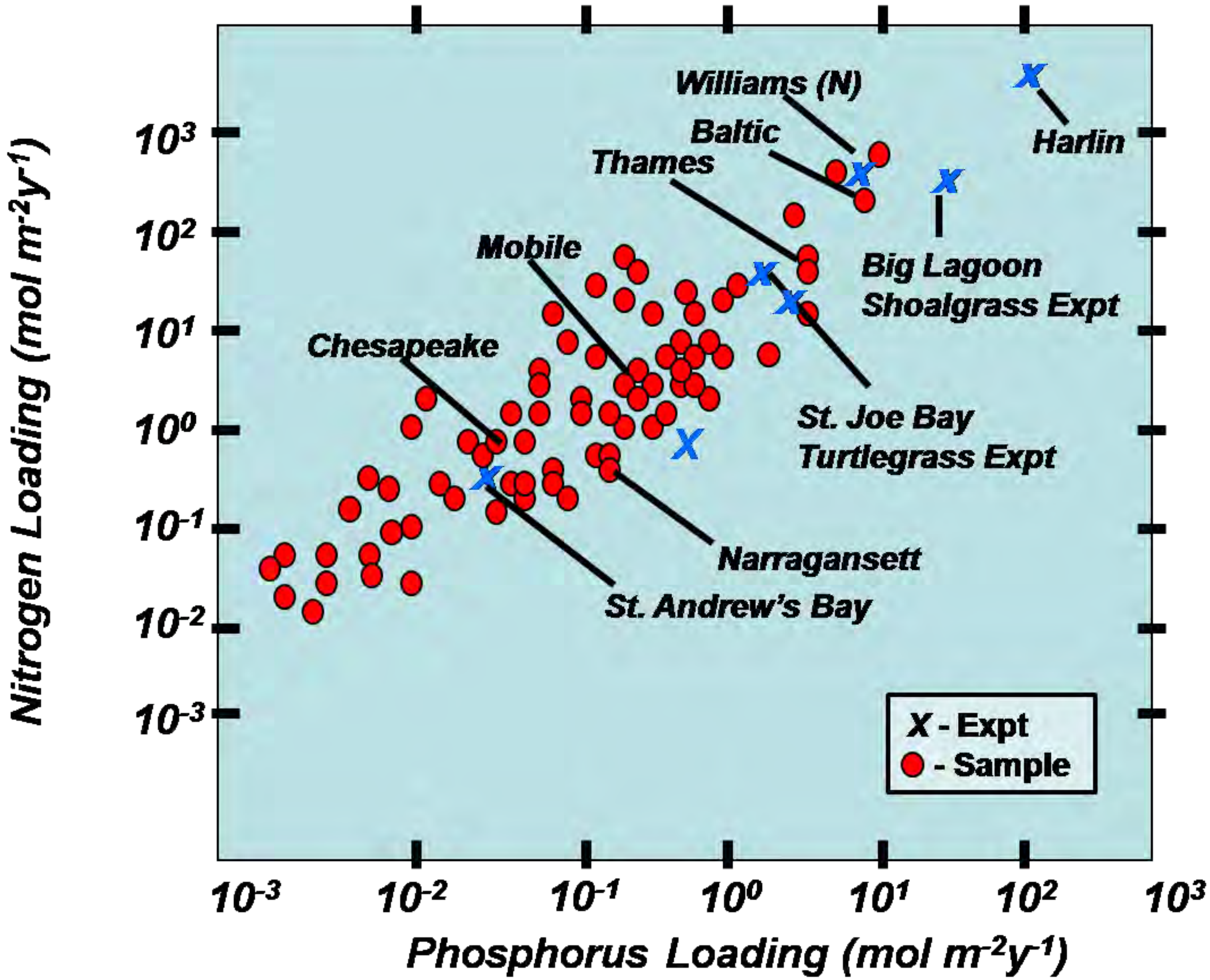
Experimental Design (1993-2005)



Nutrients Added in Turtlegrass Meadows via Osmocote

(N:P Molar ratio of 16:3)

Nutrient Loading in Coastal Systems



Source: After Nixon. 1986. J. Limnol. Soc. South Africa. 12: 43-71

Examples of Grazers Used

Peracarids:



Caridean Shrimp:


Gastropods:


Fish:

Omnivorous Pinfish

< 90mm SL mainly carnivorous

> 90mm SL mainly herbivorous

Summary of Experiments 1-5

- **Lots of significant grazer effects (fewer epiphytes and increased seagrass) and some significant nutrient effects**
- **But <u>never significant overgrowth of seagrass by algae,</u> even with few grazers**

