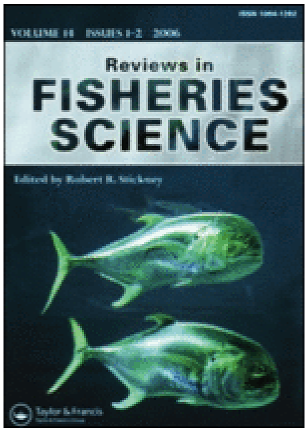

Ecological stoichiometry, biogeochemical cycling, invasive species and aquatic food webs: San Francisco Estuary and comparative systems

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Complete List of Authors:	Glibert, Patricia; University of Maryland Center for Environmental Science, Horn Point Laboratory Fullerton, David; Metropolitan Water District Burkholder, JoAnn; North Carolina State Univeristy, Center for Applied Aquatic Ecology Cornwell, Jeffrey; Univerisity of Maryland Center for Environmental Science, Horn Point Laboratory Kana, Todd; Univerisity of Maryland Center for Environmental Science, Horn Point Laboratory
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Ecological stoichiometry, biogeochemical cycling, invasive species and aquatic food webs: San Francisco Estuary and comparative systems

Patricia M. Glibert[1], David Fullerton[2], JoAnn M. Burkholder[3], Jeffrey C. Cornwell[1], and Todd M. Kana[1]

[1]University of Maryland Center for Environmental Science, Horn Point Laboratory, PO Box 775, Cambridge MD 21613; glibert@umces.edu

[2]Metropolitan Water District, 1121 L St., Suite 900, Sacramento CA 95814

[3]Center for Applied Aquatic Ecology, North Carolina State University, Raleigh, NC 27695 USA

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Key words: ammonium, Bay Delta, *Corbula*, delta smelt, *Egeria, Microcystis*, nutrient ratios, pelagic organism decline, pH effects, phosphorus limitation, stoichiotrophic imbalance

Abstract

Eutrophication has altered food webs across aquatic systems, but effects of nutrient stoichiometry have received less attention. Here, 30-year records of inorganic nitrogen and phosphorus concentrations, phytoplankton, zooplankton, invertebrates, and fish in the San Francisco Estuary were examined to collectively interpret ecosystem changes within the conceptual framework of nutrient stoichiometry and dynamics. Nutrients and nutrient ratios were highly related to many food web changes, consistent with different physiological requirements of different species or groups. This analysis suggests that nutrient changes led to a cascade of biogeochemical changes, leading, in turn, to altered stable states that were conducive to invasions of exotic macrophytes and bivalve molluscs, and to increases in the cyanobacterium *Microcystis*. Various other aquatic ecosystems have shown parallels in food web shifts linked to similar stoichiometric changes. This analysis indicates that nutrient stoichiometry is a significant driver influencing food webs in the Bay Delta. Altered nutrient supplies and associated biogeochemical changes helped invasive species thrive and led to various changes that have heretofore been considered stochastic. An overall implication is that remediation of planktivorous fish populations in the San Francisco Estuary will require significant reductions in nitrogen to restore the prior ecological stoichiometric balance.

OUTLINE

INTRODUCTION

This review applies eutrophication (e.g., Cloern, 2001), ecological stoichiometry (Sterner and Elser, 2002) and stable state theory (Scheffer et al., 1993) as an overall framework in evaluating the extent to which decadal changes in aquatic food webs in the San Francisco Bay Delta and comparative systems have resulted from human-driven changes in nutrient loads and forms. Eutrophication is the process whereby systems are enriched with nutrients with various deleterious effects, but stoichiometry relates changes in the relative elemental (e.g., nitrogen (N) and phosphorus (P)) composition in body tissue and the water column. Here, 30 years of records of inorganic N and P concentrations, phytoplankton, zooplankton, invertebrates, and fish in the San Francisco Estuary were examined to collectively interpret ecosystem changes within the conceptual framework of nutrient dynamics. The premise of this paper is that alterations in nutrient stoichiometry have profound consequences for aquatic food webs resulting from different organismal needs for different nutrients, and different abilities to sequester the nutrient that is in least supply. Stated more formally, the questions addressed in this paper are: Do systems exhibit self-assembly in fundamentally similar ways when nutrient stoichiometry is altered, and how has this been expressed in the San Francisco Bay Delta and comparative systems? Does changing nutrient stoichiometry have ecosystem effects even when nutrients are not at levels normally taken to be limiting by primary producers? If the food web changes that have occurred are related to nutrient loads, what are the biological, physiological or biogeochemical processes that help to explain, mechanistically, why such food web changes may have occurred? And, what are the management implications of such relationships?

These questions are highly relevant considering that cultural eutrophication is one of the most pressing problems affecting both coastal and freshwater ecosystems worldwide (e.g., Meybeck, 1989, Vitousek et al., 1997a,b; Howarth et al., 2002; Galloway and Cowling, 2002; Turner et al., 2003; Conley, 2009, Doney, 2010). Nutrient pollution is on the rise because of dramatic increases in human populations in many regions, and concomitant increasing demands for energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in diet that are leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Smil, 2001; Galloway and Cowling, 2002; Galloway et al., 2002; Howarth et al., 2002; Wassmann, 2005; Glibert et al., 2010a). Although eutrophication is occurring globally, nutrient export from coastal watersheds is not evenly distributed (Seitzinger et al., 2002a, 2005; Howarth et al., 2005; Glibert et al., 2006a, 2010a), nor is the export of N and P changing proportionately. There is much to be understood about the implications of changes in N:P supplies, globally and regionally for aquatic food webs. Differentiating food web changes due to nutrient loads from those due to stochastic events has important implications for restoration and management.

Nutrient enrichment interacts with aquatic food web dynamics in complex ways. At the planktonic level, many of these changes are well understood. With nutrient enrichment a shift in plankton assemblage composition is frequently observed, with large diatoms giving way to smaller phototrophs such as cyanobacteria and various flagellates (e.g., Smayda 1989; Marshall, 2003; MacIntyre et al., 2004; Finkel et al., 2010). Many of these species can be harmful to higher trophic levels, disrupting normal ecosystem function. The dominance of such species can result in a failure of normal predator-prey interactions, which in turn enhances the transfer of nutrients that sustain the blooms at the expense of competing algal species (Irigoien et al., 2005; Mitra and Flynn, 2006; Sunda et al., 2006). Such changes have implications at all levels of the food web. Increased phytoplankton and macroalgal proliferations at high nutrient levels affect seagrasses and benthic microbiota that compete for light (Harlin, 1993; Deegan et al., 2002; Burkholder et al., 2007), altering food web structure by changing the habitat needed to support fish and shellfish. All aspects of metabolism, predator-prey interactions, and species success are altered when a system is stressed by nutrient over-enrichment (Breitburg et al., 1999; Breitburg 2002).

Adding to the complexity of understanding system and food web changes due to increased nutrients is the relatively recent phenomenon of changing stoichiometry of nutrient supplies. In many parts of the developed world, as a means to reduce or control algal blooms, P reductions are being undertaken (e.g., in sewage effluents and laundry detergents), but N loads often remain elevated (Glennie et al. 2004, European Environment Agency 2005). Thus, not only have many systems undergone eutrophication, but many are showing signs of reversal due to this single nutrient reduction. Yet, even when many eutrophication symptoms are reduced, such as hypoxia and algal blooms, systems only appear to partially recover (Burkholder, 2001a,b); their food webs do not appear to return to their pre-eutrophic state.

The San Francisco Estuary, or Bay Delta, California, U.S.A. (Fig. 1) is an ideal ecosystem for addressing the questions posed above. The Bay Delta is one of the largest estuarine systems on the U.S. Pacific Coast as well as one of the nation's largest managed and engineered water systems. It is the largest source of municipal and agricultural fresh water in California, and is home to economically important fisheries. From phytoplankton to fish, the food web of this system has changed significantly over the past several decades (Alpine and Cloern, 1992; Jassby et al., 2002; Kimmerer et al., 2004; 2010; Jassby, 2008). The Bay Delta has been extensively monitored for most biological constituents over the past several decades, so this is a system rich in data with which to explore these relationships. It has also been influenced by major nutrient loads that have not only increased over time, but have also changed in composition (e.g., Van Nieuwenhuyse, 2007; Dugdale et al., 2007; Jassby, 2008; Glibert, 2010). Nitrogen loads have increased substantially since the mid-1980s, while P loads increased, then declined in the mid-1990s to levels that approximate earlier conditions.

The Bay Delta is an inverse delta, receiving the majority of its flow from the Sacramento and San Joaquin Rivers (Atwater et al., 1979; Nichols et al., 1986). The Sacramento River is the larger river, contributing about ~80% of the freshwater to the system (Jassby, 2008). The upper reaches drain 61,721 km^2, while the upper San Joaquin River drains 19,030 km^2 (Sobota et al., 2009). Major modifications to the Bay Delta have occurred over the past century, including drainage of marshes to support agriculture, installation of dikes to prevent farmland flooding, expansion and deepening of shipping lanes, and significant diversion of water to various users throughout the state (Atwater et al., 1979). The Sacramento and San Joaquin Rivers converge at the confluence of the delta, then flow into Suisun Bay, San Pablo Bay, then ultimately the Central and South Bays. River flow has varied about 10-fold in the past decades due to the effects of El Niño, prolonged droughts and ENSO wet years (Jassby, 2008).

The Bay Delta ecosystem has also been significantly modified by invasive species, including clams, bay grasses, various species of copepods, and fish over the past several decades (Carlton et al., 1990; Cohen and Carlton, 1995, 1998; Kimmerer, 2002). In fact, this system has been characterized as one of the most heavily invaded estuaries (Cohen and Carlton, 1995, 1998), with most of these invasions traced to increased trading with Asia and "discharge of ballast water, inadvertent or deliberate release of aquarium organisms, deliberate introduction for fisheries, and inadvertent release of bait organisms" (Kimmerer, 2004, p. 8; NRC, 2010). The Bay Delta has been used as an example of a system undergoing "invasion meltdown," implying that frequent invasions alter habitat and promote additional invasions (Simberloff and Von Holle 1999, Simberloff, 2006), perhaps to the point of "no return." The extent to which habitat changes brought about by nutrient enrichment has contributed to these successful invasions, as well as other food web changes, has not been explored.

The fundamental question of whether changes in the food web are a result of anthropogenic changes, especially changes in nutrient loads and balance, or whether they are the result of stochastic events, has more than academic relevance. Many management questions and actions are directly affected by the extent to which the factors contributing to the food web changes can be identified and managed. Several fish, including the delta smelt (*Hypomesus transpacificus*) and longfin smelt (*Spirinchus thaleichthys*), are on the Federal Endangered Species list or are considered threatened (Wanger, 2007a,b). Water exports have been restricted by court order in recent years in an attempt to restore these species; new habitat is being created in the hope that it will contribute positively to the restoration of the system; and major re-engineering of the flow is also being debated for the coming decades (e.g., Bay Delta

Conservation Plan, 2010, http://baydeltaconservationplan.com/BDCPPlanningProcess/ReadDraftPlan/ReadDraftPlan_copy1.aspx). Costs of these efforts are estimated in the hundreds of millions to billions of dollars at present and over the coming years.

Despite current management efforts, delta smelt have undergone further significant population declines in the past decade, along with longfin smelt, threadfin shad (*Dorosoma petenense*) and young-of-the-year striped bass (*Morone saxatilis*; Rosenfield and Baxter, 2007; Sommer et al., 2007, Baxter et al. 2010). Accelerated losses during the last decade have been termed the “Pelagic Organism Decline” (POD) period (Sommer et al., 2007, Baxter et al. 2010). Much of the debate about the declines in fish populations have been centered on the effect of the export pumps that supply the water to large aqueducts that transport it throughout the state for municipal and agricultural use.

The complexity of the Bay Delta system – hydrologically and ecologically – cannot be underestimated. Kimmerer (2004, p. 12) noted that “complex environments such as estuaries often seem not to obey general rules, but to respond in specific ways for which the general literature on estuaries provides little guidance.” The frequent changes, invasions, and effects of engineering and other management actions complicate these relationships. This paper focuses on nutrient issues that heretofore, for the most part, have not been emphasized, and suggests some “general rules” by which such systems may respond. While there have been multiple freshwater systems for which ecological stoichiometric (Sterner and Elser, 2002) and stable state principles (Scheffer et al., 1993) have been applied (described in more detail throughout this paper), there have been relatively few examples where these principles have been applied in estuaries. Recent evidence suggests that the changes in trophodynamics in the Bay Delta system may be related to nutrient changes (e.g., Wilkerson et al., 2006; Dugdale et al., 2007; Van Nieuwenhuyse, 2007; Glibert, 2010). However, ecosystem changes have not been collectively interpreted in the conceptual framework of nutrient dynamics. The multiple stressors on fish and the aquatic system in general have been, and are, the subject of multiple working groups, panels, and a National Academy Study (NRC, 2010) as the management implications are far-reaching.

This paper is written in six parts, bringing to bear the ecological principles of eutrophication (*sensu* Cloern, 2001), ecological stoichiometry (*sensu* Sterner and Elser, 2002) and alternative state theory (*sensu* Scheffer et al. 1993). Part I outlines the conceptual overviews of eutrophication, elemental stoichiometry, nutrient ratios, and alternative stable states and their inter-relation. Part II probes the long-term nutrient and organismal changes in the Bay Delta and their ecological stoichiometric relationships, beginning with phytoplankton, then zooplankton, invertebrates, fish and macrophytes along with their trophic interactions. This analysis extends that of Glibert (2010) with a more comprehensive examination of the changes in trophic components and their interactions. In Part III, the complexities of biogeochemical processes and how they relate to changes in the food web are considered. This section also develops the apparent relationships between the emergence and production of macrophytes, blooms of the toxic cyanobacterium, *Microcystis aeruginosa*, and changes in biogeochemical fluxes that may accentuate food web changes. Part IV compares the Bay Delta to selected freshwater and estuarine ecosystems, given that "the comparative method assembles the separate realizations needed for scientific inference by … recognition of information of patterns naturally occurring in temporal and spatial variations in existing conditions and phenomena" (GEOHAB, 2006, p.9). Part V compares the ecological stoichiometric and alternate stable state interpretations of changes with some prevailing views of system change in the Bay Delta. Lastly, Part VI concludes with a summary of the implications of these ideas with respect to current debates and challenges with respect to nutrient management, the development of nutrient criteria, and predictions for system recovery upon nutrient removal. Directions for further study are also suggested.

PART I: EUTROPHICATION, ECOLOGICAL STOICHIOMETRY, NUTRIENT RATIOS, AND ALTERNATE STABLE STATE THEORY

Eutrophication

Although the term “eutrophication” has been variably defined (e.g., Nixon, 1995; Richardson and Jørgensen, 1996; Andersen et al., 2006; Ferriera et al., 2010), central to all definitions is the concept that the enrichment of water by nutrients causes an enhanced biomass and/or growth rate of algae, which, in turn, leads to an undesirable disturbance in the balance of organisms present in the water and to the quality of the water body concerned (Burkholder, 2001a,b; Duarte et al. 2008; Glibert et al., 2010a). The effects of eutrophication in estuaries and marine coastal waters are generally characterized in terms of increased chlorophyll *a* in the water column, loss of dissolved oxygen leading to hypoxia or anoxia, loss of seagrasses, and loss of certain fisheries (Cloern, 2001). Increases in many harmful algal species have also been associated with eutrophication (Hallegraeff, 1993; Anderson et al. 2002, 2008; Glibert et al., 2005a,b, 2006a, 2010a; Glibert and Burkholder, 2006; Heisler et al., 2008).

The ecosystem response to eutrophication is a continual process rather than a static condition or a trophic state (Cloern, 2001; Smayda, 2006). As a result of differences in nutrient loading, estuaries on the U.S. west coast have, for example, generally been characterized as less eutrophic than east coast estuaries (Bricker et al., 2007, 2008). Historically, the concept of eutrophication was mostly applied to the natural aging of lakes, from deeper waters to a marsh (Wetzel, 2001); more recently, the terms “accelerated” or “cultural” eutrophication have been used in recognition of major human influences (e.g., Burkholder et al., 2006, 2007). Cloern (2001) identified three conceptual phases of eutrophication. In the first phase, responses in ecosystems are directly related to changes in nutrient loading; these responses included such changes as chlorophyll *a*, primary production, dissolved oxygen or other measures of system metabolism. In the second phase, it was recognized that estuaries act as filters, modulating the responses so that both direct and indirect effects can be accounted for, and that system typology (e.g., Kurtz et al., 2006; Madden et al., 2010) may also contribute to the variations in observed responses to similar nutrient loadings. Indirect effects include changes in habitat, changes in the benthos, changes in sediment biogeochemistry, and changes in food web structure, among other responses. These changes in turn influence the direct responses, which include changes in chlorophyll *a*, primary production, development of harmful algal blooms (HABs), and changes in macroalgal composition and biomass, among others. Finally, the third phase stresses interactive effects of multiple stressors on a system, including contaminants, exotic or invasive species, aquaculture development, climate change and hydrological changes (Fig. 2). Here, the conceptual Phase III model of Cloern (2001) is coupled with the ecological stoichiometric framework to further our understanding not only of the effects of nutrient loading, but also the effects of disproportionate nutrient loading (or nutrient removal). A new phase of understanding is introduced, based on the premise that food web changes may be understood and potentially predictable if stoichiometric relationships are known.

Ecological stoichiometry

Ecological stoichiometry provides a framework for "taming" the complexity of eutrophication responses. Ecological, or elemental, stoichiometry suggests that different organisms will dominate under different relative proportions of critical elements (carbon (C), N, or P) due to differences in allocation of C, N and P in the types of structures that build different types of organisms (Sterner and Elser, 2002). Different organelles have different requirements for C, N or P and, therefore, different types of organismal structures, and ultimately organisms will have different C:N:P allocations (Sterner and Elser, 2002). As noted by Hall (2009, p. 504), "Ecological stoichiometry formalizes what should be obvious: Organisms interacting in food webs are composed of different elements, such as C, N, or P. As a result, energy and nutrient flow through consumer-resource interactions obey fundamental constraints."

In particular, ribosomes are high in P relative to N; they are "the most P rich and lowest N:P organelles in cells" (Sterner and Elser, 2002, p. 73). Ribosomes are required for growth, and an increase in ribosomes is required for a cell to have an increase in growth rate. This is well illustrated for phytoplankton, for example (Geider and LaRoche, 2002; Sterner and Elser, 2002; Quigg et al., 2003; Finkel et al. 2010). Fast-growing cells have a lower N:P ratio than their more slowly growing counterparts. They have proportionately more allocation of resources to "assembly machinery" (rRNA) than to "acquisition machinery" (protein) (Elser et al., 2003; Klausmeier et al., 2004). In contrast, phytoplankton that can sustain their metabolism when resources are low – i.e., more slowly growing cells, have a higher proportion of pigments and proteins with proportionately higher N:P ratio (Sterner and Elser, 2002; Elser et al., 2000a, Elser 2006; Arrigo 2005; Finkel et al., 2010; Fig 3.). Slowly growing cells are also generally, but not always, larger in size (e.g., Malone, 1981; Kagami and Urabe, 2001; Finkel et al. 2010). Slowly growing, nutrient-stressed phytoplankton, however, may also have the capability of short-term transport of the limiting nutrient in excess of growth demands (e.g., Glibert and Goldman, 1981; Terry et al., 1985), leading to highly variable N:P ratios under transient conditions (Flynn, 2002); thus, the change in N:P ratio with algal growth rate is not necessarily a linear function (Ågren, 2004).

At the level of organismal structure, stoichiometry also varies. There is a greater need for P in skeleton and bone than in skin, heart, kidney, muscle or brain (Sterner and Elser, 2002). The latter all have a high N:P content (Sterner and Elser, 2002). Small fish, therefore, that have a higher muscle:skeleton ratio than large fish have a higher biomass N:P ratio. Whereas whole fish N content generally varies across a relatively small range, ~8-11%, whole fish P content tends to vary from ~1-5% (Sterner and George, 2000). Biomass N:P of fish generally ranges from ~5-15 (Sterner and George, 2000; Fig. 4). Piscivorous fish are generally larger than planktivorous fish, and have more bone and skeleton. As emphasized by Sterner and Elser (2002, p. 254), “as one ascends the pelagic food web...trophic groups grow increasingly nutrient and especially P rich...” Thus, fish community composition as well as fish size should change as a function of N:P ratio.

Ecological stoichiometric principles have also been invoked in predicting the overall fitness of a population. As noted by Sterner and Elser (2002), the balance of multiple chemical elements has many consequences for community dynamics. These authors state that “Stoichiometry can either constrain trophic cascades by diminishing the chances of success of key species, or be a critical aspect of spectacular trophic cascades with large shifts in primary producer species and major shifts in ecosystem nutrient cycling”. The relative balance of nutrients affects all aspects of behavior (i.e., in meeting nutritional demands), growth rate, fecundity, and ultimately the success of different populations (Jeyasingh and Weidner 2005, 2007). Biodiversity should therefore be a consequence of stoichiometry and populations should self-stabilize as a result of stoichiometric constraints.

Phototrophs generally have limited ability to dissipate nutrients because they do not actively excrete, and are more likely to reflect the stoichiometric proportions and the variability of their environment. They are more likely to follow the “you are what you eat” model (Sterner and Elser, 2002, p.16), and this has been elegantly demonstrated for many phytoplankton in culture, where, for example, it has been shown that the medium N:P ratio and the cellular N:P ratio of the chlorophyte *Scenedesmus* are very similar when grown over a range of N:P ratios in culture (e.g., Rhee, 1978). Some field comparisons of N:P stoichiometry in dissolved substrates have also compared favorably with that of particulate matter in some regions (e.g., Glibert et al. 2006b), but examples of a range of relationships between dissolved and particulate matter can be found. Many phytoplankton species or species groups do have adaptations to life under non-Redfieldian conditions. For example, cyanobacteria have a wide range of abilities to thrive at both the low and the high N:P ends of the Redfield spectrum, with many species having the capability to fix N_2 when N is limiting, and other species having the capability of reducing their P requirement at the high end. Many cyanobacteria can substitute non-P containing lipids when P is low (Van Mooey et al., 2009) and some cyanobacteria have alkaline phosphatase activity that can be more than 30-fold higher than that in diatoms (Giraudet et al., 1997). Very small cells, such as the cyanobacteria *Prochlorococcus, Synechococcus*, and the pelagophyte *Aureoumbra lagunensis* have very low P requirements, leading to very high cellular C:P or N:P ratios (Liu et al., 2001; DeYoe et al., 2007; Finkel et al., 2010). Mixotrophy provides another mechanism by which many species can thrive outside the normal Redfield range of nutrients (Burkholder et al., 2008). Cyanobacteria, diatoms and flagellates differ in size by several orders of magnitude (Finkel et al., 2010). Cell size, in turn, affects the cell's stoichiometry as well as a large range of physiological processes from resource capture to survival against predation to allelopathic interactions to motility and buoyancy (Flynn, 2002; Finkel et al., 2010).

Heterotrophs, in contrast, do not necessarily reflect the stoichiometric proportions of their chemical environment, because mechanisms of excretion and release favor the loss of non-limiting nutrients and the sequestering of the limiting nutrient (Sterner and Elser 2002; Fig. 5). Compared to plants, including microbial plants, heterotrophs are relatively inflexible in their stoichiometry (McIntyre and Flecker, 2010). Thus, heterotrophs that can sequester the nutrient in least supply relative to their needs should ultimately outcompete those that cannot effectively acquire what they need. They will become dominate, keystone species. These species further stabilize the nutrient environment by excreting, egesting, or respiring what they do not need (Sterner and Elser, 2002). The dichotomy between resource N:P ratios and consumer N:P ratios increases even more when consumers ingest nutrient-poor food; the need to dissipate excess nutrients increases (Vanni et al. 2002). Many bacteria also do not reflect the stoichiometric proportions of their resource, as they remineralize nutrients. As noted by Sterner and George (2000, p. 127), "Nutrient flux from resources to consumers and then to waste products can be thought of as a chemical reaction wherein *mass must balance*" (emphasis added). Moreover, as noted by Malzahn et al. (2007, p. 2063) based on Brett (1993), "stoichiometric needs of secondary consumers and the stoichiometry of prey are normally finely tuned." In fact, this means that fish, with their relatively inflexible skeletal requirements, have a greater likelihood to be limited by nutrients than energy or other factors (McInyre and Flecker, 2010)

Stoichiometry would thus predict that the dominant keystone predator should have a biomass N:P ratio that is inversely related to the N:P ratio of the ambient nutrient pool, and homeostasis from nutrient recycling will drive the nutrient balance of the system to be self-sustained. Yet, homeostasis comes at a cost, typically a reduction in the rates of growth or reproduction (Boersma 2000, Boersma and Kreutzer 2002, Boersma et al., 2008). Schindler and Eby (1997) showed that obligate planktivores are most likely to recycle nutrients at high N:P ratios. McIntyre and Flecker (2010, p.553), in a broad survey found that "the N:P ratio of excreted nutrient increased substantially with body size; on average, large fishes excreted relatively more N than P compared to smaller counterparts." Ecological stoichiometric principles thus suggest that many changes will occur in food webs as the N:P ratio changes (Sterner and Elser, 2002).

Biogeochemical processes are also affected by changes in nutrients. Under eutrophic conditions in shallow systems, benthic biogeochemical processes are particularly important, as these processes may sustain eutrophication and reduced oxygen levels through self-sustained feedbacks (Kemp and Boynton, 1992; Kemp et al., 2005). Return fluxes of N and P from the sediment act as a key feedback in enhancing eutrophication, and decreases in coupled nitrification/denitrification by anoxia result in a longer residence time of available N. There are multiple interacting feedbacks between nutrient cycling and biogeochemistry, food web dynamics and benthic-pelagic coupling. Overall, "disentangling….effects of anthropogenic stressors in human-altered systems and the potential for other stressors to exacerbate these effects" (Breitburg, 2002, p. 775) requires a comprehensive, multidimensional view linking nutrients to physiological responses, trophodynamics and food web structure. By applying stoichiometric principles, the expected changes in food webs and biogeochemical processes are predictable as N:P ratios increase (Fig. 6).

Many ecological stoichiometric relationships were developed in the whole-lake studies that were conducted in the 1970s-1990s (e.g., Schindler, 1974, 1977, 1988, 1990, 1991; Schindler and Fee, 1974; Schindler et al., 1987; 1993; Shapiro and Wright, 1984; Edmondson and Abella, 1988; Meijer et al., 1989; van Donk et al., 1990). Freshwaters are generally considered to be P-limited (Schindler, 1977), and there is a greater wealth of understanding of stoichiometric constraints in freshwater systems. Estuarine and coastal waters are more often considered to be N-limited at the primary producer level (Hecky and Kilham, 1988; Howarth, 1988; Howarth and Marino, 2006). However, as nutrient loads have changed in many parts of the world due to increasing N and decreasing P, this dichotomy of nutrient limitation is not the truism it once was. Sequestration of P in calcareous sediments leads to P limitation in some tropical regions (Smith, 1983; Fourqurean and Zieman, 1992; Touchette and Burkholder, 2000, and references therein). In lotic systems there is growing evidence of both N (Mosisch et al., 2001; Grimm et al., 2003) and P limitation (Martí and Sabater, 1996; Carr and Chambers, 1998), or N and P co-limitation (Rudek et al., 1991; Carr and Chambers, 1998; Elser et al., 2000a,b; Elser et al., 2007). Even in lakes, the paradigm of P limitation has recently been questioned (Elser et al., 2007; Lewis and Wurtsbaugh, 2008), although many hardwater lakes are still regarded as P-limited (Wetzel, 2001). A large-scale meta-analysis of algal response experiments across the world found no latitudinal differences in N vs. P limitation across the salinity gradient, and simultaneous N and P enrichment produced "strongly positive synergistic responses" across freshwater and marine environments (Elser et al., 2007). Nevertheless, ecological stoichiometric principles have not been rigorously examined in estuarine systems, as most current emphasis is on the effects of eutrophication or general nutrient enrichment.

Nutrient Ratios and Terminology

Nutrient stoichiometry is a comparison of nutrient ratios in solution or biomass. The concept of the Redfield ratio (Redfield, 1934, 1958), in which organismal C:N:P ratios are assumed to be in the proportion of 106:16:1 by atoms, is likely the most well-known stoichiometric relationship. Redfield (1934) documented that the N:P ratio of plankton should fall in the range of 16:1 on a molar basis, and hence deviations from this ratio (in both the particulate and the dissolved nutrient pools) have been interpreted as evidence of limitation. The Redfield ratio was developed from observations in oligotrophic waters where both biomass and nutrient concentrations are low and there is minimal interference from suspended sediments. The ratio of N:P provides a simple, easily measurable index, and total, particulate and/or dissolved N:P ratios are frequently used to evaluate nutrient status (Fisher et al., 1992; Glibert et al. 1995, 2004, 2006b). Changes in this ratio have been compared to shifts in plankton composition, yielding insight about the dynamics of nutrient regulation of plankton assemblages (e.g., Tilman 1977; Smayda, 1990; Hodgkiss and Ho, 1997; Hodgkiss, 2001; Heil et al., 2007). More recently it has been suggested that annual mean N:P ratios give a better indication of nutrient status than short-term measures of N and P (Smith, 2006), as nutrients may be uncoupled from the biomass at that same point in time due to the many processes by which nutrients are taken up, transported and and/or transformed in form.

Although N:P ratios can be useful in a relative sense, the same ratio can be obtained from vastly different numerators and denominators, as long as their proportions remain the same. Thus, an elevated N:P ratio, suggestive of P limitation, can be obtained by a depletion in P (true P limitation), or by an increase in N without a corresponding depletion in P. The latter is the case for the mouth of the Mississippi River, USA, where elevated N:P ratios have resulted from excess loading of N rather than from decreasing P (Justic et al., 1995; Rabalais et al., 1996; Turner and Rabalais, 2004; Dodds, 2006).

Most applications of N:P ratios consider only inorganic forms of N and P. Different ratios may be obtained depending on which form(s) is (are) included in the ratio (Dodds, 2003). The perspective of whether a system is N- or P-limited may be different depending on whether the N:P ratio is calculated solely with inorganic forms of N and P, or with both inorganic and organic forms. For example, on the western Florida shelf, the mean N:P ratio of the water off the Caloosahatchee River in May of 2003 was found to be considerably less than Redfield proportions when inorganic forms of N and P only were considered, leading to a conclusion of an N- limited system, but when the ratio of organic nutrients were included, the proportions suggested a P- limited system (Heil et al., 2007). Determining whether to include the organic fractions of N and P in such ratios may depend on the degree to which the organic fractions are bioavailable to the specific communities present. Unfortunately, much still is not known about the bioavailability of most organic constituents (Seitzinger et al., 2002b; Berman and Bronk, 2003). While virtually all algal species can use all forms of inorganic N and P, not all species can use organic nutrients equally well. In fact, there is no biological or chemical reason why a ratio of 16:1 on a molar basis would be an appropriate ratio for the highly variable nature of bioavailable DON and DOP. The calculation of nutrient ratios also changes depending on whether chemical interactions with particulate matter are taken into consideration. Nutrients, especially P, interact with particulate matter (via both adsorption and desorption), and result in deviation of both the particulate and dissolved N:P ratios. These interactions are discussed on more detail in Part III.

Alternate Stable State Theory

The alternate stable state theory was developed to describe the general state of shallow, productive lakes (Scheffer et al., 1993, 2003). This theory states that a system will develop a stable state condition, i.e., homeostasis will prevail, until an environmental change or disturbance occurs, altering the positive reinforcing feedbacks of homeostasis, and the population is shifted to a new stable state: hysteresis overcomes homeostasis (Scheffer et al., 1993; Scheffer and Carpenter, 2003). Such shifts can be abrupt (e.g., Tátrai et al., 2009). Communities may not return to their original state when the disturbance is removed.

Both direct and indirect interactions between and among organisms help to stabilize assemblages (Vanni, 2002). Trophic cascades and food chain interactions result from predator-prey interactions, release of organisms from predation pressure, propagated effects on both the biotic and abiotic environment and changes in availability of substrates, among many other factors. Nutrient loading, “bottom-up” control, and grazing, “top-down” control are ultimately interconnected. Their interconnectivity is at two levels. First, selective grazing alters nutrient regeneration. This has been well demonstrated, for example, at the microbial level. Macrozooplankton, such as copepods, can both enhance and reduce the flow of regenerated N. On the one hand, they release N directly, but how much and which form depends on what they ate and how long ago they ate it (Bidigare et al., 1983; Miller and Glibert, 1998). They also graze on both phytoplankton and microzooplankton, which are consumers and regenerators, respectively, of N (Caron and Goldman, 1990; Glibert, 1998). Copepods further stimulate NH_4^+ regeneration by bacteria through release of organic substrates during feeding and metabolism (Roman et al., 1988; Glibert, 1998), and by preying on larger microzooplankton that relieve smaller microzooplankton from predation, in turn resulting in higher NH_4^+ regeneration (Glibert et al., 1992; Miller and Glibert, 1998; Glibert, 1998). Similar interactions occur from size-selective predation by benthic invertebrates or fish (Vanni, 2002). Food web stability or balance thus depends on interactions at all levels, and factors that alter the balance of nutrients also alter the balance of animal-mediated recycling, leading to new relationships (Vanni, 2002). In fact, stoichiometric models suggest that the N:P ratios of release products are influenced more by algal N:P than by the grazer's own N:P (Elser and Urabe, 1999). When these principles are applied to organisms of larger biomass, the concepts are similar, but the complexity of interactions is enhanced. Larger organisms are greater sinks of nutrients than smaller organisms, and thus their impacts on nutrients are evident over longer time scales and larger space scales. Fish excretion varies in the proportion by which materials are egested (feces, pseudofeces) and excreted (urine production), as well as by the species and their osmotic environment, with NH_4^+ excretion typically being more episodic and concentrated in saltwater environments, and more dilute and continuous in freshwater environments (e.g., Randall and Wright, 1987). Nutrients are also translocated by animals, moved across physical boundaries that would otherwise prevent such mixing. Examples include translocation across the sediment-water interface, across the pycnocline, or across natural flow (Vanni, 2002). Large fish play a proportionately larger role in nutrient translocation, especially from benthic to pelagic environments (Vanni, 2002).

