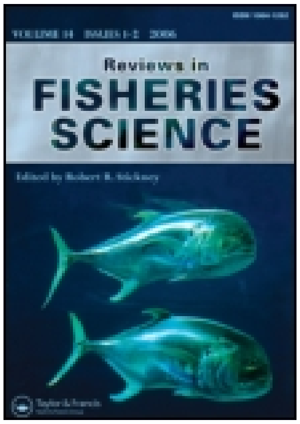

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Ecological Stoichiometry, Biogeochemical Cycling, Invasive Species, and Aquatic Food Webs: San Francisco Estuary and Comparative Systems

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Ecological Stoichiometry, Biogeochemical Cycling, Invasive Species, and Aquatic Food Webs: San Francisco Estuary and Comparative Systems

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Eutrophication has altered food webs across aquatic systems, but effects of nutrient stoichiometry (varying nutrient ratios) on ecosystem structure and function have received less attention. A prevailing assumption has been that nutrients are not ecologically relevant unless concentrations are limiting to phytoplankton. However, changes in nutrient stoichiometry fundamentally affect food quality at all levels of the food web. Here, 30-year records of nitrogen and phosphorus concentrations and ratios, phytoplankton, zooplankton, macroinvertebrates, and fish in the San Francisco Estuary (Bay Delta) were examined to collectively interpret ecosystem changes within the framework of ecological stoichiometry. Changes in nutrient concentrations and nutrient ratios over time fundamentally affect biogeochemical nutrient dynamics that can lead to conditions conducive to invasions of rooted macrophytes and bivalve molluscs, and the harmful cyanobacterium Microcystis*. Several other aquatic ecosystems considered here have exhibited similar changes in food webs linked to stoichiometric changes. Nutrient stoichiometry is thus suggested to be a significant driver of food webs in the Bay Delta by altering food quality and biogeochemical dynamics. Since nitrogen-to-phosphorus ratios have increased over time, an overall implication is that remediation of fish populations in the San Francisco Estuary will require significant nitrogen reductions to restore the historic ecological stoichiometric balance and the food web.*

Keywords ammonium, Bay Delta, *Corbula amurensis*, delta smelt, *Egeria densa*, *Microcystis*, nitrogen, nutrient ratios, pelagic organism decline, pH effects, phosphorus, stoichiotrophic imbalance

INTRODUCTION

This review integrates concepts of eutrophication (e.g., Nixon, 1995; Cloern, 2001; Wetzel, 2001), ecological stoichiometry (Sterner and Elser, 2002), and stable state theory (Scheffer et al., 1993) in an overall framework for evaluating the extent to which long-term changes in aquatic food webs in the San Francisco Bay Delta and other aquatic ecosystems 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, whereas ecological stoichiometry—consideration of nutrient ratios—relates changes in the relative elemental (e.g., nitrogen [N], phosphorus [P], and carbon [C]) composition in body tissue and the water column. Stable state theory suggests that external drivers or disturbances (here, nutrients) can shift a system from one stable state to another via interacting feedbacks.

Nutrient ratios have often been used to infer system limitation when concentrations are known to be limiting to the phytoplankton assemblage (Reynolds, 1999; Downing et al.,

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2001). A prevailing view has considered nutrient ratios to be ecologically irrelevant unless concentrations are limiting to phytoplankton growth rate. Such a narrow application of nutrient ratios, conferring importance only when concentrations limit phytoplankton growth rate, needs to be expanded in recognition of that fact that changes in nutrient stoichiometry fundamentally affect *food quality*—from the base to the apex of aquatic food webs—as well as system *biogeochemistry*, whether nutrients are limiting or not (Sterner and Elser, 2002).

The central premise of this article 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 nutrients, and that biogeochemical feedbacks associated with species assemblage changes may shift systems to new stable states. In this review, 30 years of records of inorganic N and P concentrations, phytoplankton, zooplankton, invertebrates, and fish in the San Francisco Estuary were examined to interpret ecosystem changes within the conceptual framework of nutrient dynamics. The questions addressed in this article are: *To what extent do ecosystems self-assemble as a function of nutrient stoichiometry? 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 to the issue of cultural eutrophication, which is one of the most pressing problems affecting both coastal and freshwater ecosystems worldwide (e.g., Vitousek et al., 1997a,b; Howarth et al., 2002; Galloway and Cowling, 2002; Turner et al., 2003; Conley et al., 2009; Doney, 2010). Nutrient pollution is on the rise because of dramatic increases in human population in many regions, and concomitant increasing demands for energy, increases in N and 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; Glibert et al., 2010). Although eutrophication is occurring globally, nutrient exports from coastal watersheds are not evenly distributed (Seitzinger et al., 2002a, 2005; Howarth et al., 2005; Glibert et al., 2006a, 2010), nor is the export of N and P changing proportionately. Much remains 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 changes in nutrient loads from those due to stochastic events has important implications for restoration and management. A major management implication stressed here is the importance of co-management of N and P. A common practice has been to reduce P in point sources without concomitant reductions in N while overlooking the fact that nutrient loading results in large sediment deposits of nutrients that influence the overall system for an extended period (years) after loading rates are reduced. Reductions in anthropogenic P loads can initially result in a decline in phytoplankton biomass, but the sediment "pump" of stored P replenishes P supplies in the water column, promoting benthic productivity, which, in turn, has multiple effects on the food web. If the system additionally receives N, especially in the form of ammonium (NH_4^+), it can be expected to shift to undesirable dominant species among primary producers, with ramifications extending to higher trophic levels.

Nutrient enrichment interacts with aquatic food web dynamics in complex ways. At the planktonic level, many of these changes are well understood for phytoplankton. With nutrient enrichment, biomass may increase without a change in the proportion of the dominant planktonic organisms, but, more commonly, as nutrients continue to increase, a shift in plankton assemblage composition is observed, with large diatoms giving way to smaller phototrophs, such as cyanobacteria and various flagellates (e.g., Smayda 1989; Marshall et al., 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 harmful algal blooms at the expense of competing algal species (Irigoien et al., 2005; Mitra and Flynn, 2006; Sunda et al., 2006). Such changes have ramifications at all levels of the food web. Increased phytoplankton and macroalgal proliferations at high nutrient levels affect seagrasses and benthic microalgae that compete for light (Harlin, 1993; Deegan, 2002; Burkholder et al., 2007), altering the food web structure by changing the habitat needed to support fish and shellfish. Fundamentally, 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, P reductions have been undertaken (e.g., in sewage effluents and laundry detergents), as a means to reduce or control algal blooms whereas N loads often are allowed to remain elevated (Glennie et al., 2002; 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. Nevertheless, even when many eutrophication symptoms are reduced, such as hypoxia and algal blooms, the systems only appear to partially recover (Burkholder, 2001; Burkholder and Glibert, 2011); their food webs do not appear to return to their pre-eutrophic state.

The San Francisco Estuary, or Bay Delta, California, USA (Figure 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

Figure 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 article were located. The diamond indicates the Sacremento Regional Wastewater Treatment site. Stations D4–D8 represent the stations where water chemistry data were used for this analysis (color figure available online).

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, 2004, Kimmerer et al., 2010; Jassby, 2008). The Bay Delta has been extensively monitored for most biological constituents since the 1970s, so this is a system rich in data with which to explore these relationships. It has also been influenced by major changes in nutrient loads and nutrient composition (e.g., Van Nieuwenhuyse, 2007; Dugdale et al., 2007; Jassby, 2008; Glibert, 2010). N loads have increased substantially since the mid-1980s, while P loads increased and then declined in the mid-1990s to levels that approximate earlier conditions.

The Bay Delta is an inverse delta and receives 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 ~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, flow ultimately into the Central and South Bays. River flow has varied about ten-fold in the past decades due to the effects of prolonged droughts and El Niño – Southern Oscillation 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 in the world (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; National Research Council of the National Academies [NRC], 2010; Winder et al., 2011). 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 related to nutrient enrichment have contributed to these successful invasions or other food web changes in the Bay Delta has not been explored, because it was earlier concluded that nutrients were in excess of phytoplankton demand and therefore not regulating (Alpine and Cloern, 1992; Cloern and Dufford, 2005).

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 with 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.

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 past decade have been termed the pelagic organism decline (POD) (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 article focuses on nutrient issues that heretofore, for the most part, have not been emphasized, and it suggests some general rules by which aquatic ecosystems may respond. This article develops the hypothesis that nutrient changes underlie this complexity. While there have been multiple freshwater systems to which ecological stoichiometric (Sterner and Elser, 2002) and stable state principles (Scheffer et al., 1993) have been applied (described in more detail throughout this article), there have been relatively few examples where these principles have been applied to 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 article is written in six parts, bringing to bear the ecological principles of eutrophication (sensu Nixon, 1995; 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-relations. Part II probes the long-term nutrient and organismal changes in the Bay Delta and their ecological stoichiometric relationships, beginning with phytoplankton, then zooplankton, macroinvertebrates, 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. Part III considers the complexities of biogeochemical processes and how they relate to changes in the food web. Biogeochemical feedbacks provide the mechanisms whereby food web changes are facilitated when stoichiometry changes. This section examines apparent relationships between the emergence and production of macrophytes, establishment of exotic bivalve molluscs, and blooms of the toxic cyanobacterium *Microcystis aeruginosa*. Part IV compares the Bay Delta to selected freshwater and estuarine ecosystems that have exhibited similar patterns, and Part V compares the ecological stoichiometric and alternate stable state interpretations with some prevailing views of system change in the Bay Delta. Finally, Part VI concludes with a summary of the implications of these ideas with respect to current debates and challenges associated with 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, 2001; Duarte et al., 2008; Glibert et al., 2010; Burkholder and Glibert, 2011). The effects of eutrophication are generally characterized in terms of increased phytoplankton (chlorophyll *a*) in the water column, loss of dissolved oxygen leading to hypoxia or anoxia, loss of submersed aquatic vegetation (SAV), shifts in species dominance across trophic levels, and loss of certain fisheries (Hutchinson, 1973; Cloern, 2001; Schindler, 2006). Increases in many harmful algal species have also been associated with eutrophication (Hallegraeff, 1993; Anderson et al. 2002; Glibert et al., 2005, 2006a, 2010; 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 (Hutchinson, 1973; Cloern, 2001; Smayda, 2006). Historically, the concept of eutrophication was mostly applied to the natural aging of lakes (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) suggested three conceptual phases of the understanding of eutrophication and its effects in coastal ecosystems. The first phase considers responses in ecosystems directly related to changes in nutrient loading, including such changes as chlorophyll *a*, primary production, dissolved oxygen, or other measures of system metabolism. The second phase recognizes that estuaries act as filters, modulating the responses, in turn leading to indirect as well as direct effects. Such filters include system typology (e.g., Kurtz et al., 2006; Madden et al., 2010) as well as inherent optical properties. 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, and proposes linkages to synthetic tools to guide management (Figure 2). Here, the suggested conceptual Phase III model of Cloern (2001) is coupled with the ecological stoichiometric framework (Sterner and Elser, 2002) to further understanding not only of the effects of nutrient loading, but also the effects of disproportionate nutrient loading (or nutrient removal).

Ecological Stoichiometry

Ecological stoichiometry provides a framework for "taming" the complexity of both the direct and the indirect responses of ecosystems to eutrophication. Ecological, or elemental, stoichiometry relates the organismal needs for different elements with those of available substrates or, at higher trophic levels, those of available food. Ecological stoichiometry suggests that different organisms will dominate under different relative proportions of critical elements (C, N, or P) due to differences in allocation of C, N, and P in the various structures that form the biomass of different types of organisms (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."

Thus, ecological stoichiometry is basically a comparison of nutrient ratios in solution or food and in consumer biomass. An ecological stoichiometric perspective asks the questions: *Do organisms have an elemental balance reflective of their food or their available substrates? If not, why not, and what are the*

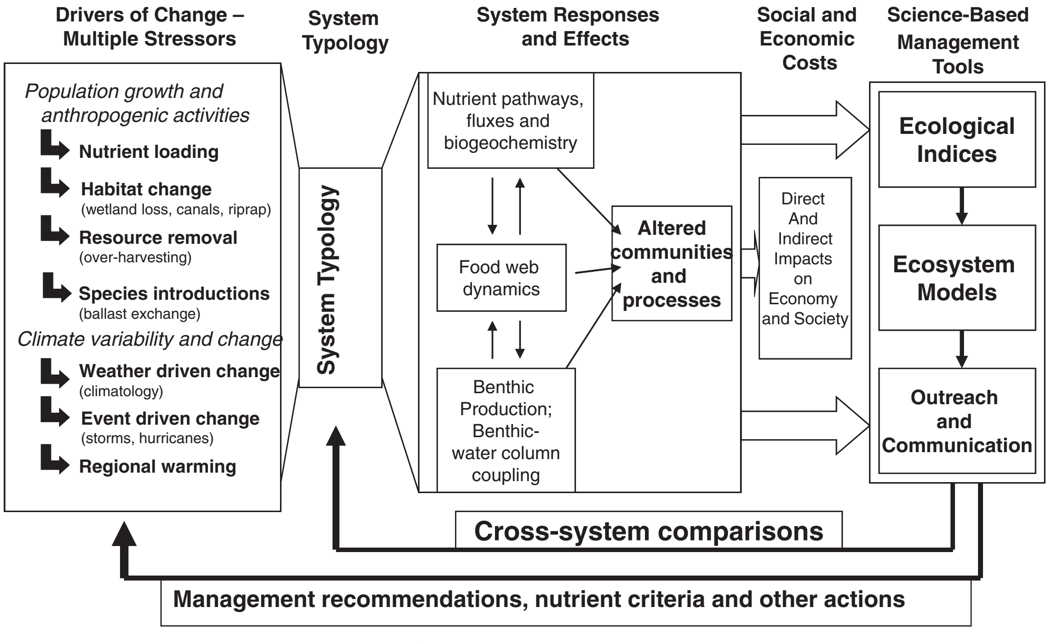

Figure 2 Modified conceptual diagram of the "phase III" model of eutrophication (Cloern, 2001) showing the complexity of interactions and effects of multiple stressors and eutrophication.

ecological consequences? 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's (1934) work indicated that the N:P ratio of phytoplankton should be approximately 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, pelagic marine waters, where both phytoplankton biomass and nutrient concentrations are low and there is minimal interference from suspended sediments. Changes in this ratio have been compared to shifts in phytoplankton composition, yielding insights about the dynamics of nutrient regulation of phytoplankton assemblages (e.g., Tilman, 1977; Smayda, 1990; Hodgkiss and Ho, 1997; Hodgkiss, 2001; Heil et al., 2007).

Elemental differences in biomass are found at all levels of organismal structure across trophic levels, from the subcellular to the macrocellular structural components (Sterner and Elser, 2002). At the subcellular level, organelles vary in their N:P content. 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 concept has been well illustrated for phytoplankton (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; high P) than to "acquisition machinery" (protein; high N) (Elser et al., 2003; Klausmeier et al., 2004). In contrast, phytoplankton species 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., 2000, Elser, 2006; Arrigo, 2005; Finkel et al., 2010; Figure 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). However, slowly growing, nutrient-stressed phytoplankton may also be capable of short-term "luxury" uptake of the limiting nutrient in excess of growth, 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).

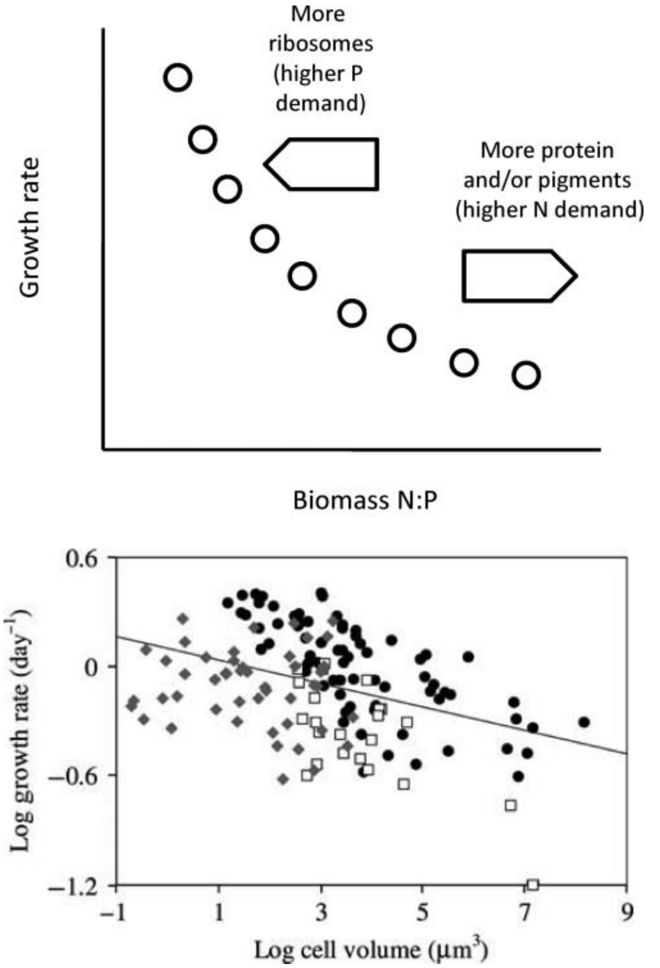

Figure 3 (A) Generalized relationships between the intrinsic growth rate of organisms and the N:P ratio in the biomass of those organisms. (B) Size dependence (cell volume, μm^3) of temperature-corrected growth rate (day^{-1}) for a range of phytoplankton functional groups: diatoms (◆), dinoflagellates (☐), and other taxonomic groups (●) (a combination of cyanobacteria, chlorophyte, haptophyte, cryptophytes, and various other groups). Line indicates 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), Oxford University Press, with permission. The data were compiled by T. A. V. Rees.