Sources: Heck et al. 2000, *L&O*; Armitage et al., 2005 *Estuaries*; Heck et al 2006, *MEPS*, Baggett et al., in press, *MEPS*

Conclusions

- **Nutrient enrichment is unlikely to cause algal overgrowth of seagrasses and subsequent seagrass loss, unless additional factors (such as overfishing) substantially reduce small grazer abundance**

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Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach

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The positive effects of epiphyte grazers were comparable in magnitude to the negative impacts of water column nutrient enrichment, suggesting that the 2 factors should not be considered in isolation of each other.

impacts on epiphyte biomass. The positive effects of epiphyte grazers were comparable in magnitude to the negative impacts of water column nutrient enrichment, suggesting that the 2 factors should not be considered in isolation of each other. Until the determinants of epiphyte grazer populations are empirically examined, it will be difficult to address the contribution that overfishing and cascading trophic effects have had on seagrass decline. Because increases in water column nutrients are documented in many regions, efforts to reduce coastal eutrophication are an appropriate and necessary focus for the management and conservation of seagrass ecosystems.

KEY WORDS: Seagrasses · Meta-analysis · Epiphyte · Nutrients · Grazers · Management · Eutrophication · Top-down/bottom-up

INTRODUCTION

Recent theoretical and empirical studies have clearly linked anthropogenic stressors to dramatic and widespread declines in the functioning of coastal marine ecosystems (Dayton et al. 1998, Lenihan & Peterson 1998, Fourqurean & Robblee 1999, Hughes et al. 2003, Stankelis et al. 2003). Among the most pervasive anthropogenic disturbances to coastal ecosystems are eutrophication (Howarth et al. 2000) and overfishing (Jackson et al. 2001). Anthropogenic changes have a particularly strong impact on ecosystem function when they affect ecologically important species such as seagrasses (Orth & Moore 1983, Short & Wyllie-Echeverria 1996, Hall et al. 1999). The prevalence of fishing pressures and nutrient loading in coastal systems and the strong experimental tradition in seagrass community ecology make seagrass beds ideal systems in which to explore the basic ecological importance of 'top-down' (i.e. higher trophic level influences, including predation) and 'bottom-up' (i.e. resource supply to primary producers) processes (Williams & Heck 2001; see Fig. 1 for a depiction of the seagrass food web).