Second, when external nutrient loads, "bottom-up" control, is altered, "top-down" control is affected via the shift in nutrient dynamics from the water column to the sediment, where nutrient reserves are accessed by those organisms capable of doing so. They, in turn, alter habitat for grazers. Thus, in shallow lakes, the typical stable states are pelagic- phytoplankton-dominated systems and littoral-macrophyte-dominated systems (Scheffer et al., 2003; Peckham et al., 2006; Mieczan, 2010). Blindow et al. (1993) specifically identified that systems dominated by macrophytes such as *Hydrilla* are in a unique stable state. Shifts from one state to another have been described as a function of turbidity and light availability (Scheffer et al., 1993), nutrient loading (McClelland and Valiela, 1998; Meiczan, 2010a), toxic ammonia levels (van der Heide et al., 2010), changes in macrophyte abundance due to mechanical harvesting (Scheffer et al., 2003), as well as other effects.

Regime shifts represent another way to conceptualize alternate stable states. Regime shifts due to climate change and stochastic events such as storms are well recognized in ecology and biogeochemical sciences. Regime shifts also involve shifts in food webs (e.g., Ives and Carpenter, 2007), through alteration in habitat or introduction of species to new areas. Such regime shifts in species have long been considered difficult to predict and model, but clues to regime shifts are provided in the variance of biomass or chemical constituents of aquatic ecosystems (Carpenter and Brock, 2006). More recent results suggest that phytoplankton changes may be a leading indicator of regime shifts in fish populations (Carpenter et al., 2008).

Recent interest in stable state theory commonly reflects efforts to restore macrophyte dominance in systems that have become dominated by phytoplankton as a consequence of increased eutrophication (e.g., Bachmann et al., 1999; Poor, 2010). In the Bay Delta, management efforts are focused on understanding how a productive, more turbid, phytoplankton system can be restored to aid endangered pelagic fish.

Summary of Part I

The fundamental questions of how systems respond to nutrient loading (eutrophication), changes in the relative composition of the nutrient pool (ecological stoichiometry) and the extent to which hysteresis overcomes homeostasis (altered stable states) are all interwoven concepts in nutrient- altered aquatic ecosystems. Trophodynamic interactions are consequences of elemental stoichiometry, physiological adaptation of autotrophs and heterotrophs, and biogeochemical nutrient feedback processes. These principles are illustrated below for the Bay Delta food web.

PART II: LONG-TERM TRENDS AND ECOLOGICAL STOICHIOMETRY RELATIONSHIPS WITH THE FOOD WEB OF SAN FRANCISCO ESTUARY

This synthesis begins with a description of the sources of data that were studied and terminology, and an overview of the long-term trends in freshwater flow, nutrients and community structure of the Bay Delta. Then, ecological principles of stoichiometry as related to each major trophic level are described, relating the available Bay Delta data to those principles. Following Smith (2006), this analysis is based on averaged data over annual scales. Nutrients loads and/or concentrations would not be expected to be synoptically related to biomass (except possibly on the microbial level), due to the various processes of uptake, transformation and grazing that occur. Annual means have been shown to be highly related to chlorophyll *a* over broad data sets worldwide (Smith, 2006; Boyton and Kemp, 2008). A comparable, broad, seasonal analysis of the Bay Delta is forthcoming. Seasonal changes in stoichiometric proportions of nutrient loads are significant, but it is assumed here that annual changes have been more significant than seasonal dynamics over the past several decades for the Bay Delta.

Data Sources and Analysis

Publically available databases (mostly 1975-2005) were used for all analyses of the Bay

Delta (Table 1). This system has an extensive monitoring program in place, covering a wide range of parameters including physical variables, water chemistry, phytoplankton, zooplankton, invertebrates, and fish. Flow data were obtained from the California Department of Water Resources Day flow record (http://www.water.ca.gov/dayflow/). The data for Sacramento outflow were used here. All nutrient, chlorophyll *a* and phytoplankton data were obtained from the Interagency Ecology Program Bay Delta and Tributary project data portal, http://www.bdat.ca.gov/. Wastewater effluent data were obtained from the Central Valley California Regional Water Quality Control Board (2010; http://www.waterboards.ca.gov/centralvalley/). Phytoplankton data, available as individual taxa counts by cell number, were grouped into dominant functional groups: Bacillariophyceae (total diatoms), Chlorophyceae (green algae), Cryptophyceae (cryptophytes), Dinophyceae (dinoflagellates), and Cyanobacteria. Individual species identifications are only considered for potentially harmful species. Cyanobacteria are underestimated in these long-term data as the recent expansion of *Microcystis* (Lehman et al., 2005, 2008, 2010; Baxa et al., 2010) is not well represented in these taxa counts. Picocyanobacteria are not included because they are not routinely enumerated. Zooplankton data were retrieved from the monthly zooplankton surveys conducted by the California Department of Fish and Game (http://www.dfg.ca.gov/delta/). The survey data do not include ciliates or bacteria. Data on abundance of the invasive clam, *Corbula amurensis* (formerly *Potamocorbula amurensis*) were also obtained from the Interagency Ecological program database (http://bdat.ca.gov/). Fish data were provided by the California Department of Fish and Game (http://www.dfg.ca.gov/delta/). Many of these data have been compiled by the National Center for Ecological Synthesis (NCEAS Project 12192, Ecosystem analysis of pelagic organism declines in the Upper San Francisco Estuary;

http://www.nceas.ucsb.edu/projects/12192), and these compilations have been used where available. Because of the wide range of organisms considered here, species are referred to by their genus names or their common names.

Data from the primary growing season, spring to fall, were averaged for most parameters (Table 1) and compared annually. All nutrient and abundance data were log transformed. Regression analysis was used for all comparisons. All data from other comparative systems were obtained from literature sources or from the authors' measurements, described where appropriate below. Note that for the years 1977 and 1979 there were many missing data records and thus these years are not included in many of the comparisons.

The geographic coverage of the chemical, microbial and invertebrate data is from the confluence of the Sacramento and San Joaquin Rivers down to roughly the bottom of Suisun Bay. However, the fish indices, such as the fall midwater trawl (FMWT) Index, may include catches from higher in the Sacramento River or from the Central and southern Delta or from the San Joaquin River above the confluence.

The analysis herein compares inorganic N to total P (DIN:TP) because organic forms of N are not available in most of the datasets considered here. Also, as noted by Dodds (2003), TP is a preferred metric due to the uncertainty of the relationship between the analytical measures of inorganic P, PO_4^{3-}, and soluble reactive PO_4^{3-}. Availability of organic forms of nutrients would undoubtedly strengthen the analysis. However, to further the analysis, comparisons are also made throughout with the individual concentrations of ammonium (NH_4^+), TP as well as phosphate (PO_4^{3-}) and with the ratio of the dominant inorganic N and P forms, NH_4^+ to PO_4^{3-}, the latter analysis specifically targets the period of its maximal change. Some species have strong relationships with N or P, others with both. In some cases where species are strongly affected by both N and P, the effects may be opposite, leading to a dampening of the relationships with DIN:TP. Some species are positively or negatively correlated with NH_4^+, but such relationships are not always readily apparent when total DIN is dominated by other forms of inorganic N. Thus, much can be learned from analysis of individual nutrients and from calculations of the ratios of different forms of the elements. Much more can be learned from multiple comparisons than from comparisons with a single parameter or ratio. As with all correlations, the variables examined may have a cause-and- effect relationship or both may be related to another variable; mechanistic explanations are provided when physiological and ecological data permit.

Long-Term Trend Overview

The long-term trends in freshwater flow, nutrient loading, and biota in the Bay Delta have been previously well described (e.g., Kimmerer et al., 2000; Kimmerer, 2002, 2004; Bennett, 2005; Jassby, 2008; Glibert, 2010). Here we provide a brief review for context, focusing on trends in the confluence of the Sacramento and San Joaquin Rivers to Suisun Bay. Each nutrient and component of the food web is then described in more detail in subsequent sections.

The early to mid-1980s represented a period of relatively high flow, whereas the late 1980s represented a period of lower flow, and the early 1990s had very low flow (Fig. 7). Flow increased in the late 1990s and decreased in the early 2000s, but this latter period of low flow was not as low as in the early 1990s.

Phytoplankton biomass (as chlorophyll *a*) was high in the 1970s, often reaching values >30 µg L^{-1}, but declined sharply in the mid-1980s following invasion of the exotic clam, *Corbula amurensis* (previously identified as *Potamocorbula amurensis;* Alpine and Cloern, 1992; Kimmerer et al., 1994; Kimmerer, 2004; Jassby 2008). The proportion of diatoms also declined in the early 1980s, coincident with an increase in NH_4^+ discharge (Glibert, 2010). Dinoflagellates, cryptophytes, and chlorophytes were generally the dominant phytoplankton groups in the late-1980s to mid-1990s (Brown, 2010). Cyanobacteria, including *Microcystis,* increased beginning in the late 1990s through the early 2000s (Lehman et al., 2005, 2008, 2010; Glibert, 2010).

Dominant copepod species also changed over time. Calanoid copepods *Eurytemora affinis and Acartia clausii* were dominant in the 1970s and early 1980s. The calanoid copepod *Sinocalanus doerrii* first appeared in the late 1970s (Orsi et al. 1983). The calanoid copepod *Pseudodiaptomis forbesi,* also an exotic species, began increasing soon thereafter, followed by the invasive cyclopoid copepod *Limnoithona tetraspina* (Orsi and Walter, 1991; Kimmerer, 2004). In the fresher reaches of the Bay Delta, and in years of higher flow, *Daphnia magna* has also been an important member of the zooplankton community (Müller-Solger et al., 2002). The clam *Corbula amurensis* first appeared in significant numbers in Suisun Bay in 1987 (Alpine and Cloern, 1992; Kimmerer et al., 1994; Kimmerer, 2004). It thus appeared around the same time that the copepod *Pseudodiaptomis forbesi* began to appear.

Pelagic fish populations changed over time, coincident with changes in lower trophic levels. Delta smelt (estimated from both summer townet (STN) or FMWT indices), as well as longfin smelt, began to decline in ~1982, but their decline accelerated beginning in ~1999, the pelagic organic decline, or POD period (Fig. 7). In contrast, other fish species increased in numbers over the time series, including largemouth bass (*Micropterus salmoides*), inland silversides (*Menidia beryllina*), threadfin shad, and sunfish (*Lepomis* spp.). Additional changes have also occurred, including increases in macrophytes, especially water hyacinth (*Eichhornia crassipes*) and Brazilian waterweed (*Egeria densa*)

In contrast to conditions in the 1960s and early 1970s when hypoxia was more frequently noted (Nichols et al., 1986), there presently are no widespread classic symptoms of eutrophication (e.g., Cole and Cloern, 1984; Kimmerer, 2004). However, localized hypoxia has been reported as well as increased frequency of cyanobacterial blooms, especially *Microcystis aeruginosa*, in the past decade (Lehman et al., 2005, 2008, 2010).

Nutrients

Both loadings and concentrations of N and P have changed significantly over time. The extent and timing of these changes differ not only between N and P, but also between forms of N. Average dissolved inorganic N (DIN) concentrations between the confluence of the San Joaquin and Sacramento Rivers (Suisun Bay region, Fig. 1) were relatively invariant for the first years of this time series, from 1975-1982, but they increased significantly after 1982, coincident with the increase in loading of N, especially NH_4^+ , from the Sacramento Regional Wastewater Treatment Plant (SRWWTP), which came on line at that time (Figs. 8 and 9). Both concentrations of effluent discharge and total loads have increased over time; the current loads of NH_4^+ are 14 tonnes day^{-1}, with concentrations that exceed 25 mg L^{-1} (Fig. 9). These conditions well exceed those that define N hypersaturation (e.g., Waiser et al., 2011).

Concentrations of total P (TP) and PO_4^{3-} tracked those of total DIN for the period of 1982--~1991, but after that concentrations declined, returning to levels approximating those of pre-1982 (Fig. 8). This decline has been suggested to be the result of removal of P from laundry detergents (Litke, 1999), as well as the loss of a number of canneries in the region which used P in their processing (Van Nieuwenhuyse, 2007). The DIN:TP ratio in the effluent from the SRWWTP also increased most significantly after 1992 (Fig. 9). As a consequence of these changes, DIN:DIP ratios increased significantly over time in the Suisun Bay region, but the change in NH_4^+:PO_4^{3-} ratios was most significant between 1987 and 1999 (Fig. 8).

Phytoplankton

The relative dominance of different phytoplankton classes changed over time in the Suisun Bay region (Figs. 10 and 11). Total chlorophyll *a* declined abruptly after 1986 (Fig. 11). Diatoms dominated from the start of the time series (1975) to ~1986, although they were already in decline by the mid-1980s when dinoflagellates and cryptophytes were increasing (Glibert, 2010; Brown, 2010). From 1986-1999, diatoms, chlorophytes, cryptophytes and cyanobacteria declined significantly, but dinoflagellate abundance was comparatively stable (Fig. 11). After 1999, increases were observed in the abundances of crytophytes and cyanobacteria, although these changes were not significant (but note the underestimation of cyanobacteria; Fig. 11).

There were no significant relationships between total chlorophyll *a* or any species groups and TP or PO_4^{3-} (Fig. 12). Declines in chlorophyll *a* and diatoms were significantly related to the increase in NH_4^+ concentrations, as were increases in dinoflagellates (Fig. 13). The dominant dinoflagellate taxon was *Peridinium*, some species of which have been shown to have toxic or alleopathic properties that can adversely affect fish (Rengefors and Legrand 2001, 2007). When the changes in phytoplankton are related to nutrient ratios, not only were the declines in chlorophyll *a* and diatoms negatively correlated with DIN:TP, but the increase in dinoflagellates was positively related to DIN:TP (Fig. 14). During the 1986-1999 period, when the change in phytoplankton was most pronounced, a significant decline in cryptophytes was significantly correlated with increasing NH_4^+:PO_4^{3-} ratios (Fig. 15).

In relation to ecological stoichiometric principles, these changes in phytoplankton abundance are generally consistent with expectations. Diatoms generally have a lower biomass N:P ratio than dinoflagellates, especially HAB dinoflagellates (Finkel et al. 2010). Low N:P should lead to higher growth rates, due to the high proportion of P required in ribosomes and biomass (Fig. 3). Moreover, diatoms may be inhibited by high concentrations of NH_4^+, and preferentially use NO_3^- under many conditions (e.g., Dugdale and Goering, 1969; Lomas and Glibert, 1999; Dugdale et al., 2007). Dinoflagellates, especially those that produce toxins, such as some members of the Peridiniales (Butow et al., 1996; Rengefors and Legrand, 2001, 2007), would be expected to differ in their biomass composition from that of the water column. The production of toxins rich in N is sometimes regarded as a dissipatory "strategy". In many algal flagellates, toxin production increases under P stress (Granéli et al., 1998; John and Flynn, 2002). Whether these toxins are used for defense or other purposes is irrelevant to their function in stoichiometric homeostasis. However, it is relevant that the freshwater *Peridinium aciculiferum* has been shown to cause recruitment failure in the larvae of the planktivorous vendace (*Coregonus albula*) in Sweden (Nyberg et al., 1998; Rengefors and Legrand, 2001). Thus, like heterotrophs, algal species with such a capability may thrive by sequestering what they need and secreting what they do not. Cyanobacteria, while generally more constrained than eukaryotic phytoplankton in their stoichiometry (Flynn, 2009), may have more flexibility when cells produce toxins. When cyanobacteria produce toxins, such as microcystins, anatoxins, and saxitoxins as secondary metabolites, the cells have a mechanism to dissipate their excess N (Carmichael 1992).

Other examples of phytoplankton community shifts in relation to nutrient changes can be found in a long-term dataset from the Neuse River Estuary, North Carolina, USA. Rothenberger et al. (2009) related an increase in NH_4^+ concentrations to increased abundance of the potentially harmful raphidophyte *Heterosigma akashiwo* and the bloom-forming dinoflagellate *Heterocapsa rotundata*. In contrast, abundances of "pfiesteria-like" dinoflagellates and *Karlodinium veneficum* were related to high TP concentrations.

The quality (form) of N also influences dominance among primary producers. The competitive advantage of different phytoplankton species has been related to their inorganic N source, NH_4^+ or NO_3^-, in combination with their P demand (Rhee, 1974; Terry et al., 1985). Shifts in N form from NO_3^- to NH_4^+ lead to shifts away from plankton assemblages dominated by diatoms to those dominated by flagellates, cyanobacteria, and bacteria, in turn shifting the composition of higher food webs (e.g., Legendre and Rassoulzadegan, 1995; Glibert, 1998; Steele et al., 2007; Collos et al., 2009; Glibert et al. 2010b).

Zooplankton

Zooplankton composition changed over time in the Suisun Bay region (Figs. 16 and 17). The calanoid copepods *Eurytemora affinis*, *Sinocalanus doerri*, *Acartia clausii*, and harpacticoid copepods decreased from roughly the start of the time series to the early to mid-1990s, although the decline in *Acartia* mostly occurred in the mid- to late-1990s (Fig. 17). The decline in these species, especially *Eurytemora*, has been interpreted to be a consequence of increased grazing after the invasive clam *Corbula amurensis* became established (e.g., Alpine and Cloern, 1992; Kimmerer, 2004). The invasive calanoid copepod, *Pseudodiaptomus*, had relatively invariant abundances for its first decade in the estuary, then declined, but may be showing a renewed increase. The concentration of the cyclopoid copepod, *Limnoithona* spp., increased significantly during the mid-1990s; this latter expansion was due to the invasion of *Limnoithona tetraspina*, a different species than was present earlier in the time series, *Limnoithona sinensis* (Bouley and

Kimmerer, 2006). Overall, the ratio of *Eurytemora*/cyclopoid copepods showed a decline in the first part of the time series, and then a relatively stable ratio of abundances (Fig. 17).

Over time, the abundances of the cladocerans *Bosmina longirostris* and *Daphnia* sp. were similar to that of *Limnoithona* spp., lower in the mid-1980s, then rising significantly until the late 1990s (Fig. 17). The mysid macrozooplankter, *Neomysis mercedis*, was abundant in the early years but declined significantly from the mid-1980s to 1999 (Fig. 17; Winder and Jassby, 2010). From 2000 to 2005, *Neomysis* began to increase in abundance once again (Fig. 17).

In relation to TP and PO_4^{3-}, the changes in *Eurytemora, Pseudodiaptomis* and harpacticoids, were not significant (Fig. 18). In contrast, the abundance of *Acartia* was significantly positively correlated with the concentration of TP, while the abundances of *Limnoithona, Sinoclanus,* and the cladocerans were significantly negatively correlated to TP (Fig. 18). For *Daphnia*, this relationship is consistent with recent modeling efforts that show that maximum *Daphnia* growth occurs in the range of ~20-40 $\mu g L^{-1}$ TP and declines with increasing TP (Persson et al., 2007; Park and Goldman, 2008).

It is interesting that *Acartia*, unlike other calanoids, showed the opposite relationship with TP, but its overall abundances were lower later in the time series compared to the earlier years (Fig. 18). *Acartia*, more of an estuarine copepod, may also be more prevalent during dry years when Suisun Bay would have greater intrusion of higher salinity water. On a seasonal basis, this copepod was found to be a spring dominant in North Carolina estuaries under nutrient-rich conditions, but the community transitioned to the cyclopoid copepod *Oithona colcarva* as silversides increased in summer (Fulton, 1984). Walve and Larsson (1999) found that *Acartia* copepodites had a higher P content than adults in Baltic waters.

In relation to NH_4^+, the abundances of *Eurytemora, Sinocalanus,*, *Pseudodiaptomis*, *Bosmina*, *Daphnia* and *Neomysis*, as well as the harpacticoids were significantly negatively correlated, but *Limnoithona* was positively correlated (Fig. 19). Thus, when zooplankton abundances were examined in relation to DIN:TP ratios for the entire time course, or to NH_4^+:PO_4^{3-} ratios for the period of its maximum change, many of the relationships were highly significant (Figs. 20 and 21). Of note are the overall significant declines in *Eurytemora, Sinocalanus, Pseudodiaptomis, Acartia*, and *Neomysis* and harpacticoids in relation to increasing DIN:TP ratios (Fig. 20) as well as the increases in *Eurytemora, Sinocalanus, Limnoithona, Daphnia* and *Bosmina* and decreases in *Acartia, Neomysis* and harpacticoids in relation to NH_4^+:PO_4^{3-} (Fig. 21).

These changes in zooplankton composition for the Suisun Bay region are consistent with ecological stoichiometric principles. If ecological stoichiometry is a driving principle shaping the food web, then consumers that can successfully sequester the nutrient in least supply should dominate and in so doing will stabilize the system at a new stable state. Calanoid copepods generally have a high N:P ratio of their biomass, ~20-35 by atoms, whereas *Daphnia* and cyclopoid copepods, have N:P ratios much closer to Redfield atomic ratios (Walve and Larsson, 1999; Sterner and Elser, 2002). Calanoid copepods thus generally retain N, while excreting nutrients in a lower N:P ratio than their biomass (i.e., they release proportionately more P), while cyclopoid copepods and cladocerans have a high P requirement in biomass, and therefore excrete nutrients in a higher N:P ratio than their biomass (i.e., they release proportionately more N; Hessen, 1997; Sterner and Elser, 2002; Fig. 22). Excretion measurements of *Acartia tonsa* under a range of conditions have shown rates to be very low, consistent with relative retention of N by these animals (Checkley and Miller, 1988; Miller and Glibert, 1998).

Thus, *Limnoithona* demonstrated a dramatic increase in relation to the NH_4^+:PO_4^{3-} ratio and similar increases were also significant for *Daphnia* and *Bosmina*, while the calanoids and harpacticoids decreased with increasing DIN:TP ratios (Figs. 20 and 21). It is of note that *Limnoithona* grazes not only phytoplankton but also ciliates, using ambush predator strategies (Bouley and Kimmerer, 2002).

Studies from whole lake experimentation suggest that the N:P ratio will alter zooplankton size, composition and growth rate, as those animals with increased RNA allocation will grow at higher rates due to increased protein synthesis rates (Sterner and Elser, 2002). While at a given protein level the percentage of N increases only modestly with growth rate, the changes in P with growth are much higher. Thus, growth rate should be negatively related to N:P ratios. Similar findings were reported from annual studies in the Baltic Sea (Walve and Larsson, 1999). Kiørboe (1989), in a laboratory study where *Acartia tonsa* was fed diatoms grown on different N concentrations, confirmed that zooplankton change their feeding rate in response to phytoplankton of different chemical composition. Moreover, egg production followed the variation in algal N content and increased with increasing algal N.

Hassett et al. (1997) compared the ecological stoichiometric constraints on zooplankton in 31 lakes and 21 marine systems. While their data were strongly suggestive of stoichiometric control, especially P constraints in the lake systems, the marine systems were not nearly as regulated. The authors noted that while N:P recycling ratios would argue for an accentuation by zooplankton of P limitation in lakes and N limitation in the oceans, systems dominated by a microbial food web may show an opposing effect. The most pronounced nutrient deficiency was found in systems that lacked large piscivores, i.e. those dominated by the planktonic food web. Bacteria and protists are also important regulators of N and P (e.g., Goldman et al., 1985; Caron et al., 1985; Dolan, 1997), but their rates and long-term trends have not been well monitored or studied in the Bay Delta.

Invertebrates

Large changes in invertebrate composition and abundance have occurred in the Bay Delta over the past several decades. Most significant is the appearance of the invasive clam, *Corbula amurensis*. Crabs (including Dungeness - *Cancer magister* - and Mitten - *Eriocheir sinensis*), have also changed over time, with significant increases in the years before the mid-1980s, then a period of highly variable abundances, followed by declines post-1999 (Fig. 23). Shrimp (*Crangon franciscorum*, *Crangon nigricauda*, and *Palaemon macrodactylus*) either showed no change or modest declines prior to 1999, followed by more substantial declines in recent years (Fig. 23). Except for *Palaemon* sp., which increased in relation to TP (but not PO_4^{3-}), none of the other invertebrate abundances were significantly related to TP. With increasing NH_4^+, *Corbula amurensis* and the crab species significantly increased and the shrimp taxa decreased. Consequently, the changes overall in *Corbula amurensis* and crabs were positively related to DIN:TP ratios, while those of shrimp were negatively related to DIN:TP ratios (Fig. 23). Shrimp can be significant sources of NH_4^+ in intertidal creeks, not only through their excretion but also via sediment bioturbation (Haertel-Bores et al., 2004).

Thus, *Corbula amurensis* appears to tolerate elevated NH_4^+ levels, and it may release higher proportions of N than P, while shrimp appear to sequester N, or are inhibited by elevated NH_4^+ concentrations and may release higher relative proportions of P. A positive relationship between *Corbula amurensis* abundance and the increase in NH_4^+ and ratios of DIN:PO_4^{3-} has previously been reported (Glibert, 2010). The relationship between P and *Corbula amurensis* is discussed further in Part IV.

Fish Composition

Fish communities have changed significantly over time in the Bay Delta. Many of these changes have previously been attributed to invasive species introductions, some intentional and some accidental. Among those identified as invasive are, “largemouth bass, white and black crappie, bluegill, threadfin shad, striped bass, inland silversides, white catfish, black and brown bullhead, and common carp” (Moyle, 2002, p.31).

Many of the planktivorous fish are in decline. Among these are delta smelt and threadfin shad, which feed on copepods generally in open waters, and longfin smelt which are more likely to feed on copepods and opossum shrimp (*Neomysis mercedis*) in brackish regions (Moyle, 2002). American shad (*Alosa sapidissima*) and striped bass are also planktivorous in their early life stages. Inland silversides have similar feeding strategies to smelt (Moyle, 2002). Delta smelt are found from Suisun Bay to the northwest delta and the lower Sacramento River (Moyle, 2002; Miller et al. in review). They preferentially feed on the calanoid copepod *E. affinis*, although the calanoid copepod *P. forbesi* has increased in importance in their diet. Increased spring mortality has been linked to the decline in food availability (Moyle, 2002; Kimmerer, 2004; Miller et al., in review).

Among the piscivorous fish in the Bay Delta are striped bass, white catfish (*Ameiurus catus*), channel catfish (*Ictalurus punctatus*), and largemouth bass. Striped bass were introduced in the late 1900s (Moyle, 2002). While successful in the early twentieth century, they have declined since the early 1980s (Fig. 24). Prevailing thoughts on the reasons for this decline include, “(1) climatic factors, (2) south Delta pumps, (3) other diversions, (4) pollutants, (5) reduced estuarine productivity, (6) invasions by alien species, and (7) exploitation” (Moyle, 2002, p. 369). Among the many factors thought to be related to the decline in delta smelt is the invasion of silversides, which share much of the same diet and habitat (Bennett and Moyle, 1996). Although catfish were not analyzed herein, they emerged in a recent analysis as among the most P-rich of fish families (McInyre and Flecker, 2010)

When the time series are examined in detail for many of these fish, several patterns are apparent. First, delta smelt, longfin smelt, splittail, threadfin shad, and yellowfin goby declined precipitously since 1999; this is the POD, pelagic organism decline (Sommer et al., 2007) (Fig. 24). Crappie (*Pomoxis* sp.), sunfish and largemouth bass increased significantly in the same years (Fig. 24). For many fish, as well, the mid-1980s was also a period of rapid or abrupt change.

Several of the changes in fish abundance were directly and significantly related to TP or PO_4^{3-} (Fig. 25). Specifically, longfin smelt, crappie, sunfish and largemouth bass abundances were significantly negatively related to TP. Interestingly, the species that have shown recent declines in abundance, while not showing an overall significant change in relation to TP, do show a change in slope when regressed against TP, all in the direction of a more positive relationship (dashed lines in Fig. 25). The abundances of longfin smelt, and striped bass (both POD species), and yellowfin goby were significantly negatively related to NH_4^+ concentrations (Fig. 26). Thus, overall, delta smelt, longfin smelt, yellowfin goby, and striped bass were negatively related to DIN:TP, and silversides, sunfish and largemouth bass were positively related to DIN:TP (Fig. 27). For the period of most rapid change in NH_4^+:PO_4^{-3} ratios, delta smelt, longfin smelt, splittail, sunfish and crappie were highly positively related to the NH_4^+: PO_4^{-3} ratio (Fig. 28).

Ecological stoichiometric principles provide insights as to why these community changes occurred. Ecological stoichiometry predicts that system shifts from low to high N:P ratios should shift from planktivores to piscivores (Sterner and Elser, 2002) (Figs. 5 and 6). Planktivorous fish and calanoid copepods have similar relationships with N:P ratios, whereas piscivorous fish have relationships with N:P ratios that are more similar to those of cyclopoid copepods. Sequestration of P in the biomass of the piscivorous fish (with more skeleton and bones) would lead to them being proportionately more abundant when P is less available in the water column. A broad survey of herbivores across freshwater and terrestrial systems also showed that herbivore C:N and C:P ratios were generally considerably lower than the C:N and C:P ratios of their food (Elser et al., 2000a). Moreover, fish excreta, like that of zooplankton, helps to support the homeostasis of nutrient ratios.

These trends also support the notion that nutrient limitation propagates up the food chain (c.f., Malzahn et al., 2007, 2010; Boersma et al., 2008). That different fish have different elemental stoichiometry is expected. Sterner and George (2000), for example, highlighted the elemental differences in the biomass of centrarchids versus cyprinids (Fig. 4). The Bay Delta trends are consistent with these concepts. The abundances of piscivores (crappie, sunfish, largemouth bass) were negatively related to TP concentrations; they have a higher P demand and can sequester this nutrient more efficiently. The planktivores, with a lower P demand, were less efficient at sequestering P and generally showed either no relationship with P or evidence of a positive relationship with P, especially in the latter years. This finding is consistent with Hendrixson et al. (2007) who showed that the plankivorous fish, less successful at sequestering P, were the most susceptible to P limitation. Hendrixson et al. (2007) also found that bluegills (*Lepomis macrochirus*) only varied in their P content by ~1% when fish from numerous sites were compared, thus underscoring their strong stoichiometric control. Grazing on P-limited copepods such as the calanoids or harpacticoids will enhance P limitation at the level of the planktivores (Boersma et al., 2008).

The notion that nutrient limitation may propagate through the food web has not been well investigated in estuarine food webs, but multiple trophic-length mesocosm experiments have elegantly demonstrated this phenomenon. In studies in which nutrients, light and food chain length were manipulated, not only did the phytoplankton assemblage under low nutrient conditions become composed primarily of cyanobacteria and chlorophytes (“intermediate” to “poor quality” food) compared to proportionately more cryptophytes and diatoms under high nutrients (“high quality” food), but fish body C and P also varied among treatments (Dickman et al., 2008). Vanni et al. (2002) examined the stoichiometry of 28 species of fish and amphibians, and their data suggested that elemental stoichiometry control was strongest when consumers ingested nutrient-poor items such as nutrient-limited algae or detritus. The effects were weaker when consumers ingested multiple food items including other animals that were apparently more nutrient-rich.

The analyses described here have not specifically considered stoichiometric requirements of larvae, nor seasonal changes. Larvae would be expected to have relatively high P demands due to their high growth rates (Boersma, 2008), and to the shift in resource allocation from muscle growth to bone and fin rays (Malzahn et al. 2007). Boersma et al.’s (2008, p. 484) review specifically noted of the potential mismatch between food quality and larval growth, “Larval fish growth typically follows the population increase of herbivorous zooplankton, which succeeds the spring bloom of phytoplankton...if for some reason the tight coupling of these dynamics becomes less...it could well be that the larval fish is faced with herbivorous zooplankton that is feeding on late-bloom phytoplankters rather than early bloom ones. Feeding on late-bloom algae automatically implies that the nutrient conditions of these algae are more depleted with respect to phosphorus and nitrogen and thus these zooplankters are a food source of suboptimal quality for larval fish.” Experimentally, nutrient limitation of larval fish has been demonstrated; P-limited tri-trophic food chains had greater effects on fish larval condition than did N-limited food chains (Malzahn et al. 2007). The trajectory of changes in phytoplankton and zooplankton in the Bay Delta over decades as well as with season are consistent with such an effect.

Fish Size

There are many reasons for changes in fish size over time and within individual fish species, a large variation in body size is frequently observed for a given life history stage (Krebs 2008). Among the reasons is the availability of adequate nutrition. When nutrition is adequate, organisms will grow faster and will reach a larger size. Ecological stoichiometry predicts that animal size should be related to water-column N:P ratios (Sterner and Elser, 2002). However, there have been variable reports of relationships between fish size and N:P in other systems. In a study of bluegills (*Lepomis macrochirus*), higher percentages of P and lower percentages of N were found in larger sized fish (Davis and Boyd, 1978). While Vanni (1996) suggested that such relationships should be evident in streams, Tanner et al. (2000) observed weak relationships at best for 20 fish taxa in Lake Superior, and Sterner and George (2000) also found weak relationships for cyprinids.

Several fish species of the San Francisco Estuary did indeed show strong correlations between their size and either TP concentrations or DIN:TP ratios (Fig. 29). Longfin smelt, threadfin shad and American shad increased significantly in length as a function of TP, while delta smelt, threadfin and American shad decreased significantly in relation to DIN:TP ratios (Fig. 29). Glibert (2010) previously reported that the size of delta smelt decreased when the zooplankton composition changed from *Eurytemora* dominance to *Pseudodiaptomus* dominance. The data for American shad, an anadromous species, are based on the fall midwater trawl surveys, which would capture the early life stages. This would suggest that early feeding is an important determinant of the ultimate size the fish attain.

Trophic Interactions

Comparisons of responses to nutrients across trophic groups provide clues to the questions raised in the introduction, and whether there is evidence of self-assembly under different nutrient conditions. Recall that stoichiometric changes should result in keystone species that are able to sequester nutrients in least supply; through their excretion or other dissipatory mechanism(s), they help to stabilize the communities. Such relationships were explored here by comparing several key species in relation to other organisms across the nutrient-time gradient.

A number of zooplankton, invertebrates and fish that varied in tandem with diatom abundance (Fig. 30). Highly significant positive correlations were found between diatom abundances and the copepod *E. affinis*, the macrozooplankter *N. mercedis*, and the shrimp *Crangon* spp. and *Paleamon macrodactylus*. Consistent with the broader observations of Jónasdóttir et al. (1998), no evidence of diatom toxicity to calanoid copepods was observed in these data. Negative correlations were found between diatom abundance and *Limnoithona* spp. (Fig. 30). Delta smelt, longfin smelt, and striped bass, both young-of-the year and adults, were positively correlated with diatom abundance, while sunfish abundance (*Lepomis* spp), was negatively correlated. It is of note that similar associations between diatoms, *E. affinis*, *Neomysis*, and smelt were also observed in St. Lawrence River estuarine transition zone (Winkler et al., 2003).