The question of whether N:P ratios or individual nutrients regulate phytoplankton growth has long been debated (e.g., Tilman and Kilham, 1976; Tilman, 1977; Bulgakov and Levich, 1999; Reynolds, 1999). Reynolds (1999, p. 29) pointedly asked the question, "When both [N and P] are 'not limiting', . . . how is it possible for the ratio of growth-saturating resources to influence the growth?" He then answered this question by stating (p. 31), ". . .there should be no selective effect, consequential upon different affinities of storage capabilities for a nutrient resource, that might distinguish between the potential performances of any pair of planktonic algae, so long as the resource concentrations are able to saturate the growth demand. If that is true, then the ratio between the (saturating) concentration of any of the resources also fails to exert any regulatory significance." This statement, which summarizes the prevailing view that nutrients are non-regulating in the Bay Delta because they are typically above levels that saturate growth demand, is based on the notion that growth rate (i.e., productivity) is the only process by which nutrients impact the ecosystem. Ecological stoichiometric theory, on the other hand, recognizes that phytoplankton nutrient composition is sensitive to available nutrients even when supplied in excess, and that the nutritional composition of the phytoplankton can play an important role in selecting and structuring the upper trophic level organisms. The emphasis is on the transfer of elements (N and P, as well as C and other elements) through the food web rather than the rate of production of organic C.

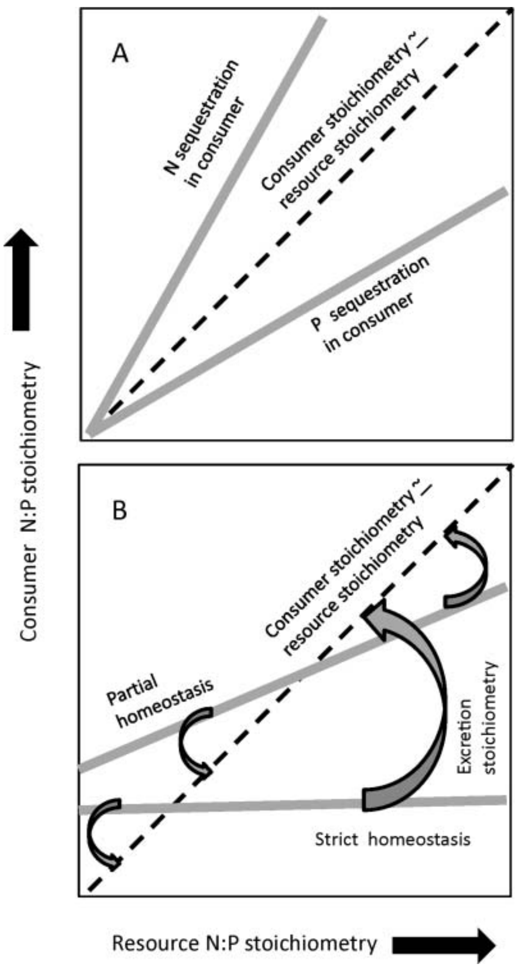

Figure 4 Schematic relationships between resource N:P (either dissolved nutrients or prey) and consumer N:P. The dashed line in both panels represents the hypothetical situation in which the consumer N:P matches that of its resource. (A) Hypothetical situations in which the consumer is either N- or P-enriched relative to its resource in a constant proportion. (B) Hypothetical situations where the consumer either partially or strictly regulates its biomass N:P regardless of the N:P of its resource. The arrows depict the extent to which the excreted or released nutrients differ in N:P from that of the consumer biomass N:P. Excretion N:P is expected to be negatively related to substrate N:P when the consumer N:P is constrained.

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). Due to the ability of many phytoplankton to take up nutrients in excess of their growth demands (e.g., Glibert and Goldman, 1981; Terry et al., 1985), they often follow the "you are what you eat" model (Sterner and Elser, 2002, p. 16), within reasonable limits (Figure 4A). This has been elegantly demonstrated for many phytoplankton in culture. 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). Extreme cellular N:P ratios are observed in cultured cells that have experienced limitation of either N or P (Rhee, 1978; Goldman et al., 1979; Geider and LaRoche, 2002) reflecting a non-homeostatic "luxury consumption" response that 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 three- to four-fold (5–19 mol N:mol P; Geider and LaRoche, 2002; Finkel et al., 2010). While it may be difficult in field data to differentiate the extent to which this variation is related to changing algal species (or taxonomic groups), culture experiments have clearly demonstrated plasticity in the N:P ratio as a function of growth condition (e.g., Quigg et al., 2003; Leonardos and Geider, 2004a,b; Finkel et al., 2010). In field comparisons, N and P stoichiometry in dissolved substrates have compared favorably with that of particulate matter in some regions (e.g., Glibert et al., 2006b), but a range of relationships between dissolved and particulate matter can be observed.The salient point is that microalgae are not homeostatic with respect to cellular N and P. Moreover, many phytoplankton species or species groups have specific adaptations to life under "non-Redfieldian" conditions (Glibert and Burkholder, 2011).

Thus, while Reynolds (1999) and others have convincingly explained how individual nutrients, not ratios, regulate the *growth* of phytoplankton, their interpretation does not address how the wide plasticity of cell quotas (sensu Droop, 1973) in algae under nutrient-saturated conditions alters the elemental *quality* of the algal food available to grazers. In other words, while primary production can constrain secondary production, N and P availability to the phytoplankton can regulate the types of organisms found in the upper trophic levels via effects of elemental composition at the primary producer level (Figure 4).

Compared to algae and other primary producers, heterotrophs are relatively inflexible in their stoichiometry (McIntyre and Flecker, 2010). 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. . .," because there is a greater need for P in skeleton and bone than in skin, heart, kidney, muscle, or brain. The latter tissues and organs all have a relatively high N content (Sterner and Elser, 2002). In aquatic food webs, small fish that have a higher muscle:skeleton ratio than large fish thus tend to have a higher biomass N:P ratio. Omnivorous fish, such as the Centrarchidae, are generally larger than planktivorous fish, have more bone and skeleton, and have particulary high P content (Sterner and Elser, 2002). Whereas whole-fish N content generally varies across a relatively small range (~8–11%), whole-fish P content tends to vary five-fold, from ~1–5% (Sterner and George, 2000; Figure 5).

In addition to the varying elemental requirements of their macromolecular structures, grazers are able to stabilize their biomass stoichiometry more than phototrophs, because they have more excretion and release pathways to eliminate the nutrients that that are not needed. By excreting, egesting, or respiring what they do not need, an effective feedback develops with respect to the element stoichiometry of their resource or prey (Figure 4B). A difference between food resource N:P ratios and consumer N:P ratios becomes established, and when consumers

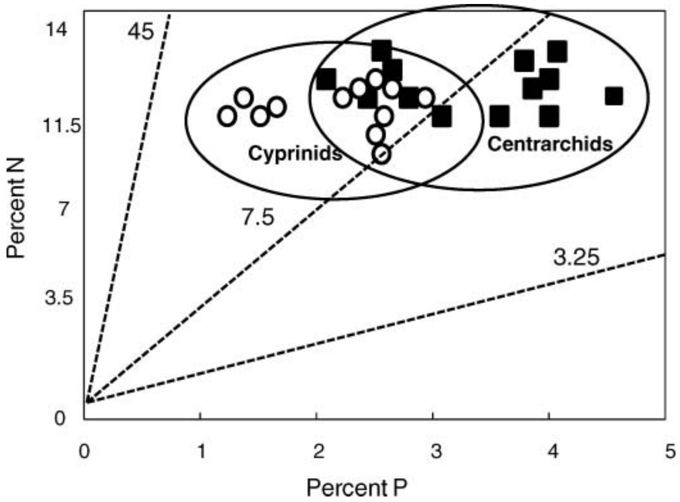

Figure 5 Relative N and P content of cyprinid and centrarchid fish. The dashed lines give three N:P ratios for perspective. Figure is modified and redrawn from Sterner and George (2000).

ingest nutrient-poor food, their need to dissipate those nutrients ingested in excess increases (Vanni et al., 2002). Ultimately, species of grazers that can sequester the nutrient in least supply relative to their needs, while dissipating what they do not need, should become the dominant (and, in some cases, the keystone) species by outcompeting grazers that cannot effectively acquire what they need and/or dissipate what they do not. 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." This means that fish, with their relatively inflexible skeletal requirements, have a greater likelihood to be limited by nutrients than by energy or other factors (McIntyre and Flecker, 2010). Larger organisms are greater sinks of nutrients than smaller organisms, and thus, their impacts on nutrients are evident over longer temporal and spatial 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). 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 nutrients increased substantially with body size; on average, large fishes excreted relatively more N than P compared to smaller counterparts." Large fish also play a proportionately larger role in nutrient translocation, especially from benthic to pelagic environments (Vanni, 1996, 2002).

Ecological stoichiometry principles would predict that the dominant predator, if its biomass N:P ratio is tightly constrained, 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-sustaining (Figure 4B). Such principles further suggest that biodiversity should be a consequence of stoichiometry, and that populations should self-stabilize as a result of stoichiometric constraints. As summarized by Sterner and Elser (2002, p. 263), the balance of multiple chemical elements has many consequences for community dynamics: "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."

Yet, homeostasis comes at a cost, typically as a reduction in the rates of growth or reproduction (Boersma, 2000; Boersma and Kreutzer, 2002; Boersma et al., 2008). 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 Weider, 2005, 2007). Stoichiometry also affects various life stages differently (Moe et al., 2005, p. 31): "[a]n organism's requirements for different elements may vary throughout its life cycle, and thus certain life stages may be more sensitive than others to variation in the stoichiometry of its resource." As a specific example, there is a greater need for C, N, and P for developing copepod juveniles, but at a later stage, while C is still needed for metabolism, more P must be allocated to eggs; thus, P-poor food can disproportionately affect egg production while not affecting survival (Færøvig and Hessen, 2003; Laspoumaderes et al., 2010).

It must be noted, however, that stoichiometric regulation of trophic interactions can be modulated when "good food goes bad" (sensu Mitra and Flynn, 2009). Many attributes of food can be altered chemically and physiologically, leading to trophic interactions that would not be anticipated strictly on the basis of elemental stoichiometry. As examples, production of allelopathic compounds or toxins, or even physical aggregation of cells, can alter trophic transfer.

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. This change alters the positive reinforcing feedbacks of homeostasis, and the system 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. Recent interest in stable state theory has occurred because of 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). Thus, the intersection of eutrophication, ecological stoichiometry, and stable state theories addresses the question: *To what extent is ecosystem structure altered when nutrient loads are altered?*

Both direct and indirect interactions among organisms help to stabilize assemblages (Vanni, 2002). Trophic cascades and food chain interactions result from predator–prey interactions, the 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 at several levels. First, selective grazing alters nutrient regeneration. This has been well demonstrated at the microbial level. For example, 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 in which form depends on what they ate and how long ago they ate it (Bidigare, 1983; Miller and Glibert, 1998). Macrozooplankton 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 the 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 that can affect multiple trophic levels (Vanni, 2002).

A second means by which bottom-up and top-down controls are interconnected relates to the coupling of the benthic and pelagic communities. When external nutrient loads (bottom-up control) are altered, top-down control is affected by the shift in nutrient dynamics from the water column to the sediment where nutrient reserves are accessed by those organisms capable of doing so. These organisms, in turn, alter the habitat for grazers. Exemplified by 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) found that systems dominated by macrophytes, such as hydrilla (*Hydrilla verticillata*), 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, 2010), toxic ammonia levels (Van der Heide et al., 2010), and 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 ecological and biogeochemical sciences. Regime shifts also involve shifts in food webs (e.g., Ives and Carpenter, 2007) through habitat alteration or species introductions into new areas. Such regime shifts in species are considered difficult to predict and model, but clues about regime shifts are provided in the variance of biomass or chemical constituents of aquatic ecosystems (Carpenter and Brock, 2006). Regime 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. 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, multi-dimensional view linking nutrients to physiological responses, trophodynamics and food web structure, and biogeochemistry.

Summary of Part I

System responses to nutrient loading (eutrophication), changes in the relative composition of the nutrient pools (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. Food web structure as a whole is highly stoichiometrically constrained. 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 THE SAN FRANCISCO ESTUARY

This section begins with a description of the sources of data that were analyzed, the data analysis approach and terminology, along with an overview of the long-term trends in freshwater flow, nutrients, and community structure of the Bay Delta. Then, ecological principles of stoichiometry relevant to each major trophic level are described, relating the available Bay Delta data to those principles. Following Smith (2006), this analysis is based on annualized data. Annual nutrient means have been shown to be highly related to chlorophyll *a* over broad data sets worldwide (Smith, 2006; Boynton and Kemp, 2008).

The stoichiometry of N and P is emphasized, as these two important macronutrients have undergone the largest changes over the past several decades. Silicate ($Si(OH)_4$) is not considered here because temporal changes in $Si(OH)_4$ have been smaller than those of N and P over the past several decades. A

Table 1 Sources of data used in this analysis and the time periods over which data were averaged. Stations identified and not shown in Figure 1 can be found on the web sites indicated

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/
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, and NZD06	http://www.nceas.ucsb.edu/
Invertebrates					
Mysid shrimp	no. m^{-3}	Log-transformed	Average of all values March–November	Stations NZ028, NZO32, NZ042, NZ048, NZO54, NZO60, and 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 of *Corbula amurensis*, March–November	EMP stations D4, D6, D7, and D8	http://bdat.ca.gov/
Fish					
FMWT catch per tow		Log-transformed	September–December	Stations 401–707 and 801–804	http://www.nceas.ucsb.edu/
FMWT index		Log-transformed	Index covers September–December trawls		http://www.dfg.ca.gov/delta/projects.asp?ProjectID=FMWT
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 and 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/

comprehensive analysis of this nutrient and its relationship to N and P merits separate analysis.

Data Sources

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 that covers 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/). All nutrient, chlorophyll *a*, and phytoplankton data were obtained from the Interagency Ecology Program Bay Delta and Tributary project data portal (accessed from http://www.bdat.ca.gov/, now available at http://www.water.ca.

gov/iep/products/data.cfm). 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 densities of individual taxa counts, were grouped into abundant functional groups: Bacillariophyceae (diatoms), Chlorophyceae (green algae), Cryptophyceae (cryptophytes), Dinophyceae (dinoflagellates), and Cyanophyceae (cyanobacteria). Individual species identifications are only considered for selected potentially harmful species. Cyanobacteria are underestimated in these long-term data because the recent expansion of *Microcystis* (Lehman et al., 2005, 2008, 2010; Baxa et al., 2010) is not well represented in the 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/); these data do not include microzooplankton. 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/, now available at http://www.water.ca.gov/iep/products/data.cfm). 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 generally referred to by their genus names or their common names rather than their species names.

The geographic coverage of the chemical, microbial, and macroinvertebrate data extends from the confluence of the Sacramento and San Joaquin Rivers to Suisun Bay, inclusive. However, the fish indices, such as the fall midwater trawl (FMWT) Index, may have included catches from higher in the Sacramento River, the central and southern Delta, and/or the San Joaquin River above its confluence with the Sacramento River.

All data from other comparative systems were obtained from literature sources or from the authors' measurements, described below.

Data Analysis

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 first tested for normality and, if found to be skewed, were log-transformed. Nutrient ratios were not transformed because they were normally distributed. Bivariate scatterplots were developed between organismal abundance and individual nutrients (total P [TP], phosphate [PO_4^{3-}], and NH_4^+ or nutrient ratios [dissolved inorganic N:TP {DIN:TP} and DIN:dissolved inorganic P {DIN:DIP}]), and Pearson correlations and/or coefficients of determination were calculated.

Pairwise relationships between biological parameters and nutrients and/or nutrient ratios were determined using both the original data and data that were adjusted for autocorrelation. The Durbin-Watson test was used to test for autocorrelation (Durbin and Watson, 1950, 1951). While only some variables displayed autocorrelation (Durbin Watson D $\sim$2), all relationships among the data were explored using several approaches. Data were analyzed as (1) original data (log-transformed if appropriate), (2) stationarized by trend (pre-whitened), (3) stationarized by first-difference, and (4) smoothed using a three-year backward moving average. The reason for applying several approaches is that different approaches for removing autocorrelation may lead to different types of errors (e.g., Pyper and Peterman, 1998). While failure to remove autocorrelation may lead to Type I errors (increased chance of concluding a correlation is significant when it is not; Jenkins and Watts, 1968), removing autocorrelation may lead to the opposite—Type II errors (failing to reject a null hypothesis of no correlation when a correlation exists; Pyper and Peterman, 1998). This comparison was also motivated by the concern summarized by Pyper and Peterman (1998, pp. 2134 and 2136) in their analysis of covariates and fish, "removing autocorrelation (low-frequency variability) may limit a researcher's ability to detect the common effect of some slowly changing variable on fish population dynamics. . . . By removing time trends, we are assuming that they are unrelated, yet there are obvious mechanisms that could produce common time trends among recruitment data such as trends in environmental variables, habitat degradation, or trends in the abundance of competitor, prey, or predator species (e.g., Butler, 1991)." By comparing all approaches here, the relative importance of directional versus cyclic (or other higher frequency) variability could be assessed. When correlations are lower for pre-whitened or first-differenced data compared to the original or smoothed data, the analysis suggests that low-frequency, slowly changing components of variability (i.e., directional changes) are dominant, whereas when pre-whitened or first-differenced correlations are greater, higher-frequency components of variability likely are greater (Pyper and Peterman, 1998). Significance was assessed at the $p < 0.05$ and 0.01 levels; n was adjusted by parameter and test to account for parameters with missing data and to account for autocorrelation in the smoothed data.