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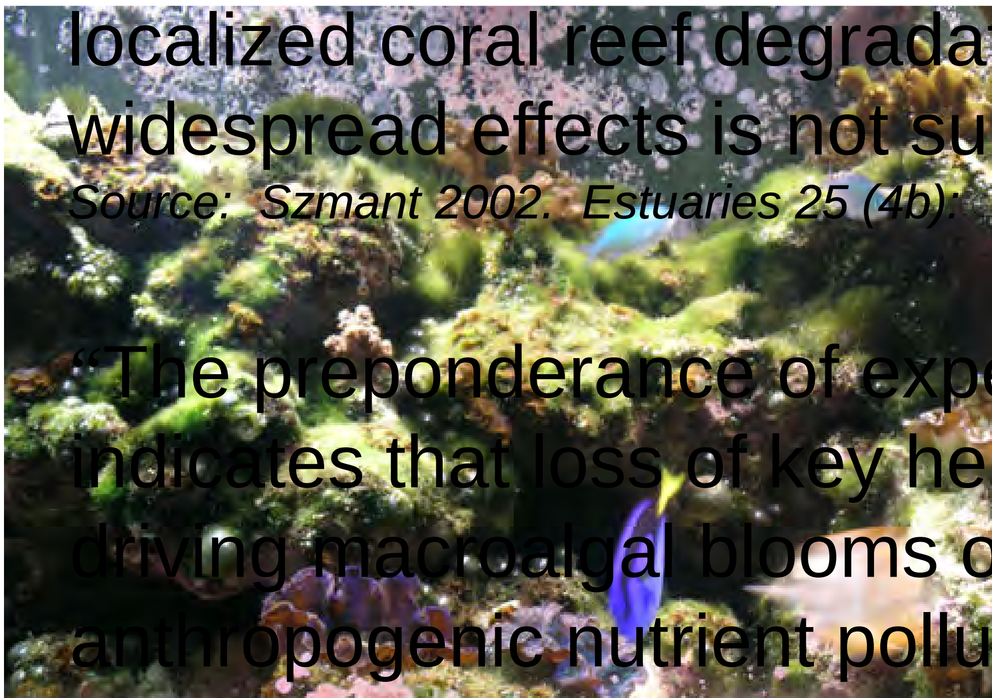
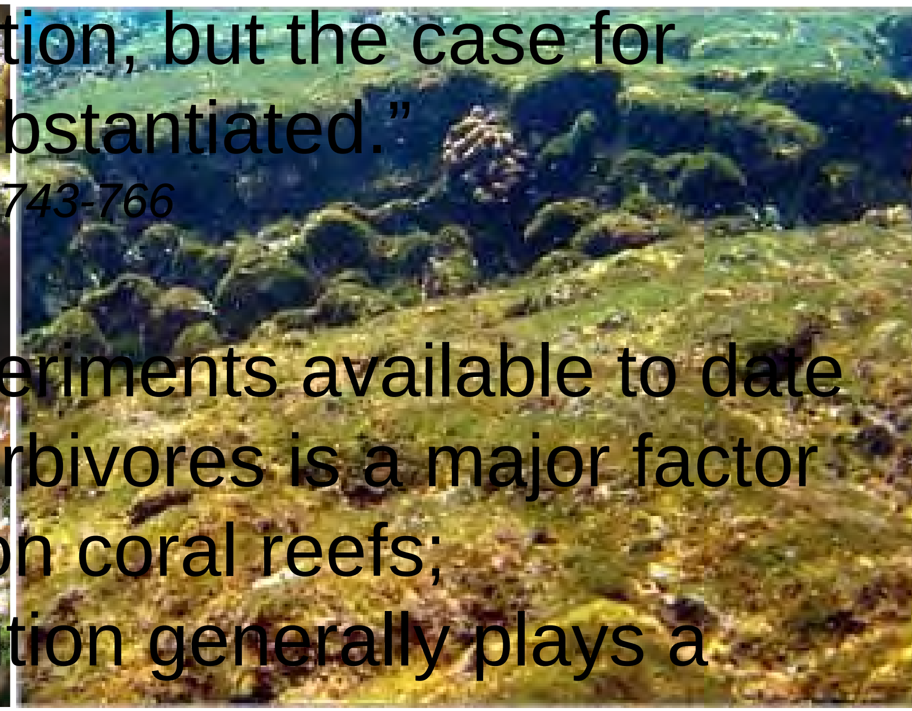
Recent Seagrass Experiments Showing Major Consumer Effects

- **McCall and Rakocinski. 2007. Grass shrimp play a pivotal trophic role in enhancing *R. maritima*. Ecology 88: 618-624.**
- **Moksnes et al. 2008. Trophic cascades in a temperate seagrass community. Oikos 117: 763-777.**
- **Jephson et al. 2008. Trophic interactions in Zostera marina beds along the Swedish coast. MEPS 369: 63-76**
- **Baden et al. (in press). Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: a broad-scale field experiment in the Baltic-Skagerrak area. Limnol Oceanogr**

Meta-analyses of Nutrients vs. Grazers in Other Benthic Habitats

Coral Reefs





"Over- enrichment can be and has been the cause of localized coral reef degradation, but the case for widespread effects is not substantiated."
Source: Szmant 2002. Estuaries 25 (4b): 743-766