Several significant negative correlations were found between dinoflagellate abundances and higher trophic levels (Fig. 31). Delta smelt (STN) annual averages declined significantly when dinoflagellates increased. The correlation was also significant between dinoflagellate abundances based on the FMWT survey data for delta smelt and longfin smelt. As noted above, the genus *Peridinium* has been reported to produce allelopathic compounds that adversely affect planktivorous vendace in the Baltic (Nyberg et al., 1998; Rengefors and Legrand, 2001). Young-of-the-year striped bass and starry flounder (*Platichthys stellatus*) also declined significantly in relation to the increase in dinoflagellates.

Calanoid copepods and either Cladocera (*Daphnia*, *Bosmina*) and/or *Limnoithona* spp. can be viewed as alternate keystone zooplankton species. While *Eurytemora* and the cladocerans generally prefer different salinities, they do co-occur (Figs. 16 and 32). The abundance of *Eurytemora* was highly significantly positively correlated with the abundances of diatoms, mysids (including *Neomysis*), longfin smelt, and striped bass. Cladocerans were positively correlated with *Sinocalanus*, longfin smelt, and crappie (Fig. 32). It is interesting to note that the relationship between the abundances of cladocerans and longfin smelt length was negative. Longfin smelt length was also negatively related to TP concentrations.

The self-assembly of the Bay Delta food web at the beginning (1975-1986) and end (1999-2005) of the time course examined here can also be seen as a function of the ratio of the major types of copepods, *Eurytemora*/cyclopoids (Fig. 34). These time periods had similar freshwater flow, and thus salinity tolerances should not be a major factor in trophic segregation. When *Eurytemora* was dominant, the system was dominated by higher relative abundances of planktivores (delta smelt, longfin smelt, yellowfin goby), but there was a shift to a more piscivore-dominated community (sunfish, largemouth bass) when cyclopoids became dominant.

Note, also, that the most recent period does not seem to be a stable one, and strong relationships are found with both the phytoplankton and fish communities.

Overall, the planktivores were negatively correlated with NH_4^+ and with DIN:TP ratios, and showed little or no relationship with changes in NH_4^+:PO_4^{3-} ratios (Fig. 35). The data suggest that the planktivores and their food, from phytoplankton to copepods, tended to either sequester N and release P, or to be highly sensitive to excess levels of NH_4^+, with exception of the dinoflagellates. Piscivore abundances were largely inversely correlated with TP, but positively correlated with NH_4^+ concentrations, DIN:TP ratios, and NH_4^+:PO_4^{3-} ratios (Fig. 35). If their biomass demands for P are higher than those of planktivores because of their higher bone density, then they would be expected to be inversely related to TP, reflecting their ability to sequester this nutrient.

Macrophytes

With progressive eutrophication, increased algal production generally occurs at the expense of seagrasses and submersed aquatic vegetation (Harlin, 1993; Burkholder et al., 2007 and references therein). Filamentous algae may replace planktonic algae (Valiela et al., 1997; Cloern, 2001; McGlathery et al., 2007). Excess N causes native seagrass loss (Burkholder et al., 1992; Short and Burdick, 1996); for example, nearly complete loss of eelgrass (*Zostera marina* L.) was reported when land-based N loading exceeded 100 kg ha^{-1} yr^{-1} (Latimer and Rego 2010). On the other hand, as nutrient stoichiometry changes, other macrophytes can proliferate (Burkholder et al., 1994; Burkholder et al., 2007, and references therein).

The macrophyte community of the Bay Delta has changed considerably over the past several decades. Native submersed aquatic vegetation has largely been replaced by invasive submersed and floating vegetation, including Brazilian waterweed (*Egeria densa*) and water hyacinth (*Eichhornia crassipes*; Lund et al., 2007; Santos et al., 2011. Although these changes have occurred in the freshwater reaches of the Bay Delta including the confluence, not in the Suisun Bay region, they have large effects on the entire ecosystem. Water hyacinth appears to have been introduced over a century ago (Finlayson, 1983; Gopal, 1987), but has increased in abundance mostly in the past several decades (Finlayson, 1983; Toft et al., 2003). By the early 1980s, water hyacinth covered ~500 ha, or ~22% of the waterways, in the Bay Delta (Finlayson, 1983). Water hyacinth grows rapidly and has been described to create somewhat similar habitat to the native pennywort (Toft et al., 2003). Although structurally the habitat may be similar, the food web is not. In the Bay Delta, regions heavily overgrown by water hyacinth have been shown to have different epiphytic amphipod species and also a distinctly different fish-invertebrate food web compared to that supported by native pennywort (Toft et al., 2003). Overgrowth of water hyacinth has led to major efforts to control its spread as it blocks waterways. In the late 1990s, chemical control of more than 900 ha of hyacinth in the Bay Delta cost approximately $1,000,000 (CDBW, 1998; Toft et al., 2003; Anderson, 2003), but chemical control has been found not to be a cost-effective mitigation strategy (Khanna et al., 2009)

The first appearance of *Egeria* in the Bay Delta is thought to have been in the 1960s, but it is documented to have increased significantly during the decade of the 1980s (Jassby and Cloern, 2000) and even more in the 1990s, after the drought (Anderson, 1999). Although estimated to contribute ≤10% of the Bay Delta productivity (Jassby and Cloern, 2000), it covers more than ~2,400 ha (6,000 acres) of area in varying densities (Anderson, 1999; 2003; Hestir et al., 2008, 2010). Of >800 sites sampled in 2007 and 2008 in the central Delta, *Egeria* was found in >50% of the samples, about half of which were monospecific patches (Santos et al., 2011).

Moreover, in the same study, it was found that >60% of the waterways were covered with submersed plant canopy, most of which, especially in summer, was the non-native *Egeria* (Santos et al., 2011). It appears to be a species well adapted to thrive in an altered nutrient and light regime. Under relatively low light, it develops apical shoots more rapidly than under high light, allowing it to reach more light-rich surface waters faster (Rodrigues and Thomaz, 2010).

Egeria has been identified as an ecological engineer (Yarrow et al., 2009, *sensu* Jones et al., 1994). As its coverage increases, it affects nutrients via uptake, decreases turbidity by sediment trapping, increases light availability, and is also thought to positively affect zooplankton since it provides a refuge from predation (Fig. 36). As these beds trap sediments, they also alter water flow (Gacia and Duarte, 2001; Wetzel, 2001). In the Bay Delta, decreased turbidity has been noted in macrophyte areas (Hester et al., 2010). Higher abundance of macro-suspension feeders, including bivalve molluscs, also generally occurs in vegetated areas. As summarized by Marba et al. (2006), this is due to "enhanced rates of recruitment within canopies (Duggins et al., 1990; Boström and Bonsdorff, 2000), shelter from predation (Peterson and Heck, 2001) and high abundance of food availability." The extent to which invasive, structurally complex species alter habitat – and therefore food webs – is a function not only of their biomass, but the extent to which they replace other structurally complex submersed macrophyte species or adds new structure to an otherwise more open habitat (Martin and Valentine, 2010).

Macrophyte beds serve as habitat for largemouth bass. These fish nest among the submersed vegetation, and they contribute to the development of clearer water by their voracious grazing on planktivorous fish (Moyle, 2002). In the Bay Delta, largemouth bass are increasing (Fig. 24), and this increase has been linked to the habitat provided by beds of *Egeria* (Conrad et al., 2010). Brown and Michniuk (2007) documented an increase in alien centrarchids in macrophyte habitats in recent years as well, compared to surveys of decades past. Macrophyte beds also are excellent habitat for carp. Grass carp (*Ctenopharyngodon idella*), for example, are omnivorous, but are preferentially herbaceous as adults and prefer plants such as *Hydrilla* and *Egeria* (Moyle, 2002).

Published stoichiometry data of *Egeria* suggest a plant that has a high N:P content (Yarrow et al., 2009). Among marine seagrasses, Romero et al. (2006, p. 245) noted that "when nutrients are abundant, leaves seem to be the 'preferred' site for uptake; in contrast, when nutrients are scarce, root uptake is maximized" and more biomass is allocated to leaves in N-rich environments. Although generalized, this information collectively suggests that in dense vegetation stands, the dominant macrophytes might be expected to have a high biomass N:P ratio, while the dominant fish would be expected to be comparatively large in size and have a low biomass N:P ratio.

Summary of Part II

Patterns in the abundance of various members of the aquatic community in the Bay Delta, from phytoplankton and macrophytes to zooplankton, invertebrates, and fish, appear to follow trends related to ecological stoichiometric 'rules'. Members of different trophic levels were found to have different correlations with N and P, as did taxa within trophic levels. The patterns are consistent with the general notion that the community becomes proportionately more P-rich with increasing levels of consumers (Sterner and Elser, 2002).

PART III: ECOLOGICAL STOICHIOMETRY AND BIOGEOCHEMICAL INTERACTIONS

Ecological stoichiometric principles, and the data described above, support the expectation that large piscivores should increase in abundance as levels of P in the ambient environment decrease. Yet, these fish have higher metabolic demands for P in their biomass structures. If large fish with a high P demand dominate in environments where the ambient N:P ratio is high, the question arises: What is the source of the P? These organisms may be efficient at sequestering the needed element, but it must be available in order to be taken up. Additionally, to what extent are other biogeochemical processes altered when stoichiometry changes? What feedbacks may help to sustain an altered ecosystem structure?

Sediment chemistry observations in estuaries show that concentrations of nutrients in the sediments are significantly higher than in the water column. Sediments represent enormous stores of both P and N; porewater NH_4^+ concentrations have been documented to reach up to 1 mM (=14 mg L^{-1}) and PO_4^{3-} more than 50 µM (=1.6 mg L^{-1}) in a wide range of environments (e.g. Udy and Dennison, 1997; Touchette and Burkholder, 2000). In the Bay Delta, where P has been measured in the upper few cm of sediment, concentrations were 5-10 µM g^{-1} in the confluence region, but significantly higher in the more freshwater sites when samples were collected in fall of 2001 (Nilsen and Delaney, 2005). Sediment enrichment of PO_4^{3-} and NH_4^+ have been well described for other estuarine systems (e.g. the Potomac River, USA; Fig. 35), whereas NO_3^-, a key substrate for denitrification, does not typically accumulate in porewater. Locked in sediments as mineral or strongly adsorbed species, much of the P is not biologically available. In freshwater systems (Carlton and Wetzel, 1988; Wetzel, 2001) as well as marine habitats, several biogeochemical and chemical processes serve to mobilize this P, making it available for organismal uptake. These abiotic and biotic processes are described below, followed by a description of the interactions of altered geochemical and biogeochemical processes as they affect the food web.

Abiotic Release of P from Saltwater Intrusion

In non-calcareous freshwater sediments, P is most often bound to iron oxyhydroxides (FeOOH, Compton et al., 2000; Jordan et al. 2008). The FeOOH-bound P may be delivered to estuaries with transport of suspended solids, or may become adsorbed to particulates when P is discharged from other sources, such as from point source discharge. When this bound P meets saline or sulfate-rich water, either from transport down-estuary, or from salt intrusion to sediments, formation of iron sulfide minerals releases P to overlying water (Caraco et al. 1989; Jordan et al., 2008; Lehtoranta et al., 2009). The sulfides in salt water compete with the Fe, releasing P and precipitating Fe(II); this has been termed the iron conveyer belt (Jordan et al., 2008). A simplified representation of the net process is:

$$\mathrm{FeOOH(s)\cdot H_2PO_4^-(ads) + H_2S \rightarrow FeS\ (s) + H_2PO_4^-\ (aq)} \qquad (1)$$

where (s) refers to sediment, (ads) refers to adsorbed, and (aq) refers to aqueous. In freshwater, FeOOH-bound P may be released under anoxic conditions, but the cycle of Fe binding of P begins anew when oxygen is encountered again (Carignan and Flett, 1981). In the Bay Delta, high concentrations of Fe-bound P in sediments have previously been reported (Nilsen and Delaney, 2005).

The iron conveyor belt has been demonstrated clearly in studies of P fluxes in the Patuxent River Estuary, a tributary of Chesapeake Bay (Jordan et al., 2008). There, Fe-bound P was found to decline with increasing salinity. Furthermore, highest concentrations of dissolved P in river transects were found in the region of the river where salinity ranged from ~2-4. When PO_4^{-3} concentrations for the Bay Delta are plotted as a function of specific conductance for all data available for the 30 year record (Fig. 37), the near universality of the change in P availability can be seen at ~200 μmhos cm^{-1}, corresponding to the fresh to low salinity zone.

In Tomales Bay, California, USA, Chambers et al. (1995) estimated that release of PO_4^{-3} from Fe-bound P was ~12% of the benthic flux of P in sediments that were sulfide rich. In the Patuxent Estuary, release from iron oxides was estimated to contribute ~30% of dissolved PO_4^{-3} to the estuary, with point source discharges contributing another 50-60%. The contribution of this flux is highest in summer when rates of SO_4^{-2} and Fe(III) reduction are highest (Boynton et al., 1995, 2008; Jordan et al., 2008).

The influence of salinity on sediment nutrient cycling differs for N and P. Seitzinger et al. (1991) suggested that lower denitrification efficiencies in salt water compared to freshwater arise, at least in part, due to decreased adsorption of NH_4^+ at higher ionic strengths which leads to poor efficiency of nitrification. Porewater NH_4^+ concentrations decline, rather than increase with salinity, leading to a significant difference in the flux rates of these elements with regard to salinity (Jordan et al., 2008; Weston et al., 2010). Whereas rates of NH_4^+ flux are higher in freshwater, P flux rates are higher in salt water (Jordan et al., 2008 and references therein), and this can accentuate the discrepancy between N:P ratios along the salinity gradient. Caraco et al. (1989) showed that the relative efficiency of return of sediment P to the water column was directly related to the concentration of sulfate in the overlying water. Sulfate concentrations in brackish water can be 100-500 times higher than freshwater, leading to increased dominance of sulfate reduction as a metabolic pathway. The increased production of H_2S results in loss of P-binding iron oxide surface area. Regardless of salinity, the supply of labile organic matter to sediment remains a key determinant of sediment N fluxes.

Comparisons of the NH_4^+: PO_4^{3-} ratio along the salinity gradient of four sub-estuaries of Chesapeake Bay (Patuxent, Potomac, Choptank and Bush Rivers) revealed a common switch from molar ratios >16 to <16 as salinity increased, with the major breakpoint at salinities of 1-4 (Hartzell and Jordan, 2010). These changes were mostly due to changes in P, not N. These comparative results are suggestive that similar P-Fe-S interactions could enhance sediment PO_4^{-3} effluxes in the Bay Delta, particularly in the low salinity zone.

Biota-Mediated P and N Fluxes

Abiotic processes are significant, but are not the only pathways by which P and N may be mobilized into solution. Macrophytes such as *Egeria* are able to take up P from the sediment. *Egeria* obtains P from both the water column and the sediment, but the relative importance of the water column or the sediment as a P source depends on the ambient concentrations in each of these media (Moeller et al., 1988; Wetzel, 2001; Feijoo et al., 2002). *Egeria* thus has the physiological capability to balance its N demand by water-column uptake, and its P demand by sediment uptake in waters with high N:P. It may have been a successful "invader" due to its adaptive physiology, making it a suitable species to do well in an environment in which the water column is rich in NH_4^+, and the sediment rich in PO_4^{3-}. Classic work by Barko and Smart (1980) showed that PO_4^{3-} turnover in the interstitial water increased 1,000-fold in sediments supporting Eurasian milfoil or *Egeria* growth.

Egeria, and the related invasive macrophyte *Hydrilla* (*Hydrilla verticillata*), can reach very high biomass levels and can attain very high growth rates. In dense productive stands, the aqueous environment can become limited by free CO_2. However, these plants are well suited to grow well under low CO_2 due to well developed CO_2 concentrating mechanisms (Bowes, 1987; Bowes and Salvucci, 1989; Lara et al., 2002). Leaf polarity allows these plants to regulate the equilibrium of HCO_3^- at the leaf surface, thus allowing CO_2 to enter the plant. In a closed system, the depletion of CO_2 (aq) during photosynthesis increases pH as the dissolved inorganic carbon system shifts towards an increased dominance of HCO_3^- and CO_3^{2-} according to the reaction:

$$CO_2 + H_20 <\text{-}> H_2CO_3 <\text{-}> HCO_3 + H^+ <\text{-}> CO_3^{2-} + 2\ H^+ \qquad (2)$$

Hydrilla and *Egeria* are thus able to use HCO_3^-, and elevate pH of the surrounding water as they photosynthesize. Although measurements of pH for the Suisun Bay region have not been regularly taken for the duration of the time series of interest, long-term general trends in pH for a range of stations in the Bay Delta show similar patterns, including a increase since the mid-1990s (Fig. 38A,B). High-frequency measurements show a diel oscillation with late-day pH elevations during the summer growing season (Fig. 38C), and pH values in excess of 10 have been recently recorded in the western Delta (Lindemuth 2010). The pH increase is related to 1) photosynthetic DIC uptake, 2) the rate of air-sea exchange of pCO_2 to replenish the depleted CO_2 (aq), 3) resupply of CO_2 (aq) via respiration and 4) the pH-buffering capacity of the water (e.g., Stumm and Morgan, 1981). In fact, *Hydrilla*, while having the capability to grow well at a pH of 5-9, attains a growth rate 10-fold higher when the pH is 9 than in lower pH growth conditions (Spencer and Bowes, 1985; Bowes, 1987). Thus, high productivity leads to elevated pH, which has a positive effect on growth rate of these plants. Conversely, low pH and/or increases in sulfate, which also reacts with HCO_3^-, have been shown to be detrimental to *Egeria* (Mulsow and Grandjean, 2006).

As pH increases, the fundamental physical-chemical relationships related to P adsorption-desorption changes. Enhancement of sediment P release under elevated water-column pH conditions has been observed in eutrophic lakes (i.e., Andersen, 1974; Drake and Heaney, 1987; Jensen and Andersen, 1992; Xie et al. 2003) and tidal freshwater/oligohaline estuaries (Seitzinger, 1991). Indeed, PO_4^{-3} flux from the sediment in the Potomac Estuary increased from < 5 µmol m^{-2} h^{-1} to nearly 30 µmol m^{-2} h^{-1} in < 24 h when pH increased from 7.8 to 9.5 (Fig. 39). The effect of pH 10.5 is far greater, however: PO_4^{-3} efflux increased to >100 µmol m^{-2} h^{-1} in 24 h, and continued to increase to >160 µmol m^{-2} h^{-1} when these high pH values were sustained for 100 h (Fig. 39). Organisms that can tolerate a high pH and high NH_4^+ thus form the base of the food web in these stands. In turn, they benefit from a source of PO_4^{-3} not otherwise available from the water column. Estimates of P release from *Egeria* stands in Arkansas, USA, have been estimated to range from 0.13 to 0.36 µM L^{-1} d^{-1} for a stand corresponding to 132 cm^2 of plant area and a density of 788 g m^{-2}, when direct release and direct release plus decomposition are considered, respectively (Arnott and Vanni, 1996, based on data from Barko and Smart, 1980).

Altered Biogeochemical Processes and Effects under Conditions of High Benthic Primary Productivity

Elevated pH resulting from high productivity by macrophytes affects the biogeochemical cycling of N, including the chemistry of NH_4^+-NH_3 and processes such as nitrification, denitrification, and dissimilatory NO_3^- reduction to NH_4^+ (e.g., Huesemann et al., 2002; Kemp et al., 2005). The form of NH_4^+-NH_3 is a function of pH based on the reaction:

$$NH_3 + H_2O \overset{Kb}{<\!\!-\!\!>} NH_4^+ + OH^- \qquad (3)$$

where K_b is the equilibrium constant (Bange, 2008). At elevated pH's, the proportion of NH_3 to $\Sigma NH_3 + NH_4^+$) increases; the salinity dependence of K_b results in increase in the proportion of

NH_3 at lower pH under freshwater conditions than under brackish/marine conditions. The penetration of elevated pH into aquatic sediment results in a shift of porewater NH_4^+ to NH_3. With a large pool of adsorbed NH_4^+ in equilibrium with porewater NH_4^+ (Rosenfeld, 1979; Cornwell and Owens, in review), particularly in freshwater (Seitzinger, 1991), a large pool of bound NH_4^+ can be released to the pore water as NH_3, leading to elevated fluxes of $\Sigma(NH_3 + NH_4^+)$. Moreover, at high pH, direct volatilization of NH_3 from *Egeria* has been observed (Reddy et al., 1987).

Elevated pH values also alters bacterial metabolism (Tank et al., 2009). Both bacterial production and respiration have been shown to be negatively affected by alkaline pH resulting from high rates of macrophyte photosynthesis which, in turn, affects C cycling and energy flow and reduces rates of remineralization (Tank et al., 2009). The bacteria *Nitrosomonas* and *Nitrobacter* are inhibited by NH_3, and their inhibition in turn reduces nitrification. Without nitrification, the effects of elevated NH_4^+ and NH_3 are sustained (Russo, 1985; Kemp et al., 2005). Macrophytes also release dissolved organic carbon (DOC; Wetzel, 2001; Mateo et al., 2006). Estimates of the quantity of DOC released vary widely, and depend on the species and their physiological state, but fall in the range of 5-10% of total carbon fixed (Brylinsky, 1977; Moriarty et al., 1986; Ziegler and Benner, 1999). The importance of this flux to ecological stoichiometry is that DOC enhances bacterial production and may shift local metabolism, especially sediment metabolism from autotrophic to heterotrophic (Ziegler and Benner, 1999), in turn accelerating nutrient recycling and potentially secondary production (Marba et al., 2006). Microbial activity typically is enhanced in vegetated regions (e.g., Nielsen et al., 2001; Wetzel, 2001), leading to accelerated rates of nutrient cycling (Marba et al., 2006).

Increasing NH_4^+ shifts aquatic communities to dominance by phototrophs with higher

NH_4^+ tolerance, for example, dinoflagellates and macrophytes such as *Egeria*. As NH_4^+ increases, organisms that are tolerant of it increase; as primary production increases, pH increases, and the equilibrium shifts to NH_3. Feedback inhibition of the food web then occurs due to the toxic effects of NH_3. There are multiple physiological effects to exposure to high NH_3 levels. Shrimp, for example, alter their ability to osmoregulate, with the degree of disruption a function of both concentration as well as time of exposure (Lin et al., 1993). Values of pH >9.7 have also been found to be lethal for some shrimp species (Shaw, 1981). Toxic effects of unionized NH_3 on fish are multi-faceted and can include damage to the gill epithelium, stimulation of glycolysis and suppression of the Krebs cycle, uncoupling of oxidative phosphorylation and inhibition of ATP production and disruption of osmoregulation and effects on liver and kidneys, and suppression of the immune system, leading to susceptibility to infection (Tomasso et al., 1980; Alabaster and Lloyd, 1982; Russo, 1985; Adams and Bealing, 1994; Camargo and Alonso, 2006). Collectively these effects can lead to reduced feeding activity, fecundity, and survivorship (Alonso and Camargo, 2004). Toxic effects of NH_3 on physiology can intensify when other chemical pollutants or hypoxia occur, because of additive and synergistic effects (Alabaster and Lloyd, 1982; Russo,1985; Mugnier et al., 2008; Camargo and Alonso, 2006). High pH alone, as well, has been found to be stressful for many fish species, resulting in reduced spawning and, in some cases, direct mortality (Smith et al., 1958; Calabrese, 1969; Moyle, 2002). Largemouth bass, for example, are more tolerant of moderate hypoxia compared to smallmouth bass (Furimsky et al. 2003), but are stressed by pH values above 9 (Moyle, 2002).

High pH has also been shown to adversely affect some seagrasses; massive die-offs have been related to episodic pH events and associated elevated NH_3 (van der Heide et al., 2010).

Ammonia toxicity is known for many vascular plants (Britto and Kronzucker, 2002). Growth of seagrasses *Ruppia drepanensis* and *Z. marina* has been significantly depressed under NH_4^+ enrichment (mean pH 8.5), unrelated to light attenuation from algal overgrowth (Santamaría et al., 1994; van Katwijk et al., 1997). In the Santamaría et al. (1994) and van Katwijk et al. (1997) studies, sediment and water-column NH_4^+ were high relative to levels typically found in seagrass habitats, with die-off occurring at 3-220 µM NH_4^+N (=0.42-3.08 mg L^{-1}) in the water column, and at 500-1,600 µM NH_4^+N (=7.00-22.4 mg L^{-1}) in the sediment porewater. Earlier work by Thursby and Harlin (1982) had also shown that maximum rates of root NH_4^+ uptake by *Z. marina* were substantially compromised during periods when leaves were exposed to increased NH_3 (15-30 µM). The authors hypothesized that the observed response was associated with higher basipetal translocation of N products relative to acropetal translocation.

Toxic effects of NH_4^+ and NH_3 on the common calanoid copepods, *Eurytemora* and *Pseudodiaptomus*, have been reported in the Bay Delta (Flores et al. 2010). For example, *Pseudodiaptomus* reproduction rates are negatively affected, as are nauplii and juvenile growth rates (Flores et al., 2010). Suppression of productivity and reduction in the proportion of primary: bacterial productivity have been reported for other N-hypersaturated systems as well (Waiser et al., 2011), and such impacted systems have been identified to be significant sites of ecological change (Brooks et al., 2006).

Tolerance for NH_3 and its excretion in bivalves are other adaptations to long periods of emergence. Most bivalves excrete NH_3 after short emergence periods as a mechanism to avoid NH_3 toxicity during the acidosis that develops during emergence (e.g. Widdows and Shick, 1985; Schick et al., 1988). However, adaptations of the freshwater clam *Corbicula fluminea* apparently differ: In *C. fluminea* there was no evidence of immediate NH_3 release following 2-4 days in air;

rather, maximal excretion rates occurred 15 h after re-submergence and were maintained for at least 35 h (Byrne et al., 1991b). Rates of release increased up to 4-fold for 2-day exposures at 25°C (Byrne et al., 1991b). This species may fundamentally change its metabolism during these exposure periods by suppressing protein catabolism and NH_3 production, and/or by storing and subsequently deaminating amino acids such as alamine (Gainey 1978). When emersed, *C. fluminea* shows little NH_3 production, but after return to the water, elevated excretion rates suggest a shift in metabolism.

Within the significant tidal range of Suisun Bay (Smith and Cheng, 1987), a similar mechanism in the clam *Corbula amurensis* would provide an additional physiological explanation for the strong long-term relationships with NH_4^+ and NH_4^+: PO_4^{3-} (Fig. 23) (Glibert, 2010).

Macrophyte Production, Calcification, and Bivalves

Aquatic macrophytes alter sediment $CaCO_3$ dissolution rates due to aerobic respiration (Burdige and Zimmerman, 2002). In *Egeria*, as in various other macrophytes that are capable of using bicarbonate (Allen and Spence, 1981), inorganic carbon is taken up through the abaxial surface, and hydroxyl ions are released through the adaxial surface. Thus, the pH is lower on the lower side and high on the upper side (Prins et al., 1982; Raven, 1984). With this polarity, $CaCO_3$ may precipitate on the side of hydroxyl ion release. $CaCO_3$ production rates in temperate to tropical seagrass beds range from <0.1 to >7 g $CaCO_3$ m^{-2} d^{-1} (Gacia et al., 2003 and references therein). Extracellular Ca^{+2} concentrations have also been associated with the ability of the plant to endure stress; *Egeria* produces H_2O_2 and induces leakage of other electrolytes (Marre et al., 1998).

The pK of calcium carbonate is 7.9. As the pH rises, the reaction

$$Ca(HCO_3)_2 \leftrightarrow CaCO_3 + H_2CO_3 \qquad (4)$$

is driven to the right, thus increasing calcification. While the effects of vegetation on biogeochemistry can be large, these effects are also species-specific and depend on sediment characteristics. In macrophyte communities, calcifying fauna represent the dominant epibiota (Marba et al., 2006). These epiphytes have been shown to be preferred sources of food for fish such as sunfish (*Lepomis* spp.) (e.g., Werner and Hall, 1979; Schramm and Jirka, 1989; Toft et al., 1983). Larger organisms with more bone also have a greater need for Ca than do smaller organisms; shad, for example, increase their Ca in biomass from 1% to 6% when their length increases from 20 to 120 mm (Pilati and Vanni, 2007).

The precipitation of $CaCO_3$, a complex process in bivalves, requires significant PO_4^{3-} as well as Ca^{2+} (Asana and Ito, 1956). Total P requirements in shellfish are high (Asano and Ito, 1956); in fact, in a comparison of net incorporation rates of P in fish and shellfish, those of the shellfish were higher (Asana and Ito, 1956). In the Bay Delta, there is a strong long-term correlation between water-column DIN:TP ratios (and DIN:PO_4^{-3} ratios) and abundance of the clam, *Corbula amurensis* (Fig. 23) (Glibert, 2010); there is also a strong long-term relationship between pH and *C. amurensis* abundance (Fig. 40). This species invaded the Bay Delta in 1987, at the start of a several-year period of drought (Alpine and Cloern, 1991; Kimmerer 2004). Some freshwater bivalves appear to be particularly well adapted to sustain drought and dry periods, and such adaptations relate, as well, to Ca metabolism. The freshwater clam *Corbicula fluminea*, another invader of freshwater habitats including the Bay Delta (Lucas et al., 2002), mobilizes shell $CaCO_3$ to retard the effects of acidosis that results from long periods of aerial exposure or hypoxia (Byrne et al., 1991a). Concentrations of Ca in sediment porewater in regions occupied by clams would be expected to be much higher than that of sediments where clams are not abundant. In addition to metabolic fluxes, dead clam shell dissolution contributes to such concentrations and help to sustain elevated concentrations in a positive feedback. Zebra mussels (*Dreissena polymorpha*), invaders in the Laurentian Great Lakes, many rivers in the midwestern USA., and much of Europe, sustain a net loss of Ca when the pH falls below 6.8 (Heath, 1993).

Suspension-feeding bivalves can also increase seagrass productivity because their biodeposits are a conduit between the pelagic and the benthic communities, bringing particulate nutrients to the benthos in the form of algae and increasing nutrient availability to the benthos through their regeneration (Peterson and Heck, 2001; Heck and Orth, 2006). Suspended sediments depress photosynthesis in seagrasses (e.g., Ralph et al., 2006; Touchette and Burkholder, 2007); however, macrophytes with an ability to enhance gas exchange across the leaf surface by floating are not as affected. The rates and pathways by which bivalves release particulate and dissolved nutrients to the rhizosphere and the water column also influences stock re-establishment and associated eutrophication impacts (Newell, 1988; Rice, 2000; Peitros and Rice, 2003; Burkholder and Shumway, 2011, and references therein). Reduction of turbidity by filter feeders also can increase light availability of macrophytes.

Corbula spp. burrows a few centimeters into the sediment, with at least a portion of its siphon remaining in the water column. This animal has a pelagic larval stage that typically is in the water column for several weeks in spring, and it accelerates rates of calcification in summer when temperatures and pHs are elevated (Hrs-Brenko, 2006). Larvae survive well under oxygen stress (Rosenberg, 1977), and in enclosed bays with high sedimentation and reduced hydrodynamic flow (Solis-Weiss et al., 2004). *Corbula gibba* has been shown to have higher survival rates under hypoxic conditions, especially adults, than under oxygen-replete conditions

(Holmes and Miller, 2006). It can become dominant in hypoxic, systems, but otherwise is a relatively poor competitor (Holmes and Miller, 2006).

Biological and Biogeochemical Feedbacks and Microcystis *Abundance*

Positive feedback interactions between clam production, excretion, altered biogeochemical processes, and nutrient accumulation help to explain why shifts in algal assemblage composition occur when clams are abundant (Glibert, 2010). Macroinvertebrates are well recognized to be sensitive indicators of anthropogenic impacts in lakes and estuaries (Chainbo et al., 2010) and *Corbula* spp. is well documented to be a bioindicator of pollution (FAO/UNEP, 1986). They are considered to be rapidly growing "r-selected" species (Gray, 1979; Hrs-Brenko, 2006). The virtual disappearance of chlorophyll *a* from Suisun Bay since 1987 has been attributed to the proliferation of *Corbula amurensis* (Alpine and Cloern, 1991; Kimmerer, 2002; Jassby et al., 2002). Diatoms had declined from this system a few years earlier than the invasion, and during the late 1980s there was a shift to increasing abundance of chlorophytes, dinoflagellates, cryptophytes and cyanobacteria (Figs. 10 and 11) (Glibert, 2010). The cyanobacterium *Microcystis* is commonly observed in the upper (fresher) reaches of the Bay Delta, not in Suisun Bay where *Corbula amurensis* is most common. Instead, the upper reaches of the Bay Delta have a higher prevalence of *Corbicula fluminea* (Lucas et al., 2002). Although cyanobacteria increased in abundance in the mid-1980s, their abundance and their ecosystem impacts have escalated significantly in the past decade (Lehman et al., 2005, 2008, 2010).

Links between zebra mussels and *Microcystis* have been examined in various systems (discussed below; Sarnelle et al., 2005), and these findings may be analogous to the relationship between invasive clams and *Microcystis* in the Bay Delta. Excretion by zebra mussels is significantly higher than that by crustacean zooplankton (Conroy et al., 2005). Ecological stoichiometric principles have been examined with respect to zebra mussel invasions of Swedish Lakes (Naddafi et al., 2009). While nutrient stoichiometry was not linked to mussel fitness, the zebra mussels tolerated low P and that their stoichiometry was altered by both food quantity and quality.

Numerous studies have suggested a linkage between the increased prevalence of cyanobacteria blooms and either reduced stocks of planktivorous fish (e.g. Reinertsen et al., 1989; Hessen, 1997) or increases in invasive bivalve molluscs (e.g., Bykova et al., 2006). Both trophic cascade effects and altered nutrient cycling from changes in nutrient release have been thought to be the linking mechanisms. Nutrient loading can interact with resource removal through trophic cascading: Depletion of large grazers (including invertebrates) results in decreased predation on macro- and microzooplankton, leading to reductions in microzooplankton populations and increases in algal blooms in the nutrient-enriched environment (Merrell and Stoecker, 1998; Stibor et al., 2004; Vadstein et al., 2004). In cyanobacteria-dominated reservoirs in Australia, a trophic link between mesozooplankton and *Cylindrospermopsis* has been suggested (Ying et al., 2010). Mesozooplankton preferentially consume algae other than *Cylindrospermopsis*, in turn releasing P that is rapidly taken up by the cyanobacteria. This phenomenon may be germane with respect to increases in *Microcystis* blooms not only in the Bay Delta, but also in many other systems affected by invasive species.