Nutrient Ratios and Terminology

Although N:P ratios can be useful in a relative sense, the same ratio can be obtained from markedly 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 (non-limiting) P. The latter is the case, for example, 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). Nutrient ratios are applied here to illustrate the potential stoichiometric regulation of the food web (i.e., through food quality and biogeochemistry influences) rather than to infer the potential for nutrient limitation of phytoplankton assemblages.

Most applications of N:P ratios consider only inorganic forms of N and P. Different ratios may be obtained depending upon the form(s) specifically included in the ratio (Dodds, 2003, 2009). The perspective of N or P limitation or availability may be different depending upon whether the N:P ratio is calculated solely with inorganic forms of N and P, or with both inorganic and organic forms, or with the particulate fraction only, or with just the dissolved fractions. For example, on the western Florida shelf, the mean N:P ratio of the water off the Caloosahatchee River in May of 2003 was considerably less than Redfield proportions when only inorganic forms of N and P 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). Karl et al. (2001) reported similar findings for the Hawaii time series station. Determining whether to include the organic fractions of N and P (DON and DOP) in such ratios may depend upon the degree to which the organic fractions are bioavailable to the specific organisms present. Unfortunately, much still is not known about the bioavailability of most organic N and P constituents (Seitzinger et al., 2002b; Berman and Bronk, 2003). While nearly all algal species can use all forms of inorganic N and P, their use of organic nutrients is much more variable. The calculation of nutrient ratios also changes depending upon whether chemical interactions with particulate matter are taken into consideration. Nutrients, especially P, interact with particulate matter (via both adsorption and desorption), and the interactions can result in deviations in both particulate and dissolved N:P ratios. Dissolved inorganic PO_4^{3-} (=DIP) is equivalent to soluble reactive phosphate, SRP, but is referred to as PO_4^{3-} or DIP throughout.

Thus, because different nutrient ratios may give different perspectives on nutrient relationships, both DIN:TP and DIN:DIP were used here. In accordance with recommendations by Dodds (2009), DIN:TP can serve as a "reliable surrogate" for total N:TP (TN:TP), understanding that such a substitute may underestimate the true TN:TP.

Table 2 Abbreviations and acronyms used throughout the text

DIN	Dissolved inorganic nitrogen
DIP	Dissolved inorganic phosphorus; used here interchangeably with phosphate, PO_4^{3-}; equivalent to soluble reactive phosphorus
DON	Dissolved organic nitrogen
DOP	Dissolved organic phosphorus
FMWT	Fall midwater trawl fish index
POD	Pelagic organism decline; the rapid decline in numerous planktivorous fish species in the Bay Delta since 1999
SAV	Submersed aquatic vegetation
SRP	Soluble reactive phosphorus
SRWWTP	Sacramento Regional Wastewater Treatment Plant
STN	Summer townet fish index
TN	Total nitrogen
TP	Total phosphorus
WWTP	Wastewater treatment plant
X2	In the Bay Delta, the distance from the Golden Gate Bridge at which salinity is measured to be 2

The most frequently used abbreviations and acronyms used throughout this review are summarized in Table 2.

Long-Term Trend Overview

The long-term trends in freshwater flow, nutrient loading, and biota in the Bay Delta have been previously described (e.g., Kimmerer et al., 2000; Kimmerer, 2002, 2004; Bennett, 2005; Jassby, 2008; Glibert, 2010). Here, a brief review is provided for context, focusing on trends associated with the region between the confluence of the Sacramento and San Joaquin Rivers to Suisun Bay. Each nutrient and component of the food web is 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 (Figure 6). Flow

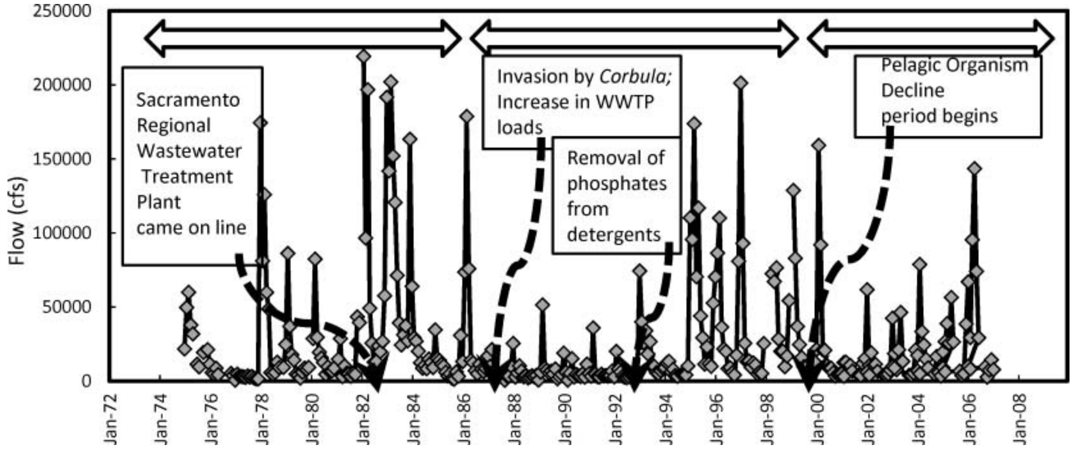

Figure 6 Time course of the change in freshwater outflow from the Bay Delta over time and notations indicating the time of major changes in nutrients and the food web. The arrows along the top of the graph depict the major time periods that are described in text. The first time period is from the start of the time series up to the time when the WWTP discharge began. The second time period encompassed the period of major change in N and P. The third time period corresponds to the "POD." The text boxes and dashed arrows highlight key events.

Table 3 Average nutrient concentration (mg L^{-1}), nutrient ratio (wt:wt), and chlorophyll *a* (μg L^{-1}) for time periods shown and overall percent change in the parameter from the first to third time period

Time period	Ammonium	Nitrate + nitrite	DIP	TP	DIN:TP	DIN:DIP	Chlorophyll *a*
1975–1986	3.70	17.40	2.19	4.71	4.48	9.63	9.03
1987–1999	4.47	25.79	2.83	4.79	6.31	10.70	2.16
2000–2005	5.36	25.62	2.29	3.81	8.12	13.53	2.40
Percent change	44.9	47.2	4.5	−19.1	81.25	40.5	−73.4

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 $> 30\ \mu g\ L^{-1}$, but declined sharply in the mid-1980s following invasion of the exotic clam, *Corbula amurensis* (Alpine and Cloern, 1992; Kimmerer et al., 1994; Kimmerer, 2004; Jassby, 2008). Diatom relative abundance also declined in the early 1980s, and 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).

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 a decade later, 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 invasive 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* increased in abundance.

Pelagic fish populations changed over the past few decades, often coincident with changes in the 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 declines accelerated beginning in ∼1999, referred to as the POD period. In contrast, other fish species increased in numbers over the time series, especially largemouth bass (*Micropterus salmoides*) and sunfish (*Lepomis* spp.). Additional changes included increases in invasive macrophytes, especially water hyacinth (*Eichhornia crassipes*) and Brazilian waterweed (*Egeria densa*).

Nutrients

In contrast to conditions in the 1960s and early 1970s when hypoxia was more frequently noted (Nichols et al., 1986), there presently are no such widespread "classic" symptoms of eutrophication (e.g., Cole and Cloern, 1984; Kimmerer, 2004). Eutrophication has been thought to have been reduced due to major changes in sewage discharge (diversions and forms of nutrients discharged) since the 1970s (Jassby, 2008). However, localized hypoxia has been reported, as well as increased frequency of cyanobacterial blooms, especially *Microcystis aeruginosa*, within the past decade (Lehman et al., 2005, 2008, 2010).

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 DIN concentrations (Figure 7) were relatively invariant for the first years of this time series (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, consolidating numerous smaller facilities that were

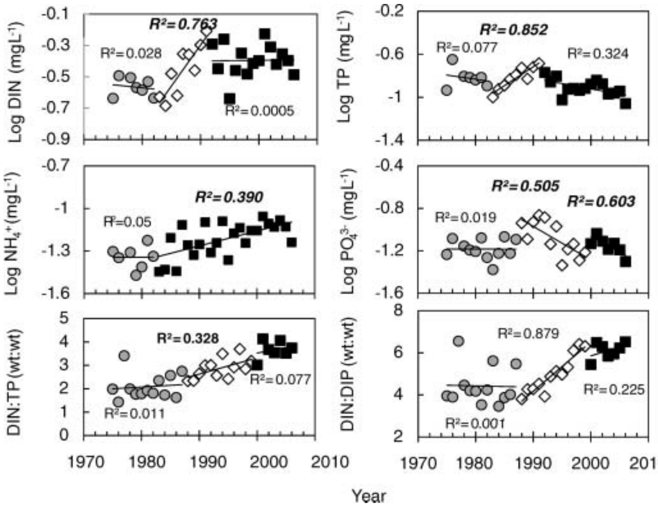

Figure 7 Changes over time in the major inorganic nutrients and inorganic nutrient ratios (log-transformed data) in the confluence of the Sacremento and San Joaquin Rivers to Suisun Bay from 1975–2005. Note that different nutrients changed in different periods of the time course, and thus, the delineation of the time periods by symbols differs from those of subsequent graphs; these individual time periods highlight the periods of major change. For panels showing total inorganic N (DIN) and TP, the time course highlights 1975–1982 (●), 1983–1992 (◇), and post-1992 (■). For PO_4^{3-}, DIN:TP, and DIN:DIP, the time course highlights the periods of 1975–1986 (●), 1987–1999 (◇), and post-1999 (■). For NH_4^+, the time course highlights the period of 1975–1982 (●) and post-1982 (■). Coefficients of determination (R^2) of all time periods are shown; those indicated in bold are significant at $p < 0.05$, those in bold italic are significant at $p < 0.01$. Note that in addition to the trends in time periods indicated, the overall trends in NH_4^+ ($R^2 = 0.21$, $p < 0.05$), DIN:TP ($R^2 = 0.65$, $p < 0.01$), and DIN:DIP ($R^2 = 0.46$, $p < 0.01$) were significant.

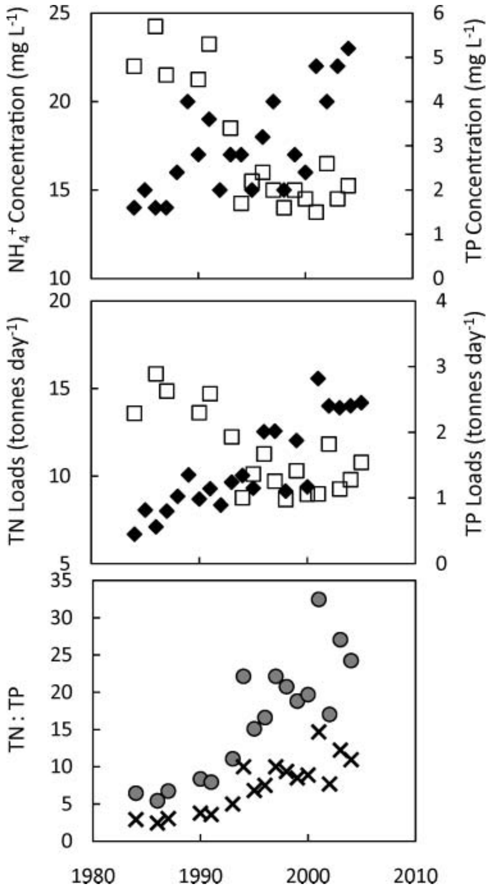

Figure 8 Change in concentrations and total loads (NH$_4^+$ or TN, ◆ TP, ☐) and DIN:TP (molar basis, ● weight basis, X) over time in the wastewater effluent of the SRWWTP, located on the Sacramento River.

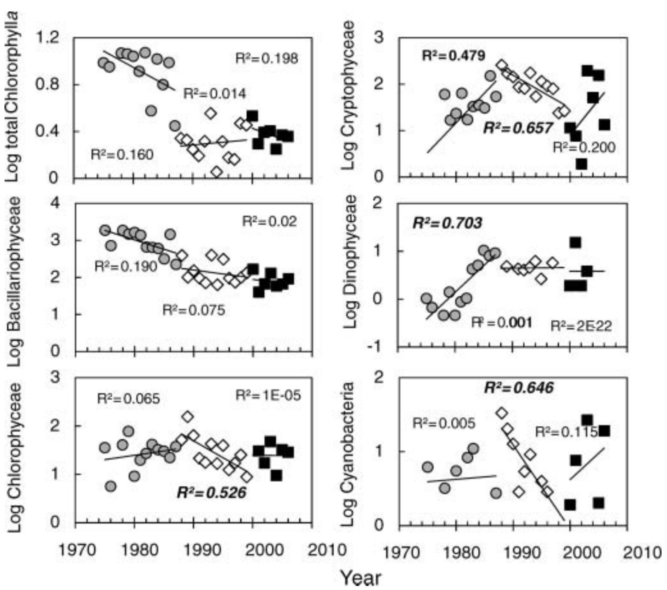

Figure 9 Change in the concentration of chlorophyll *a* (log μg L^{-1}) and abundances of the major classes of eukaryotic phytoplankton and prokaryotic cyanobacteria (log cells mL^{-1}) over the time course. Coefficients of determination (R^2) are given for each major time period (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). Those coefficients indicated in bold are significant at $p < 0.05$, and those in bold italics 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 declines in chlorophyll *a* and diatoms over the entire time course were significant ($R^2 = 0.57$ and 0.68, $p < 0.01$), as was the increase in dinoflagellates ($R^2 = 0.30$, $p < 0.05$).

located upriver (Figures 7 and 8 and Table 3). Both concentrations of effluent discharge and total loads have increased over time; present-day loads of NH$_4^+$ are 12 tonnes day^{-1} (14 tonnes TN), corresponding to concentrations in excess of 25 mg L^{-1} (~1,800 μM-N; Figure 8).

Concentrations of TP, PO$_4^{3-}$, and DIN tracked each other for the period of 1982–~1991, but after that, P concentrations declined, returning to levels approximating those of pre-1982 (Figure 7, Table 3). This decline has been related to the removal of P from laundry detergents (Glibert, 2010), as well as the loss of canneries in the region that had used P in their processing (Van Nieuwenhuyse, 2007). As a consequence of the increased N loads but decreased P loads (Figure 8), DIN:TP and DIN:DIP increased over time (Figures 7 and 8).

Phytoplankton

The relative dominance of different phytoplankton groups has changed over time (Figure 9). Total chlorophyll *a* declined abruptly after 1986 (Figure 9). 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 relatively stable (Figure 9). After 1999, there was no significant increase in the abundances of crytophytes and cyanobacteria (Figure 9; but note the above-described underestimation of cyanobacteria).

The overall changes in total chlorophyll *a* or the abundance of any algal group relative to concentrations of TP or PO$_4^{3-}$ were not significant when compared as log-transformed data, but there were significant negative correlations in chlorophyll *a*, diatoms (Bacillariophyceae), and green algae (Chlorophyceae) and increases in cryptophytes and dinoflagellates with TP and/or PO$_4^{3-}$ when the data were detrended (Figure 10, Table 4). Declines in chlorophyll *a,* diatoms, and cyanobacteria were significantly correlated with the increase in NH$_4^+$ concentrations in both the original and detrended data (Figure 11, Table 4). When the changes in phytoplankton are considered with respect to nutrient ratios, not only were the declines in chlorophyll *a* and diatoms negatively correlated with DIN:TP and DIN:DIP ratios in the original and detrended data, but also the increase in dinoflagellates was positively correlated with DIN:TP ratios (Figure 12, Table 5). These changes in phytoplankton abundance are generally consistent with expectations from ecological stoichiometric principles. Diatoms tend to have a lower biomass

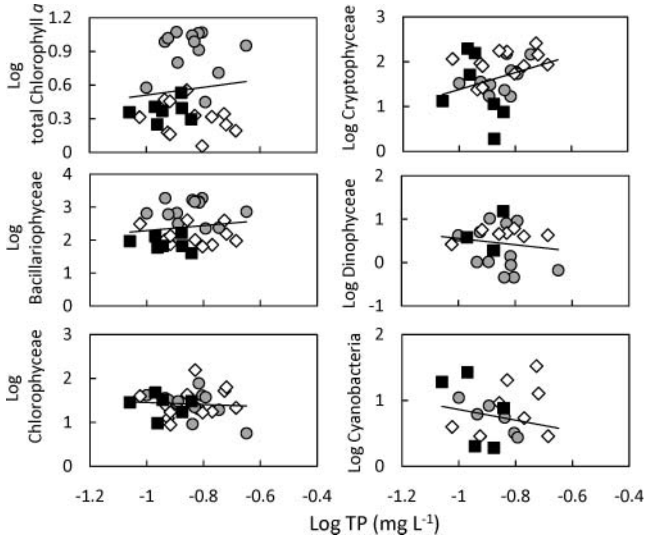

Figure 10 Change in the concentration of chlorophyll *a* (μg L^{-1}) and abundances of the major classes of phytoplankton (log cells mL^{-1}) over the time course in relation to TP (mg L^{-1}) (all data were log-transformed). The major periods are represented by different symbols (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). While these correlations were not significant ($p > 0.05$), several significant relationships emerged when the data were detrended (see Table 4).