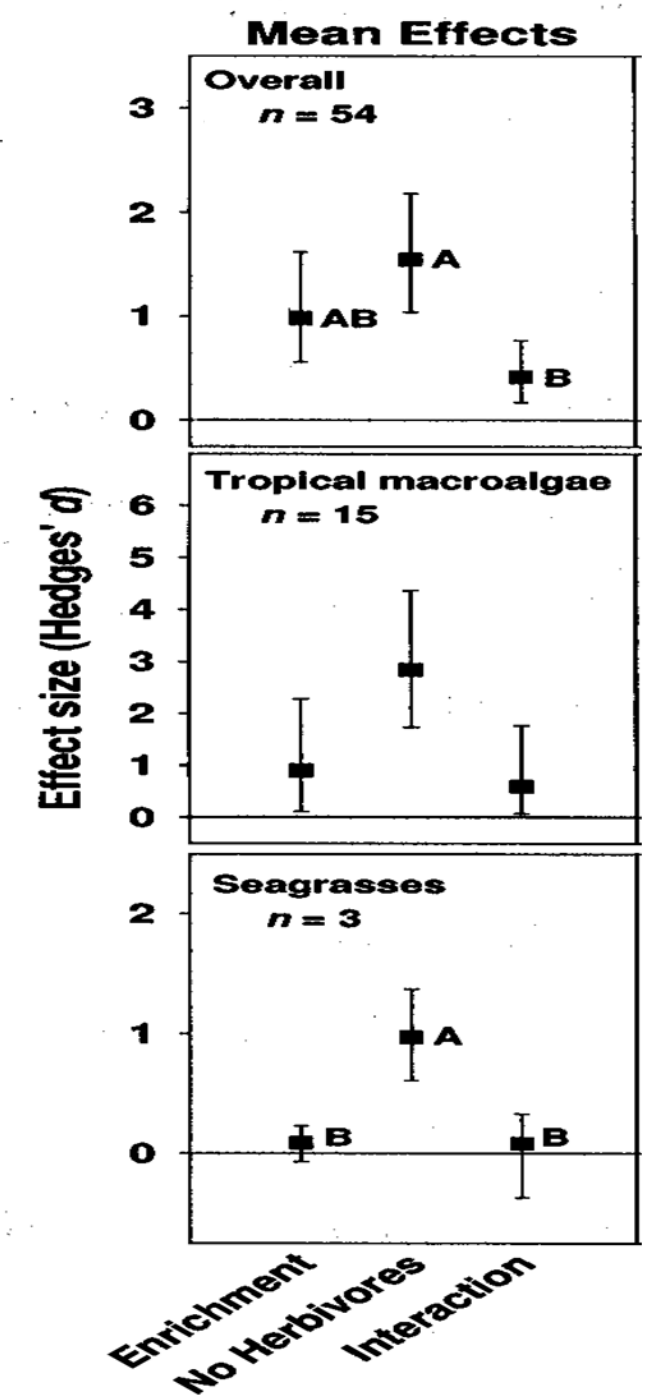
"The preponderance of experiments available to date indicates that loss of key herbivores is a major factor driving macroalgal blooms on coral reefs; anthropogenic nutrient pollution generally plays a more minor role." *Source: Sotka & Hay 2009. Coral Reefs 28: 555-568*

Meta-analyses for All Marine Primary Producers

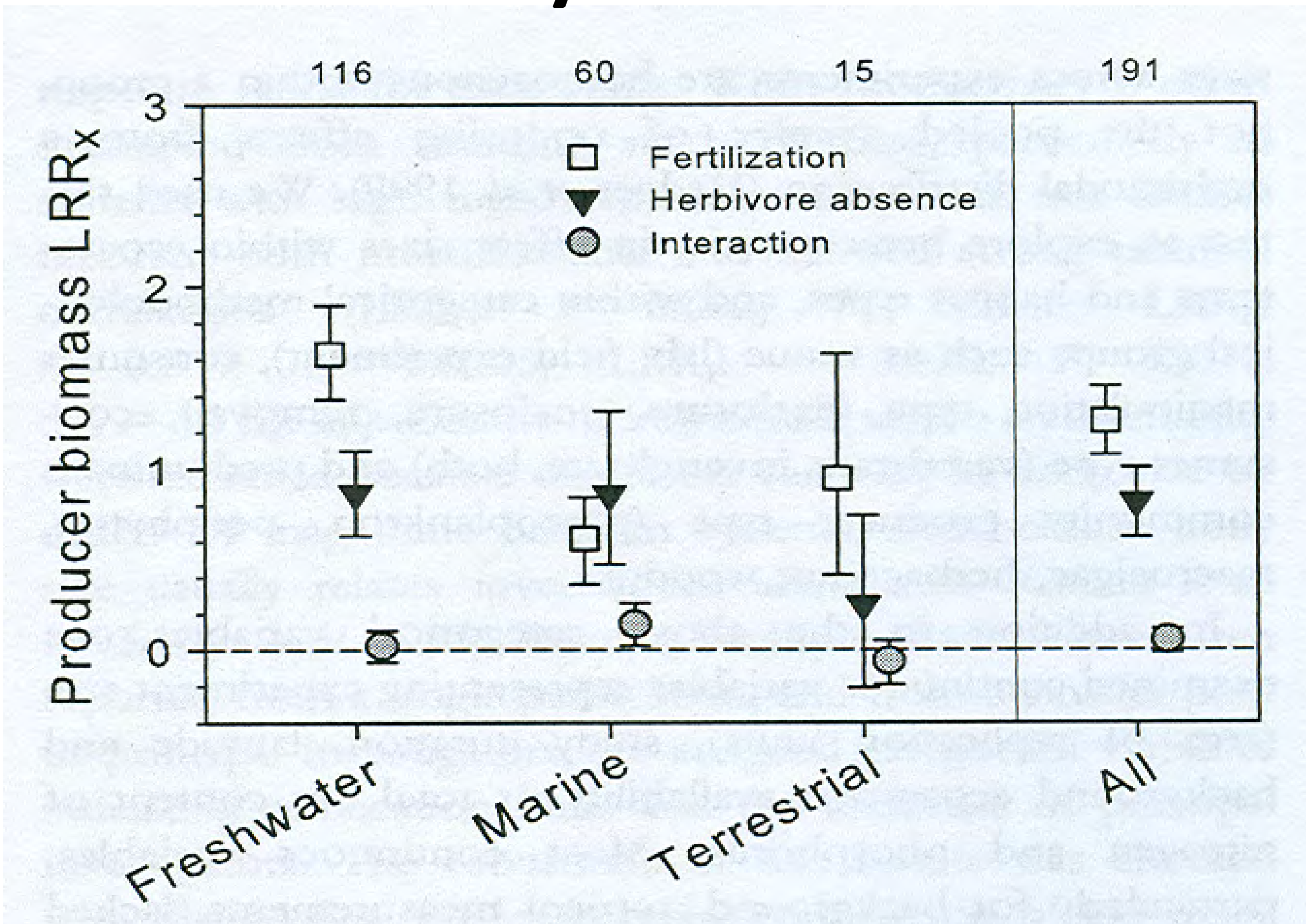
Results of meta-analyses on mean effects for primary producers overall, tropical macroalgae, and seagrasses. A positive *d* indicates an increase in primary producer abundance.