Microcystins appear to adversely affect growth and development of daphnids, with offspring showing decreased growth and survival even if the offspring were raised in microcystin-free conditions; effects are age and dose-dependent (Dao et al., 2010; Ortiz-Rodríguez and Wiegand, 2010). Wang et al. (2010) showed that *Microcystis* developed in experimental systems when zooplankton were included in the enclosures, but not in those where zooplankton were removed prior to the start of the experiment. It has similarly been noted that *Microcystis* blooms in lakes typically co-occur when small-sized zooplankton dominate (Allen, 1977; Edmondson and Lutt, 1982; Wang et al., 2010). The effect of microcystins on *Daphnia* in the Bay Delta has not been examined, but greater detrimental effects on the copepod *Eurytemoras* than on the copepod *Pseudodiaptomus* have been observed in that system (Ger et al., 2010).

Various studies have related increasing N and increasing N:P ratios to increased toxicity of *Microcystis*. In Daechung Reservoir, Korea, *Microcystis* toxicity was related not only to an increase in N in the water, but also to cellular N content (Oh et al., 2001). In P-limited chemostats, Oh et al. (2000) observed that while *Microcystis* growth declined as the degree of P limitation increased, more microcystins were produced as the extent of P limitation increased. In addition, the more toxic microcystin-LR form was produced compared to microcystin-RR (Fig. 41). Excess N has also been related to microcystin production under controlled chemostat conditions (Van de Waal et al., 2009, 2010). In the Philippines, increased *Microcystis* was associated with high N but not P loading, and its cellular P content (cell quota) was low (Baldia et al., 2007). In the Huron River, Michigan, USA, *Microcystis* has been associated with molar water column N:P ratios ranging from 40 to 80 (Lehman, 2007). Similar relationships were reported for a field survey of Hirosawa-no-ike Pond, Kyoto, Japan, where the strongest correlations between microcystins and nutrients were found at high concentrations of NO_3^- and NH_4^+. Moreover, seasonal bloom maxima were associated with extremely high water column N:P ratios ranging from 40-90 (Ha et al., 2009). In the field and in culture, the molar cellular N:P of *Microcystis* has varied from ~10 to more than 30 (Tsukada et al., 2006). Thus, both abundance and toxicity of *Microcystis* appear to be enhanced under high water-column N:P ratios. This would suggest that *Microcystis*, unlike many phytoplankton, does not follow the "you are what you eat" model" (Sterner and Elser, 2002, p. 16), but instead functions stoichiometrically more like a heterotroph, in this case sequestering P and releasing excess N in the form of the toxin, microcystin. It may also have the capability to reduce its P requirement by lipid substitution, although this has not been directly shown for this species, but has for other cyanobacteria (Van Mooey et al., 2009). From its C-concentrating capability (e.g. Paerl, 1983) to its P metabolism and its tolerance and/or preference for NH_4^+, *Microcystis* appears well adapted to the current environment of the Bay Delta where pH values fluctuate and can become elevated on episodic bases, and where N:P ratios have inceased over time.

Broad surveys have been undertaken to assess relationships between cyanobacteria and water-column N:P ratios. Some of these surveys have included all cyanobacteria (including the N_2- fixing species), others only *Microcystis*. Downing et al. (2001) examined data from 99 lakes from around the world and reported that total P or total N were better predictors of cyanobacteria than N:P ratios. Others have shown that low N:P ratios can favor cyanobacteria (e.g., Smith, 1983; Stahl-Delbanco et al., 2003). *Microcystis* is able to tolerate elevated N:P ratios, and thus its dominance under high N:P ratios may also reflect the decline in other species without such tolerances. Cyanobacteria do not have to grow faster at elevated N:P than at lower N:P values to become abundant; they merely have to grow faster than competing species groups (Glibert, 2010). Clearly, there is great plasticity in the ability of cyanobacteria to grow in a wide range of environments, including elevated N:P environments. It is also possible that some cyanobacteria, such as *Synechococcus*, flourish under high levels of water-column P (c.f., Finkel et al., 2010), while others, such as *Microcystis*, are especially good at sequestering P, leading to negative correlations.

Summary of Part III

Conceptually the relationships between changes in pH and altered salinity and the major biogeochemical processes are summarized in Fig. 42, while the changes over time and the shift in dominant biogeochemical processes are depicted in Fig. 43. While the interactions among the biogeochemistry and biology and their changes over time are complex, the important point is the interconnectedness of these relationships. This analysis suggests that these changes in biological communities are not a result of stochastic events but, rather, the result of a cascade of changes in biogeochemistry resulting from the major driver, changes in nutrient loading over time. Reductions in P loading from external sources drive the system toward increased importance of sediment dynamics and thus sediments as a source of P. The food webs that are supported are thus different from those supported when the water column is the source of P. Macrophytes, such as *Egeria*, and *Microcystis* are physiologically well adapted to these altered nutrient flux regimes. The communities of fish change accordingly.

PART IV: COMPARATIVE ECOSYSTEMS

The changes over time in the Bay Delta have been described as uniquely complex, driven primarily by the wide range in effects of invasive species and alterations in habitat (e.g., Alpine and Cloern, 1992, Bennett and Moyle, 1996; Cohen and Carlton, 1998; Kimmerer, 2004). This notion of unique complexity for the Bay Delta is not supported by the following analysis of other aquatic systems. Instead, the information illustrates similarities with the Bay Delta in terms of 1) changes in state from a system with high chlorophyll *a* and high pelagic productivity to one dominated by macrophytes, or vice versa, as a function of nutrient loading; 2) invasions of bivalves following P removal; 3) associations between high macrophyte production, invasive bivalves, piscivorous fish, and *Microcystis* growth, and/or 4) reductions in invasive species following targeted nutrient reduction measures.

Lake Washington

A classic example of a system that has sustained shifts to new stable states following P removal is Lake Washington. This large, deep lake (surface area 8,959 ha; 32.2 km long x 2.4 km wide; maximum depth 65 m, mean depth ~18 m, with ~128 km of shoreline; Koehler et al., 2006) is surrounded by the city of Seattle, Washington, USA, and historically was degraded by major sewage inputs (Edmondson, 1996). In 1922, a diversion was created to carry the raw sewage from 30 outfalls away from the lake into nearby Puget Sound, and algal blooms and fish kills soon abated. However, in 1930 sewage effluents began to be discharged into the lake again, this time from treatment plants in outlying communities, and ~76 million liters of sewage without nutrient removal had been discharged daily into the lake over the period from 1930 to 1962. Hypoxia increased along with blooms of noxious cyanobacteria, mostly as potentially toxic *Planktothrix* (formerly *Oscillatoria*) *rubescens* and various N_2- fixing species.

In the 1960s, Seattle and the surrounding communities adopted zero sewage discharge policies for Lake Washington. Removal of P from effluent was undertaken, and P levels declined precipitously (Krebs, 2008). By 1970 phytoplankton growth had decreased to levels that had not been seen since the early 1950s, along with obvious improvements in water quality and aesthetics. Zooplankters such as *Daphnia* spp. became increasingly abundant (Edmondson and

Litt, 1982). This increase was enhanced in part by an increase in longfin smelt that consume a major *Daphnia* predator, the opossum shrimp *Neomysis mercedis*, which declined sharply. The decline in *Neomysis* in Lake Washington, like that in the Bay Delta, corresponded with the period of P removal. It should be noted that these changes, influenced by ecological stoichiometry, are also being modified by influences of global warming, which is now uncoupling the influence of the "keystone" grazer *Daphnia* on phytoplankton and cyanobacteria are again on the increase in Lake Washington (Winder and Schindler 2004a,b). With increased warming of the upper water column, daphnids are beginning to decline. Ecological stoichiometric changes and climate change synergistically affect food web structure.

Potomac River, Chesapeake Bay

The Potomac River has undergone many similar changes to those in the San Francisco Estuary (Table 2, Fig. 44). The Potomac River has been heavily impacted by nutrient inputs for over a century, with cyanobacterial blooms evident in the 1930s (Krogmann et al., 1986). Nutrient inputs to the Potomac have been strongly affected by management actions (Table 2), starting with treatment that removed 75% of point-source P loading by 1976, and with a P detergent ban, so that there was a total decrease of more than 95% from peak levels (Jaworski and Romano 1999). Nitrification was added to the treatment plant processing in the early to mid 1980s, resulting in decreased NH_4^+ loading, and from the early 1990s to the present, effluent loading has decreased more than 50% from the early 1990s to the present (Jaworski and Romero, 1999; Jaworski et al., 2007).

An invasion by *Corbicula fluminea* was first noted in the mid-1970s, and its abundance peaked in the late 1980s, exceeding 2,500 individuals m^{-2} (Dresler and Cory, 1980; Phelps, 1994). Its abundance subsequently declined, coincident with the efforts to remove N from effluent (Phelps, 1994; Cummins et al., 2010; Fig.44A). Its presence in the 1980s was associated with declines in phytoplankton abundance due to the grazing pressure it imposed (Cohen et al., 1984).

When N:P ratios increased in the late 1970s, chlorophyll *a* declined and submersed vegetation increased. *Hydrilla verticillata*, an invasive species, expanded its range shortly after P removal and this was associated with a decrease in water-column chlorophyll *a* (Rybicki and Landwehr, 2007; Ruhl and Rybicki, 2010; Fig. 44B). The extent of *Hydrilla* coverage was directly related to the N:P ratios of the effluent (Fig. 44C). After the nitrification-denitrification system was installed at that treatment plant several years later, the relative abundance of this exotic species declined while the abundance of native grasses and vegetation increased (Ruhl and Rybicki, 2010).

Microcystis, which had been a major component of the phytoplankton assemblage in the 1960s, declined in abundance with the installation of more advanced sewage treatment in the 1970s. However, over time, *Microcystis* returned. The percent of samples collected in which >10% of the phytoplankton cells were *Microcystis* was also highly correlated with the N:P ratio in the total load of nutrients to the river (Tango et al., unpubl. data; Fig. 44D).

Fish composition also changed over time, and some of these changes can be related to nutrient stoichiometry. Bay anchovy decreased and both spottail shiner and largemouth bass increased (http://www.dnr.state.md.us/fisheries/juvindex/index.asp#Indices) in proportion to N:P ratios that reflected changes in either total nutrient loads or effluent (Fig. 44E,F). Overall, the ratio of pelagic:demersal fish declined (Kemp et al., 2005; www.noaa.chesapeakebay.net) and these changes related to the N:P ratio in the effluent (Jaworski et al., 2007; Fig. 44G).

Hudson River

Point source nutrient loading to the Hudson has been contentious for many decades (Brosnan et al., 2006). Peak loading of N and P occurred in the 1930s, with a rate of ~125 tonnes d^{-1} and ~13 tonnes d^{-1}, respectively. Secondary treatment plants were constructed in the 1980s, and N loads decreased by ~30%. Reductions in P by ~60%, from a maximum of 36 mt d^{-1} in the 1970s, was achieved by the 1990s through secondary treatment and P removal from detergents. The exception to these river nutrient trends is the lower Hudson, where, loads of both N and P *increased* due to the Ocean Dumping Ban Act of 1988, which required several municipalities to cease ocean disposal, and from New York City's use of a P-based buffer to reduce pipe corrosion (O'Shea and Brosnan, 2000; Brosnan et al., 2006). The total N and P loads to the Hudson are now on the order of 43 x 10^3 tons N yr^{-1} and 4.8 x 10^3 tonnes P yr^{-1}, of which 53% of the N and 77% of the P are from point source discharges (Howarth et al., 2006).

The Hudson, like the Bay Delta, has been heavily impacted by invasive species. The dominant species of concern include the zebra mussel, black bass, water chestnut, Atlantic rangia (*Rangia cuneata*), and the Asian shore crab (*Hemigrapsus sanguineus*) (Strayer, 2006). These species "came from Europe or the Great Lakes through shipping activities, the Erie Canal, or deliberate introduction" (Strayer, 2006, p. 296). Zebra mussels were first detected in the Hudson in 1991 and by 1992, when P reductions had been implemented, were well established (Strayer, 1992). Their impact on the chlorophyll *a* and zooplankton populations of the river was large, and planktivorous fish soon became food limited (Caraco et al., 1997; Pace et al., 1998, Strayer, 2006). Annual May-October chlorophyll *a* dropped from ~20 μg L^{-1} to ~4 μg L^{-1} after 1993 when zebra mussels were well established (Cole and Caraco, 2006). Common copepods in the Hudson now include two cyclopoids, *Diacyclops bicuspidatus thomasi* and *Halicyclops* sp. (Pace and Lonsdale, 2006).

Increases in largemouth bass and bluegill have been observed since nutrients have changed and, analogous to the Bay Delta, the length of American shad has decreased since P removal and zebra mussel invasion (Stanne et al., 2007). There have also been large increases in water chestnut (*Eleocharis dulcis*), an aggressive macrophyte that was first observed in the Hudson in the 1930s. It has especially increased during recent decades, with “larger beds reaching 10-100 hectares in extent” (Strayer, 2006, p. 302). In these dense beds, oxygen depletion occurs (Caraco and Cole, 2002). The small estuarine invasive clam, *Rangia*, was first detected in 1988 and has spread significantly since that time (Strayer, 2006). Overall, the Hudson has displayed a trajectory of responses similar to those of the Bay Delta, with a shift from a productive pelagic system to one dominated by benthic production. These changes were all accelerated in the Hudson in the early to mid-1990s when P removal measures were most significant. The ratio of N:P loads from all sources to the Hudson also increased from the early 1970s to the mid-1990s (Howarth et al., 2006).

Microcystis is now a concern in the Hudson River as well (Fernald et al., 2007). It had been problematic years earlier, but disappeared from the river soon after zebra mussels invaded (Smith et al., 1998). Laboratory studies indicated that it was preferentially grazed by the mussels (Baker et al., 1998; Baker and Levinton, 2003). Recent phytoplankton record reveals that *Microcystis* blooms have returned, and by 2005 it contributed more than 45% of the total summer algal biomass (Fernald et al., 2007). The recent reports have linked these blooms to increased temperature, but the pattern is also consistent with an altered biogeochemical pathway of nutrient cycling following the increased dominance of both macrophytes and zebra mussels.

The Laurentian Great Lakes and other U.S. Lakes

Lake Ontario has been well monitored for several decades and changes in nutrient loading and trophic dynamics are well characterized. Point source reductions in P began in this system in the late 1970s, and phytoplankton assemblage composition abruptly changed. The largest declines were noted in chlorophytes, dinophytes, bacillariophytes and cryptophytes (Nicholls et al., 2002). More than a decade later, zebra mussels became established and community composition changed in favor of smaller-sized phytoplankton species, including *Microcystis* (Nicholls et al., 2002; Mills et al., 2003). The zooplankton community shifted, as well, to increased abundance of cyclopoids and *Daphnia* (Mills et al., 2003). In fact, *Daphnia*, which comprised less than 15% of the zooplankton community prior to P removal, increased to 30-50% after P removal (Mills et al., 2003). Water-column N:P ratios in the early 1970s were near Redfield proportions, but now exceed 50 (reviewed by Mills et al., 2003). Medeiros and Molot (2006) similarly correlated the increase in microcystin cyanotoxins in Lake Ontario with the reduction in total P from the major municipal treatment plant, but they raised the possibility that other geochemical changes, including increases in iron, additionally may have occurred. Both invasion by zebra mussels and a shift from planktivorous to piscivorous fish were also associated with the reduction in P, including a dramatic decrease in rainbow smelt (Mills et al., 2003).

The same pattern of *Microcystis* increase after zebra mussel invasion was observed in western Lake Erie and in Saginaw Bay of Lake Huron (Lavrentyev et al., 1995; Budd et al., 2001). In contrast to the feeding studies of the zebra mussels in the Hudson River (Baker et al., 1998; Baker and Levinton, 2003), in Saginaw Bay *Microcystis* was not grazed by zebra mussels, and this has been inferred as one of the causative mechanism for the expansion in *Microcystis* in more recent years (Fishman et al., 2010).

In Lakes Huron and Erie, this relationship was attributed to selective rejection of *Microcystis* in zebra mussel pseudofeces (Vanderploeg et al., 2001). In a survey of 61 lakes in Michigan, a strong association between invasive zebra mussels and *Microcystis* was observed, but only for lakes with P levels less than 25 µg L^{-1} (Raikow et al., 2004). Knoll et al. (2008, p. 448), in a follow-up to the Raikow et al. (2004) study, found that in 39 lakes in southern Michigan, those with zebra mussels had, “3.3 times higher microcystin concentrations and 3.6 times higher biomass of *Microcystis*.” Although they did not clearly identify a specific mechanism leading to this relationship, ecological stoichiometric hypotheses were invoked, relating the relative retention of P, and excretion of N by the mussels as one factor that would enhance this relationship. It is not surprising, considering that ecological stoichiometry and biogeochemistry collectively appear to promote invasions, that zebra mussels and *Microcystis* blooms are predicted to continue to expand into such “oligomesotrophic” systems (Raikow et al. 2004).

The reduction in external P loadings during the 1970s followed by exotic mussel species invasions in the 1980s has affected benthic algal production, as well as phytoplankton, in the Great Lakes. In a manner analogous to *Microcystis*, which first declined and then increased years later following external P reductions, the benthic green filamentous alga *Cladophora* also proliferated after external P reductions. As summarized by Burkholder (2009), “As a ‘poster child’ of the 1960s ecology movement in the United States, *Cladophora glomerata* [and likely other *Cladophora* species] focused international attention on the west basin of Great Lake Erie where it proliferated in response to phosphorus pollution, then drifted into shore in rotting masses from major seasonal die-offs that were sometimes measured in tonnes of fresh weight

[Bootsma et al. 2005, and references therein; Higgins et al., 2006]….From the 1960s through the early 1980s, massive growth of *Cladophora* characterized the rocky shorelines of Lakes Erie and Ontario, as well as localized areas of Lakes Michigan and Huron….Research indicated that elevated inorganic phosphorus [P_i] concentrations were the most important cause of the blooms, and led to multi-billion dollar upgrades in wastewater treatment plants and detergent P bans. TP and *Cladophora* markedly decreased in the lower Great Lakes. The Great Lakes recently have become a *Cladophora* story of 'déjà vu.' Ironically, dissolved P_i concentrations during the spring season have increased again in nearshore waters throughout Lake Erie since the late 1980s from metabolic wastes and feces of mass invasions of exotic zebra mussels and quagga mussels (*Dreissena bugensis*), which now dominate the nearshore benthic environment. Recent surveys have indicated that the mean peak biomass of *Cladophora* is similar to historic values in Lake Erie during the 1960s-1970s, and shorelines along portions of Lakes Ontario, Michigan, and Huron are again being fouled by rotting *Cladophora* growth."

In the lower San Francisco Estuary, *Cladophora* bloomed sporadically in the 1970s (e.g., Luoma and Cloern 1982). However, filamentous algae in the Bay Delta are not routinely assessed and, thus, trends over time cannot be quantified, although *Cladophora* is known to be present (e.g. Cohen, 1998; Anderson, 2003)

Florida Lakes

Many Florida lakes have undergone very similar changes to those of the Bay Delta. West Lake Tohopekaligo, central Florida, well known for its exceptional bass fishing, has had enormous changes in community composition and in nutrients over the past 20 years (Bonvechio and Bonvechio, 2006). Nutrients, especially P, were removed from this system in the late 1980s due largely to sewage treatment upgrades. Water-column N:P ratios increased (James et al. 2007). *Hydrilla* emergence soon followed, with a change from 0-83% coverage (Bonvechio and Bonvechio, 2006). Total phytoplankton chlorophyll *a* concentrations declined in the lake. In Lakes Wales and Baldwin, other *Hydrilla*-infested lakes, largemouth bass, black crappies and sunfish species all are common (Colle and Shireman, 1980; Bonvechio and Bonvechio, 2006). *Microcystis* is common in many of these Florida lakes as well and has been for many years (Bugham et al. 1971).

In a re-analysis of data on the relationship between aquatic macrophytes and largemouth bass in 56 lakes in northern and central Florida (data of Hoyer and Canfield, 1996), a significant correlation was found between percent cover by macrophytes and the molar TN:TP ratio (Fig. 45).

Florida also provides an example of the reversal of eutrophication following nutrient removal. Tampa Bay is considered a restoration success story following the removal of nutrients from wastewater effluent. Nitrogen loads in the 1970s were approximately 8200 tonnes annually (Greening and Janicki, 2006). The estuary was heavily impacted by these nutrients, with phytoplankton and macroalgal blooms, hypoxic and anoxic conditions and depauperization of the benthos, as well as a significant loss of native seagrass (Greening and Janicki, 2006). Over the subsequent decade, N in sewage effluents was reduced 90%, to 3 mg L^{-1}; N loads from fertilizer manufacturing operations were reduced and stormwater regulations also were improved to reduce N loads (Johansson and Greening, 2000). By the early 1990s, N loads were reduced by more than half of the 1970s levels. Since these reductions, chlorophyll *a* target levels have been reached, and native seagrass has begun to recover; indeed, seagrass acreage has increased 25% (Greening and Janicki, 2006).

In Lake Apopka, Florida, in the 1940s, there was an overgrowth of macrophytes, and fish were abundant. When PO_4^{3-} increased due to PO_4^{3-} mining, the lake became turbid and production shifted from the benthos to the pelagic (Bachmann et al., 1999). While there is considerable controversy regarding the development of the hypereutrophic state in Lake Apopka in the 1940s and whether it was gradual or episodic (e.g., Bachmann et al., 1999; Schelscke et al., 2000; Schumate et al., 2002), there is no disagreement that the food web shifted when the lake shifted from macrophyte to algal dominance in response to P loading.

European Lakes and Estuaries

In the Ebro River Estuary, where an 18-year time series of nutrients and biota have been examined, significant changes in the food web have occurred as nutrient loadings have changed. From the mid-1980s to the mid-1990s, P loading rates were consistently high, and NH_4^+ loading increased. Both dropped precipitously in the mid-1990s (Ibáñez et al., 2008). For P, this drop was from ~2.8 kt y^{-1} to <0.5 kt y^{-1}. However, total N load did not decrease to the same extent because NO_3^-+NO_2^- loads were not reduced. Consequently, mean values of DIN:DIP increased over 4-fold from the early 1990s to the mid-2000s. Total water chlorophyll *a* declined by ~10-fold, macrophyte production increased, sediment retention and transparency increased, and invasive bivalves increased, including *Dreissena polymorpha* and *Corbicula fluminea* (Ibáñez et al., 2008). These changes were attributed to the reduction in P loads (Ibáñez et al., 2008). In the Dutch Delta, Lake Veere provides another example of system change upon PO_4^{3-} removal; when PO_4^{3-} was reduced, following the restoration of exchange with the tidal marine eastern Scheldt, there was an increase in bivalves among other ecosystem changes (Wijnhoven et al., 2010).

In another example of the relationship between P reduction and zebra mussels, a study of the recovery of eutrophication in Lake Velume, The Netherlands, showed that zebra mussels expanded following P reduction (Ibelings et al., 2007). The zebra mussels in turn, like the macrophytes, acted as keystone species, further structuring the food web including fish. Lakes in southern Sweden have shown similar patterns: Lake Krankesjön shifted to a clear state when P was reduced, with a concomitant expansion of pondweed and piscivorous fish, while Lake Tåkern displayed a reduction in submersed vegetation, and increased chlorophyll *a* when nutrients, especially P, increased (Blindow et al., 2006; Hargeby et al., 2007). Zebra mussels were also highly associated with *Microcystis* in 47 sites in lakes in northern Ireland and all of these lakes had toxic blooms (Mooney et al., 2010). These studies further support the notion that feedback mechanisms help to stabilize systems in new states.

Summary of Part IV

The general trajectory of responses of the comparative systems described here are summarized in Table 3. Most of the changes in invasions of zebra mussels occurred in the late 1990s in the US (Fig. 46), the period coinciding with the most rapid removal of P throughout much of the US and Europe. It is possible that the similarity of these trends is coincidence – that serendipity resulted in these systems having similar food webs when nutrients were altered, and/or that similar ballast water pressures were exerted across the oceans at similar times. In addition, more classical explanations such as differences in food availability and cover (e.g., Crowder and Cooper, 1982; Colle et al., 1987) may explain the associations between macrophytes and centrarchids. However, the physiology of the resident organisms and biogeochemical pathways lends support to the premise that similar trophic structure, including the appearance of *Microcystis,* in many of these systems resulted from similar nutrient dynamics, biogeochemistry and food web interactions that resulted, in turn, from changes in stoichiometry and the relative abilities of different types of organisms to either sequester nutrients and/or tolerate those (e.g., NH_4^+) in excess.

PART V: ECOLOGICAL STOICHIOMETRY AND PREVAILING VIEWPOINTS

The interpretation of changes in the food web structure of the Bay Delta as a function of stoichiometric changes in nutrients is seemingly at odds with many of the prevailing perspectives of how this system has become stressed over time. Nutrients have not been linked to the decline in fish or the change in species dominance at all levels for multiple reasons. Nixon and Buckley (2002), in a review of the relationships between nutrient loadings and fish production, discussed the evolution of the concept of linking nutrients to fish, and tracked how this concept generally fell out of favor. Among the reasons cited was the recognition that “the last 100 years of marine research revealed a much richer and more complex marine environment than anyone working in the 1900 could have imagined, ultimately leading to the conclusion by Micheli (1999) that there is “...virtually no link between nutrient delivery or availability and secondary production in marine coastal waters” (Nixon and Buckley, 2002, p.784). This rich complexity of effects has led to a range of interpretations with respect to changes in the food web in the Bay Delta, most of which have not involved the notion of nutrient control.

Nutrients have recently been considered in the context of potential inhibition of diatoms by NH_4^+ (Wilkerson et al. 2006; Dugdale et al., 2007). The possibility of ‘bottom up’ control of fish populations in the Bay Delta has been largely dismissed for several reasons: most nutrients are at levels that saturate phytoplankton growth; phytoplankton growth is considered to be regulated primarily by light limitation (Cole and Cloern, 1984); NH_4^+ is generally a preferred form of nitrogen for phytoplankton uptake; the pH of the receiving waters is generally in the range that prevents formation of the toxic NH_3; and NH_4^+ levels are typically below the criteria considered by the U.S. Environmental Protection Agency (EPA) to be toxic to aquatic organisms (McCarthy et al., 1977; Millero, 2006; Jassby, 2008; U.S. EPA, 2009). In addition, some analyses of nutrient effects have considered only total N or P and chlorophyll *a*, rather than nutrient form and phytoplankton composition (e.g., Jassby, 2008). As a consequence, relationships between nutrients, production or food web effects have been ambiguous (Jassby 2008). Moreover, because many physical, chemical and biological factors potentially influence and modify other factors, the system as a whole is considered highly complex. Thus, prior efforts that used standard multifactor correlative analyses of the ecosystem data have not been successful at identifying causality with any degree of certainty (Bennett and Moyle, 1996; Sommer et al., 2007, Mac Nally et al., 2010, Thompson et al., 2010).

Prevailing views about changes in the Bay Delta food web emphasize invasive species, light limitation of primary production, potential inhibition by NH_4^+, alteration in flows, including export pumping, alterations in habitat, and climate change as major stressors (Linville et al., 2002; Davis et al., 2003; Lehman, 2004; Lehman et al., 2005; Bennett, 2005; Sommer et al., 2007; Jassby, 2008, Baxter et al., 2010). Both the prevailing viewpoints and the stoichiometric viewpoint underscore that the system is stressed and complex. The prevailing views are examined here in comparison to stoichiometric interpretations. The effects of climate act synergistically with many of these stressors in the Bay Delta and elsewhere (e.g., Lehman, 2000; Burkholder et al., 2006, Paerl et al., 2006; Cloern et al., 2007; Paerl and Scott, 2010).

Invasive species

Food web changes in the Bay Delta ecosystem largely have been interpreted in the context of invasive species introductions (e.g., Alpine and Cloern, 1992; Cohen and Carlton, 1995, 1998; Kimmerer et al., 1994; Kimmerer, 2004). From the copepods *Pseudodiaptomus* and *Limnoithona* to *Corbula*, *Egeria*, *Microcystis* and others, the system has been heavily changed by altered trophodynamics. These species have been introduced by various mechanisms – ballast water, inadvertent introductions from bait or ornamental organisms, and the rate of introductions is large. Our premise here, however, is that without alterations in nutrient biogeochemistry, these organisms most likely would not have become established. Nutrients thus provide a mechanism whereby "invasional meltdown" can be accelerated (Simberloff and Von Holle 1999).

The invasion of clams has often been considered to be the major factor modifying the primary production in this system (Alpine and Cloern, 1992; Jassby et al., 2002, 2003; Kimmerer, 2004). While there is little doubt that invasive species can alter ecosystems (Elton 1958), it is now also recognized that "it is difficult to separate the effects of exotic species on ecosystems from those triggered by other anthropogenic stressors" (Vitousek et al., 1996; Martin and Valentine, 2010). This review has raised the hypothesis that anthropogenic stressors in the form of changing nutrient loads, from simultaneous reductions in P and increases in N loading, led to conditions favorable for the establishment of invasive macrophytes and bivalves. Their establishment, in turn, led to conditions favorable to cyanobacterial blooms and altered fish communities. Thus, the ultimate driver was a change in nutrient loads. While species may be introduced from non-native habitats via many mechanisms, they can only become established when the nutrient biogeochemistry is favorable for their success. Introduction of species alone is not sufficient for them to become established.

Light Limitation of Primary Producers

Dissolved nutrients generally have been perceived to play, at most, a minor role in controlling the succession of biota in the Bay Delta over the last 30 years and that primary production is considered to be mainly controlled by light. This notion stems from a number of modeling studies of phytoplankton productivity as applied to the San Francisco Estuary (Cloern et al., 1995; Cloern,1999; Jassby et al., 2002). The results of the models indicated that over much of the estuary, particularly the upper estuary, ambient nutrient concentrations over the last ~30 years were generally well in excess of the demand for those nutrients given the available light in the water column to drive photosynthesis: i.e., the phytoplankton were strongly light-limited and not nutrient-limited for growth. The models of Cloern (Cloern et al., 1995; Cloern 1999) were developed to simulate phytoplankton primary productivity in the San Francisco Bay Estuary based on the availability of resources (light and nutrients) in the system and empirical 'physiological' relationships. The influence of nutrients was formulated using assumptions of uptake kinetics with respect to ambient concentrations and an interactive term with light harvesting to account for photoacclimative changes in chlorophyll *a*:carbon (Chl:C) ratios under different nutrient stress levels. The models were parameterized using mean relationships from large datasets (Cloern 1999). Importantly, however, the wide plasticity in nutrient uptake kinetics between species and within species under varying growth conditions was not considered (e.g., Rhee, 1973; Burmaster and Chisholm, 1979; Gotham and Rhee, 1981; Goldman and Glibert, 1982, 1983; Morel, 1987). A subsequent model developed by Jassby et al. (2002), which did not include a nutrient term, exhibited good fidelity with independent productivity measurements, suggesting that primary productivity was independent of nutrients in the system. Therefore, the models have been taken to be substantially accurate in the limited context of distinguishing light from nutrient limitation of C production by the phytoplankton.

Do these phytoplankton productivity model results really indicate that there are minimal nutrient effects on the phytoplankton assemblage of the Bay Delta? A fundamental premise of the previous modeling approaches was that primary production of reduced C is the principal factor that links phytoplankton to the grazer community and upper trophic levels. This is a conventional approach for determining the amount of energy (as reduced C) that would be available to upper trophic levels, but it ignores the transfer of elements other than C. It is analogous to studying nutrition by only counting calories. In contrast, within the context of ecological stoichiometry, it is the processing and transfer of N and P by and through the phytoplankton assemblage that drives the fitness of species at higher trophic levels (Sterner and Elser, 2002; Allen and Gillooly, 2009; Schoo et al., 2010; Malzahn et al., 2010). No insight into these aspects of community response can be drawn from the existing, carbon-based primary production models. As illustrated in the analyses above, nutrients that are at levels normally taken to be saturating or near-saturating do influence the elemental composition of the phytoplankton and therefore affect, differentially, the transfer of N and P to upper trophic levels.

Although the Redfield ratio is often used to infer elemental composition in phytoplankton, the actual elemental composition of microalgae in culture and phytoplankton in nature is highly variable (Geider and LaRoche, 2002; Finkel et al., 2010). Extreme ratios are observed in cultured cells that have experienced limitation of either N or P (Rhee, 1978; Goldman et al., 1979; Geider and La Roche, 2002) reflecting a non-homeostatic ‘luxury consumption’ response which is characteristic of microalgae (Goldman and Glibert, 1983). Significantly, under nutrient-replete growth conditions (i.e. saturating ambient concentrations), variation in the N:P ratio of microalgae can be on the order of 3-4-fold (5 to 19 mol N:mol P;

Geider and LaRoche 2002; Finkel et al., 2010).

The extent to which this variation is related to algal species (or taxonomic groups) or to plasticity in the N:P ratio as a function of growth condition is debated (e.g. Quigg et al., 2003; Leonardos and Geider, 2004a,b; Finkel et al., 2010). While C flow through the ecosystem may control rates of primary production, N and P availability and form may control species composition and trophic transfer. This concept is similar to that proposed by Malone et al. (1996), and has been illustrated in Chesapeake Bay and Moreton Bay, Australia (Malone et al., 1996; Glibert et al. 2006b): the same nutrients do not necessarily regulate biomass and productivity.

Potential Inhibition of Diatoms by NH_4^+

The potential inhibition of shellfish and fish by high levels of NH_4^+ and, under levels of high pH, NH_3, was described in Part III, although, with few exceptions, these effects have been considered to be small in the Bay Delta.

The effect of NH_4^+ on diatom production has received considerable recent attention in the Bay Delta (e.g., Wilkerson et al. 2006, Dugdale et al., 2007;Van Nieuwenhuyse, 2007; Jassby, 2008; Glibert, 2010). Many diatoms physiologically prefer, and in some cases require, nitrate (NO_3^-) over NH_4^+. This is the fundamental basis of the discrimination between bew and regenerated production (*sensu* Dugdale and Goering, 1969). NO_3^- may be used in the energy balance of these cells (Lomas and Glibert 1999). However, most algae physiologically prefer NH_4^+. Some of the first observations that NH_4^+ is assimilated by algae first, and only then does NO_3^- get assimilated, were from batch culture experiments in the 1930's, 40's and 50's (e.g., Ludwig 1938, Harvey 1953). Some of the early field demonstrations of this phenomenon were by MacIsaac and Dugdale (1969, 1972), followed by research in the Chesapeake by McCarthy et al. (1975, 1977). In the San Francisco Bay, Wilkerson et al. (2006) and Dugdale et al. (2007), based on enclosure experiments, found that diatoms grew only after NH4+ concentrations were drawn down to <4 µM (0.056 mg L^{-1}).