N:P ratio than dinoflagellates, especially harmful dinoflagellates species (Finkel et al., 2010). Low biomass N:P ratios should lead to higher growth rates, due to the high proportion of P required in ribosomes and biomass (Sterner and Elser, 2002; Figure 3), and diatoms generally have higher growth rates than dinoflagellates (e.g. Harris 1986, and references therein).

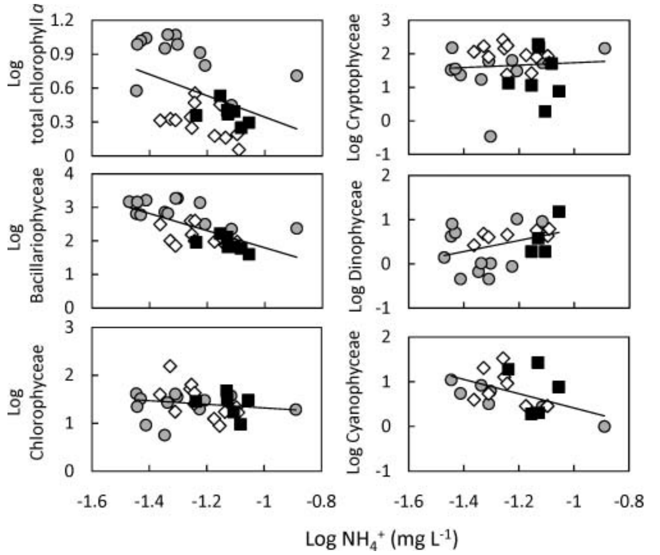

Figure 11 As for Figure 10, except in relation to NH_4^+ (mg L^{-1}) (all data were log-transformed). The correlations for total chlorophyll *a*, diatoms (Bacillariophyceae), and cyanobacteria were significant for these and/or the detrended data ($p < 0.05$; see Table 4).

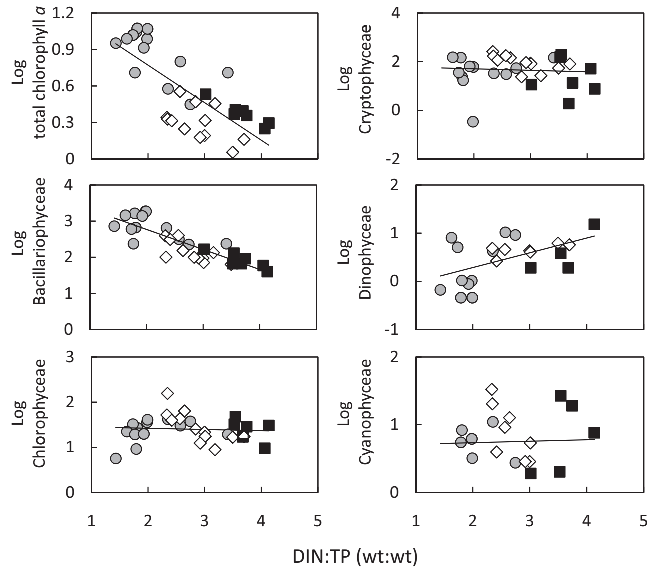

Figure 12 As for Figure 10, except in relation to DIN:TP (wt:wt) (abundance data were log-transformed). The correlations for total chlorophyll *a*, diatoms (Bacillariophyceae), and dinoflagellates (Dinophyceae) indicated significant relationships ($p < 0.05$). Note that chlorophyll *a* and diatoms (Bacillariophyceae) also showed significant correlations with DIN:DIP ($p < 0.05$; see Table 4).

Zooplankton

Although not included here due to lack of long-term data, the importance of microzooplankton in the San Francisco food web is recognized. The trophic link between phytoplankton and microzooplankton has been demonstrated and may represent an important mediator of C flow and nutrients to the mesozooplankton (Rollwagen-Bollens et al., 2006, 2011).

The composition of macrozooplankton has changed over time in the Bay Delta (Figure 13). The calanoid copepods *Eurytemora*, *Sinocalanus*, *Acartia*, 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 (Figure 13). The decline in these species, especially *Eurytemora*, has been interpreted to be a consequence of increased grazing after the invasive clam *Corbula* 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 and then declined, but it appears to be increasing again. Abundance of the cyclopoid copepod *Limnoithona tetraspina* increased significantly during the mid-1990s, whereas earlier in the time series a different species of *Limnoithona*, *L. sinensis*, was present (Bouley and Kimmerer, 2006). Overall, the ratio of *Eurytemora affinis*/cyclopoid copepods showed a decline in the first part of the time series, and then a relatively stable ratio of abundances (Figure 13).

Over time, the abundances of 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 (Figure 13). The mysid macrozooplankter *Neomysis*

Table 4 Correlation coefficients (r) for the organisms and nutrients shown

	TP (mgL^{-1})				PO_4^{3-} (mgL^{-1})				NH_4^+ (mgL^{-1})			
Organism	Original data	Pre-whitened	First-differenced	Three-year moving average	Original data	Pre-whitened	First-differenced	Three-year moving average	Original data	Pre-whitened	First-differenced	Three-year moving average
Phytoplankton												
Chlorophyll *a* ($\mu g\ L^{-1}$)		−0.44*			−0.33	−0.57**			−0.43*	−0.34	−0.45**	−0.37
Bacillariophyceae (cells mL^{-1})		−0.51**				−0.62**	−0.39*		−0.57**	−0.60**	−0.60**	−0.54**
Chlorophyceae (cells mL^{-1})			−0.44**				−0.43**	−0.413*				0.36
Cryptophyceae (cells mL^{-1})		0.36						0.40*				
Dinophyceae (cells mL^{-1})							0.48**		0.35			
Cyanobacteria (cells mL^{-1})									−0.54*	−0.59*		0.40
Zooplankton												
Eurytemora (individ. m^{-3})		−0.58**			−0.38*	−0.72**		−0.34	−0.37*		−0.56**	−0.40*
Sinocalanus (individ. m^{-3})	−0.43*			−0.43*	−0.66**			−0.65**	−0.49**		−0.61**	
Acartia (individ. m^{-3})	0.56**	0.41*		0.58**	0.39*	0.44*	0.37*			0.45*	0.70**	
Pseudodiaptomus (individ. m^{-3})		−0.45	−0.75**	−0.46		−0.50*	−0.83**		−0.72*	−0.65**	−0.66**	−0.85*
Harpacticoids (individ. m^{-3})				0.48*								−0.48*
Limnoithona (individ. m^{-3})	−0.70**	−0.70**		−0.76**	−0.41*	−0.64**		−0.47*	0.46*			0.54**
Daphnia (individ. m^{-3})	−0.50**	−0.75**	−0.51**	0.54**	−0.71**	−0.72**	−0.75	−0.75**	−0.44*	−0.38*	−0.44*	
Bosmina (individ. m^{-3})	−0.70**	−0.83**	−0.32	−0.74**	−0.85**	−0.85**	−0.34	−0.86**	−0.57**	−0.59**		−0.43*
Neomysis (individ. m^{-3})	0.39*			0.53**			0.46**		−0.49**	−0.53	−0.63*	−0.68**
Invertebrates												
Corbula (count/grab)		0.50*	0.38			0.48*	0.47*		0.64**	0.55*	0.60*	0.84**
All crabs (individ. m^{-2})		0.42*							0.53**	0.42*		0.49*
Crangon (individ. m^{-3})									−0.57**	−0.42*	−0.33	−0.59**
Palaemon (individ. m^{-3})	0.41*								−0.44*			−0.64**
Fish												
Delta smelt (STN index)	0.60**	0.51*	0.45*	0.42							−0.35*	
Delta smelt (FMWT index)				0.52**			−0.50**					
Longfin smelt (FMWT index)		−0.62**			−0.72**	−0.80**		−0.68**	−0.64**	−0.57*		−0.52**
Splittail (FMWT index)				−0.35	−0.51**	−0.49*		−0.68**	−0.34			−0.37
Threadfin shad (FMWT index)			−0.33*	−0.53**								
Striped bass (FMWT index)				0.32					−0.58**			−0.81**
Yellowfin goby (FMWT catch per tow)				0.32			−0.58**		−0.47**	−0.42*	−0.48*	−0.36
Starry flounder (FMWT catch per tow)		0.45*			−0.39*	−0.42*		−0.47*				
Crappie (relative abundance)	−0.65**	−0.69**	−0.39	−0.63**	−0.69**	−0.68**	−0.41	−0.81**				
Sunfish (relative abundance)	−0.69**	−0.58**		−0.83**	−0.46*	−0.65**		−0.53**				0.40*
Largemouth bass (relative abundance)	−0.51**	−0.48**	−0.41*	−0.81**		−0.54**	−0.49**	−0.46**			−0.40*	0.35
Silversides (relative abundance)						0.37*			0.48**	0.44*		0.52**

For each nutrient, the first column shows the correlations of the original data (log-transformed), the second column shows the correlations of the trend stationary data, the third column shows the correlations of the difference stationary data, and the fourth column shows the correlations of the data transformed as three-year backward moving averages. The correlations are for the entire time series. Only values for $p < 0.10$ are shown; values that are significant at $p < 0.05$ are indicated by *, and those significant at $p < 0.01$ are indicated by **. Negative correlations are highlighted in blue and positive correlations are highlighted in pink ($p < 0.05$ [lighter shade] and 0.01 [darker shade] only).

Table 5 Correlation coefficients (r) for the organisms and nutrient ratios shown

Organism	DIN:TP (wt:wt)				DIN:DIP (wt:wt)			
	Original data	Pre-whitened	First-differenced	Three-year moving average	Original data	Pre-whitened	First-differenced	Three-year moving average
Phytoplankton								
Chlorophyll *a* (μg L^{-1})	−0.76**	−0.40*	−0.57**	−0.77**	−0.53**		−0.57**	−0.50**
Bacillariophyceae (cells mL^{-1})	−0.53**	−0.58*	−0.45**	−0.93**	−.63**		−0.45**	−0.72**
Chlorophyceae (cells mL^{-1})								−0.42*
Cryptophyceae (cells mL^{-1})								−0.41*
Dinophyceae (cells mL^{-1})	0.53*		0.48*	0.49*	0.36			
Cyanophyceae (cells mL^{-1})			−0.33					
Zooplankton								
Eurytemora (individual m^{-3})	−0.75**	−0.34	−0.55**	−0.83**	−0.46**		−0.54**	−0.53**
Sinocalanus (individual m^{-3})	−0.42*			−0.34		0.49**		
Acartia (individual m^{-3})	−0.41*		0.40*	−0.60**	−0.45**		0.40*	−0.56**
Pseudodiaptomus (individual m^{-3})	−0.66**	−0.64**		−0.80**				−0.62**
Harpacticoids (individual m^{-3})	−0.69**			−0.90**	−0.66**		−0.39	−0.76**
Limnoithona (individual m^{-3})	0.68**			0.73**	0.81**	0.45*		0.88**
Daphnia (individual m^{-3})		−0.35						
Bosmina (individual m^{-3})		−0.35	0.44				0.44*	
Neomysis (individual m^{-3})	−0.88**	−0.62**	−0.54**	−0.96**	−0.81**	−0.62**	−0.52**	−0.93**
Invertebrates								
Corbula (count/grab)	0.67**	0.51*	0.73**	0.81**	0.45*			0.56*
All crabs (individual m^{-2})	0.53**	0.48*		0.58**				0.54**
Crangon (individual m^{-3})	−0.76**	−0.49**	−0.43*	−0.77**	−0.49**			
Palaemon (individual m^{-3})	−0.74**		−0.40*	−0.93**	−0.57**		−0.47*	−0.76**
Fish								
Delta smelt (STN index)	−0.41*		−0.36*				−0.36*	
Delta smelt (FMWT index)	−0.36*			−0.35				
Longfin smelt (FMWT index)	−0.65**	−0.60**		−0.64**				
Splittail (FMWT index)	−0.36	−0.42*		−0.33		0.38*		
Threadfin shad (FMWT index)			0.64*	0.56**	0.35*	0.35*	0.60**	0.50**
Striped bass (FMWT index)	−0.73**			−0.86**	−0.58**			−0.77**
Yellowfin goby (FMWT catch per tow)	−0.49**	−0.45*	−0.64**	−0.43*				0.34
Starry flounder (FMWT catch per tow)	−0.38*			−0.50**				
Crappie (relative abundance)						0.34		
Sunfish (relative abundance)	0.63**			0.77**	0.73**	0.42*		0.84**
Largemouth bass (relative abundance)	0.46*			0.80**	0.48**	0.39*		0.75**
Silversides (relative abundance)	0.54**		−0.40*	0.74**		−0.39*	−0.40*	0.49**

For each nutrient ratio, the first column shows the correlations of the original data (organism data log-transformed), the second column shows the correlations of the trend stationary data, the third column shows the correlations of the difference stationary data, and the fourth column shows the correlations of the data transformed as three-year backward moving averages. The correlations are for the entire time series. Only values for $p < 0.10$ are shown; values that are significant at $p < 0.05$ are indicated by *, and those significant at $p < 0.01$ are indicated by **. Negative correlations are highlighted in blue, and positive correlations are highlighted in pink ($p < 0.05$ [lighter shade] and 0.01 [darker shade] only).

mercedis was abundant in the early years but declined significantly from the mid-1980s to 1999 (Figure 13; Winder and Jassby, 2010). From 2000 to 2005, *Neomysis* began to increase in abundance once again (Figure 13).

In relation to TP and PO_4^{3-} concentrations, *Limnoithona*, *Daphnia*, and *Bosmina* were negatively correlated in the original data, and *Eurytemora* and *Pseuodiaptomus* were also correlated in the detrended data (Figure 14, Table 4). In contrast, *Acartia* abundance was significantly positively correlated with TP and PO_4^{3-} concentrations (Figure 14, Table 4). For *Daphnia*, this relationship is consistent with recent modeling efforts that show that maximum *Daphnia* growth occurs in the range of ∼20–40 μg L^{-1} TP and declines with increasing TP (Persson et al., 2007; Park and Goldman, 2008).

In relation to NH_4^+, the abundances of *Eurytemora*, *Sinocalanus*, *Pseudodiaptomis*, harpacticoids, *Daphnia*, *Bosmina*, and *Neomysis* were significantly negatively correlated, while those of *Acartia* (detrended analysis only) and *Limnoithona* were positively correlated (Figure 15, Table 4). Thus, when zooplankton abundances were examined in relation to DIN:TP and DIN:DIP ratios, many of the relationships were highly significant (Figure 16, Table 5). Of particular note are the overall significant declines in *Eurytemora*, *Acartia*, *Pseudodiaptomis*, and *Neomysis* in relation to increasing

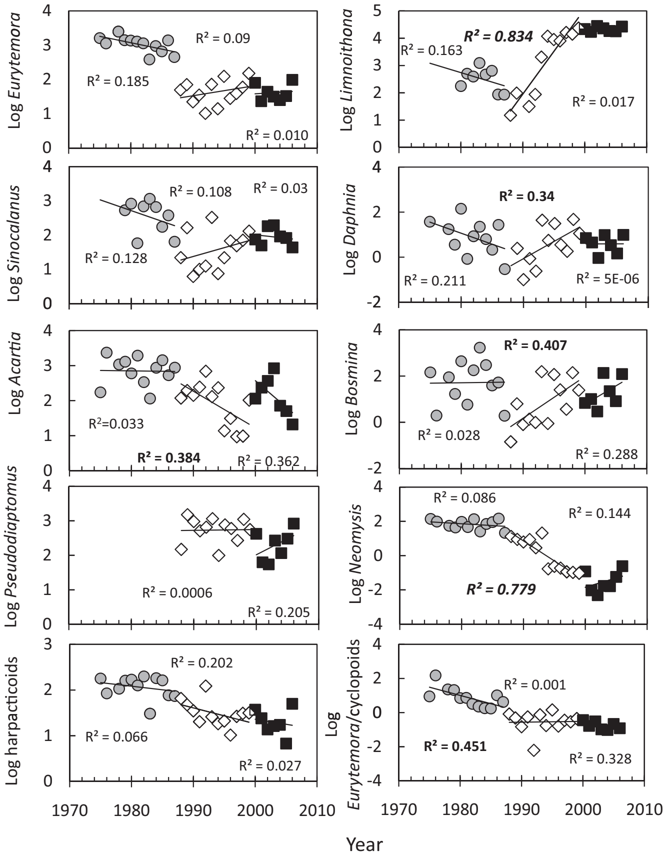

Figure 13 Change in the abundance of the major groups or taxa of zooplankton (as individuals m^{-3} and as the ratio of *Eurytemora affinis*/cyclopoids) over time (all data were log-transformed). Coefficients of determination (R^2) are given for each major time period (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). Those indicated in bold are significant at $p < 0.05$, and those indicated in bold italic are significant at $p < 0.01$. The analysis indicates significant changes over a major time period for most taxa. Among the significant negative relationships over the entire time period (1975–2005) were the declines in *Eurytemora* ($R^2 = 0.65$, $p < 0.01$), *Neomysis* ($R^2 = 0.83$, $p < 0.01$), and the *Eurytemora affinis*/cylopoid ratio ($R^2 = 0.65$, $p < 0.01$).