"Herbivores consistently had stronger effects than did nutrient enrichment for both tropical macroalgae and seagrasses"

Source: Burkepile and Hay, Ecology 2006.



Nutrients vs. Herbivore Effects across Systems



Log response ratio (LRR = 'effect size') of fertilization, herbivore absence and their interaction on producer biomass across ecosystems. An LRR is significant when the 95% CIs do not overlap the dashed line of zero effect, and is distinct from other LRRs when 95% CI do not overlap. **Source: Gruner et. al (2008) Ecology Letters 11: 740-755**

Overall Conclusions

- **Grazer effects and nutrient effects are both significant and they interact, but most often grazer effects explain more variance in algal biomass**

- **It is well past time to change the conventional wisdom that nutrient supply (and not consumers) primarily determines benthic algal abundance in coastal waters**

Practical Implications

- **Reducing nutrient input into coastal waters, usually at great expense, will not eliminate benthic algae and lead to recovery of habitats such as seagrass beds or coral reefs if food webs have been altered so that algal mesograzers are not present**

Heck and Valentine 2007. The primacy
of top-down effects in benthic coastal ecosystems.
Estuaries and Coasts 30: 1-11.

To Recap

- What I am **<u>not</u>** saying: nutrients don't matter or that they do not lead to algal overgrowth.

- What I **<u>am</u>** saying: that algal grazers usually explain as much, or more, variation in algal abundance than nutrients.

- Therefore, the only logical conclusion is that **<u>nutrients and fisheries must be co-managed</u>** to promote the rehabilitation of coastal ecosystems.

Some Unanswered Questions

- Are we wrong about the importance of grazers because the scale of studies has been too small or too short? **Possibly. Solution: Larger, embayment-scale studies.**

- Are there latitudinal differences in the stimulatory effects of nutrients on algae (i.e., more impacts in cold than warm climates)? **Maybe. Solution: Studies in cold waters. However, recent work in Sweden by Moksnes et al (2008, Oikos) has also shown stronger Top-Down effects. Current work in 2009 in Australia will also be informative.**

Some Unanswered Questions (2)

- Herbivores prefer nitrogen rich plants (see Preen 1995; Goecker et al. 2005), and they grow faster on N-rich foods, so how can palatable, N-rich filamentous green algae accumulate in eutrophic waters? **Only because there must be very few grazers present.**
- Can chemically defended taxa (e.g., red and brown algae) become abundant even in the face of intense grazing? **Probably, and drift algal mats (reds and browns) may be an example**

Some Unanswered Questions (3)

- Won’t low D.O. in algae-rich areas prevent grazers from surviving? **This can happen, but we must explain why grazers did not control algae before they became so abundant they caused low D.O. (Similar to the issue of latitudinal gradients in grazer control).**