When NH_4^+ is present in high concentrations, it can become inhibitory to NO_3^- uptake (Syrett and Morris, 1963; Eppley et al. 1969; Conway et al., 1976). The analysis provided herein is consistent with a physiological inhibition of diatoms. Diatoms declined in direct proportion to the increase in NH_4^+ over time, but further experimental data would be required to evaluate cause-and-effect of the patterns shown here (Fig. 13). The mechanisms of NO_3^- inhibition by NH_4^+ have long been known, although there is still much to be understood about species specific differences. Active NO_3^- reductase (the enzyme involved in NO_3^- reduction in the cell) is generally not formed when NH_4^+ is present (Syrett, 1981). In some cells there is a reversible inactivation of NO_3^- reductase after addition of NH_4^+. In other cells, an irreversible inactivation of NO_3^- reductase (NR) occurs with NH_4^+ addition. The difference depends on species, cell growth conditions, and whether the addition of NH_4^+occurs in the light (when NR is active) or dark (when NR is inactive). There is much yet to be learned about the species differences, time scales and physiological regulation of this interaction.

Food Limitation

Food limitation of the food web has been invoked by numerous researchers (Bennett and Moyle, 1996; Jassby et al. 2002, 2003), ultimately linked to the declines in chlorophyll *a*. The Jassby et al. (2002) analysis compared nutrient values from the long-term monitoring data to average nutrient uptake kinetics by phytoplankton and found that classic "limitation" occurred in

<1% of the samples. The authors interpreted this information to mean that if nutrients were in excess, they would have no impact on production. Such an approach, however, fails to recognize that species shifts occur under different nutrient regimes – even in the absence of classic limiting conditions – and that these shifts have propagating effects through the food web. There is no lack of food in the Bay Delta, but there *is* a lack of food of the nutritional quality that would support planktivorous fish. Moreover, quantifications of food quality on the basis of C is an incomplete perspective. Detrital C appears to be abundant (e.g., Müller- Solger et al., 2002), but this may result in metabolic costs to consumers, including altered metabolic rate and growth rate (Plath and Boersma, 2001; Hessen and Andersen 2008). Disposal of excess C appears to have major impacts on organismal fitness, and like the other stoichiometric arguments posed above, can affect ecological interactions at the ecosystem level (Hessen and Andersen, 2008).

Variations in Flow and Habitat Suitability

Of considerable interest to resource managers in the Bay Delta have been the effects of hydrologic changes on pelagic fish (e.g., Nichols et al., 1986; Jassby et al., 1995; Kimmerer, 2002; Moyle et al., 2010). The question of relationships between hydrology and biodiversity are also of importance in many systems (e.g., Ferreira et al., 2009). In the Bay Delta, flow is rigorously managed and measured by the location where salinity is equal to 2, measured as the distance from the Golden Gate Bridge ("X2"; Jassby et al., 1995; Kimmerer, 2004). It has been thought that regulation of flow will lead to improved conditions for endangered fish. Relationships have been reported between X2 and chlorophyll *a*, *Eurytemora, Acartia*, rotifers, mysids, bay shrimp, and various fish species, including delta smelt, longfin smelt, splittail and starry flounder (Kimmerer, 2002). Interestingly, these relationships were noted to change after

1987.

Nutrients provide a mechanism for these relationships and why they changed with time: X2 is strongly correlated with PO_4^{3-}, TP and NH_4^+ (Fig. 46). Thus, when the nutrients changed due to changes in loading, the relationships with X2 changed. The time course of the interconnected changes in biogeochemistry and trophodynamics shown herein suggest that while flow may have been an important mechanism of nutrient dilution or supply in prior decades, increases in flow that occurred in the early 1990s did not result in a recovery of the food web because the biogeochemistry of the system had changed. Given the auto-correlative nature of X2 and nutrients, interpretations of effects of flow-related relationships should also consider the potential for ecological stoichiometric relationships to provide the mechanistic explanation. Changes in nutrients also suggest why relationships between fish abundance and X2 changed around 1987: this was a time of rapid change in nutrient loads.

A relationship has also been developed between X2 and a habitat index for delta smelt, an index which uses salinity, turbidity, and temperature to define the spatial distribution of habitat suitability. This index explained 26% of the variability in delta smelt over the past 3 decades (Feyrer et al., 2010). Interestingly, the authors note that additional abiotic factors might add more explanatory power to their model, “but it should be noted that these other factors would not likely increase our estimates of suitable habitat – they could only reduce them” (Feyrer et al., 2010). The habitat index, like that of X2, is highly correlated with nutrients (Fig. 46); thus, inclusion of nutrients should increase rather than decrease the confidence in identifying suitable habitat. Nutrients do explain the changes in phytoplankton and zooplankton well (Figs. 18-21) and, in turn, these changes have strong correlations with delta smelt. A recent analysis of the factors contributing to the decline in delta smelt underscores food limitation of that species, linked to changes in zooplankton composition over time (Miller et al., in review).

Moyle et al. (2010) has suggested that variability and disturbance are required to re-establish the native fish populations. They argue that the changes over time in fish populations are the result of, “an altered physical environment in which the Delta has become simplified into a channelized conveyance system to support export of fresh water from and through the Estuary during summer and to reduce freshwater outflows at other times of year. Suisun Bay and Suisun Marsh have become essentially a brackish water system, while San Francisco Bay has become more consistently a marine system, as shown by fish distributions” (Moyle et al., 2010). This notion is based on the premise that when disturbance is low, the system moves to an equilibrium where those species whose competitive abilities are low may be lost (Krebs, 2008). Interestingly, in aquatic systems, homeostasis tends to dampen the effects of disturbance (Krebs, 2008). Our focus here on nutrients and Moyle et al.’s (2010) focus on physical habitat both recognize that changes have led to altered stable states structured by keystone species and “ecological engineers.” Moyle et al. (2010) acknowledge that water quality is important in multiple ways, that their analysis is highly speculative, that freshwater brings many of the nutrients required to fertilize the food web, and that excessive nutrients, including effluent from large treatment plants needs to be addressed.

Exports of Water

A significant amount of the water supply for the State of California is extracted from the Bay Delta, via extensive pumps, aqueducts, and other engineering infrastructure (Brown et al., 2009). Fish declines have been associated with water extractions, as fish become entrained in the pumping facilities. Water restrictions in recent years, however, have not led to the expected change in fish populations, based on the assumption that export pumping was the cause of fish declines. Because exports are generally related to freshwater flow, being higher when flow is greater, there are correlations between exports and nutrients, the strongest of which is with TP (R^2 for exports and TP =0.206, $p<0.05$, not shown). Years of higher flow, hence years of higher exports, have lower TP. If planktivorous fish are less successful at sequestering P when it is comparatively low, then exports would appear to have a relationship with the decline in these fish. However, as was the case for X2 and the index of habitat, these measures are all correlated with nutrient availability. Given that nutrients affect fish size and all aspects of their metabolism and fitness, correlations between exports and fish abundance may be strengthened when fish are stressed. They may become more susceptible to other stressors.

Summary of Part V

The trajectory of responses to nutrients has set in motion a cascade of interacting effects. Thus, to varying degrees, nutrients, flow, X2, invasive species and climate change are all related to the observed changes in the food web and it is not surprising that some of these relationships are statistically significant. The trajectory of responses to changing nutrients over time provides a new conceptual model for the decline in pelagic species in recent years, the POD. The current conceptual understanding is based on multiple factors ranging from predation and water exports (top down control), to prior abundance levels (life history and density-dependent effects), to changes in the physical and chemical environment to changes in food availability and quality (Sommer et al. 2007, Baxter et al., 2010). In contrast, the stoichiometric interpretation suggests that many of these factors and changes are linked (Fig. 48). Nutrient changes, and the biochemical changes that follow as a consequence, alter the environment to make it conducive to invasive species, and differential nutrient metabolism and homeostasis drives the system away from planktivores to piscivores. The stoichiometric interpretation underscores that nutrient control – especially N control – is central to the recovery of the endangered pelagic fish.

PART VI: CONCLUSIONS, IMPLICATIONS AND RECOMMENDATIONS

Conclusions

Elemental stoichiometry and alternate stable state theory provide a unifying framework for understanding the complexity of responses not only in the San Francisco Bay Delta but also more generally in many comparative systems. Ecological stoichiometry affects systems by setting elemental constraints on the growth of organisms. This, in turn, affects the relationships between predators and prey, and they, in turn, modulate the environment through nutrient regeneration which differs from organism to organism based on their elemental requirements. Growth also alters the physical and chemical environment through pH changes, habitat alteration, light environment, and substrate, among other factors. These factors become powerful regulators of the food web in a complex interactive fashion. An overarching driver is the importance of bottom up control. Top-down control can be considered as a secondary effect, that is, a consequence of altered nutrients. This interpretation is consistent with Ware and Thompson's (2005) insights from a broad survey of the relative contributions of "bottom-up" vs. "top-down" factors that potentially control fish catch in the coastal waters of the western U.S.; they, too, reported that bottom-up factors were the most important. This interpretation does not preclude strong top-down control of selected component organisms. The distinction is that, at the overall ecosystem level, the structuring of species is affected by alterations in nutrients.

The powerful similarity in responses by the comparative systems described here supports the need for a new phase of understanding of nutrient loading impacts. In Cloern's (2001) Phase III model of eutrophication, interactions of multiple stressors and nutrients result in complex interactions and changes in plankton and benthic communities (Fig. 2). We have shown several common responses of complex aquatic ecosystems to increased or sustained N loading and concomitant P reductions. These commonalities, including reduced levels of chlorophyll *a*, increased SAV (particularly macrophyte) growth and a shift in dominance to large, piscivorous fish, have been, in some cases, interpreted as oligotrophication (e.g., Anderson et al., 2005; Collos, 2009). However, an additional feature that these ecosystems have in common is susceptibility to invasive species, particularly bivalve molluscs. Systems in which either N or P, but not both, are controlled are in a unique trophic state, neither eutrophic nor oligotrophic; they have been forced into a state of *stoichiotrophic imbalance*. Stoichiotrophic imbalance can occur throughout the eutrophication process, but the nutrient and trophodynamics that become established represent a different state than that which develops along the eutrophic continuum.

Ecological stoichiometry thus provides the basis for understanding how and why nutrients may be important regulators of trophodynamics even when they are not at levels normally taken to be limiting for phytoplankton production. Moreover, stoichiometric regulation can be important for food web dynamics even when changes in these nutrients and their ratios are not widely divergent from Redfieldian proportions.

1. The trajectory of ecosystem responses illustrated here suggest that as nutrient stoichiometry changed over time, and the system simultaneously shifted from high flow to low flow to high flow, it did not return to the same condition (e.g., Fig. 34). While complex, the Bay Delta is not uniquely complex among estuaries or, indeed, among aquatic ecosystems (Kimmerer

(2004). Nutrient enrichment can destabilize the dynamics of consumers, the "paradox of enrichment" (Naddafi et al. 2009), and this appears to have occurred in the Bay Delta in a manner similar to other systems. When flow returned to high levels after the mid-1980s drought, bivalves had become established and the biogeochemistry of the system was altered relative to pre-drought conditions. A new stable state had emerged, setting in place the conditions that accelerated further ecosystem change. The new condition no longer provided the same relationships between fish abundance and flow as had the earlier condition; nutrient effects overwhelmed flow effects.

The analysis here extends that of Glibert (2010), who also examined both NO_3^-:NH_4^+ ratios and N:P ratios and their effects on the food web in the Bay Delta. Using cumulative sums of variability analyses (CUSUM; e.g., Page, 1954) applied to nutrient changes, as well as major trophic components, Glibert (2010) conceptualized three different major food webs over time: a diatom-*Eurytemora*-delta smelt period prior to 1982; a mixed phytoplankton (cryptophytes-green algae-other flagellates)-*Pseudodiaptomus*-bass-shad period from 1982 to ~2000; and a cyanobacteria-*Limnoithona*-silverside-largemouth bass-sunfish period post-2000. CUSUM comparative curves provide visually accentuated patterns, allowing interpretations of commonalities in timing of shifts in variables. Comparison of CUSUM curves allowed visualization of how long different components of the food web exhibited similar trends relative to their long-term means (Glibert, 2010). Both sets of analyses (this study and Glibert, 2010) showed strong correlations between changes in the food web and nutrients. Both also demonstrated changes in fish populations as a function of DIN:P and NH_4^+; and both identified the timing of these changes. The stoichiometric and biogeochemical constraints presented above provide the mechanisms for why these food webs changed as they did. Regressions of CUSUM curves and those of raw data do not give the same value, and would not be expected to. Yet, the CUSUM analyses and the raw data comparisons provided here show common trends and provide similar conclusions. Understanding the system from a mechanistic, biogeochemical, and physiological perspective, one could make the case that it was inevitable that diatoms declined under conditions of high NH_4^+ loads, that the copepod population became dominated by a cyclopoid and that macrophytes and cyanobacteria would proliferate when P was reduced but NH_4^+ loads remained and that other associated changes would follow. Comparisons across systems have provided even more powerful evidence of commonalities in changes in food webs when nutrient stoichiometry is altered.

The conclusion is that P control, without concomitant N control, has unintended consequences. As seen for the Bay Delta here and in previous analyses (Van Nieuwenhuyse, 2007) and in the comparative systems describe above, P reductions do result in a decline in chlorophyll *a*. Where cyanobacterial blooms had previously been problematic, they declined initially, as in the Potomac River. However, once benthic primary producers take hold, and their productivity increases, the sediment pump of stored P begins to provide this nutrient in sufficient quantities that organisms such as *Microcystis* can become established, or re-established. If the system is also one receiving N in the form of NH_4^+, only those organisms able to tolerate high concentrations are apparently able to thrive. These organisms include cyanobacteria, the cyclopoids and the piscivorous fish. Thus, it appears that it is the interplay of P sequestration and NH_4^+ tolerance that results in new dominants. Once the sediment pump of P has become established, the system can be viewed as having reached a tipping point, one in which further reductions in P will likely only result in an exacerbation of the problem. One can therefore envision two control strategies. One would involve increasing P load, and the other decreasing the N load. Increasing P contains the risk of pushing the system in the direction of a classical eutrophied system, with concomitant increase in oxygen-stressed waters and unfavorable changes in the benthic community. Reductions in N is the other strategy. Reductions in N (and especially NH_4^+) will allow those organisms otherwise intolerant of NH_4^+ (or intolerance for other organisms that tolerate NH_4^+, e.g. dinoflagellates), from diatoms to fish, to compete. The challenge for managers is how to recognize when such a tipping point has occurred and when aggressive P reductions will therefore be counter-productive. This conclusion therefore is in contradiction with those of Carpenter (2008) and Schindler et al. (2008), who view P reductions as the sole solution to eutrophication, but confirms that of Howarth and Paerl (2008), Conley et al. (2009) and Paerl (2009), who view both N and P control to be necessary. Control of P works to a point, but appears not to be able to overcome the biogeochemical pumping of P in systems when sediments are laden with P. Initial responses, such as chlorophyll *a* and bloom reductions in response to P control may give managers a false sense of success. But, once the threshold of biogeochemical control has been crossed, more P control is not the solution.

State shifts have often been illustrated by marble-in-cup diagrams (e.g., Scheffer et al., 1993, 2001; Amemiya et al., 2007). The likelihood of an ecosystem (marble) being moved to a new state (new cup) is a function of system resilience. When the dynamic structure of the ecosystems is changed, restoration of the original stable state is much more difficult, if possible. Changes in nutrient loading can be a destabilizing factor in trophodynamics. Predictions of the potential success of “habitat” restoration for native species have been difficult (Brown, 2003). Without consideration of nutrients in the Bay Delta, such restoration efforts will likely remain unpredictable. Reconstruction of habitat is under consideration because it had been thought that fish were “habitat limited” due to the hydrological changes and severe loss of tidal wetlands in the Bay Delta (Kimmerer et al., 2005; Feyrer et al., 2010). More habitat is thought to be beneficial in exporting C. However, if the habitat is in a reach of the Bay Delta where N:P favors cyanobacteria and macrophytes, return of native fish that depend on plankton, such as diatoms with a different nutritional requirements and content, will be unlikely.

The analysis further supports the nutrient regulation hypotheses advanced by Wilkerson et al. (2006), Dugdale et al. (2007), and Van Nieuwenhuyse (2007). While Wilkerson et al. (2006) and Dugdale et al. (2007) have suggested that the controlling nutrient is N, especially NH_4^+ inhibition of NO_3^- uptake by diatoms, Van Nieuwenhuyse (2007) hypothesized that P limitation of phytoplankton developed over time. The biogeochemical regulations of these fluxes are intertwined. These findings underscore that without reductions in N loads, restoration of the food web leading to pelagic delta smelt will be difficult at best (Glibert 2010).

It is encouraging that restoration efforts in the Potomac are showing evidence of reduction in exotic species and a return of more native vegetation following the reduction in wastewater N (Ruhl and Rybicki 2010). Similarly, a 57% reduction in N loading in Tampa Bay between the 1980s and 2002 led to extensive recovery of native seagrasses, and a similar recovery was observed for Sarasota Bay following a 46% reduction in its N loading (Johansson and Greening, 2000; Tomasko et al., 2005; Ralph et al., 2006). New requirements for effluent removal from the major wastewater treatment plant on the Sacramento River call for reductions in N loading from the current 14 tonnes day^{-1} to 8 tonnes day^{-1} (2.2 mg L^{-1} NH_4^+ + 10 mg L^{-1} NO_3^-, at a permit capacity of 181 mgd) in the coming decade through implementation of nitrification and denitrification (Central Valley Regional Water Quality Control Board 2010). This would result in a significant drop in effluent DIN:TP ratios. Riverine N:P is not expected to change to this extreme, however, due to other nutrient loading sources (Sobota et al., 2009).

Elemental stoichiometry provides the theory, and the Potomac River and Tampa Bay provide examples, that the Bay Delta's food web will likely be altered favorably under this projected nutrient regime. Inasmuch as P levels are approximately what they were in the early 1970s when the food web supported fishes such as delta smelt, it is N that must be reduced, rather than P that should be increased, to achieve this balance.

Implications

A number of broader implications emerge from this analysis.

(1) The patterns in invasions of species in the Bay Delta and the comparative systems described herein are generally supportive of the emerging concept that invasions are not strictly stochastic events, but that environmental changes interact with vectors of invasion to enhance their success (e.g., Hobbs, 2000; Kolar and Lodge, 2000). There have been numerous other examples where ecosystems disturbance has been associated with the opportunity for species to colonize and for populations to expand (Hobbs and Huenneke, 1992; Hobbs, 2000). That the pattern of trophic cascade is similar in systems ranging from the Bay Delta to the Potomac River to the lower Great Lakes and elsewhere is powerful confirmation of the similar paths that systems undergo in biogeochemistry and biological interactions when nutrients are altered. Changes in land use, nutrient loading, and climate-related changes have all been associated with successful species invasions (Carlton 2000). To this list we add the interacting effects of P reductions and static or increasing N loads.

(2) There has been much debate about nutrient regulation and limitation, most recently in a set of papers about the potential importance of N vs. P in estuaries (Schindler et al., 2008; Schindler and Hecky, 2008; Howarth and Paerl, 2008, Carpenter, 2009; Conley et al.,

2009). Schindler argued that P is the limiting nutrient in lakes, and therefore eutrophication can be controlled by controlling that nutrient. Others have argued for the need for control of both nutrients in estuarine and freshwater systems (e.g., Paerl et al., 2004; Howarth and Marino, 2006; Howarth and Paerl, 2008; Conley et al., 2009; Paerl, 2009). The synthesis provided here bears on this argument in several ways. Nitrogen is no longer the limiting nutrient in many estuarine systems; it is the excess of N loading that is of concern, not its lack of supply. Reductions in P have indeed reduced chlorophyll *a* levels in many systems, and this change in phytoplankton biomass has frequently been referred to as oligotrophication. However, systems rarely can be restored to pre-eutrophic conditions (Burkholder, 2001a,b). Moreover, the shift to an alternate stable state does not *a priori* mean that the system is returned to its natural, un-eutrophied, state because that system may be much more susceptible to invasions of nonindigenous species. Nutrient ratios *do* matter, especially at the level of community dynamics and structure, and as P has been controlled without the concomitant control of N, the change in N:P can alter food web dynamics and biogeochemistry. While individual species and processes respond to single nutrients, the relative proportion of N and P collectively alters metabolism, species composition, and food webs.

(3) In what has become a much-referenced paper in a very short period of time, Duarte et al. (2008) discussed the pathways of return of an ecosystem following nutrient removal – the "Return to Neverland" (sensu the children's story of Peter Pan and Wendy). They surveyed the literature for systems that have undergone nutrient loading and nutrient reductions to determine if there were common patterns. The trajectories of response were complex and varied. Duarte et al. attributed this to "shifting baselines," recognizing that systems have changed due to invasions, extinctions, overfishing, climate change and other factors; thus, any expectation that

the system will return to that which it was decades before is a flawed assumption. They did not, however, differentiate those systems where stoichiometry had been altered. Despite the difficulty in predicting exactly how individual systems will respond, Duarte et al. (2008, p 6) underscore that “efforts to reduce nutrient inputs to eutrophied coastal ecosystems have indeed delivered important benefits by either leading to an improved status of coastal ecosystems or preventing damages and risks associated to further eutrophication.” A stoichiometric perspective aids our understanding of how systems return to a new – or altered – stable state.

(4) Global change patterns suggest that acidification of the oceans and its effects on physiology and biodiversity is a major emerging issue (e.g., Fabry et al., 2008; Hendriks et al., 2010; Kroeker et al., 2010; Vézina and Hoegh-Guildberg, 2010 and references therein). Shown here, as well as in many other reports (Pedersen, and Hansen**,** 2003a,b; Søderberg and Hansen**,** 2007), highly productive aquatic systems are, instead, sustaining alkalinification. The consequences for biogeochemical and related trophic dynamic changes at high pH are as large as those at reduced pH values. The range of pH fluctuations under highly productive systems, up to several pH units, is much higher than what is occurring and expected under acidification. Effects of variable pH must be better understood across the range of environmentally relevant pH values, including the alkaline range.

(5) One of the most common “currencies” of trophodynamic studies is C. Many studies normalize rates or mass to C. When food quality (i.e., nutritional content) is linked to food web outcome, however, feedback effects and nutrient biogeochemical processes also play large roles in species success. Indeed, it has been suggested that food quality is a measure of grazer success, and that low food quality (as measured by high C:N or high C:P ratios) should dampen predator-prey relationships (Hessen 1997). Food quality is also important to consider in

detritus-based food webs. Detritivores consume the least nutritionally balanced foods and thus have lower growth rates than their planktivorous or piscivorous counterparts (Sterner and Elser, 2002). In keeping with this notion for the Bay Delta, Sobczak et al. (2005) found that while detritus may support a significant fraction of the heterotrophic metabolism of the system, it did not seem to support pelagic food webs leading to higher trophic levels. The findings here suggest that strengthened insights may be gained by use of additional denominators – that P and N “currency” yields insights not found with C “currency.” While productivity is a function of C, community composition is more strongly linked to N and P. Conceptualizing all change as a function of C transfer and productivity may lead to a flawed conclusion that productivity, biomass, and species composition are all regulated by a single element (MacIntyre and Flecker, 2010).

(6) Many trophic interactions are interpreted in the context of the requirements by grazers for acquisition of particular fatty acids, as a measure of the food quality of algae (e.g., Ågren et al., 1990; Coutreau and Sorgeloos, 1997; Weers and Gulati 1997). However, cellular biochemical constituents, including lipids and proteins, are strongly influenced by the elemental composition of the cells. While some cyanobacteria may be able to alter their phospholipid content in relation to P stress (Van Mooey et al. 2009), for example, some green algae have been shown to have higher lipid content under P limitation (e.g., Kilham et al. 1997). Stoichiometry of N and P may be a better determinant of food quality than lipid content.

(7) Cyanobacteria may do well at both ends of the Redfield spectrum. Most previous focus on P reductions has been based on the assumption that N limitation will lead to cyanobacterial blooms because many cyanobacterial species are capable of N_2 fixation; thus, if N-limiting conditions do not occur, cyanobacteria blooms may be reduced or avoided (e.g.,

Downing et al., 2001). However, *Microcystis* often occurs in *high* N:P ambient conditions, making it an enigmatic bloom former under the prevailing assumption that high N:P will drive the ecosystem away from cyanobacteria. Its success apparently is a function of its ability to garner its requisite P from enhanced biogeochemical cycling. Stoichiometric homeostasis (Fig. 5) may be yet another explanation for release of nutrient-rich toxins, not only by *Microcystis*, but potentially by other harmful algal species, including dinoflagellates.

(8) Various indices and metrics have been developed to measure eutrophication status (e.g., Llansó et al., 2003; Corbett et al., 2005; Buchanan et al., 2005; Lacouture et al., 2006; Bricker et al., 2007; Williams et al., 2010; US EPA, 2010). However, virtually all of these indices are measures of the classic symptoms of eutrophication – increase in chlorophyll *a*, decline in SAV, extent of hypoxia, or HABs. There are as yet no quantitative indices of the impacts of altered stoichiometry. As noted above, systems that are manipulated stoichiometrically through removal of one, but not both nutrients, are neither eutrophic nor oligotrophic. Application of the traditional eutrophication indices will lead to the erroneous conclusion that these systems are not nutrient stressed. A new suite of indicators needs to be developed to more accurately characterize these systems. Such indicators will need to vary depending on which end of the stoichiometric continuum a system may lay. For systems with high N:P ratios, these indicators could include extent of coverage of SAV by invasive macrophytes, decline in chlorophyll *a*, extent of cyanobacteria blooms, bivalve invasions, and piscivore/planktivore abundance, calanoid/cyclopoid ratios, and sediment release of P and N, as examples.

(9) The alternate stable states that have been documented here and in comparative systems suggest that there may be additional societal considerations about which state is

preferred. The Bay Delta management arena has coped with societal implications of water use with regard to protections of an endangered species. Shown here is a dichotomy of stable states of fish communities. Saving the endangered delta smelt will be at the cost of success of many of the recreational fish species that the public enjoys, such as largemouth bass. To save delta smelt will require that the system be returned to one that has many characteristics of a eutrophic system, with higher chlorophyll *a* levels, higher turbidity, and less benthic vegetation. Most communities that are coping with systems in altered stable states are attempting to shift to a system with more piscivores, not fewer, and clearer water, not more turbid.

(10) Regulation of a single nutrient without recognition of the role of nutrient stoichiometry serves to displace in space the impacts of eutrophication (Fisher et al., 1992; Hagy et al., 2004; Paerl et al. 2004). While production and chlorophyll *a* biomass may be held in check in the river or estuary due to P limitation, the N is displaced downstream where it eventually intercepts adequate levels of P to form blooms, either in the estuarine reach of the system – or even offshore (Fig. 49). Such effect has been documented for the Neuse River Estuary, the mesohaline reach of Chesapeake Bay and southern Baltic Sea in the Sweden archipelago region; eutrophication effects increased in these areas when P reduction strategies were put in place upstream (Fisher et al., 1992; Paerl et al., 2004). Many marine HABs are increasing (GEOHAB, 2006; Heisler et al., 2008), and even those species that were previously thought to be unrelated to nutrient pollution, such as *Noctiluca scintillans*, the classic "red tide" former, have recently been found to be associated with offshore transport of excess N, mediated through N cycling and trophic transfer (Harrison et al., in press). Thus, in a transect from an N-impacted river to the sea, stoichiometric proportions change significantly, and when P is controlled upstream, algal blooms are displaced either downstream or offshore. Dilution does not solve the problem, it just

displaces it.

Recommendations for Further Study

While compelling, the ecological stoichiometric model raises many questions that need further analysis in the San Francisco Estuary. The synthesis provided herein is based on a reconstruction of biogeochemical and trophic interactions based on historical data. Using comparative systems, it was shown that similar dynamics have developed in other systems affected by similar stressors. A "weight of evidence" approach, from trend analysis to physiological and biogeochemical mechanisms, steeped in ecological theory, was used to construct the scenarios of change described here. However, regulation of the food web by nutrient controls is directly testable, and there is much that needs to be explored to test these relationships directly.

In 1985, Cloern and Nichols outlined a number of research questions regarding the importance of nutrients and nutrient processes that were understudied in the San Francisco Estuarine system. Although some progress has been made on some of these issues, many remain. These include, "sediment dynamics and transport, primary production of benthic microalgae, virtually all aspects of microbial ecology and biogeochemistry, the nature and role of microzooplankton, sources and fates of toxic contaminants (particularly organic compounds), nutrient budgets, and riverine inputs of organic material" (Cloern and Nichols, 1985, p. 236).

In 2011, many of the same research questions can be outlined, including:

(1) What are the dynamics of sediment nutrient fluxes and how do they vary spatially and seasonally within the Bay Delta?

(2) To what extent do the common dinoflagellates of the Bay Delta produce toxins

and if so, what organisms and life stages are particularly susceptible? Are delta smelt larvae among those potentially affected? How does nutrient stoichiometry alter the toxicity of these dinoflagellates?

(3) What are the organic sources of nutrients, and how does their stoichiometry compare to the inorganic forms presented here? How do they vary spatially and temporally? How do they contribute to the nutrition of the primary producers?

(4) How do rooted versus floating invasive macrophytes differ in their alteration of biogeochemical fluxes of nutrients, and how does this vary with nutrient stoichiometry? How does the metabolism of these plants compare to that of native vegetation?

(5) What are the seasonal and spatial patterns in abundance of bacteria? What is the stoichiometry of bacteria, and does it change over time?

(6) What is the stoichiometry of the microzooplankton and does it change over time and space?

(7) What is the biomass stoichiometry of the fishes of the Bay Delta? Do fish of varying species change in growth rate and size in relation to varying quality of nutrients in their diet?

(8) Do stoichiometric changes or changes in flow have a greater effect on fish metabolism?

(9) How does the stoichiometry of the invasive fauna compare with that of native species?

(10) What are the synergistic effects of stoichiometric changes in ambient nutrients and other stressors on the Bay Delta food web, such as changes in temperature, pH, or light?

Answers to these questions, attainable through studies in controlled laboratory or mesocosm settings or field measurements, would greatly advance understanding about the factors controlling the food web of San Francisco Estuary and would advance the knowledge base and tools for managers to make informed decisions regarding the future of the Bay Delta.

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Table Legends

Table 1. Sources of data used in this analysis and the time periods over which they were averaged.

Table 2. Time line of changes in the Potomac River subestuary. WWTP is wastewater treatment plant, most of which is discharged from the Blue Plains Facility.

Table 3. Descriptive comparison of the major food webs changes in comparative systems after the reduction of P from the system and an associated increase in the N:P ratio. Further details of all of these changes are described more fully in text. Blank entries are those for which insufficient data are available to evaluate.

Figure Legends

1. Map of the San Francisco Estuary and the Sacramento-San Joaquin Bay Delta. The region outlined in the box represents the region where virtually all of the stations examined in this paper were located. Stations D4 –D8 represent the stations where water chemistry data were used for this analysis.

2. Modified conceptual diagram of the "phase III" model of eutrophication (Cloern, 2001) showing the complexity of interactions and effects of multiple stressors and eutrophication.

3. (A) Schematic depiction of the relationship between phytoplankton cell size and the N:P ratio of their biomass. (B) Size dependence (cell volume, μm^3) of temperature-corrected growth rate (day^{-1}) for a range of phytoplankton functional groups: diatoms (filled circles), dinoflagellates (open boxes) and other taxonomic groups (grey diamonds, a combination of cyanobacteria, chlorophyte, haptophyte, cryptophyte and various other groups). Line is the least-squares regression of all data ($\log \mu = -0.06 \log V + 0.1$; $r^2 = 0.15$). This figure is reproduced from Finkel et al. (2010), J. Plank. Res., Oxford University Press, with permission. The data were compiled by T.A.V. Rees.

4. Relative N and P content of cyprinind and centrarchid fish. Figure is modified and redrawn from Sterner and George (2000).

5. Top: Schematic relationships between resource N:P and consumer N:P. Where resource

(or prey) and consumer stocihiometry do not balance, it reflects either P or N sequestration by the consumer. Bottom: Consumer biomass N:P and excretion N:P are expected to be negatively related.

6. Expected changes in various components of the food web as the N:P ratio increases, based on ecological stoichiometry principles. The upper panel is a general depiction of trends in N:P ratios over time.

7. Time course of the change in freshwater outfow from the Bay Delta over time and the major changes in nutrients and the food web that have occurred. The arrows along the top of the graph depict the major time periods that are described in text. The first time period is from the start of the time series up to the time when the wastewater treatment plant discharge began. The second time period encompassed the period of major change in nutrients. The third time period is that taken to represent the period of the pelagic organism decline.

8. Changes over time in the major inorganic nutrients and inorganic nutrient ratios (log-transformed data) in the confluence to Suisun Bay from 1975-2005. Note that different nutrients changed in different periods of the time course, and thus the delineation of the time periods by symbols differs from those of subsequent graphs; the individual time periods highlight the periods of major change. For panels exhibiting total inorganic nitrogen (DIN) and total phosphorus (TP), the time course highlights 1975-1982 (circles), 1983-1992 (diamonds), and post-1992 (squares). For PO_4^{3-} and NH_4^+: PO_4^{3-}, the time course highlights the periods of 1975-1986 (circles), 1987-1999 (diamonds) and post-1999 (squares). For NH_4^+, the time course

highlights the period of 1975-1982 (circles), and post 1982 (squares). Finally, for DIN:TP, the time course is shown as a continuous trend (squares). Coefficients of determination (R^2) of all time periods are shown; those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$.

9. Change in concentrations of NH_4^+, TP, and DIN:TP over time in the effluent of the wastewater from the Sacramento Regional Wastewater Treatment Plant, located on the Sacramento River. Total loads have also increased over time. For NH_4^+, current loads are 14 tonnes day^{-1}.

10. Change in the abundance (log cells mL^{-1}) of the major classes of eukaryotic phytoplankton and prokaryotic cyanobacteria in the lower Sacramento River to Suisun Bay region from 1975-2005.

11. Change in the concentration of chlorophyll *a* (log µg L^{-1}) and abundances of the major classes of eukarytotic phytoplankton and prokaryotic cyanobacteria (log cells mL^{-1}) over the time course. Coefficients of determination (R^2) are given for each major time period (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The analysis indicates a significant change in abundance over one or more major time periods for diatoms (Bacillariophyceae), green algae (Chlorophyceae), cryptophytes (Cryptophyceae), dinoflagellates (Dinophyceae) and cyanobacteria. In addition, the decline in chlorophyll *a* over the entire time course was significant (R^2=0.57, $p<0.01$).