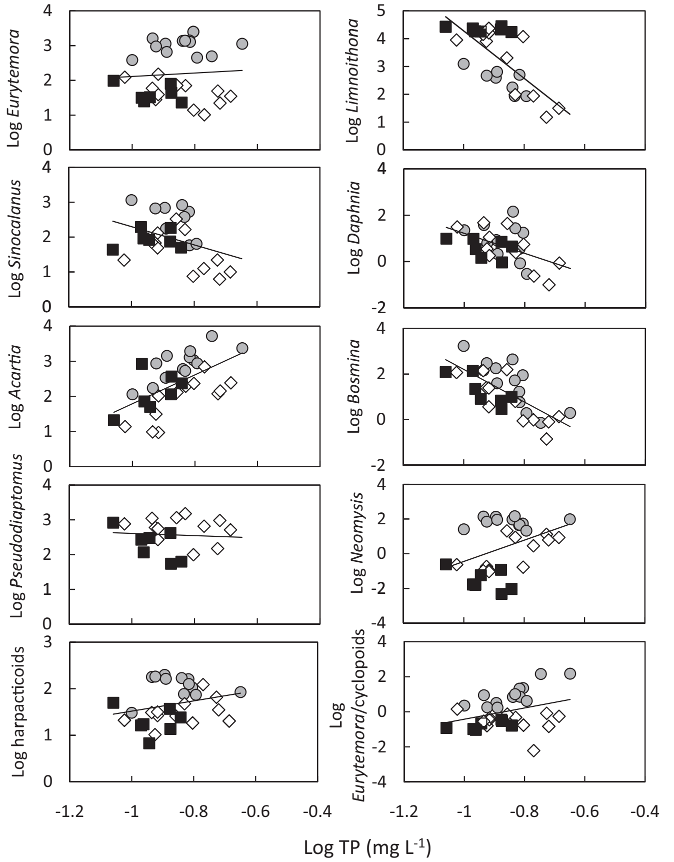

Figure 14 Change in the abundance of the major groups or taxa of zooplankton (as individuals m^{-3} and as the ratio of *Eurytemora*/cyclopoids) over the time course in relation to TP ($mg\ L^{-1}$) (all data log-transformed). The major periods are represented by different symbols (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). The correlations for all taxa and groups except the harpacticoids were significant ($p < 0.05$) for these and/or the detrended data (see Table 4).

DIN:TP or DIN:DIP ratios (Figure 16), as well as the increases in *Limnoithona* (Figure 16).

These changes in zooplankton composition are consistent with ecological stoichiometric principles that predict that consumers that successfully sequester the nutrient in least supply relative to their needs should dominate and, in so doing, may stabilize 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; Figure 17). In direct measurements under a range of conditions, NH_4^+ excretion measurements of the calanoid copepod *Acartia tonsa* have been very low, consistent with relative retention of N by these animals (Checkley and Miller, 1988; Miller and Glibert, 1998).

Studies from whole-lake experimentation suggest that the N:P ratio is linked to alterations in 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). Similar findings were reported from annual studies in the Baltic Sea (Walve and Larsson, 1999). Hassett et al. (1997) compared the ecological stoichiometric constraints on zooplankton in 31 lakes and 21 marine systems, and their data were strongly suggestive of stoichiometric controls, especially P constraints in the lake systems. In their comparison, the most pronounced nutrient deficiency was found in systems that lacked large piscivores, i.e., those dominated by the planktonic food web. In a laboratory study where *Acartia tonsa* was fed diatoms grown on different N concentrations, Kiørboe (1989) confirmed that this zooplankter changes its feeding rate in response to phytoplankton of different chemical composition—thus, in response to food quality.

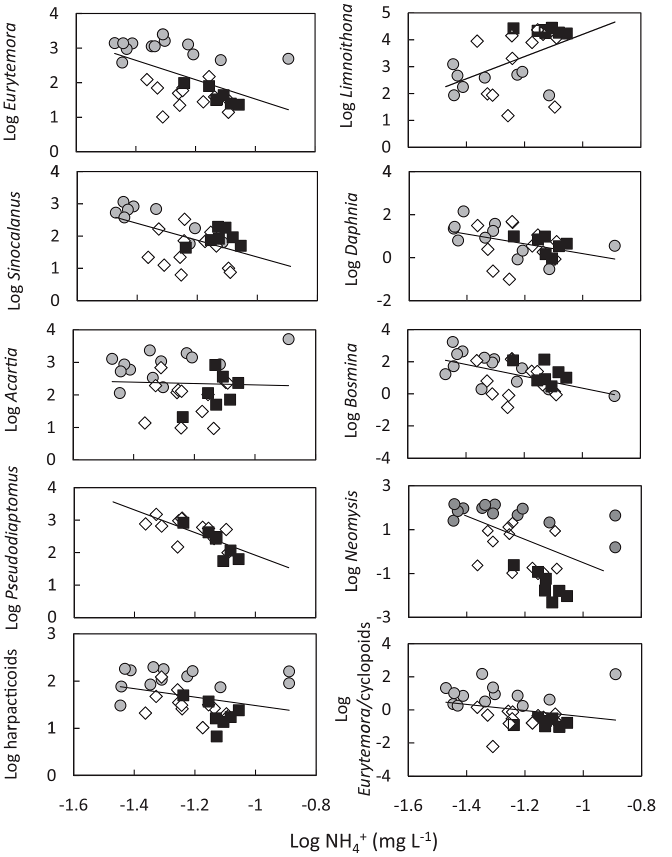

Figure 15 As for Figure 14, except in relation to NH_4^+ (mg L^{-1}) (all data were log-transformed). All correlations for all taxa and groups and for the ratio of *Eurytemora*:cyclopoids were significant ($p < 0.05$) for these and/or the detrended data (see Table 4).

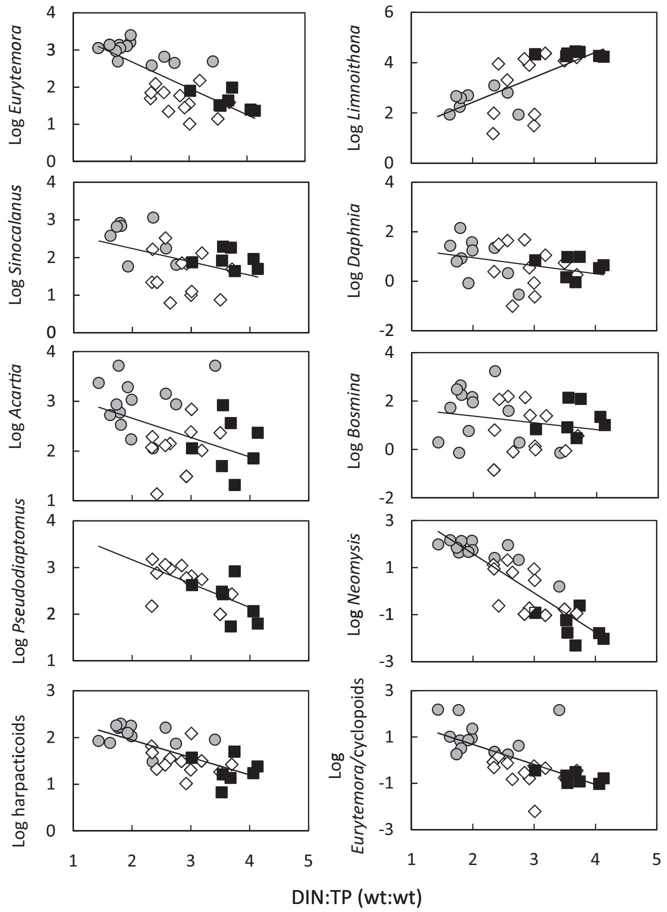

Figure 16 As for Figure 14, except in relation to DIN:TP (wt:wt) (abundance data were log-transformed). All correlations for all taxa and groups were significant ($p < 0.05$) for these and/or the detrended data. Note that the correlations for *Eurytemora*, *Sinocalanus*, *Acartia*, harpacticoids, *Limnoithona*, *Bosmina*, and *Neomysis* with DIN:DIP were also significant ($p < 0.05$) for these and/or the detrended data (see Table 4).

Macroinvertebrates

Major changes in macroinvertebrate 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 *Cancer magister*–Dungeness and *Eriocheir sinensis*–Chinese mitten) have also changed over time, with significant increases in the years before the mid-1980s, then a period of highly variable abundance, followed by declines post-1999 (Figure 18). Shrimp (*Crangon franciscorum*–crangonid, *Crangon nigricauda*–blacktail, and *Palaemon macrodactylus*–Oriental) either showed no change or modest declines prior to 1999, followed by more substantial declines in recent years (Figure 18). *Corbula* abundances were positively correlated with TP and PO_4^{3-} in the detrended data (Table 4). The abundances of *Corbula* and the crab species were significantly positively correlated with NH_4^+ concentrations, while abundances of the shrimp taxa were negatively correlated with NH_4^+ (Figure 18, Table 4). Consequently, the changes overall in *Corbula* and crabs were positively correlated with DIN:TP ratios, while changes in shrimp were negatively correlated with DIN:TP or DIN:DIP ratios (Figure 18, Table 5).

Stoichiometric interpretation of these relationships suggests that *Corbula* may tolerate elevated NH_4^+ levels and may release higher proportions of N than P, whereas shrimp appear to sequester N or are inhibited by elevated NH_4^+ concentrations and may release higher relative proportions of P.

Fish Composition

The changes in fish community composition have also been significant. 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).

As described above, many of the planktivorous fish are in decline (Figure 19). 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

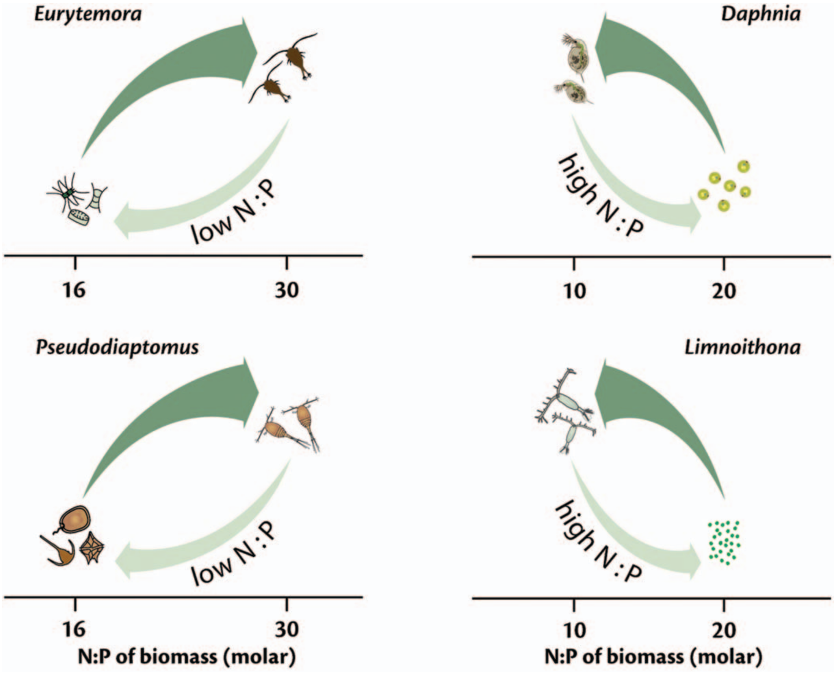

Figure 17 Conceptual diagram of the ecological stoichiometric relationship between different phytoplankton and zooplankton genera. The *x*-axis represents the biomass N:P of the organisms. The wide arrow represents ingestion of the phototrophs by the grazer; the lighter arrow represents nutrient regeneration 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 (color figure available online).

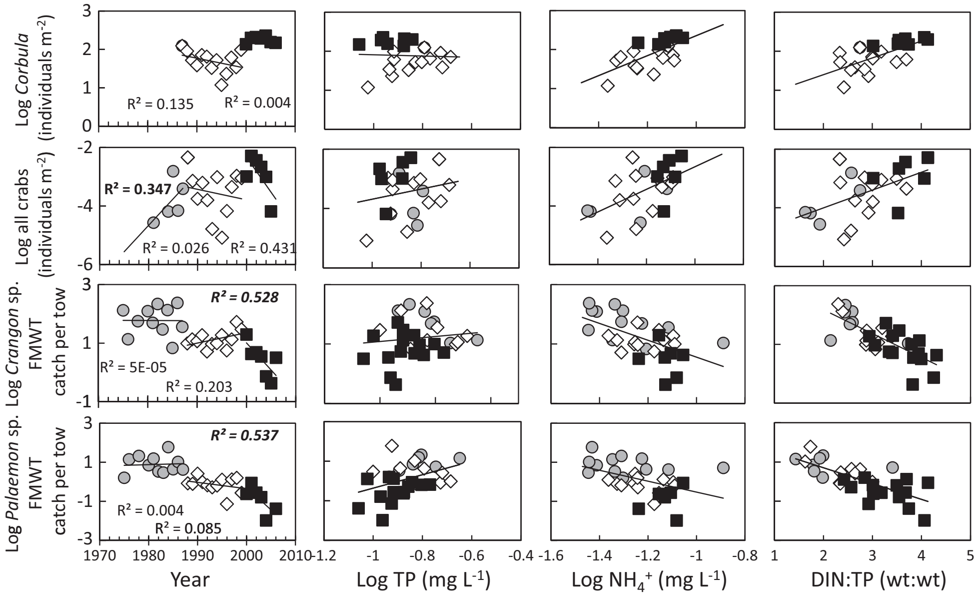

Figure 18 Change in the abundance of *Corbula amurensis* (individuals m^{-2}), crabs (*Cancer magister* and *Eriocheir sinensis,* individuals m^{-2}), shrimp (*Crangon franciscorum*, *Crangon nigricauda,* and *Palaemon macrodactylus*, FMWT catch per tow) over the time course and in relation to TP, NH_4^+, and DIN:TP ratios (all data except DIN:TP log-transformed). Coefficients of determination (R^2) are given for each major time period (1975–1986, ●; 1987–1999, ◇; and post-1999, ■) over the time course. Those indicated in bold are significant at $p < 0.05$, those in bold italics are significant at $p < 0.01$. The analysis indicates a significant change in abundance of the "crabs" grouping over the first major time period and declines in the shrimp species in the third 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 0.65, $p < 0.01$, respectively). The relationships between changes in *Corbula*, "all crabs," and *Palaemon* and TP were significant ($p < 0.05$), as were all species and NH_4^+ and DIN:TP for these and/or the detrended data (see Table 4).

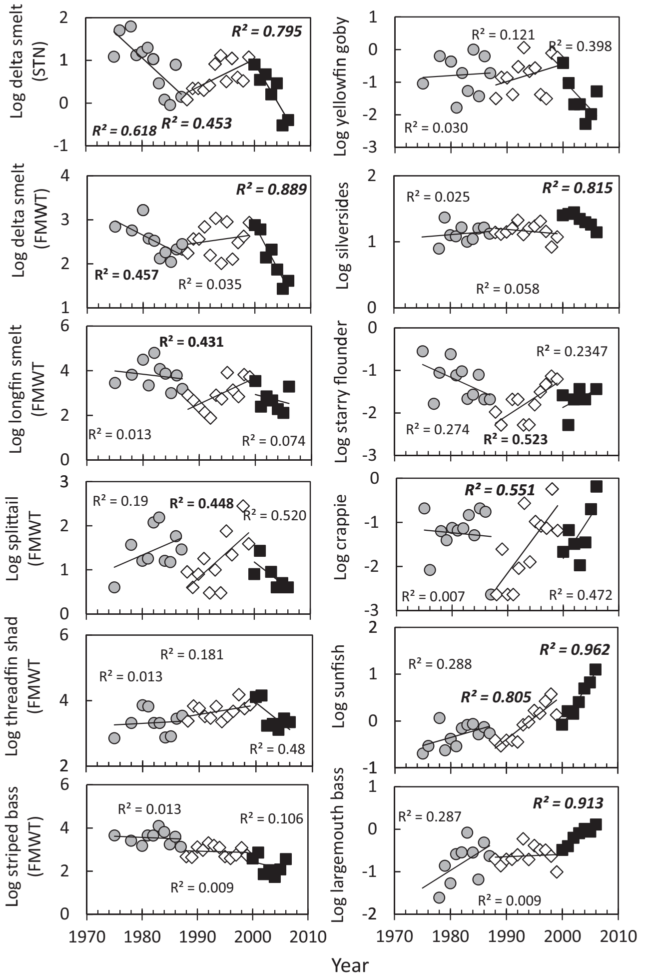

Figure 19 Change in the abundance of major fishes (all data were log-transformed) over the time course. Delta smelt are shown for the STN and FMWT indices. Longfin smelt, splittail, threadfin shad, and striped bass are shown for the FMWT index. Yellowfin goby and starry flounder are FMWT catch per tow. Inland silversides, crappie, sunfish, and largemouth bass are shown as relative abundance based on the beach seine data. Coefficients of determination (R^2) are given for each major time period (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). Those indicated in bold are significant at $p < 0.05$, those in bold italics are significant at $p < 0.01$. The analysis indicates significant changes over one or more major time periods for 9 of the 12 taxa. Although changes were not significant for individual time periods for striped bass, they were significant for the entire time course ($R^2 = 0.671$, $p < 0.01$). Several other species also had significant changes over the entire time course.