12. Change in the concentration of chlorophyll *a* (µg L^{-1}) and abundances of the major classes of phytoplankton (log cells mL^{-1}) over the time course as a function of TP (mg L^{-1}) (all data log transformed). Coefficients of determination (R^2) are given for the entire time course only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. Coefficients of determination (R^2) values in parentheses represent the respective relations with PO_4^{3-} rather than TP. None of these regressions indicated a significant relationship ($p > 0.05$).

13. As for Figure 8, except as a function of NH_4^+ (mg L^{-1}) (all data log transformed). The regressions for NH_4^+ versus total chlorophyll *a*, diatoms (Bacillariophyceae), and dinoflagellates (Dinophyceae) indicated significant relationships.

14. As for Figure 8, except as a function of DIN:TP (wt:wt) (all data log transformed). The regressions for DIN:TP ratios versus total chlorophyll *a*, diatoms (Bacillariophyceae), and dinoflagellates (Dinophyceae) indicated significant relationships.

15. As for Figure 8, except as a function of NH_4^+: PO_4^{3-} (wt:wt) for the period of time only over which the change in this ratio was most significant (1987-1999) (all data log-transformed). Only the regression for NH_4^+:PO_4^{-3} ratio versus crytophytes (Cryptophyceae) indicated a significant relationship.

16. Change in the abundance of the major groups or taxa classes of zooplankton (individuals

m^{-3}) in the lower Sacramento River to Suisun Bay region from 1975-2005.

17. Change in the abundance of the major groups or taxa of zooplankton (as organisms mL^{-1}, and as the ratio of *Eurytemora*/cyclopoids) over time (all data log transformed) . Coefficients of determination (R^2) are given for each major time period (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The analysis indicates significant changes over a major time period for all taxa except *Sinocalanus*, *Pseudodiaptomus*, and harpacticoids. However, over the entire time period (1975-2005), the changes in *Sinocalanus* and harpacticoids were significant ($R^2=0.136$, $p<0.05$, and $R^2=0.622$, $p<0.01$, respectively).

18. Change in the abundance of the major groups or taxa of zooplankton (as organisms mL^{-1} and as the ratio of *Eurytemora*/cyclopoids) over the time course as a function of TP (mg L^{-1}) (all data log transformed). Coefficients of determination (R^2) are given for the entire data set only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. Regression values in parentheses represent the respective relations with PO_4^{3-} rather than TP. The regressions for TP and/or PO_4^{-3} versus *Eurytemora*, *Sinocalanus*, *Acartia*. *Limnoithona Daphnia*, *Bosmina*, and *Neomysis* indicated significant relationships.

19. As for Figure 17, except as a function of NH_4^+ (mg L^{-1}) (all data log transformed). All regressions indicated significant relationships except for NH_4^+ versus *Acartia* and the ratio of

Eurytemora:cyclopoids.

20. As for Figure 17, except as a function of DIN:TP (wt:wt) (all data log transformed). All regressions indicated significant relationships except for DIN:TP versus *Daphnia* and *Bosmina.*

21. As for Figure 17, except as a function of NH_4^+: PO_4^{3-} (wt:wt) for the period of time only over which the change in this ratio was most significant (1987-1999) (all data log transformed). All regressions indicated significant relationships except for NH_4^+: PO_4^{3-} versus *Pseudodiaptomus* and the ratio of *Eurytemora*:cyclopoids.

22. Conceptual diagram of the ecological stoichiometric relationship between different phytoplankton and zooplankton genera. The X axis represents the biomass N:P of the organisms. The wide arrow represents ingestion of the phototrophs by the grazer; the lighter arrow represents nutrient regeneration in the grazer's excretions. Note that the stoichiometry of the regenerated nutrients differs with zooplankton taxon and the N:P ratio of the food on which they graze.

23. Change in the abundance of *Corbula amurensis*, crabs (*Cancer magister* and *Eriocheir sinensis*), shrimp (*Crangon franciscorum* and *Crangon nigricauda*, and *Palaemon macrodactylus)* over the time course and as a function of TP, NH_4^+, and DIN:TP ratios (all data log-transformed). Coefficients of determination (R^2) are given for each major time period (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares) for the time course, and for the entire data set only as a function of nutrients. Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The analysis indicates a significant change in

abundance of the "crabs" grouping over the first major time period. In addition, over the entire time course (1975-2005), the changes in *Crangon* sp. and *Palaemon* sp. were significant (R^2= 0.51 and 0.654, p<0.01, respectively).

24. Change in the abundance of major fishes (data log transformed) over the time course. Coefficients of determination (R^2) are given for each major time period (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at p<0.05, those by bold italic are significant at p<0.01. Data for delta smelt are shown based on the summer townet survey (STN) and the fall midwater trawl index (FMWT), while longfin smelt, splittail, striped bass and threadin shad.are from the FMWT index; yellowfin goby, and starry flounder are FMWT catch per tow data; and inland silversides, crappie, sunfish and largemouth bass are relative abundances from beach seine data. The analysis indicates significant changes over one or more major time periods for 9 of the 12 taxa. Although changes were significant for individual time periods for striped bass, they were significant for the entire time course (R^2=0.671, p<0.01).

25. Change in the abundance of major fishes over the time course as a function of TP (mg L^{-1}) (all data log transformed). Coefficients of determination (R^2) are given for the entire data set only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at p<0.05, those by bold italic are significant at p<0.01. Regression values in parentheses represent the respective relations with PO_4^{3-} rather than TP. Dashes lines represent the trends for the post 1999 data only. The regressions for TP and/or PO_4^{3-} versus delta smelt (STN but not FMWT), longfin

smelt, splittail, yellowfin goby, starry flounder, crappie, sunfish, and largemouth bass indicate significant relationships.

26. As for Figure 24, except as a function of NH_4^+ (mg L^{-1}) (all data log-transformed). The regressions for NH_4^+ versus longfin smelt, yellowfin goby, striped bass, and sunfish indicate significant relationships.

27. As for Figure 24, except as a function of DIN:TP ratio (wt:wt) (all data log-transformed). The regressions for DIN:TP ratio versus delta smelt (STN but not FMWT), longfin smelt, yellowfin goby, striped bass, silversides, starry flounder, sunfish and largemouth bass indicate significant relationship.

28. As for Figure 24, except as a function of NH_4^+: PO_4^{3-} ratio (wt:wt) (all data log transformed) for the period of time only over which the change in this ratio was most significant (1987-1999). The regressions for NH_4^+:PO_4^{-3} ratio versus delta smelt (STN but not FMWT data), longfin smelt, starry flounder, crappie, and sunfish indicate significant relationships.

29. Change in fish length indicated as a function of TP (mg L^{-1}) and DIN:TP (wt:wt) (all nutrient data log transformed). Coefficients of determination (R^2) are given for the entire data set only. Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The regressions for length versus TP indicate significant relationships for longfin smelt, threadfin shad, and American shad; the regressions for length versus DIN:TP ratio indicate significant relationships for delta smelt (FMWT), threadfin shad, and American shad.

30. Comparisons between abundances of various food web components and diatom (Bacillariophyceae) abundance (units as previously given; all data log-transformed). Coefficients

of determination (R^2) are given for the entire data set only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. All regressions shown are significant.

31. Comparisons between abundances of various components of the food web and dinoflagellate (Dinophyceae) abundance (units as previously given; all data log-transformed). Coefficients of determination (R^2) are given for the entire time course only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. All regressions shown are significant.

32. Comparisons between abundances of various food web components and abundance of the zooplankter *Eurytemora* or of total cladocerans (units as previously given; all data log-transformed). Coefficients of determination (R^2) are given for the entire time course only, although the major periods are represented by different symbols (1975-1986, circles; 1987-1999, diamonds; and post 1999, squares). Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. All regressions shown are significant.

33. Comparisons of the average planktivore and average piscivore abundance as a function of TP, NH_4^+, DIN:TP ratio, and NH_4^+: PO_4^{-3} ratio over the entire time course (all data log-transformed). Coefficients of determination (R^2) are given for the entire time course only. Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The regression analyses indicate significant relationships between planktivores and both NH_4^+ and the DIN:TP ratio, and significant relationships between piscivores and TP, the DIN:TP ratio, and

the NH_4^+: PO_4^{-3} ratio.

34. Comparison of abundance of the major classes of phytoplankton, zooplankton and fish as a function of the *Eurytemora*/cyclopoid ratio for two periods of the time course: 1975-1983 (circles) and 1999-2005 (squares).These time periods represent the beginning years of the time course and the years encompassing as the Pelagic Organism Decline (POD) period. Coefficients of determination (R^2) are given for each major time period. Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The analysis indicates significant relationships between the *Eurytemora*: cyclopoids ratio and the DIN: DP ratio, cyanobacteria, *Bosmina*, and delta smelt (STN or FMWT data).

35. Pore water profiles of PO_4^{3-} and NH_4^+ from May 2004 at Freestone Point on the Potomac River, Chesapeake Bay, USA. This figure illustrates the main characteristics of Potomac River pore water chemistry. Data are from Bailey et al. (2006).

36. Schematic depiction of *Egeria densa* as an “ecosystem engineer”. As *Egeria* increases, turbidity decreases, and light increases, Also, nutrients are taken up by the plants (but may be mobilized from the sediment; see text). Zooplankton increases due to the ability to find refuge from predation, but phytoplankton decrease due to zooplankton grazing. Figure redrawn from Yarrow et al. (2010).

37. Relationship between the concentration of PO_4^{3-} (mg L^{-1}) and the specific conductance (µmhos cm^{-1}). Data shown are bimonthly averages for the time series for a station located near the confluence.

38. Annual average pH for (A) various stations (from Suisun Bay to lower San Joaquin and upper Sacramento River) in the Bay Delta over time, and (B) mean of annual average pH of these stations over time. Panel C gives a snapshot of diel fluctuations in pH from 17 June to 1 July, 2009, in the Grantline Canal, as measured from an *in situ* pH data sonde. Data are from http://bdat.ca.gov (panel A) and http://cdec.water.ca.gov/ (panel C).

39. Change in rate of flux of PO_4^{3-} from cores taken from a *Hydrilla*-dominated reach of the Potomac River, Chesapeake Bay, USA, and experimentally manipulated to alter the pH (data from Bailey et al. 2006).

40. Annual abundance of *Corbula amurensis* (individuals m^{-2}) at stations located from the confluence to Suisun Bay as a function of mean annual average pH. Coefficients of determination (R^2) was significant at $p<0.01$.

41. Left: Relationship between the N:P atomic ratios and the concentrations of different microcystin toxins [MC-LR, MC-RR, and MC-(LR + RR)] of *Microcystis aeruginosa* grown in laboratory P-limited cultures. Right: The microcystin-production rate and microcystin content of *M. aeruginosa* at each growth rate in laboratory P-limited cultures. Figure reproduced from Oh et al. (2000), *Appl. Envir. Microbiol.* with permission.

42. Conceptual diagram of the effect of altered pH and altered salinity on the processes of exchange of PO_4^{3-} and NH_4^+ from the sediment to the water column. With a rise in pH, or a shift to higher salinity, sediment flux of NH_4^+ and PO_4^{3-} increase via the mechanisms described in text.

pH also alters the equilibrium between NH_4^+ and NH_3, leading to higher NH_3 at high pHs.

43. Conceptual depiction of the change over time in major nutrients, flow, dominant biogeochemical processes, and the food web of the Bay Delta. The first panel represents the period from 1975 to ~1982, when flow was low, and diatoms and *Eurytemora* were the dominant phytoplankton and zooplankton, respectively, and smelt were common. The second panel represents the period from ~1982-1986 when flow was high, and NH_4^+ was increasing. During this period the food web began to change. Under very low flow conditions, depicted by the third panel, and representing ~1987-1995, the NH_4^+ load was high but PO_4^{3-} began to decrease. The food web also began to change significantly, with changes in the dominant phytoplankton and zooplankton, increasing abundance of macrophytes, increased importance of sediment nutrient processes, and increase in piscivores. Finally, post 1995, NH_4^+ loads remain high, while PO_4^{3-} loads have decreased. Sediment biogeochemical processes are of increasing importance in nutrient processing, macrophyte production is important and piscivorous fish have increased. At the microbial level, *Microcystis* is more common and the zooplankton is dominated by *Limnoithona*.

44. Comparative nutrient and food web relationships for the Potomac River. Panel (A), the change in N:P ratio of all loads (filled squares), and of the wastewater effluent only (open squares) as a function of time from the mid 1960s to 2005. Indicated also on the time course is the first appearance of the invasive *Corbicula fluminea* clams, as well as its maximum abundance and the time when it began to decline. Data derived from Dresler and Cory (1980), Jaworski et al. (2007), and Cummins et al.(2010). Panel (B), the change in abundance of submersed aquatic vegetation, in this case dominated by *Hydrilla* (closed squares), and the

change in chlorophyll *a* in the water column (open squares). Data derived from Jaworski et al. (2007). Panel (C), the relationship between the abundance of SAV (dominated by *Hydrilla*) and the N:P in the wastewater effluent. Data derived from Jaworski et al. (2007). Panel (D), the relationship between the frequency of occurrence of water column samples enriched with >10% *Microcystis* (by cell count) and the N:P in the total nutrient load. *Microcystis* data are courtesy of P. Tango, from Maryland Department of Natural Resources monitoring program data; nutrient data are from Jaworski et al. (2007). Panel (E), the abundance of Bay anchovy (log relative abundance as geometric mean catch per haul) as a function of N:P of the total nutrient load; panel (F), the abundance of spottail shiner (log relative abundance as geometric mean catch per haul) as a function of N:P in the effluent. Fish data from panels E and F are from Maryland Department of Natural Resources, Fisheries Service http://www.dnr.state.md.us/fisheries/ , and nutrient data are from Jaworski et al. (2007). Panel (G), the ratio of pelagic:demersal fish as a function of the N:P ratio in the effluent. Fish data are from Kemp et al. (2005) and www.noaa.chesapekaebay.net and nutrient data are from Jaworski et al. (2007).

45. Relationship between the percent cover of Florida lakes by *Hydrilla* or other macrophytes and the molar N:P ratio. Data are derived from data of Hoyer and Canfield (1996). Coefficient of determination (R^2) is significant at $p<0.05$. Note that although a linear relationship is drawn, the data appear to suggest a rapid change at a molar ratio of ~100.

46. Change over time in the extent of the invasion of zebra mussels across the USA. Data are from USGS (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/).

47. Comparison of the relationships between TP, PO_4^{3-}, NH_4^+, and the DIN:TP ratio versus X2 (the isohaline where salinity = 2, measured as distance from the Golden Gate Bridge) and versus the habitat index (defined by salinity, temperature and turbidity relationships; Feyrer et al., 2010) for the time course from 1975-2005. Coefficients of determination (R^2) are given for the entire data set. Those indicated by bold are significant at $p<0.05$, those by bold italic are significant at $p<0.01$. The analysis indicates significant relationships between X2 and TP, PO_4^{3-}, and NH_4^+ concentrations, and significant relationships between the habitat index and PO_4^{-3}, NH_4^+, and the DIN:TP ratio.

48. Comparison between the conceptual understanding of the factors related to the Pelagic Organic Decline (POD) as described by Sommer et al. (2007) and the conceptual understanding described in this analysis.

49. Conceptual diagram of a generalized estuary affected by high NH_4^+ loading from a point source discharge, but with reduced P loads. The immediate impact zone has the potential to have strong negative impacts on organisms, either through direct toxicity or indirect inhibition effects. As the NH_4^+ moves downstream, processes such as nitrification (depicted as an arrow from NH_4^+ to NO_3^-) may convert subtsantial amounts of N from NH_4^+ to NO_3^-. If macrophytes are common in this reach of the system, recycling of P from the sediment may result in increased P availability, although numerous organisms may effectively take this up and sequester it. Moving further downstream into the brackish estuarine zone, nitrification may continue, resulting in increased availability of NO_3^- relative to NH_4^+. Together with P release from the sediments, and/or with inputs of P from oceanic sources, blooms of diatoms or other algae may occur in this region, and the excessive production may result in hypoxia, seagrass loss, etc. The effectiveness

of the estuarine filter (*sensu* Cloern 2001) will depend on the size of the estuarine, residence time, depth and many other factors. When N loading is very high, it will not all be effectively taken up in the riverine and estuarine segments, and will be exported offshore. The export may be in the form of dissolved (inorganic or organic) or particulate N. When sufficient P is available in offshore sources, additional blooms may develop. A succession of blooms may also occur, with increasing importance of mixotrophic organisms expected in such a progression.

Parameter	Units	Data Transformation	Temporal period averaged	Spatial area averaged	Source/Reference
Water Quality					
Ambient nutrients	mg-N L^{-1}, mg-P L^{-1}, or µM	Log transformed	Average of all values March - November	EMP Stations D4, D6, D7, and D8	http://bdat.ca.gov/
Turbidity	NTU	Normal	Average of all values March – November	EMP Stations D4, D6, D7, and D8	http://bdat.ca.gov/
Conductivity	µmhos/cm	Normal	No averaging	EMP Station D24 at Rio Vista	http://bdat.ca.gov/
pH		Normal	Average of all values March - November	EMP Stations D4, D6, D7, and D8	http://bdat.ca.gov/
Effluent nutrient loads	mg-N L^{-1} or µM	Normal	Monthly or annual	Point source discharge	Central Valley Regional Water Quality Control Board
Phytoplankton					
Total chlorophyll a	µg L^{-1}	Log transformed	Average of all values March - November	EMP Stations D4, D6, D7, and D8	http://bdat.ca.gov/
Species composition	Cells mL^{-1}	Log transformed	Average of all values March - November	EMP Stations D4, D6, D7, and D8	http://www.nceas.ucsb.edu/
Zooplankton					
Species composition	no. m^{-3}	Log transformed	Average of all values March - November	Stations NZ028, NZO32, NZ042, NZ048, NZO54, NZO60, NZD06	http://www.nceas.ucsb.edu/

Invertebrates					
Total Bay Shrimp	no. m^{-2}	Log transformed	Average of all values of *Cancer franciscorum, C. nigricauda* and *Palaemon macrodactylus* March – November	Bay Study Stations 427 – 736, 837	http://www.nceas.ucsb.edu/
Mysid shrimp	no. m^{-3}	Log transformed	Average of all values March – November	Stations NZ028, NZO32, NZ042, NZ048, NZO54, NZO60, NZD06	http://www.nceas.ucsb.edu/
Total crabs	no. m^{-2}	Log Transformed	Average of all values of *Cancer magister* and *Eriocheir sinensis* March – November	Bay Study Stations 427 – 736, 837	http://www.nceas.ucsb.edu/
Clams	count/grab	Log Transformed	Average of all values *Corbula amurensis* March – November	EMP Stations D4, D6, D7, and D8	http://bdat.ca.gov/
Fish					
Fall midwater trawl (FMWT) Catch per tow		Log Transformed	September – December	Stations 401 – 707, 801 – 804	http://www.nceas.ucsb.edu/
Fall midwater trawl (FMWT) index		Log Transformed	Index covers September – December Trawls		http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT

Summer townet (STN) index		Log Transformed	Index covers June-July Trawls		http://www.dfg.ca.gov/delta/projects.asp?ProjectID=TOWNET
FMWT Fish length	mm	Catch weighted average. (Reject years with counts <6)	September – December	Stations 401 – 707, 801 – 804	http://bdat.ca.gov/
Beach seine	Relative abundance	Log Transformed	September – December		http://bdat.ca.gov
Other Abiotic parameters					
X2	km	Normal	Average of all values March - November	Distance of salinity =2 isohaline from Golden Gate Bridge	http://www.water.ca.gov/dayflow/
Exports	cfs	Normal	Average of all values March - November	Total SWP + CVP Pumping	http://www.water.ca.gov/dayflow/

Table 2. Time line of changes in the Potomac River subestuary. WWTP is wastewater treatment plant, most of which is discharged from the Blue Plains Facility.

~ Years	Environmental Change	References
1900 - 1970	P Discharges from WWTP increase, peaking at ~$4.0 \cdot 10^6$ kg y^{-1} (100 kg m^{-2} y^{-1}). Dissolved oxygen reaches minima ~1940.	(Jaworski and Romano 1999)
Late 1970's	With tertiary treatment and a P detergent ban, WWTP discharges of P decrease to $1.0 \cdot 10^6$ kg y^{-1} by 1976,	(Jaworski and Romano 1999)
	Corbicula fluminea invades river, with variable but often high abundance until the early 1990's	(Phelps 1994)
Early to Mid 1980's	Nitrification added to WWTP leading to NO_3^- discharge, rather than NH_4^+. Large upswing in surface water dissolved oxygen.	(Jaworski et al. 2007; Ruhl and Rybicki 2010)
1983-1991	Secondary drop in WWTP discharge of P to < 0.1 by 1986.	(Jaworski and Romano 1999)
	SAV resurgence in the Potomac occurs, peaking with ~ 2000 ha of coverage dominated by *Hydrilla verticillata*.	(Rybicki and Landwehr 2007)
1984-1986	Fish surveys suggest large and small mouth bass populations doubled with increasing SAV	(USEPA 1993)
1986-present	SAV coverage decreased below peak levels, with low coverage in the mid-1990's and a resurgence in the early 2000's	(Orth et al. 2010)
Mid 1990's	N loading from WWTP peaks at > $1 \cdot 10^7$ kg y^{-1}	(Jaworski and Romano 1999)
Early-1990's to present	N loading from WWTP decreases about 50% due to nitrification/denitrification	(Jaworski et al. 2007)

Table 3. Descriptive comparison of the major food webs changes in comparative systems after the reduction of P from the system and an associated increase in the N:P ratio. Further details of all of these changes are described more fully in text. Blank entries are those for which insufficient data are available to evaluate.

	San Francisco Estuary	**Potomac River**	**Hudson River**	**Great Lakes**	**Florida Lakes**	**Lake Washington**	**Ebro River**
Phytoplankton							
Change in Chl a	Decrease	Decrease	Decrease	Decrease	Decrease	Decrease	Decrease
Change in *Microcystis* occurrence	Increase	Initial decrease, then resurgence	Initial decrease, then resurgence	Initial decrease, then resurgence		Decrease	
Zooplankton							
Change in species group	Increase in cyclopoids and cladocerans	Increase in cyclopoids and cladocerans	Increase in cyclopoids and cladocerans	Increase in cyclopoids and cladocerans		Increase in cyclopoids and cladocerans	
Fish							
Change in dominant feeding strategy	Decrease in planktivores: piscivores	Decrease in planktivores: detritivores	Decrease in planktivores	Decrease in planktivores: piscivores	Decrease in planktivores: piscivores		
Bivalves							
Change in dominant species	Increase in *Corbula*	Increase in *Corbicula, Rangia*	Increase in *Dreissena, Rangia*	Increase in *Dreissena*			Increase in *Dreissena, Corbicula*
Shrimp							
Change in dominant species	Decrease in *Neomysis*					Decrease in *Neomysis*	
Submerged Vegetation							
Change in abundance	Increase	Increase	Increase		Increase		Increase
Dominant species	*Egeria, Eichornia*	*Hydrilla*	*Hydrilla, Eleocharis*		*Hydrilla*		*Hydrilla*

Figure 1
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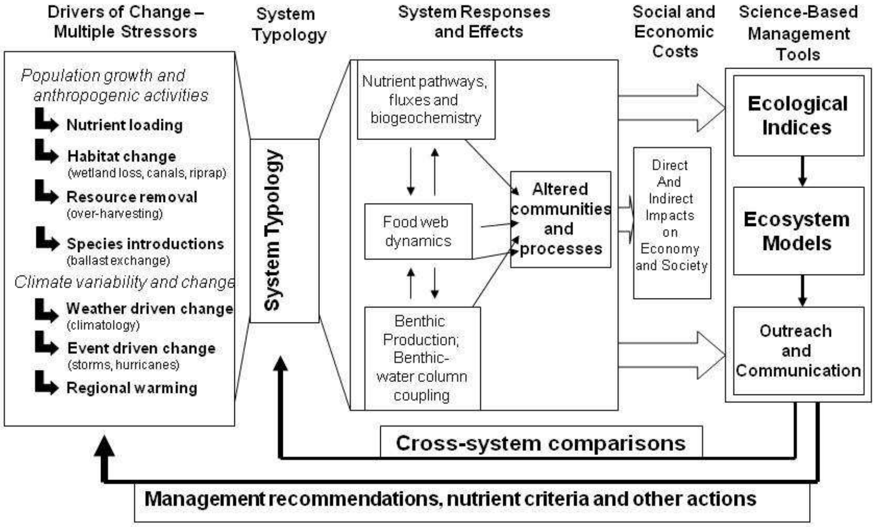

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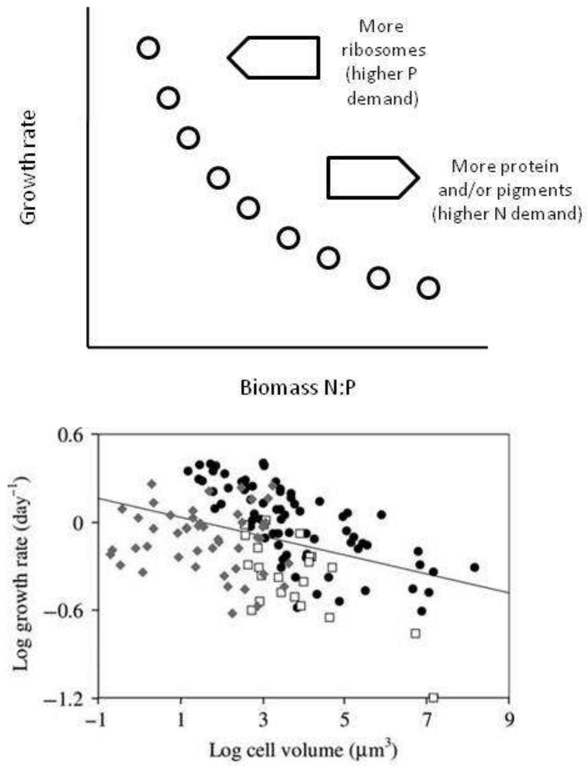

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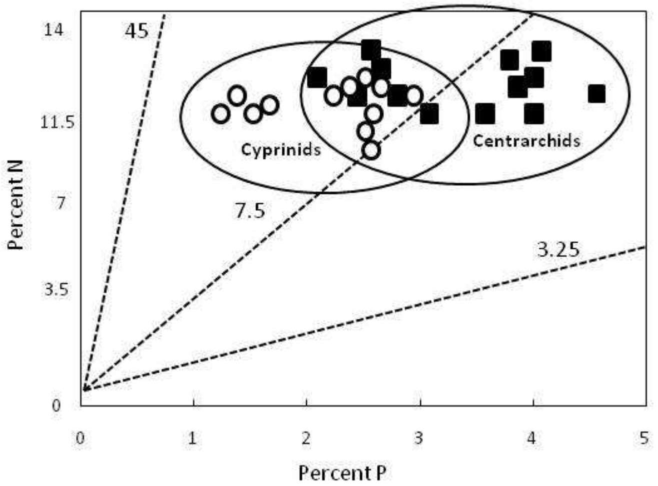

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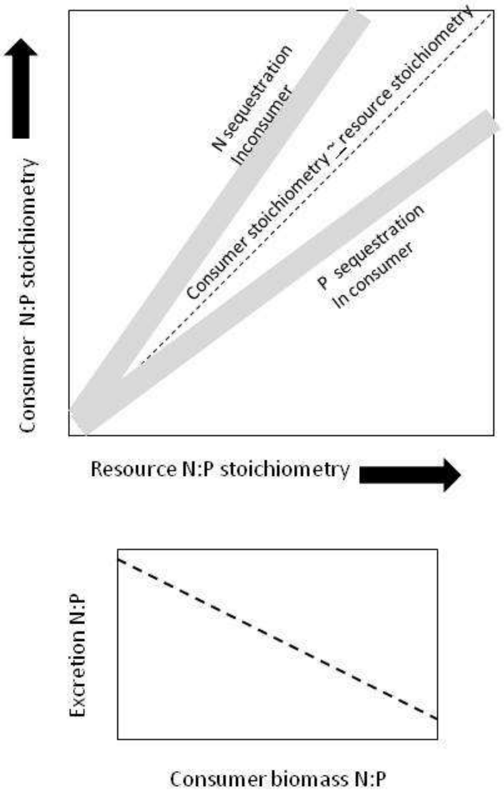

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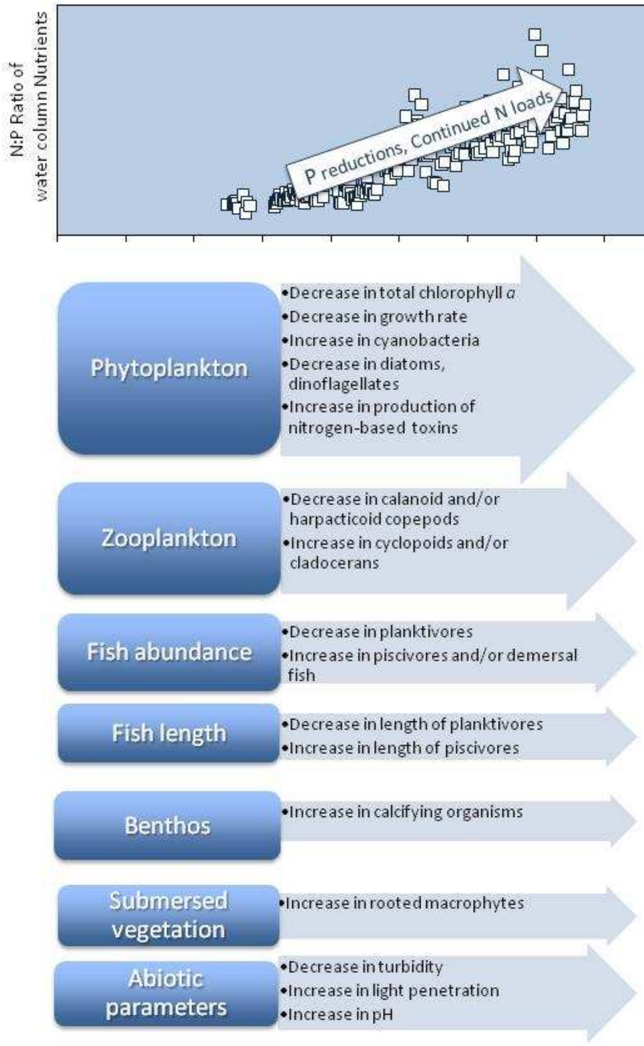

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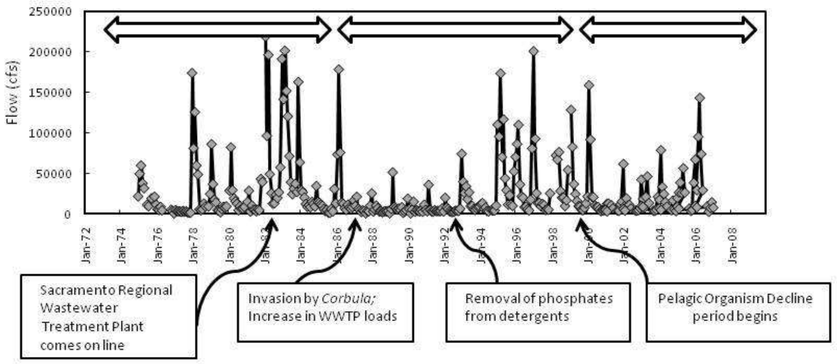

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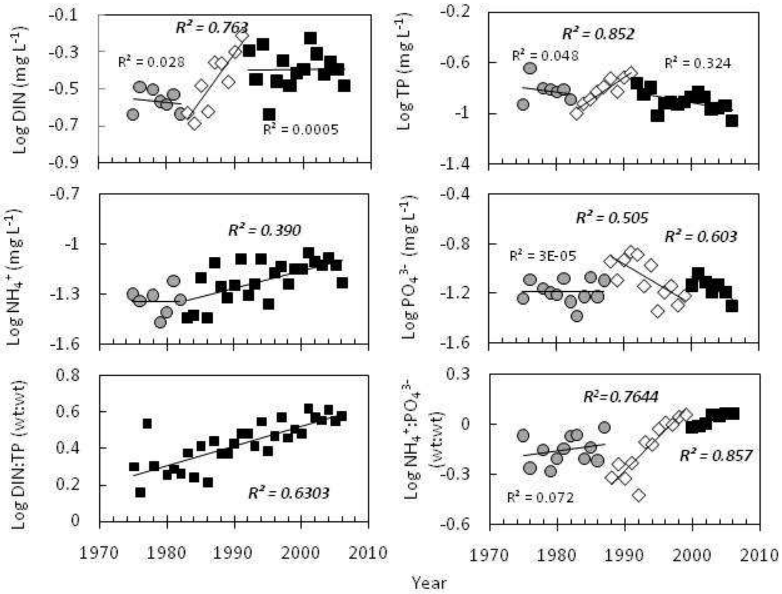

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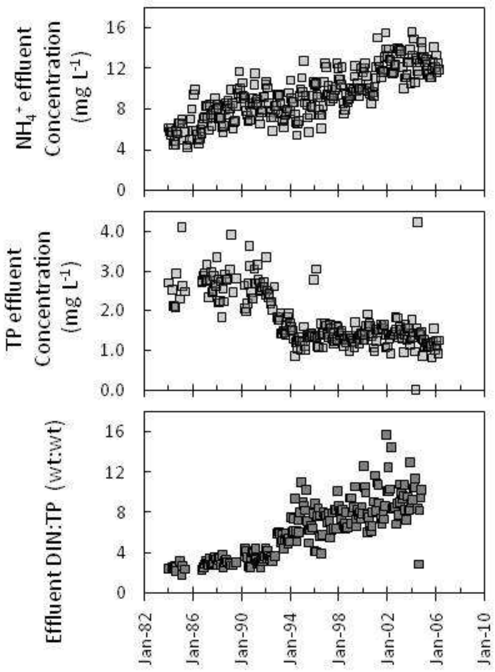

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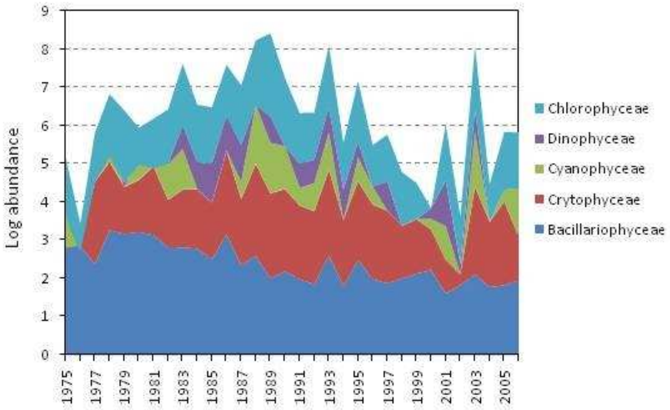

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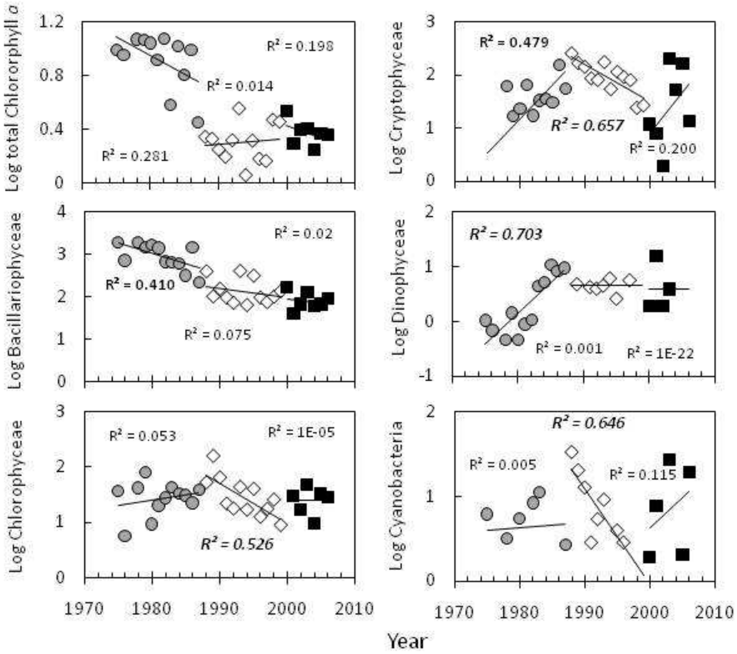

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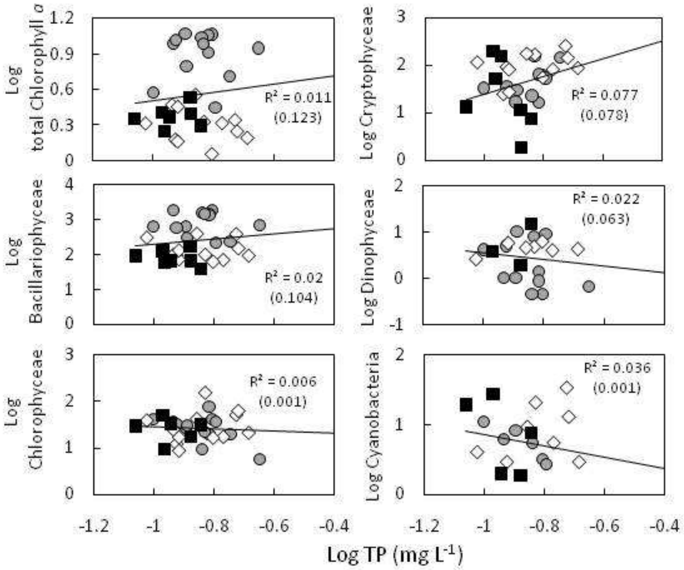

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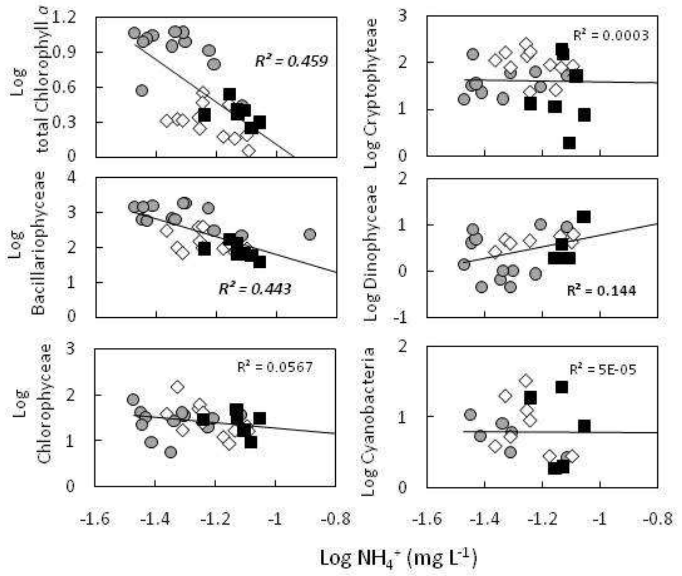

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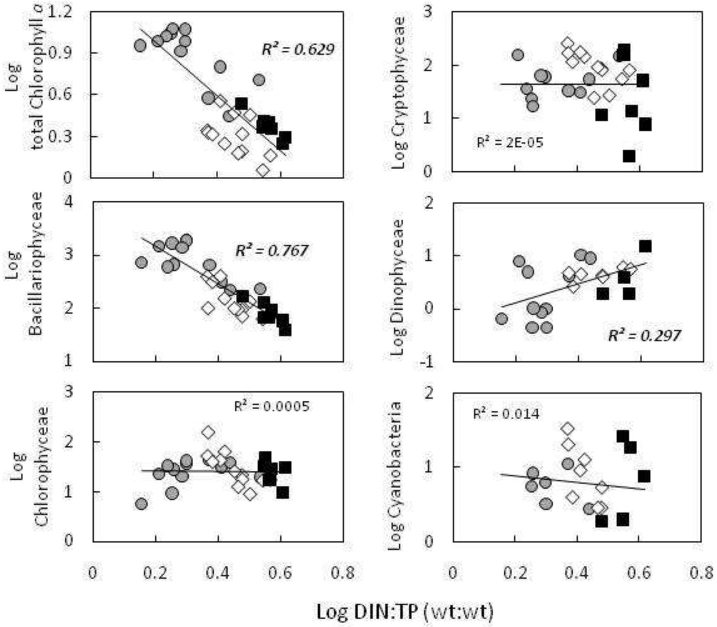

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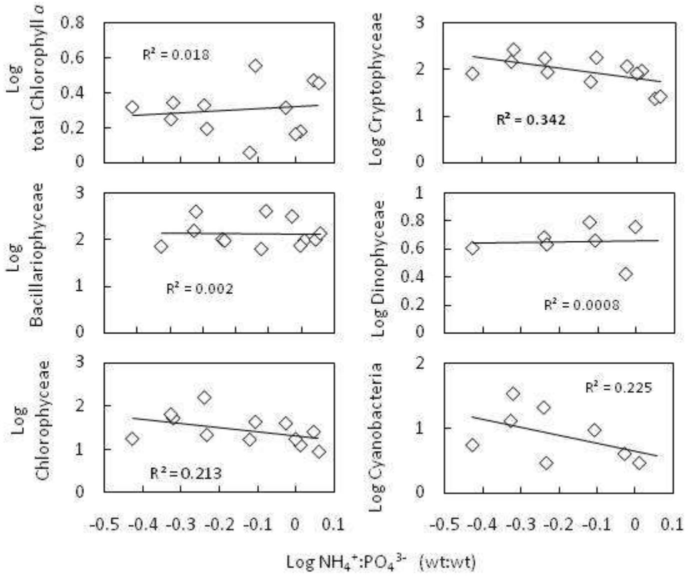

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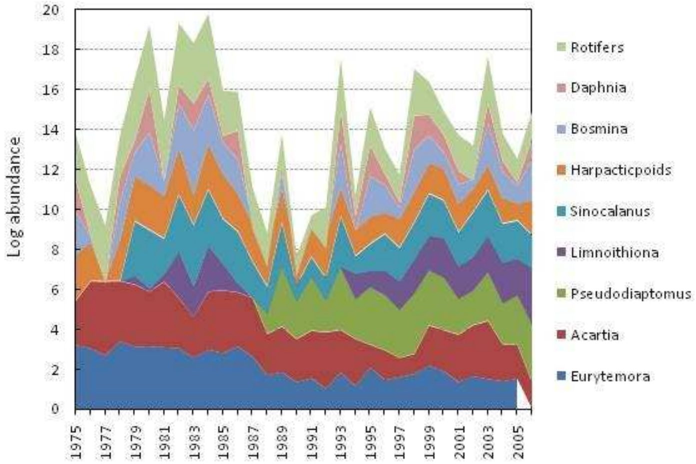

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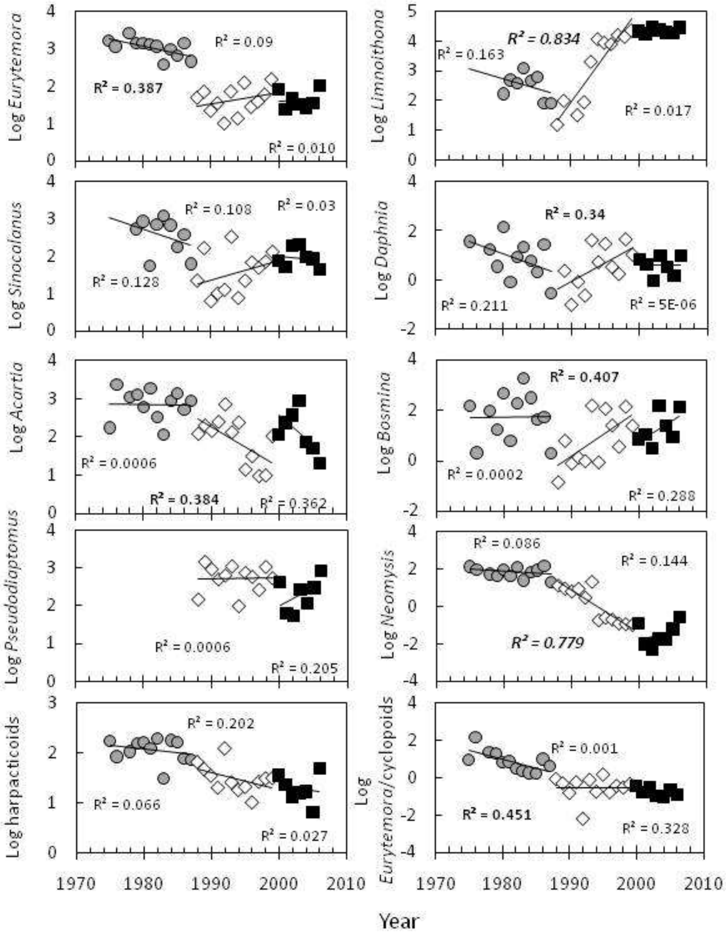

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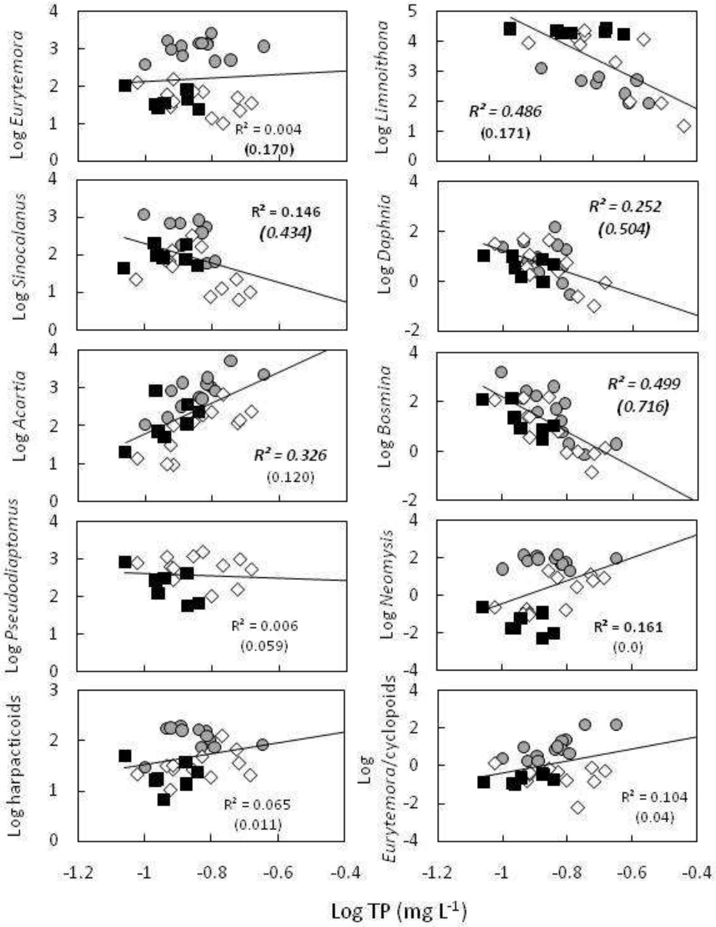

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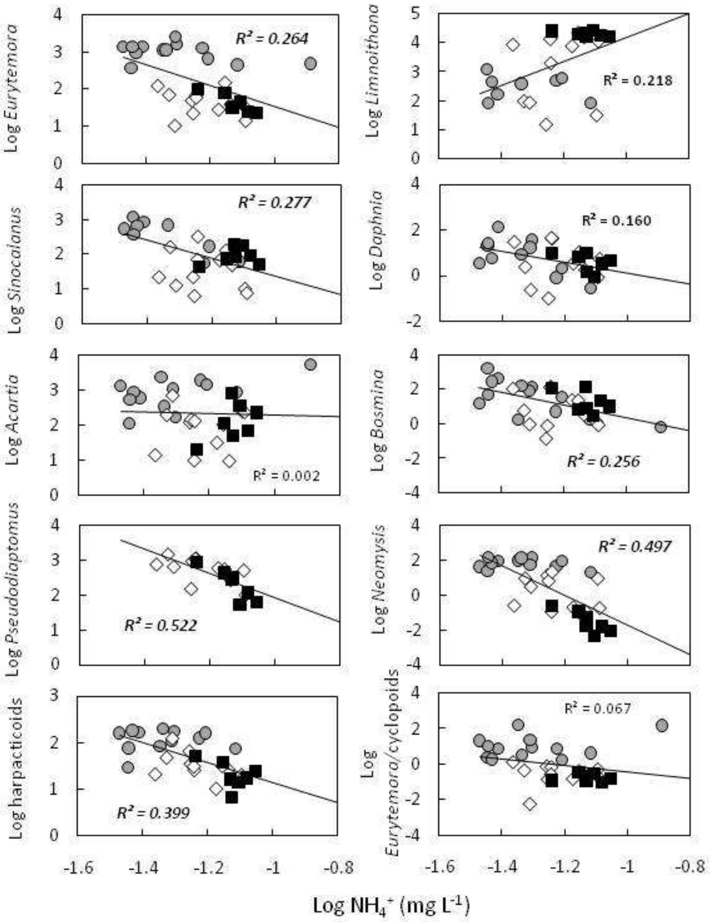

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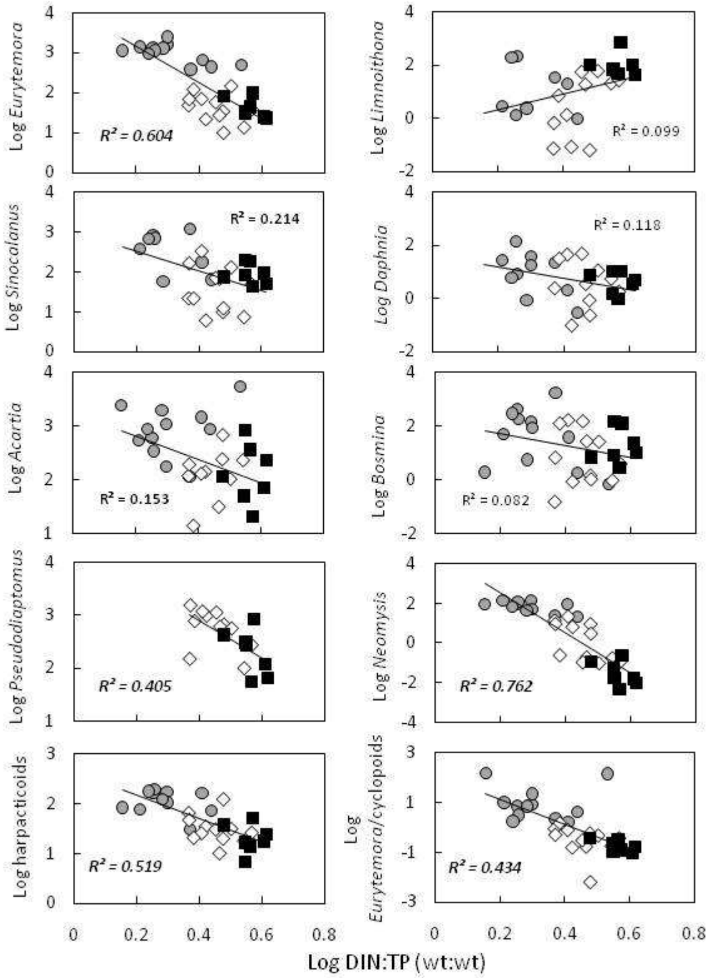

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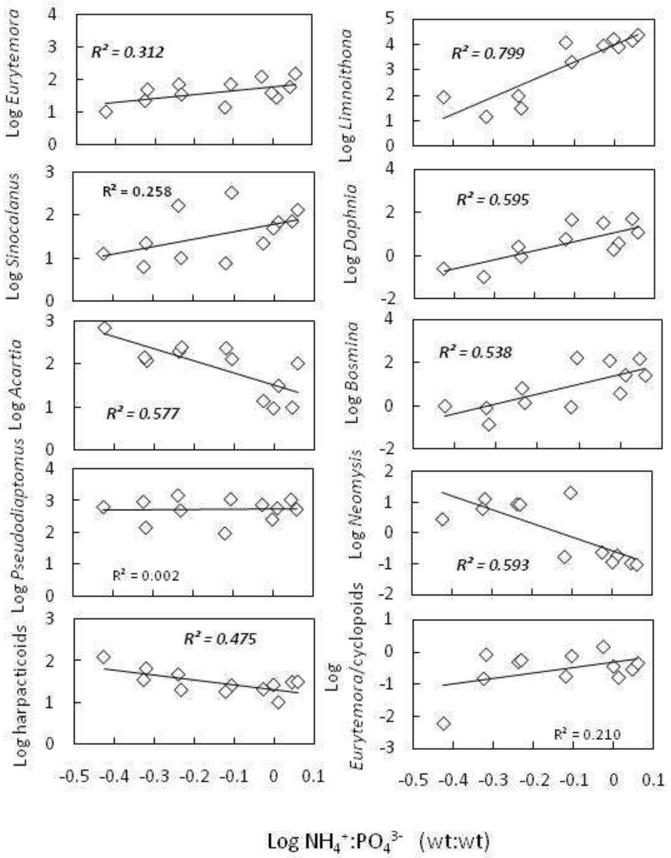

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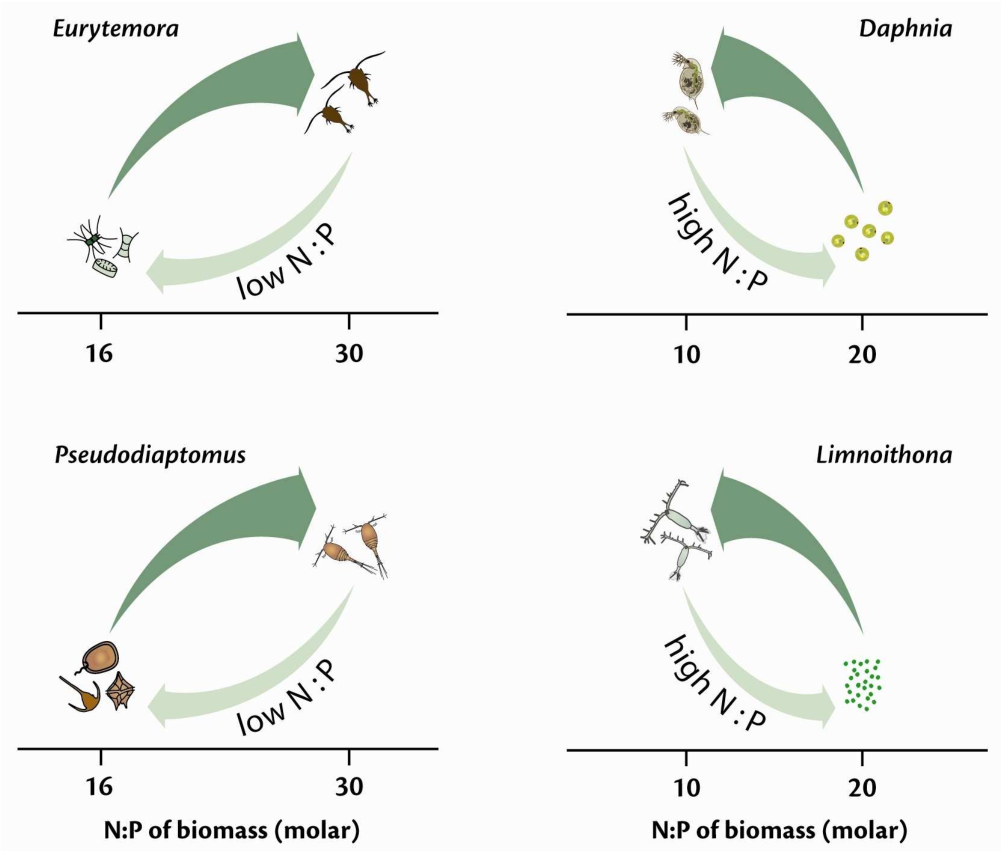

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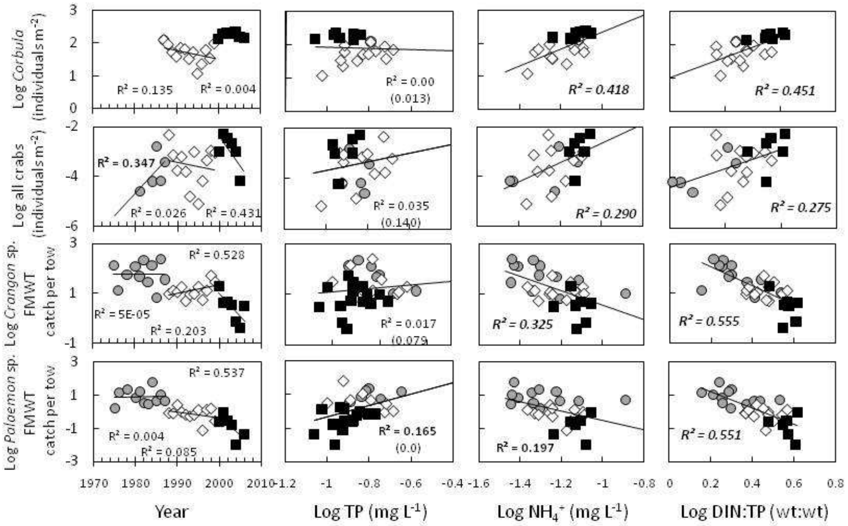

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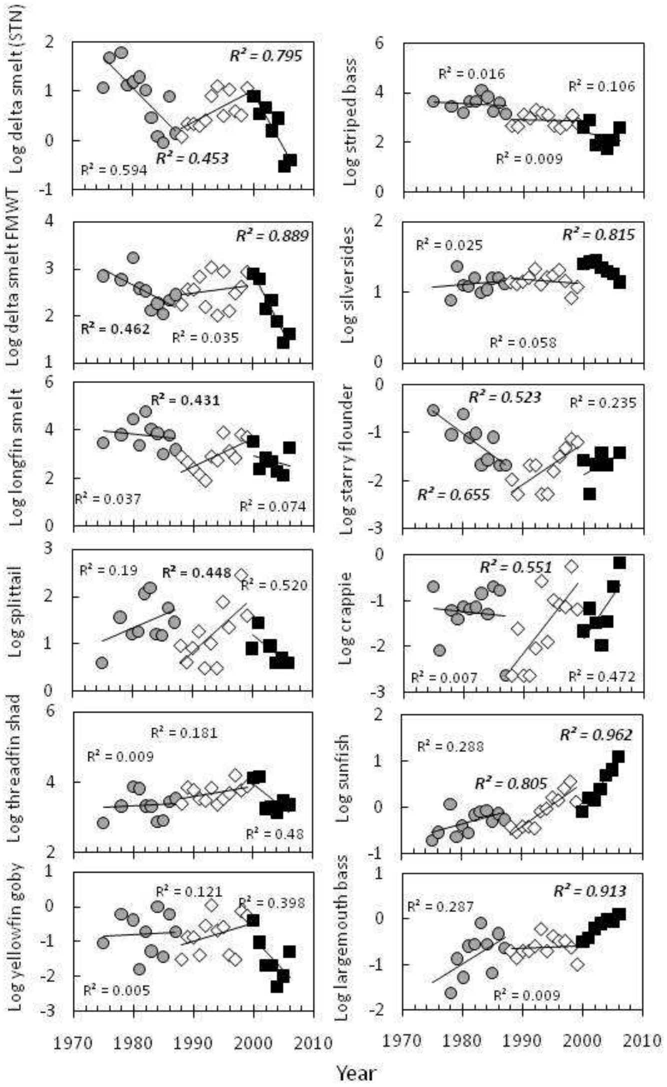

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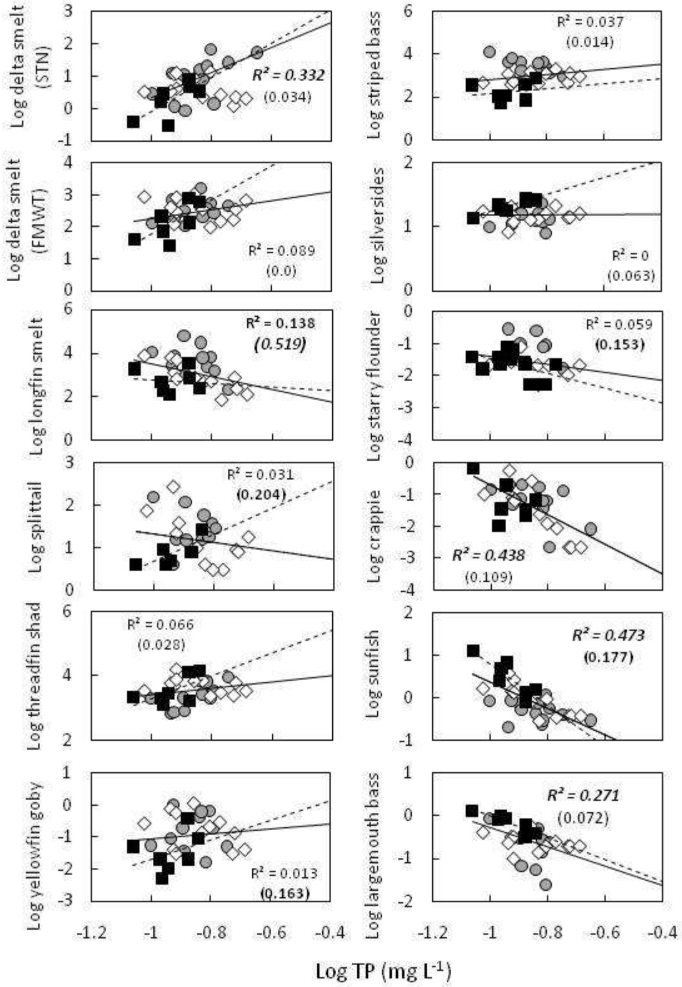

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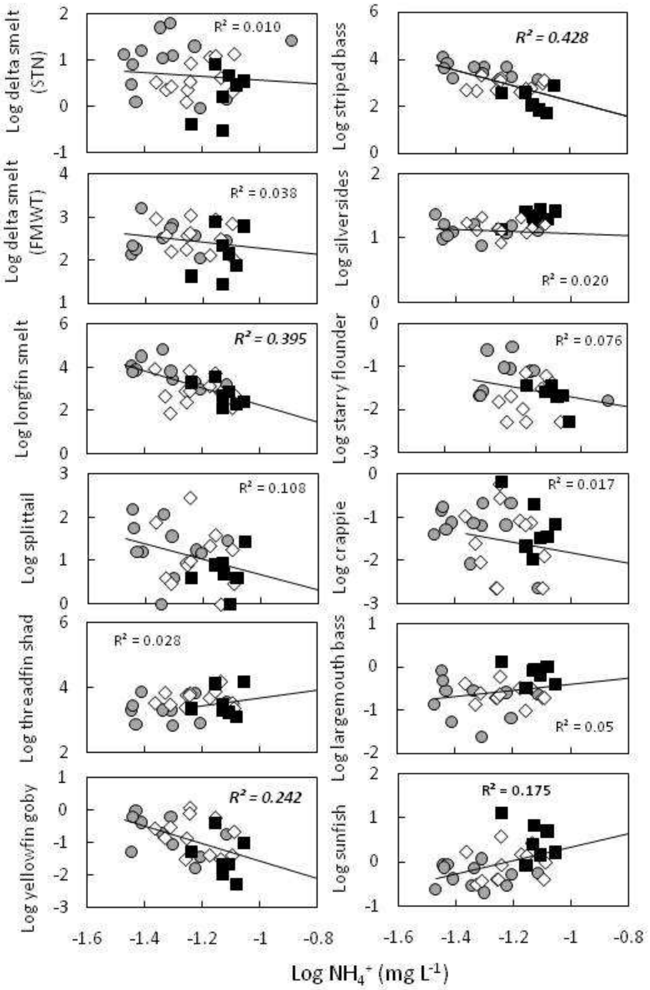

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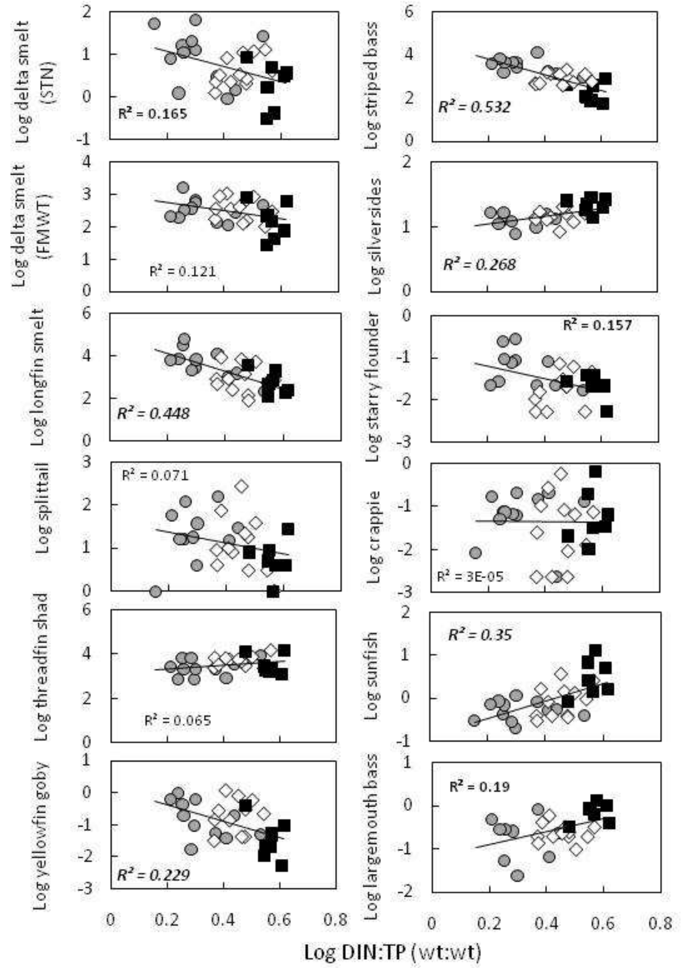

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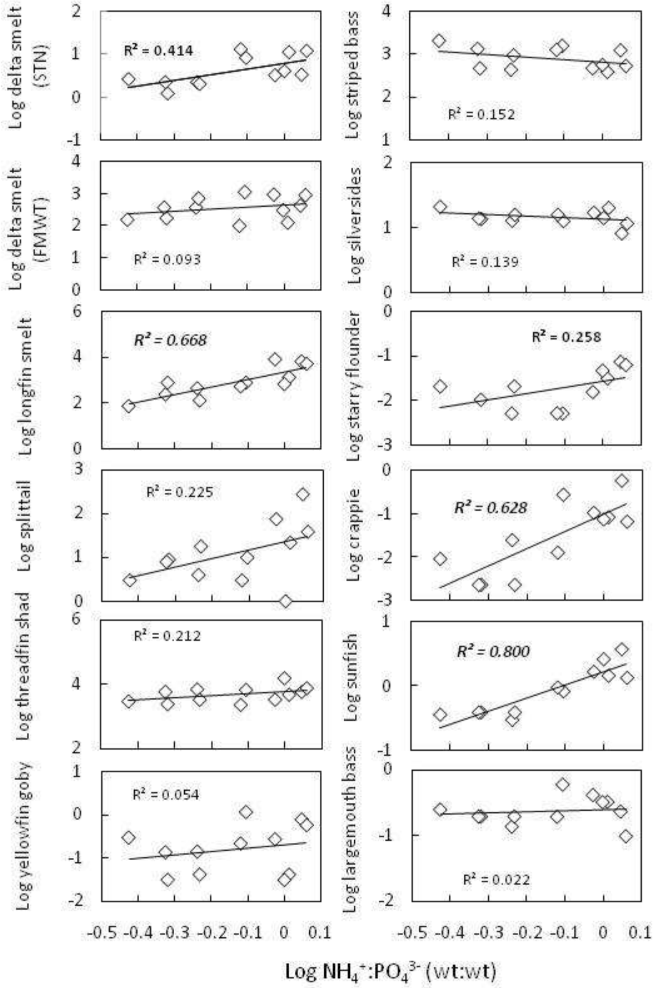