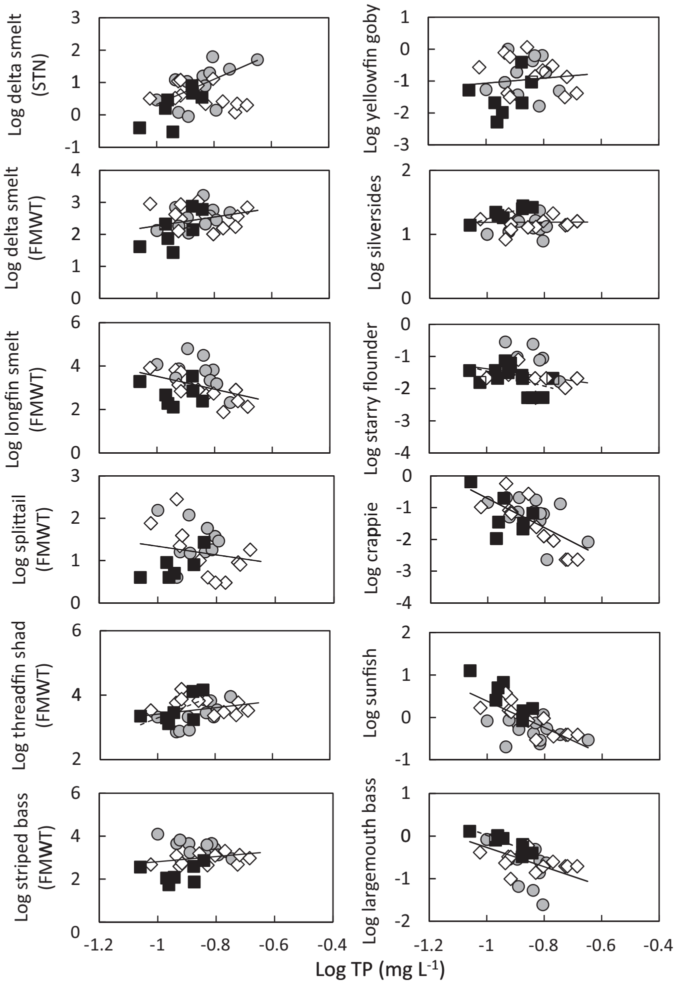

Figure 20 Change in the abundance of major fishes over the time course in relation to TP (mg L^{-1}) (all data were log-transformed). Abundances are as described in Figure 21. The major periods are represented by different symbols (1975–1986, ●; 1987–1999, ◇; and post-1999, ■). The correlations for delta smelt (STN but not FMWT), longfin smelt, crappie, sunfish, and largemouth bass were significant in these data, and for threadfin shad and starry founder in the detrended data ($p < 0.05$; see Table 4).

and opossum shrimp (*Neomysis*) in brackish regions (Moyle, 2002). 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). They preferentially feed on the calanoid copepod *Eurytemora*, although the calanoid copepod *Pseudodiaptomis* has increased in importance in their diet. Increased spring mortality has been linked to the decline in their food availability (Moyle, 2002; Kimmerer, 2004).

Striped bass were introduced in the late 1900s (Moyle, 2002). While successful in the early 20th century, the young of the year (which dominate the FMWT index) have declined since the early 1980s (Figure 19). Prevailing thoughts on the reasons for this decline include, "(1) climatic factors, (2) south Delta pumps, (3) other [water] 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).

Among the omnivorous fish in the Bay Delta are striped bass, white catfish (*Ameiurus catus*), channel catfish (*Ictalurus punctatus*), and largemouth bass. Crappie (*Pomoxis* sp.); sunfish and largemouth bass increased significantly in the same years (Figure 19). 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 correlated with TP or PO_4^{3-} concentrations (Figure 20, Table 4). Specifically, delta smelt (STN index) was

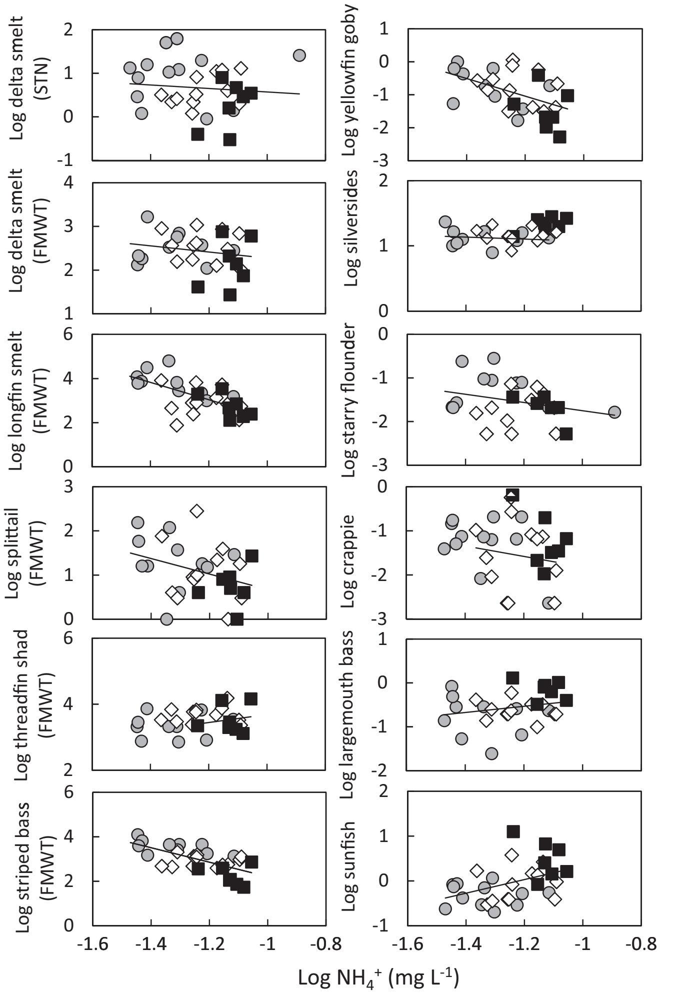

Figure 21 As for Figure 20, except in relation to NH_4^+ (mg L^{-1}) (all data were log-transformed). The correlations for all fish except delta smelt FMWT, splittail, threadfin shad, crappie, and sunfish were significant ($p < 0.05$) in these and/or the detrended data (see Table 4).

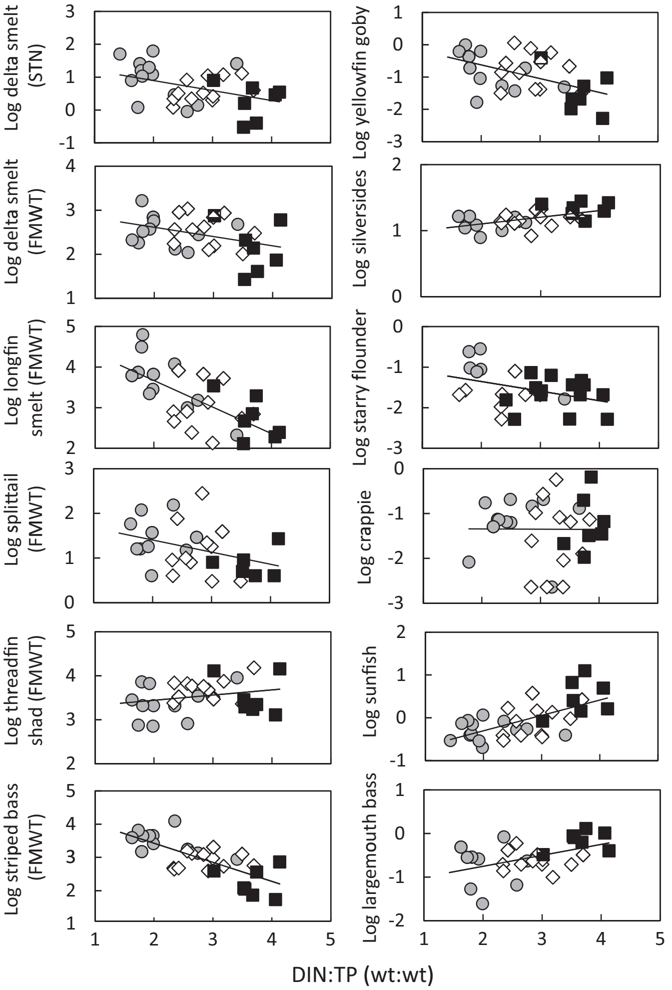

Figure 22 As for Figure 20, except in relation to DIN:TP ratio (wt:wt) (all abundance data were log-transformed). The correlations for all fish except crappie were significant ($p < 0.05$) in these and/or the detrended data. Note that most of these correlations were also significant for DIN:DIP as well (see Table 4).

positively correlated with TP, while abundances of longfin smelt, splittail, starry flounder, crappie, sunfish, and largemouth bass were significantly negatively correlated with TP and/or PO_4^{3-} in the original and detrended data. The abundances of longfin smelt, striped bass, and yellowfin goby were significantly negatively correlated with NH_4^+ concentrations, while those of inland silversides were positively correlated (Figure 21, Table 4). Thus, overall, delta smelt (STN index), longfin smelt, striped bass, and yellowfin goby were negatively correlated with DIN:TP or DIN:DIP ratios, while threadfin shad, sunfish, and largemouth bass were positively correlated with DIN:TP or DIN:DIP ratios (Figure 22, Table 5).

These trends also support the premise that nutrient stoichiometry propagates up the food chain (cf., Malzahn et al., 2007, 2010; Boersma et al., 2008). Ecological stoichiometry theory predicts that systems that shift from low to high N:P ratios should sustain shifts from planktivores to piscivores or omnivores (Sterner and Elser, 2002). The abundances of omnivores or piscivores (crappie, sunfish, largemouth bass) were negatively related to TP concentrations; they have a higher P demand and seemingly can sequester this nutrient more efficiently. The planktivores, with a lower P demand, are apparently 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 of the time series. Planktivorous fish and calanoid copepods have similar relationships with N:P ratios, whereas omnivorous fish have relationships with N:P ratios that are more similar to those of cyclopoid copepods (Table 5). Sequestration of P in the biomass of the omnivorous fish (with more skeleton and bones) would lead to them being proportionately more abundant when P is less available in the water column.

These findings are consistent with Hendrixson et al. (2007), who showed that the plankivorous fish, less capable of 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, underscoring strong stoichiometric control. Grazing on P-limited copepods, such as the calanoids or harpacticoids, is considered to enhance P limitation at the level of the planktivores (Boersma et al., 2008). In studies in which nutrients, light, and food chain length were manipulated, the phytoplankton assemblage under low nutrient conditions shifted primarily of cyanobacteria and chlorophytes ("intermediate-" to "poor-quality" food) compared to proportionately more cryptophytes and diatoms under high nutrients ("high-quality" food), and fish body C and P also varied accordingly (Dickman et al., 2008). Vanni et al. (2002) examined the stoichiometry of 28 species of fish and amphibians, and their data suggested that elemental stoichiometric controls were 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 considered stoichiometric requirements of larvae or 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 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 P and N 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, and 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 relative to biomass demands. When nutrition is adequate, organisms should grow faster and should reach a larger size. Furthermore, body N:P should decline with animal size due to the higher P demand of larger organisms (Davis and Boyd, 1978). However, there have been variable reports of relationships between fish size and N:P. 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). On the other hand, Sterner and George (2000) found weak relationships for cyprinids, and Tanner et al. (2000) observed weak relationships for 20 fish taxa in Lake Superior.

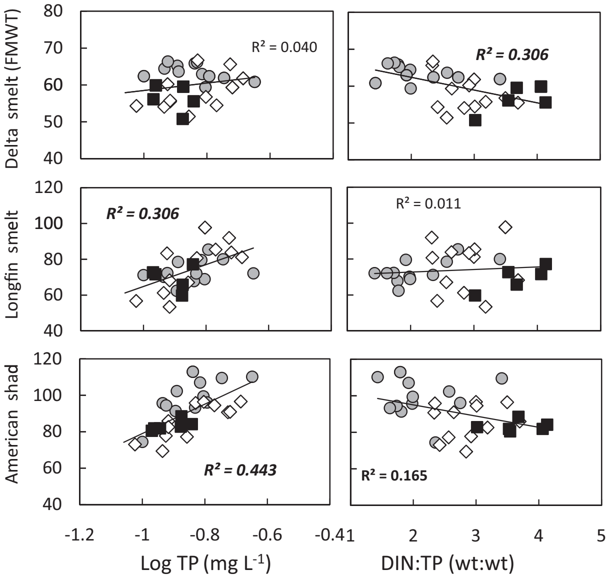

Figure 23 Change in fish length as a function of TP (mg L^{-1}; log-transformed) and DIN:TP (wt:wt). Coefficients of determination (R^2) are given for the entire data set only (symbols as in Figure 19). Those indicated by bold are significant at $p < 0.05$, those by bold italic are significant at $p < 0.01$. The correlations for length versus TP indicate significant relationships for longfin smelt and American shad; the correlations for length versus DIN:TP ratio indicate significant relationships for delta smelt (FMWT) and American shad.

Several fish species of the San Francisco Bay Delta showed strong correlations between their size and either TP concentrations or DIN:TP ratios (Figure 23). Longfin smelt and American shad increased significantly in length with increasing TP, while delta smelt and American shad decreased significantly in relation to DIN:TP ratios (Figure 23). 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 FMWT 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 answering the following questions posed in this analysis, namely: *To what extent do ecosystems self-assemble in a manner consistent with nutrient stoichiometry?* and *Does changing stoichiometry have ecosystem effects even when nutrients are not at levels normally taken to be limiting?* Such relationships were explored here by comparing several key species in relation to other organisms across the nutrient-time gradient.

Diatom abundance varied positively with total chlorophyll *a*, most zooplankton, *Crangon* and *Palaemon* abundance, delta smelt (STN), longfin smelt, and striped bass in the original and the smoothed data (Table 6). In contrast, dinoflagellates, *Limnoithona*, the "all crabs" grouping and sunfish, largemouth bass, and silversides varied negatively with total diatom abundance (Table 6). Most of the same relationships also held when associations with *Eurytemora* were compared (Table 6). It is noteworthy that similar associations between diatoms *Eurytemora* and *Neomysis* and smelt were also observed in the St. Lawrence River estuarine transition zone (Winkler et al., 2003).

Several negative correlations were found between dinoflagellate abundances and higher trophic levels (Table 6). Delta smelt (STN and FMWT) and longfin smelt were negatively correlated with dinoflagellates. Starry flounder (*Platichthys stellatus*) also declined as dinoflagellates increased (Table 6). The dominant dinoflagellate taxon was *Peridinium*, some species of which have been shown to have allelopathic properties that can adversely affect fish (Rengefors and Legrand, 2001, 2007). It is noteworthy that for many algal flagellates, production of bioactive substances increases under P stress (Granéli et al., 1998; John and Flynn, 2002). Most of the correlations between trophic groups were greater for the original and the smoothed data compared to the detrended data. These findings are consistent with the idea that detrending removed a "*common* mechanism influencing [these] data series" (Pyper and Peterman, 1998, pg. 2136). The common mechanism is suggested to be nutrients.

Overall, the Bay Delta food web at the beginning (1975–1986) and end (1999–2005) of the time course shows correspondence with the ratio of the major types of copepods, *Eurytemora affinis*/cyclopoids (Figure 24). These time periods had similar freshwater flow; thus, salinity tolerances should not have been a major factor in food web structuring. When *Eurytemora* were abundant in the early years, the system had higher relative abundances of planktivores (delta smelt, longfin smelt, yellowfin goby). In the later years when cyclopoids became dominant, there was a shift to a more omnivore-dominated community (sunfish, largemouth bass).