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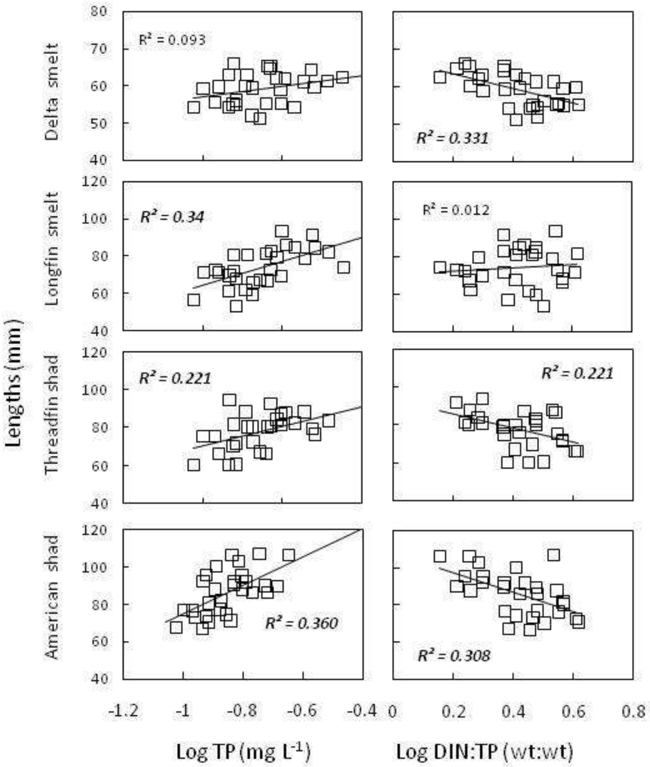

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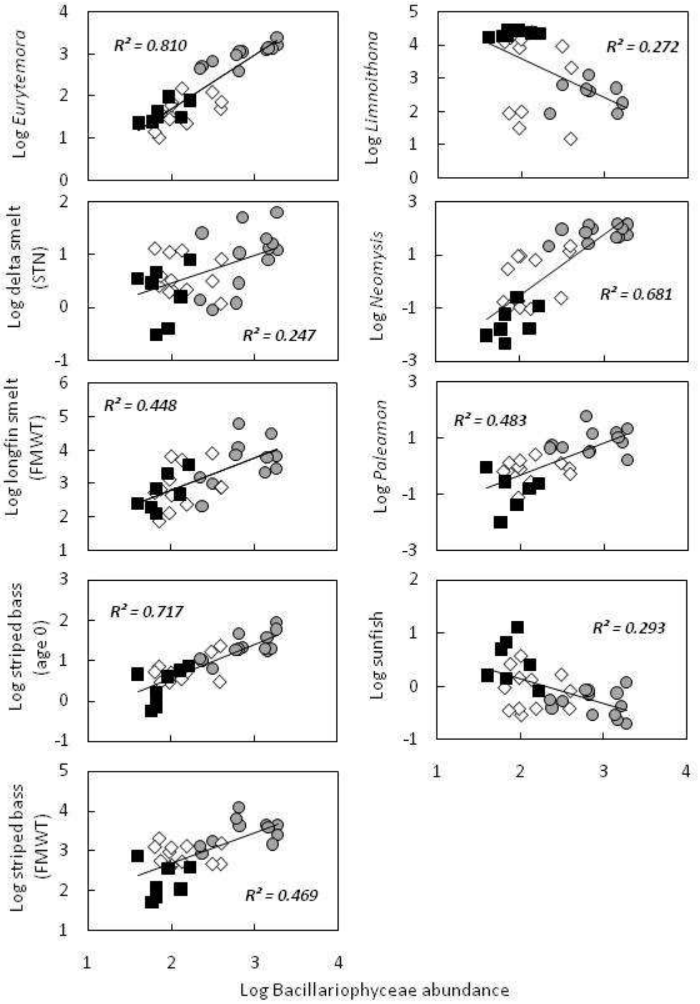

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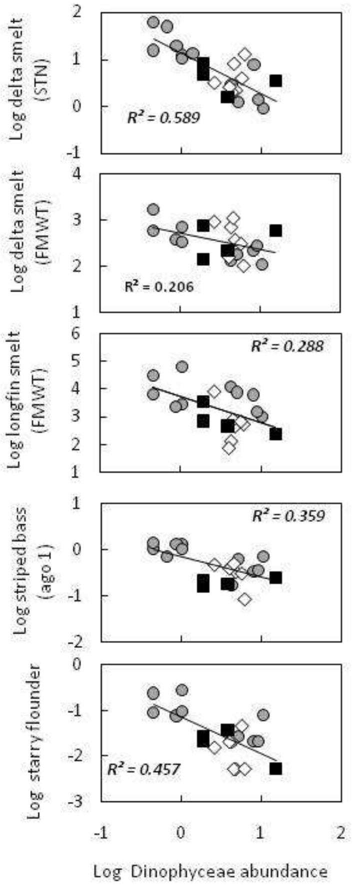

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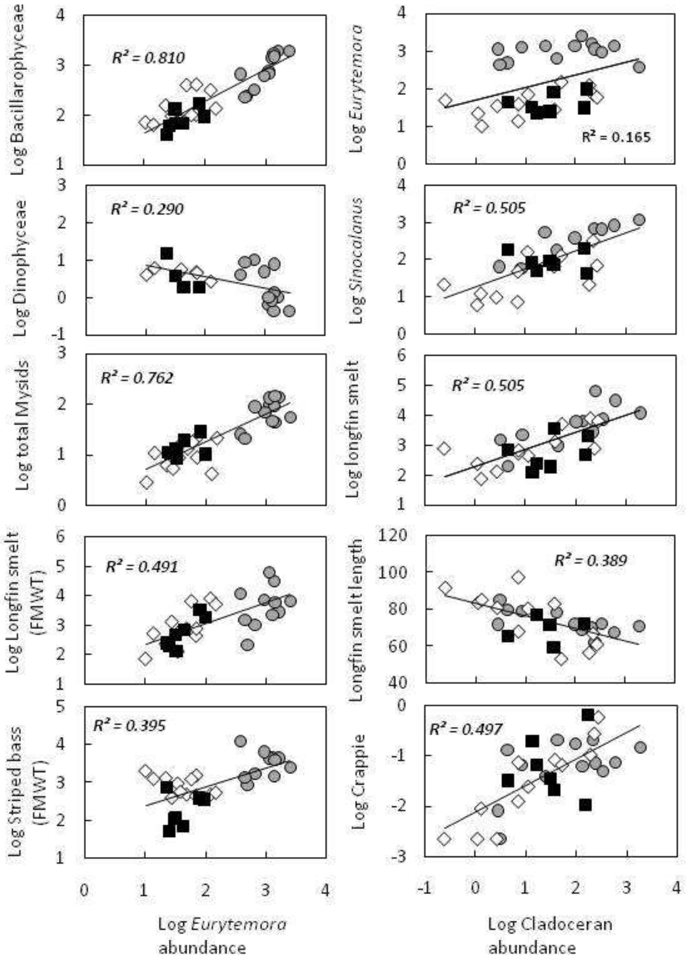

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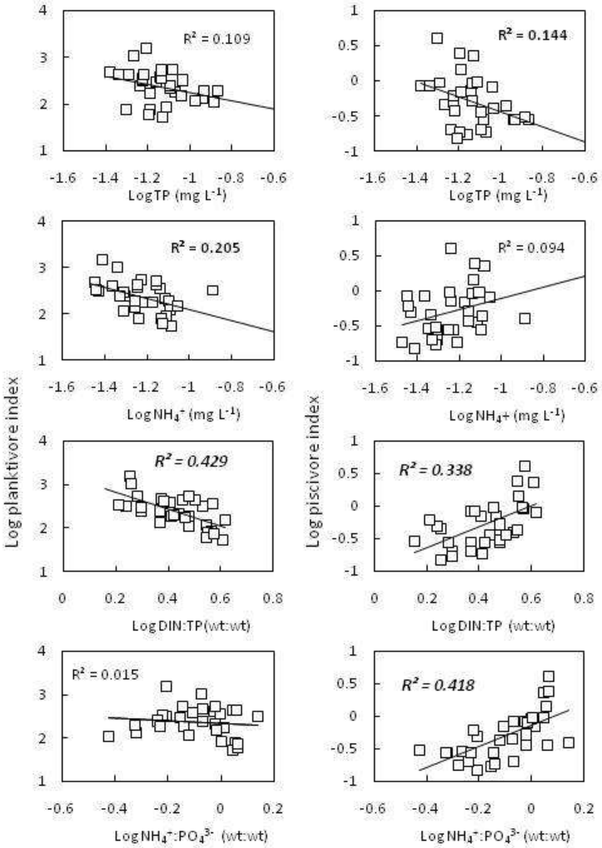

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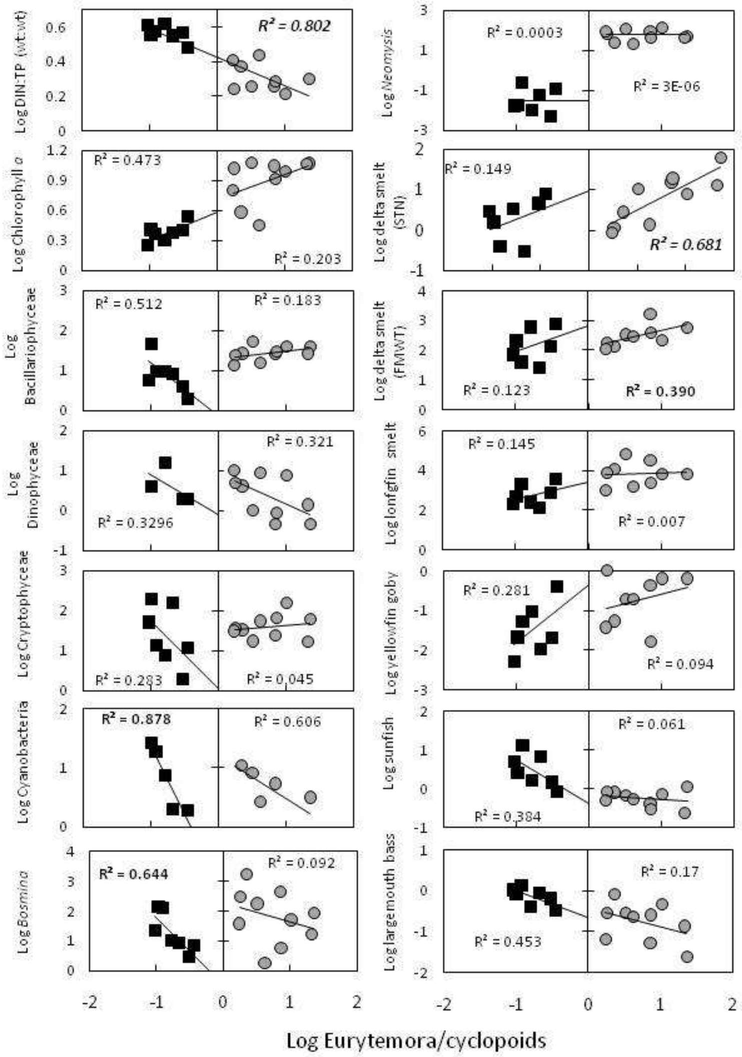

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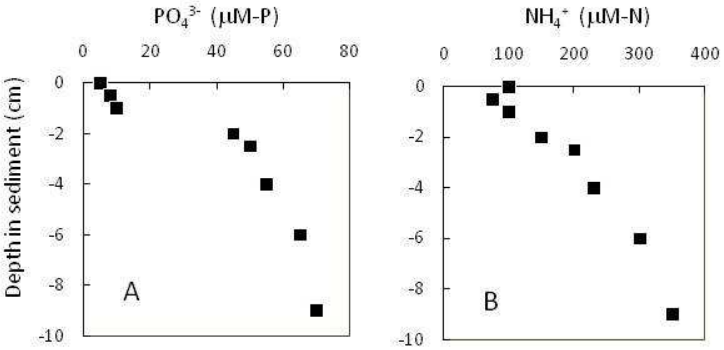

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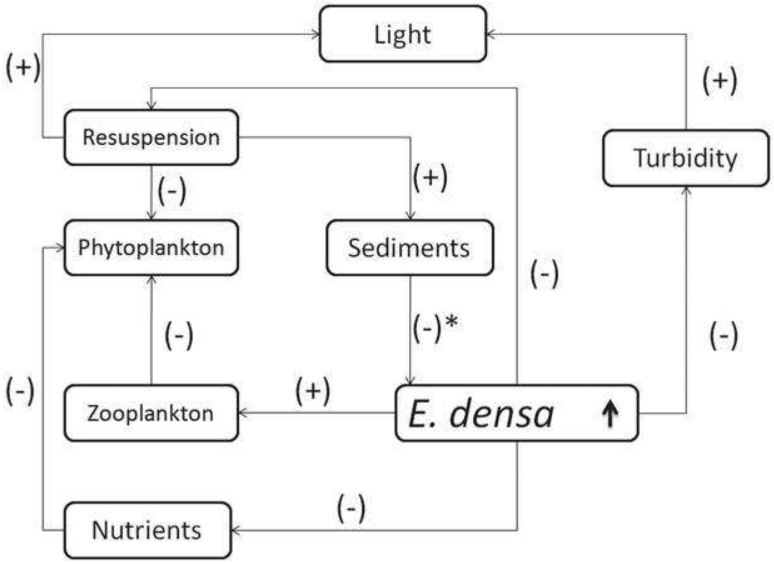

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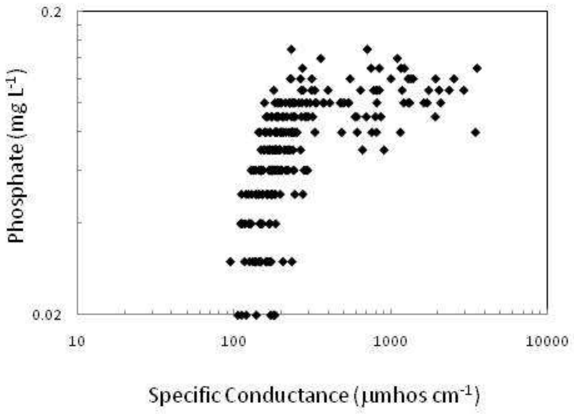

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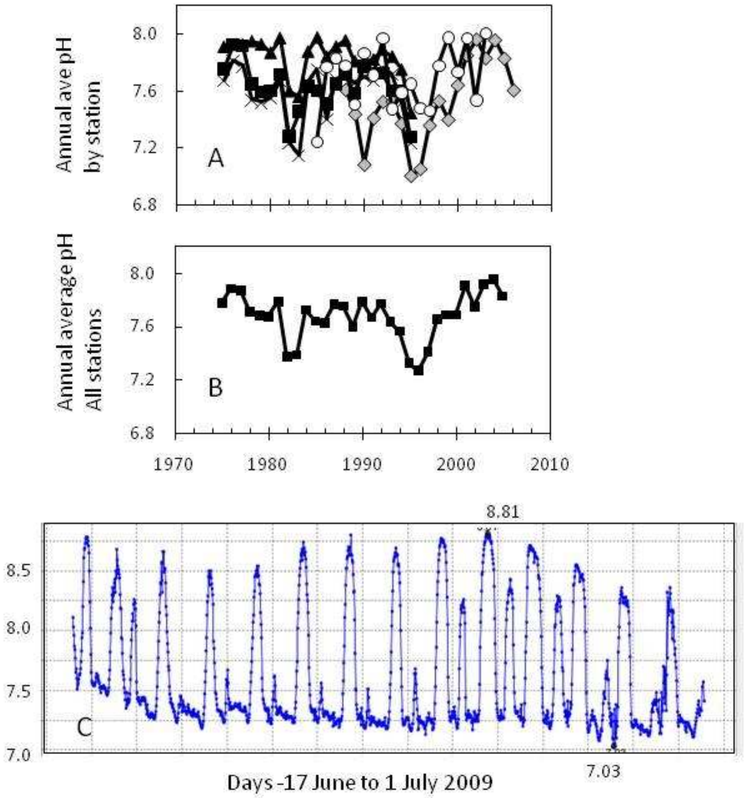

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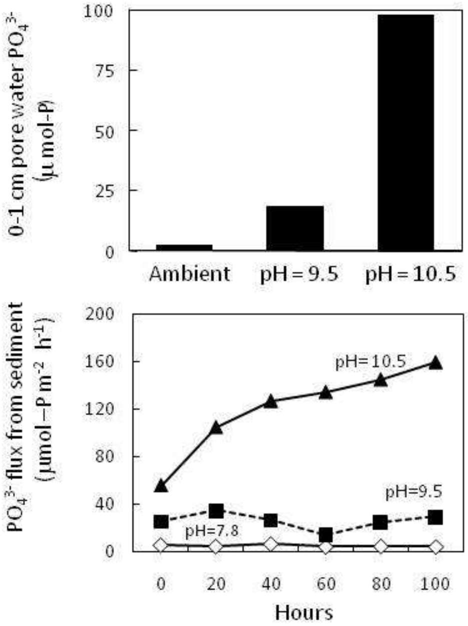

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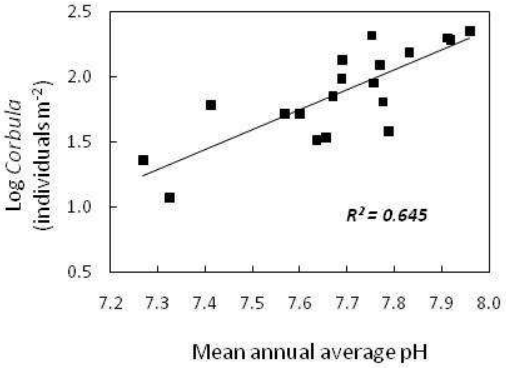

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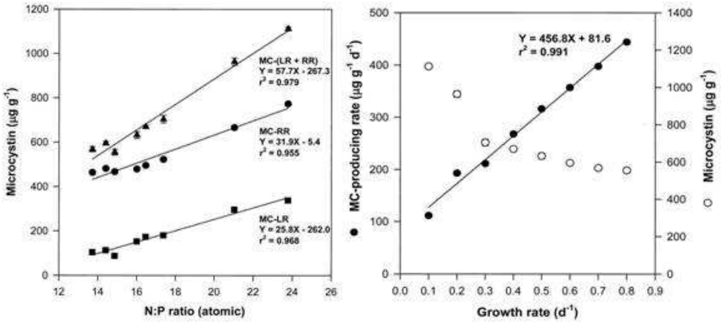

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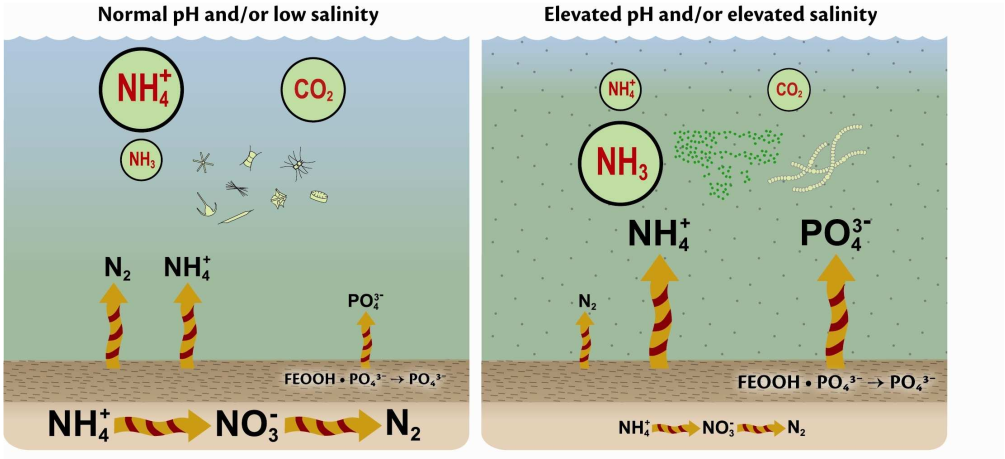


Figure 42
187x85mm (300 x 300 DPI)

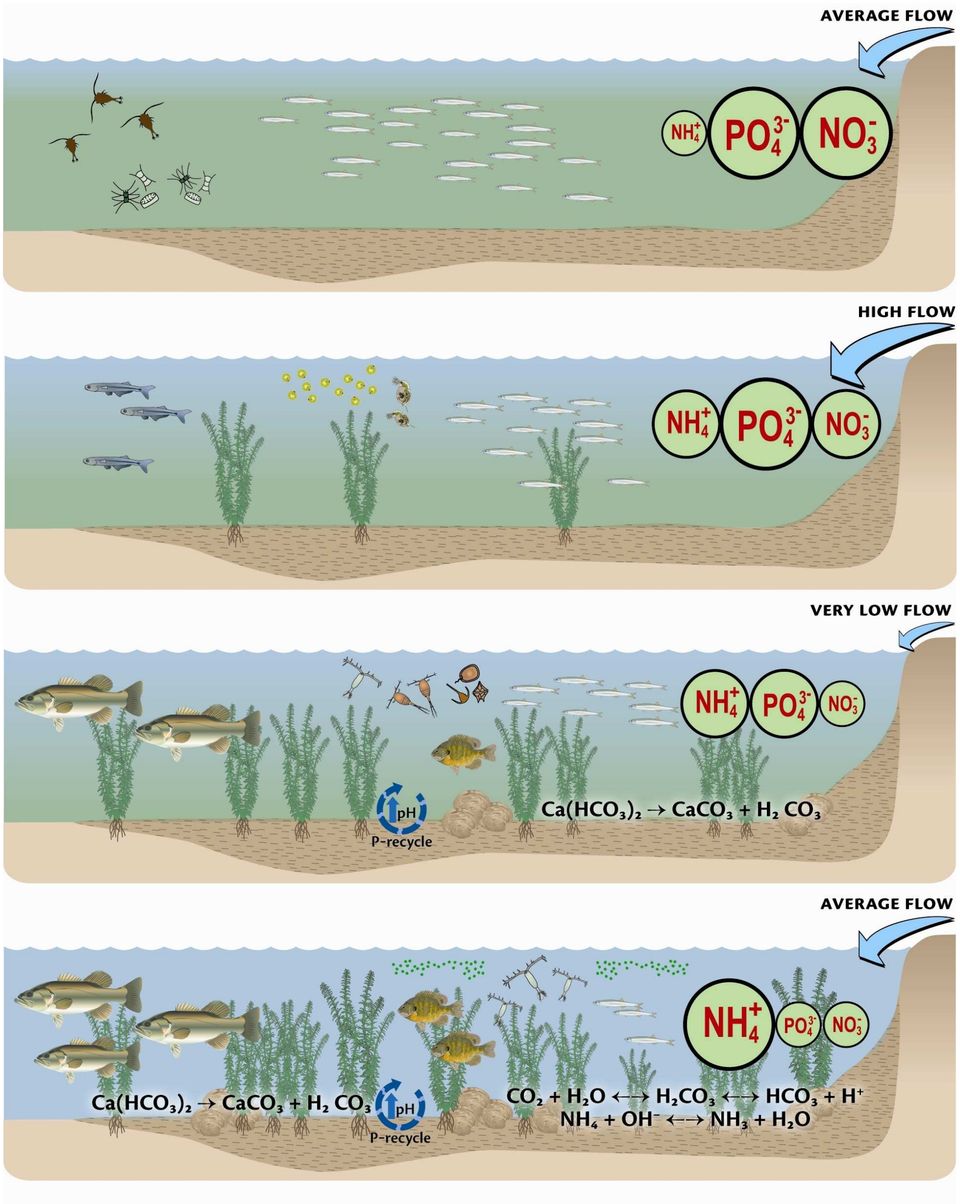


Figure 43
164x207mm (300 x 300 DPI)

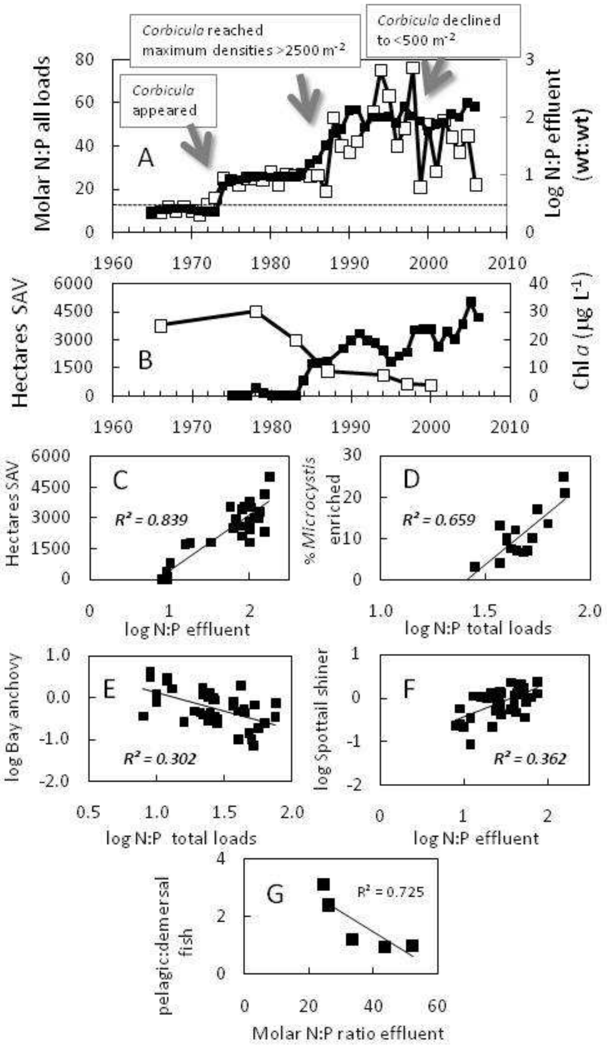


Figure 44
190x254mm (96 x 96 DPI)

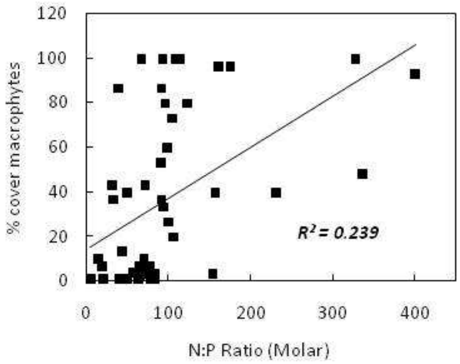


Figure 45
190x254mm (96 x 96 DPI)

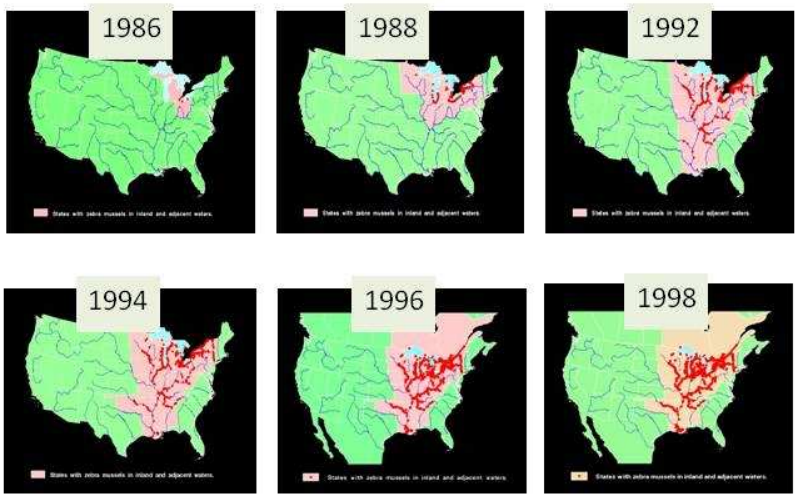


Figure 46
190x254mm (96 x 96 DPI)

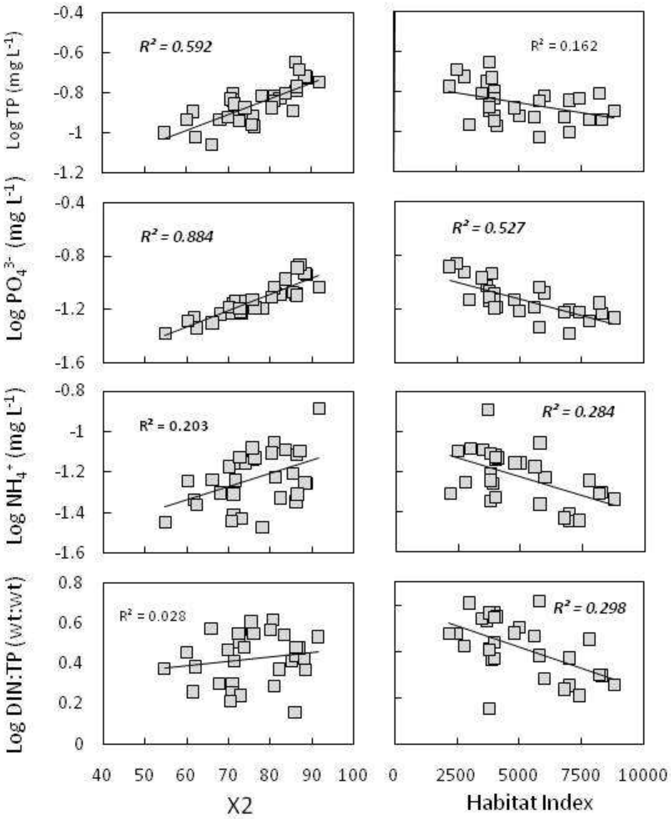


Figure 47
190x254mm (96 x 96 DPI)

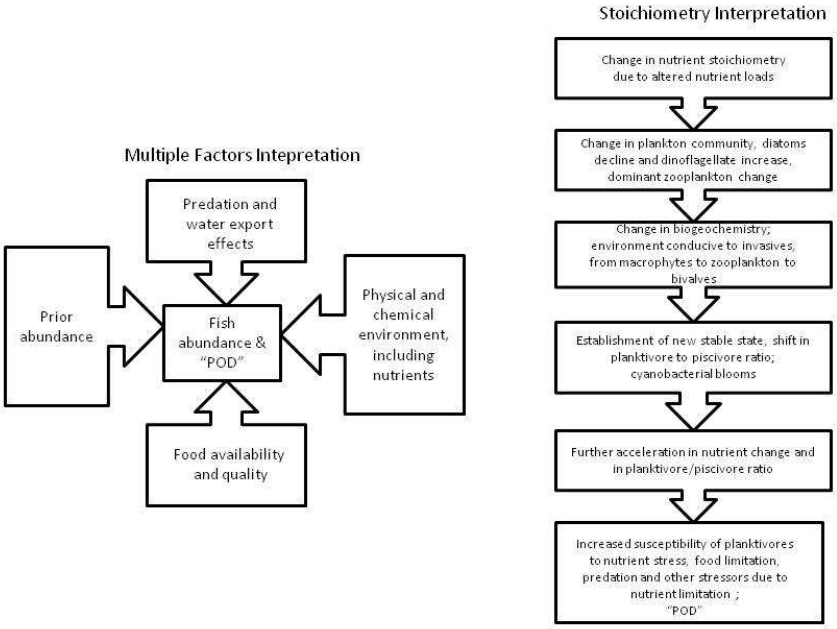
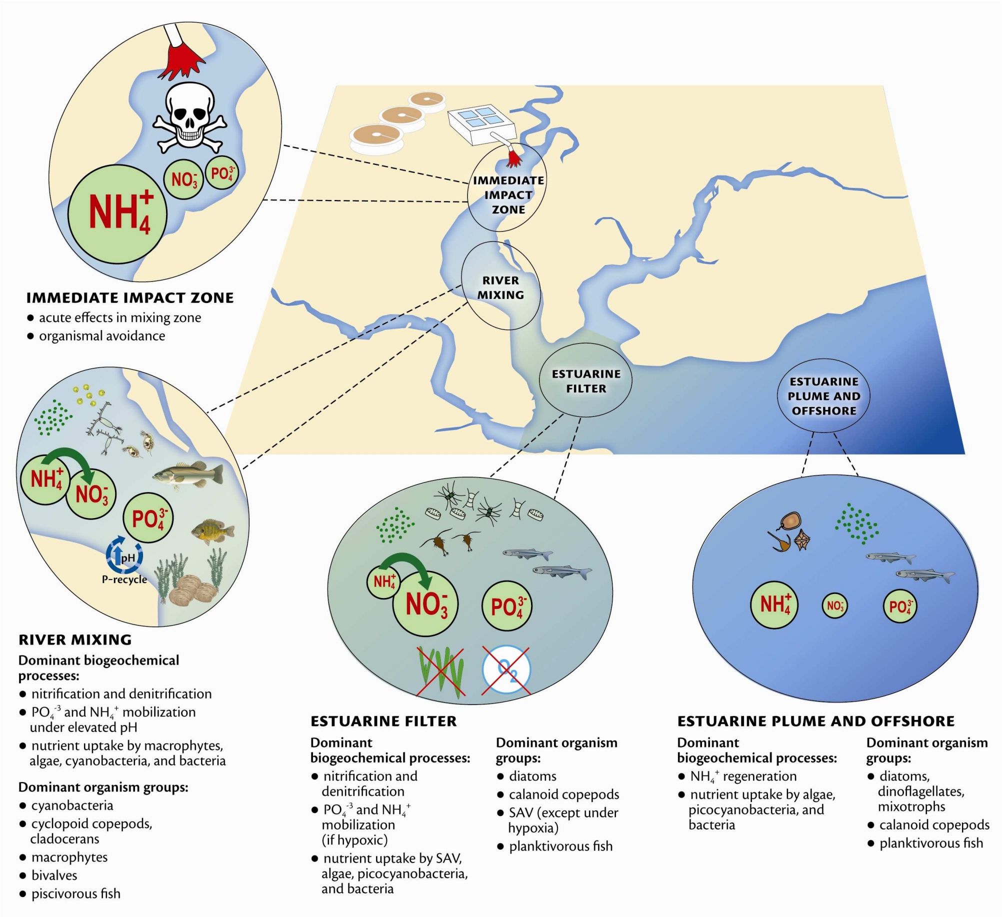


Figure 48
254x190mm (96 x 96 DPI)



IMMEDIATE IMPACT ZONE

- acute effects in mixing zone
- organismal avoidance

RIVER MIXING

Dominant biogeochemical processes:

- nitrification and denitrification
- PO_4^{-3} and NH_4^+ mobilization under elevated pH
- nutrient uptake by macrophytes, algae, cyanobacteria, and bacteria

Dominant organism groups:

- cyanobacteria
- cyclopoid copepods, cladocerans
- macrophytes
- bivalves
- piscivorous fish

ESTUARINE FILTER

Dominant biogeochemical processes:

- nitrification and denitrification
- PO_4^{-3} and NH_4^+ mobilization (if hypoxic)
- nutrient uptake by SAV, algae, picocyanobacteria, and bacteria

Dominant organism groups:

- diatoms
- calanoid copepods
- SAV (except under hypoxia)
- planktivorous fish

ESTUARINE PLUME AND OFFSHORE

Dominant biogeochemical processes:

- NH_4^+ regeneration
- nutrient uptake by algae, picocyanobacteria, and bacteria

Dominant organism groups:

- diatoms, dinoflagellates, mixotrophs
- calanoid copepods
- planktivorous fish

Figure 49
232x212mm (300 x 300 DPI)