Macrophytes

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

The macrophyte community of the Bay Delta has changed considerably over the past several decades. Native SAV has largely been replaced by invasive submersed and floating vegetation, including *Egeria densa* and water hyacinth (*Eichhornia crassipes*) (Lund et al., 2007; Santos et al., 2011). Although these changes have disproportionately occurred in the freshwater reaches of the Bay Delta, including the confluence, they potentially have large effects on the entire ecosystem. Water hyacinth apparently was 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 ~22% of the waterways, in the Bay Delta (Finlayson, 1983). Water hyacinth grows rapidly and has been described to create habitat somewhat similar 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 because 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 (California Department of Boating and Waterways [CDBW], 1998; Toft et al., 2003; Anderson, 2003; www.dbw.ca.gov/Environmental/EgeriaDensaGenifo.aspx), 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 increased significantly during the 1980s (Jassby and Cloern, 2000) and even more in the 1990s after a major drought (Anderson, 1999). Although estimated to contribute $\leq$ 10% of the Bay Delta productivity (Jassby and Cloern, 2000), it has been estimated to cover more than ~2,400 ha of area in varying densities (Anderson, 1999, 2003; Hestir et al., 2008, 2010). Of more than 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, more than 60% of the waterways were covered with submersed plant canopy, most of which, especially in summer, was *Egeria* (Santos et al., 2011). This species appears to be 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).

Table 6 Correlation coefficients (r) for various organisms shown and diatom (Bacillariophyceae), dinoflagellate (Dinophyceae) or *Eurytemora* abundance

	Diatoms (cells mL^{-1})				Dinoflagellates (cells mL^{-1})				Eurytemora (individual m^{-2})			
Organism	Original data	Pre-whitened	First-differenced	Three-year moving average	Original data	Pre-whitened	First-differenced	Three-year moving average	Original data	Pre-whitened	First-differenced	Three-year moving average
Organism												
Phytoplankton												
Chlorophyll *a* ($\mu g\ L^{-1}$)	0.87**	0.70**	0.45*	0.92**	−0.58**			−0.59*	0.93**	0.84**	0.75**	0.96**
Bacillariophyceae (cells mL^{-1})	x	x	x	x	−0.61**			−0.59*	0.89**	0.70**	0.80**	0.95**
Chlorophyceae (cells mL^{-1})								0.61*				
Cryptophyceae (cells mL^{-1})										−0.32		
Dinophyceae (cells mL^{-1})	−0.61**	−0.34		−0.59**	x	x	x	x	−0.52**			−0.55*
Cyanobacteria (cells mL^{-1})								0.46				−0.46
Zooplankton												
Eurytemora (individual m^{-3})	0.89**	0.70**	0.80**	0.95**	−0.52*			−0.55*	x	x	x	x
Sinocalanus (individual m^{-3})	0.55**			0.54*		−0.47*		−0.71**	0.67**			0.43*
Acartia (individual m^{-3})	0.41*		−0.67**	0.71**				−0.48*	0.51**		−0.64**	0.70**
Pseudodiaptomus (individual m^{-3})	0.44			0.61*			−0.45*		0.40			
Harpacticoids (individual m^{-3})	0.69**			0.93**	−0.39			−0.50*	0.74**	0.34		0.89**
Limnoithona (individual m^{-3})	−0.52**		0.37	−0.57*					−0.39	0.47		−0.43
Daphnia (individual m^{-3})	0.46*	0.60**	0.51*	0.47*	−0.36			−0.62*	0.41*	0.48*		0.43
Bosmina (individual m^{-3})	0.40*	0.65**							0.38*	0.61**		0.37
Neomysis (individual m^{-3})	0.81**		0.51**	0.88**		0.46			0.75**		0.56**	0.76**
Invertebrates												
Corbula (count/grab)	−0.42			−0.75**			0.43					
All crabs (individual m^{-2})	−0.50*	−0.41		−0.51*	0.33*		−0.49*				0.59**	
Crangon (individual m^{-3})	0.74**	0.44*	0.52**	0.82**	−0.41			−0.50	0.72**	0.41*	0.59**	0.78**
Palaemon (individual m^{-3})	0.69**			0.90**				−0.47	0.72**		0.40*	0.85**
Fish												
Delta smelt (STN index)	0.46**			0.55*	−0.76**	−0.57**		−0.81**	0.46**		0.60**	0.59*
Delta smelt (FMWT index)	0.37*				−0.45*	−0.45*		−0.67**				
Longfin smelt (FMWT index)	0.67**	0.65**		0.70**	−0.54**			−0.45*	0.70**	0.68**		0.75**
Splittail (FMWT index)	0.32*								0.40*	0.37*		0.52*
Threadfin shad (FMWT index)				−0.64**				0.52*			−0.50**	−0.65**
Striped bass (FMWT index)	0.68**			0.81**		0.51*			0.63**			0.72**
Yellowfin goby (FMWT catch per tow)	−0.34		0.39*				−0.52*				0.53**	
Starry flounder (FMWT catch per tow)	0.34	0.41*		0.60**	−0.67**	−0.49*		−0.75**	0.59**	0.53**	0.33*	0.70**
Crappie (relative abundance)										0.54**		0.39
Sunfish (relative abundance)	−0.50**	0.33		−0.63**					−0.40*	0.57**		−0.48*
Largemouth bass (relative abundance)	−0.40**		0.40*	−0.64**	0.41			0.44	−0.41*	0.36		−0.52*
Silversides (relative abundance)	−0.53**			−0.68**				0.58*	−0.52*			−0.66**

All parameters were log-transformed. For each data series, the first column shows the correlations of the original data (log-transformed), the second column shows the correlations of the trend stationary data, the third column shows the correlations of the difference stationary data, and the fourth column shows the correlations of the data transformed as three-year backward moving averages. The correlations are for the entire time series. Only values for $p < 0.10$ are shown; values that are significant at $p < 0.05$ are indicated by *, and those significant at $p < 0.01$ are indicated by **. Negative correlations are highlighted in blue, and positive correlations are highlighted in pink ($p < 0.05$ [lighter shade] and 0.01 [darker shade] only).

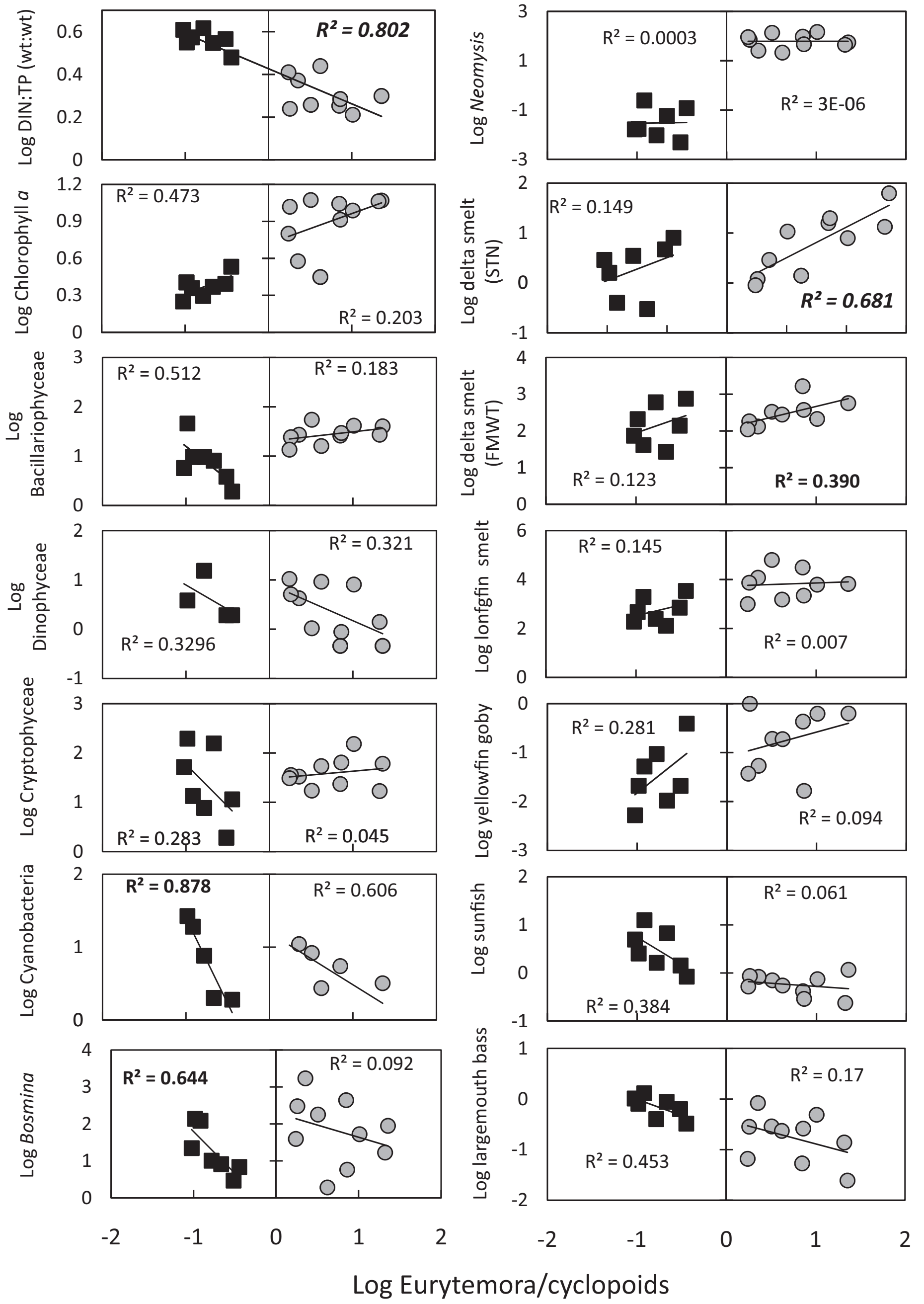

Figure 24 Comparison of abundance of the major groups of phytoplankton, zooplankton, and fish as a function of the *Eurytemora affinis*/cyclopoid ratio for two periods of the time course: 1975–1986 (●) and 1999–2005 (■). These time periods represent the beginning years of the time course and the years encompassing the POD. Among the significant relationships are those of the *Eurytemora affinis/*cyclopoid ratio and the DIN: TP ratio, cyanobacteria, *Bosmina*, and delta smelt (STN or FMWT data) ($p < 0.05$).

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 by providing a refuge from predation (Figure 25). 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 (Hestir 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

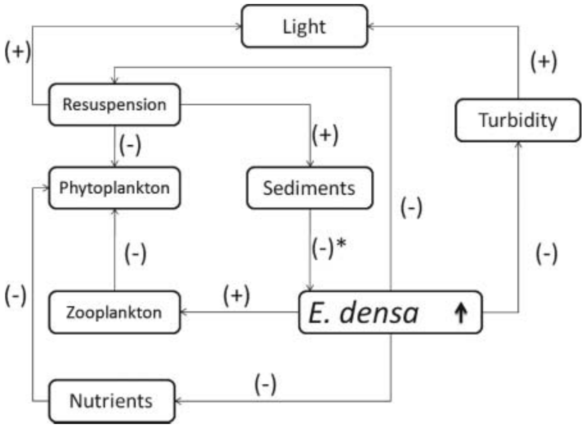

Figure 25 Schematic depiction of *Egeria densa* as an "ecosystem engineer." As *Egeria* increases, turbidity decreases, and light increases, Also, nutrients are taken up by the plants (but may be mobilized from the sediment; see text). Zooplankton increases due to the ability to find refuge from predation, but phytoplankton decrease due to zooplankton grazing. Figure reproduced from Yarrow et al. (2009) with permission.

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 also the extent to which they replace other structurally complex submersed macrophyte species or add new structure to an otherwise more open habitat (Martin and Valentine, 2010).

Macrophyte beds provide habitat for largemouth bass. These fish nest among the submersed vegetation (Moyle, 2002). In the Bay Delta, largemouth bass are increasing (Figure 19), 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. From a stoichiometric viewpoint, *Egeria* biomass differs from that of the dominant fish that thrive in these beds; published stoichiometry data of *Egeria* suggest a plant that has a high N:P content (Yarrow et al., 2009), while the dominant fish would be expected to 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 follow trends predicted by ecological stoichiometry theory. Members of different trophic levels were found to have different correlations with N and P, as did taxa within trophic levels. These patterns are consistent with the general premise that the fish community becomes proportionately more P-rich with increasing levels of consumers (Sterner and Elser, 2002). The patterns are also consistent with the increased development of a benthic food web following reduction in P loading. The comparisons of trends in taxa based on original versus detrended data illustrates that the most significant relationships with nutrients were robust even when autocorrelation was removed (an expected result since most parameters did not have significant autocorrelation).

PART III: ECOLOGICAL STOICHIOMETRY AND BIOGEOCHEMICAL INTERACTIONS

Ecological stoichiometric principles, and the data described above, suggest that there is a negative relationship between ambient levels of P in the environment and the abundance of piscivorous or omnivorous fish. As described above, such fish have higher metabolic and structural demands for P in their biomass than do smaller, more planktivorous fish and, thus, may be more efficient at sequestering the needed element. However, these large fish increased when P loads were reduced, leading to elevated N:P in the water column. The question arises: *What is the source of the P that supports these fish?* These organisms may be efficient at sequestering the needed element, but it must be available in order to be taken up. The related questions are thus: *To what extent are nutrient biogeochemical processes altered when the stoichiometry of land-based sources changes? What nutrient feedbacks may help to sustain an altered ecosystem structure?* From a stoichiometric perspective, altered biogeochemical pathways serve to provide the mechanism whereby nutrient dynamics supporting trophodynamics are changed. A stoichiometric perspective also suggests that altered biogeochemical pathways may shift environments so as to make them more conducive to the success of different species, some of which may be invasive. The hypothesis posed here is that through alterations in nutrient loads and resulting biogeochemical changes, the Bay Delta became a conducive environment for the invasion of *Egeria* and, in turn, *Corbula* and *Microcystis*.

Years of nutrient loading may result in large sediment reservoirs of nutrients for a considerable time (years) after the rate of loading is reduced (Chapra and Canale, 1991; Wetzel, 2001; Carpenter, 2005). Sediment chemistry measurements 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 and references therein; Figure 26). In the Bay Delta, where P has been measured in the upper few cm of sediment, concentrations were 5–10 μmol 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). 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 mobilize this P, making it available for organismal uptake. These abiotic and biotic processes are described below,

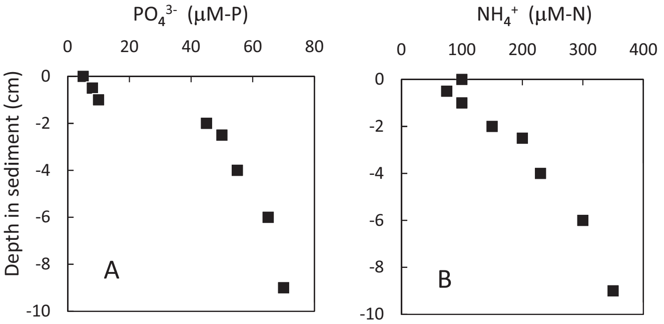

Figure 26 Pore water profiles of PO_4^{3-} and NH_4^+ from May 2004 at Freestone Point on the Potomac River, Chesapeake Bay, USA. This figure illustrates the main characteristics of Potomac River pore water chemistry. Data are from Bailey et al. (2006).

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 it may become adsorbed to particulates when P is discharged from other sources, such as from point source discharges. When this bound P meets saline or/and sulfate-rich water, either from transport down-estuary or from salt intrusion to sediments, the formation of iron sulfide minerals releases P to the overlying water (Caraco et al., 1989; Jordan et al., 2008; Lehtoranta et al., 2009). The sulfides produced in saline sediments preferentially bind 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

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

where (s) refers to solid phase, (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 been reported (Nilsen and Delaney, 2005).

This "iron conveyor belt" has been demonstrated 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 in the 30-year record for a station just outside Suisun Bay (Figure 27), an increase can clearly be seen. Thus, as salinity moves inland, more P is released from the sediments. The drier the season or year, the more P should flux from the sediment; the wetter the season or year, the smaller this flux.

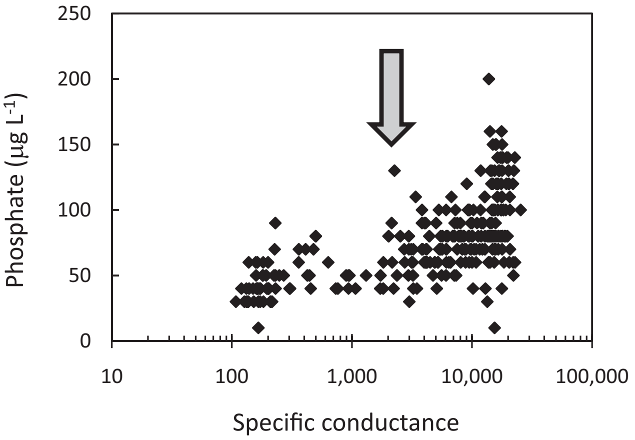

Figure 27 Relationship between the concentration of PO_4^{3-} (μg L^{-1}) and the specific conductance (μmhos cm^{-1}). Data shown are bimonthly averages for the time series for station D8 located near Suisun Bay. The arrow indicates the conductance approximately equal to a salinity of 2.

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).

Salinity has an opposite effect on N fluxes compared to P fluxes. Whereas P flux rates are higher in saltwater, rates of NH_4^+ flux are higher in freshwater (Jordan et al., 2008 and references therein), and this can accentuate the discrepancy between N:P ratios along the salinity gradient. Consistent with this idea, one study was conducted on benthic fluxes of nutrients in the upper Bay Delta in late summer, and rates of PO_4^{3-} efflux ranged from insignificant to ∼0.06 mmole $m^{-2}d^{-1}$, considerably lower than rates previously found for the more saline reaches of the estuary and considerably lower than those of NH_4^+ (Kuwabara et al., 2009). Comparisons of the NH_4^+: PO_4^{3-} ratio along the salinity gradient of four sub-estuaries of the Chesapeake Bay (Patuxent, Potomac, Choptank, and Bush Rivers) revealed a common switch from molar ratios >16 to <16 as salinity increased, with a major breakpoint in the salinity range of 1–4 (Hartzell and Jordan, 2010). Seitzinger et al. (1988) suggested that lower denitrification efficiencies in saltwater 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. Regardless of salinity, the supply of labile organic matter to sediment remains a key determinant of sediment N fluxes.

Biota-Mediated P and N Fluxes

Abiotic processes are significant, but they are not the only pathways by which P and N may be mobilized into solution. Macrophytes such as *Egeria* take up nutrients from the sediment and the water column; the relative importance of these two sources depends on the ambient concentrations in each (Moeller et al., 1988; Wetzel, 2001; Feijoo et al., 2002). *Egeria* has a high N:P content (Yarrow et al., 2009) and 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 ratios. 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, can attain high biomass levels and very high growth rates. In dense, productive stands, the environment for these two submersed plants can become limited by free CO_2, but both species have well-developed C-concentrating mechanisms (Bowes, 1987; Bowes and Salvucci, 1989; Lara et al., 2002; Pierini and Thomaz, 2004). In a (relatively) closed system, CO_2 (aq) depletion during photosynthesis increases pH, and the dissolved inorganic C system shifts toward increased dominance of HCO_3^-:

$$\mathrm{CO_2{+}H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO_3^-{+}H^+ \leftrightarrow CO_3^{2-}{+}2H^+} \quad (2)$$

Hydrilla and *Egeria* are able to use HCO_3^- efficiently with the consequence of elevating the pH of the surrounding water. In fact, hydrilla, while capable of growing well across a pH of 5–9, has a ten-fold higher growth rate at pH 9 than in lower pH conditions (Spencer and Bowes, 1986; Bowes, 1987). Thus, the elevated pH from high productivity 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).

Although measurements of pH for the Suisun Bay region have not been taken regularly over the time series of interest, long-term general trends in pH at a range of stations in the Bay Delta show similar patterns, including an increase since the mid-1990s (Figures 28A,B). High-frequency measurements show a diel oscillation with late-day pH elevations during the summer growing season (Figure 28C), and pH values > 10 have been recorded in the western Delta (Lindemuth, 2010).

As pH increases, the fundamental physical–chemical relationships related to P adsorption–desorption change. 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). For example, PO_4^{3-} flux from the sediment in the Potomac River increased from <5 μmol m^{-2} h^{-1} to nearly 30 μmol m^{-2} h^{-1} in <24 hr when the pH increased from 7.8 to 9.5 (Figure 29). The effect of pH 10.5 is far greater, however, as PO_4^{3-} efflux increased to > 100 μmol m^{-2} h^{-1} in 24 hr and continued to increase to > 160 μmol m^{-2} h^{-1} when these high

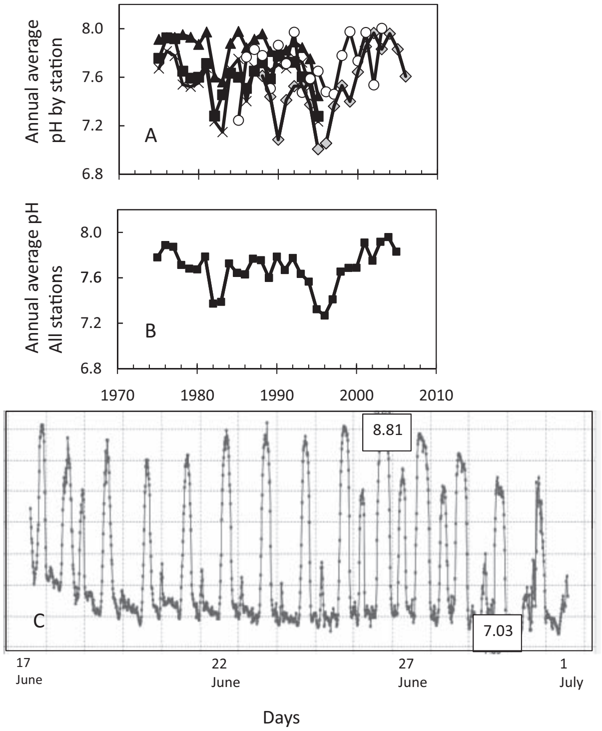

Figure 28 (A) Annual average pH for various stations (from Suisun Bay to lower San Joaquin and upper Sacramento River) in the Bay Delta over time, (B) mean of annual average pH of these stations over time, and (C) snapshot of diel fluctuations in pH from 17 June 2009 to 1 July 2009 in the Grantline Canal, 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).

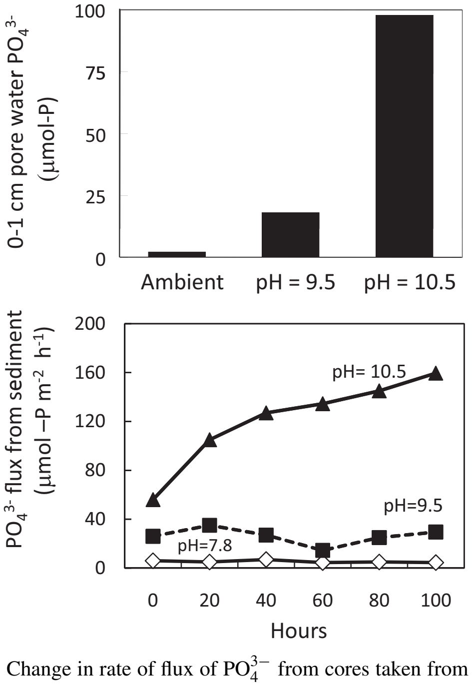

Figure 29 Change in rate of flux of PO_4^{3-} from cores taken from a *Hydrilla*-dominated reach of the Potomac River, Chesapeake Bay, USA, and experimentally manipulated to alter the pH (data from Bailey et al. 2006).

pH values were sustained for 100 hr (Figure 29). Organisms that can tolerate high pH and high NH_4^+ (such as *Egeria*) thus form the base of the food web in these stands. In turn, their metabolism affects the availability of benthic PO_4^{3-}. Rates of release of P 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} (Arnott and Vanni, 1996, based on data from Barko and Smart, 1980).

In summary, benthic sources of P are mobilized and can support the food web through two important mechanisms: salt intrusion resulting in localized abiotic exchange, and elevated pH resulting from highly productive macrophyte communities. Increased production in *Egeria* stands, which promote increased pH over diel cycles, may provide an important mechanism whereby P becomes available, and this can, in turn, fuel other components of the benthic food web.

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

Several other biogeochemical pathways are altered when pH is elevated due to highly productive benthic macrophytes under such conditions: First, 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

$$NH_3 + H_2O \xleftrightarrow{K_b} NH_4^+ + OH^-, \qquad (3)$$

where K_b is the equilibrium constant (Bange, 2008). At elevated pH, the proportion of NH_3 to $\Sigma(NH_3 + NH_4^+)$ increases; the salinity dependence of K_b results in an increase in the proportion of NH_3 at lower pH under freshwater conditions than under brackish/marine conditions. Moreover, at high pH, direct volatilization of NH_3 from *Egeria* has been observed (Reddy et al., 1987).

Elevated pH also alters bacterial metabolism (Tank et al., 2009). Both bacterial production and respiration can 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, elevated NH_4^+ and NH_3 are sustained (Russo, 1985; Kemp et al., 2005). 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 tolerate it increase; as primary production increases, pH increases, and the equilibrium shifts to NH_3. Feedback inhibition of the food web may occur 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 and exposure time (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, 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_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). Both taxa are negatively correlated with NH_4^+ in the long-term data (Table 4). Suppression of productivity and reduction in the proportion of primary productivity and bacterial productivity have been reported for other N-hypersaturated systems as well (Waiser et al., 2011), and such impacted systems have been identified as significant sites of ecological change (Brooks et al., 2006).

Macrophyte production can also alter the biogeochemistry of calcification by increasing the pH, and macrophytes alter sediment $CaCO_3$ dissolution rates through aerobic respiration (Burdige and Zimmerman, 2002). 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. In macrophyte communities, calcifying fauna often represent the dominant epibiota (Marba et al., 2006). These fauna are preferred sources of food for fish, such as sunfish (e.g., Werner and Hall, 1979; Schramm and Jirka, 1989; Toft et al., 2003). 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).

In addition to changes in availability of epiphytic biota, bivalve molluscs are important calcifiers. The precipitation of $CaCO_3$, a complex process in bivalves, requires significant PO_4^{3-} as well as Ca^{2+} (Asana and Ito, 1956). TP 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). Concentrations of Ca^{+2} in sediment porewater in areas occupied by clams would be expected to be much higher than in sediments where clams are not abundant. In addition to metabolic fluxes, shell dissolution from dead clams can contribute to such concentrations and help to sustain elevated Ca^{+2} concentrations in a positive feedback.

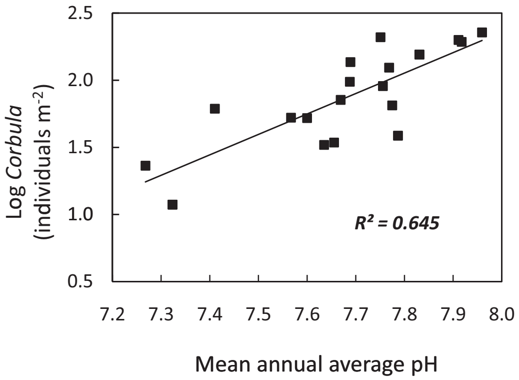

Figure 30 Annual abundance of *Corbula amurensis* (log of individuals m^{-2}) at stations located from the confluence to Suisun Bay in relation to mean annual average pH. Coefficient of determination (R^2) was significant at $p < 0.01$.

As shown above, 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* (Figure 18, Table 5) (Glibert, 2010). There is also a strong long-term positive relationship between pH and *Corbula* abundance (Figure 30). This species invaded the Bay Delta in 1987 at the start of a several-year drought (Alpine and Cloern, 1992; 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. *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 is typically in the water column for several weeks in spring, and it accelerates rates of calcification in summer when temperature and pH are elevated (Hrs-Brenko, 2006).

Biological and Biogeochemical Feedbacks and Microcystis *Abundance*

Positive feedback mechanisms thus exist between macrophyte production, pH, nutrient efflux, and calcification. Additional 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). Although cyanobacteria increased in abundance in the mid-1980s, the abundance of *Microcystis* has escalated significantly in the past decade (Lehman et al., 2005, 2008, 2010). *To what extent might the increase in* Microcystis *in the Bay Delta be a consequence of such positive feedbacks?*

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., 1986; 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. *Microcystis* is also a superior algal competitor under elevated pH; like *Egeria*, it has highly effective C-concentrating mechanisms, allowing it to sustain photosynthesis when other algae become C-limited (Jähnichen et al., 2007 and references therein).

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 is significantly higher by zebra mussels than by crustacean zooplankton (Conroy et al., 2005). Ecological stoichiometric principles have been examined with respect to zebra mussel invasions of lakes in Sweden (Naddafi et al., 2009). While nutrient stoichiometry was not directly linked to mussel fitness, zebra mussels tolerated low P, and their stoichiometry was altered by both food quantity and quality.

Toxin production by *Microcystis* provides yet another positive feedback. Cyanotoxins, such as microcystins, appear to adversely affect growth and development of daphnids, with offspring of toxin-exposed daphnids showing decreased growth and survival even if they were subsequently raised in microcystin-free conditions (Dao et al., 2010; Ortiz-Rodríguez and Wiegand, 2010). Wang et al. (2010) showed that *Microcystis* developed in experimental systems when zooplankton were included, but not in enclosures where zooplankton were removed prior to the experiment. *Microcystis* blooms in lakes typically occur when small-sized zooplankton dominate (Allan, 1977; Edmondson and Litt, 1982; Wang et al., 2010). The effect of microcystins on *Daphnia* in the Bay Delta has not been examined, but in laboratory experiments with copepods, more detrimental effects have been observed on *Eurytemora* than on *Pseudodiaptomus* (Ger et al., 2010).

Various studies have related increasing N and increasing N:P ratios to increased toxicity of *Microcystis*. In the 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 P limitation increased, more microcystins were produced. In addition, the more toxic form, microcystin-LR, was produced compared to microcystin-RR (Figure 31). Excess N has also been related to microcystin production under controlled culture conditions (e.g., Lee et al., 2000; Vézie et al., 2002; Downing et al., 2005;

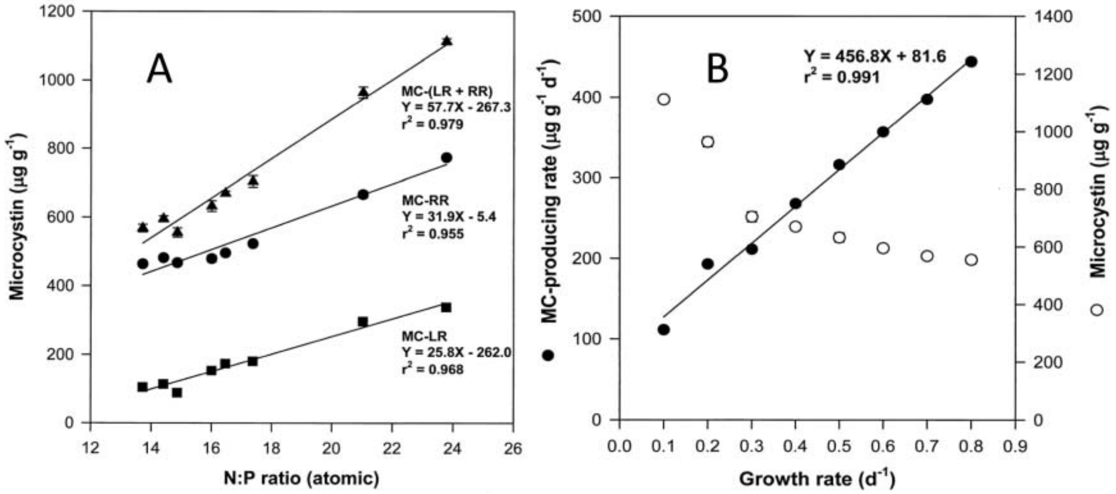

Figure 31 (A) Relationship between the N:P atomic ratios and the concentrations of different microcystin toxins (MC-LR, MC-RR, and MC-[LR + RR]) of *Microcystis aeruginosa* grown in laboratory P-limited cultures. (B) The microcystin-production rate (●) and microcystin content (○) of *M. aeruginosa* at each growth rate in laboratory P-limited cultures. Figure reproduced from Oh et al. (2000) with permission.

Van de Waal et al., 2009). In the Philippines, increased *Microcystis* was associated with high N loading 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; the strongest correlations between microcystins and nutrients were found at high concentrations of NO_3^- and NH_4^+, and seasonal bloom maxima occurred at high water-column N:P ratios ranging from 40–90 (Ha et al., 2009). In both field studies and in culture, the molar cellular N:P ratio 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" stoichiometric model (Sterner and Elser, 2002, p. 16), but instead functions stoichiometrically more like a heterotroph, in this case, sequestering P and potentially releasing excess N in the form of the toxin microcystin. It may also have the capability to reduce its P requirement by lipid substitution, as shown for other cyanobacteria (Van Mooey et al., 2009). From its C-concentrating capability (Jähnichen et al., 2007) to its P metabolism and its tolerance and/or preference for NH_4^+, *Microcystis* appears well adapted to the present environment of the Bay Delta where pH values fluctuate and can become elevated on episodic bases and where N:P ratios have increased over time.

Broad surveys have been undertaken to assess relationships between cyanobacteria and water-column N:P ratios. Some of these have included all cyanobacteria (including the N_2-fixing species), others only *Microcystis*. For example, Downing et al. (2001) examined data from 99 lakes from around the world and reported that TP or TN 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* can tolerate elevated N:P ratios, and thus, its dominance under high N:P ratios may also reflect the decline in other species that lack such tolerance. 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.

Summary of Part III

Conceptually, the relationships examined between changes in pH and altered salinity and the major biogeochemical processes are summarized in Figure 32, while the changes over time and the shift in dominant biogeochemical processes are depicted in Figure 33. While the interactions among the biogeochemistry and biology and their changes over time are complex, the important point is the interconnectedness of these relationships. Changes in external nutrient loads can drive changes in internal ecosystem biogeochemistry and, in turn, trophodynamics. This analysis suggests that increasing dominance over time of macrophytes, clams, and *Microcystis*, along with more omnivorous fish that are fueled by a benthic food web, are not a result of stochastic events (random invasions) but, rather, are related to a cascade of changes in biogeochemistry resulting from changes in nutrient loading over time as a major driver. This analysis supports the premise that reductions in P loading from external sources drive aquatic systems toward increased importance of sediment dynamics and toward the sediments as a major source of P. The food webs that are supported are different from those supported when the water column is the major source of P; they are benthic-dominated. Macrophytes, such as *Egeria*, and phytoplankton, such as *Microcystis*, are

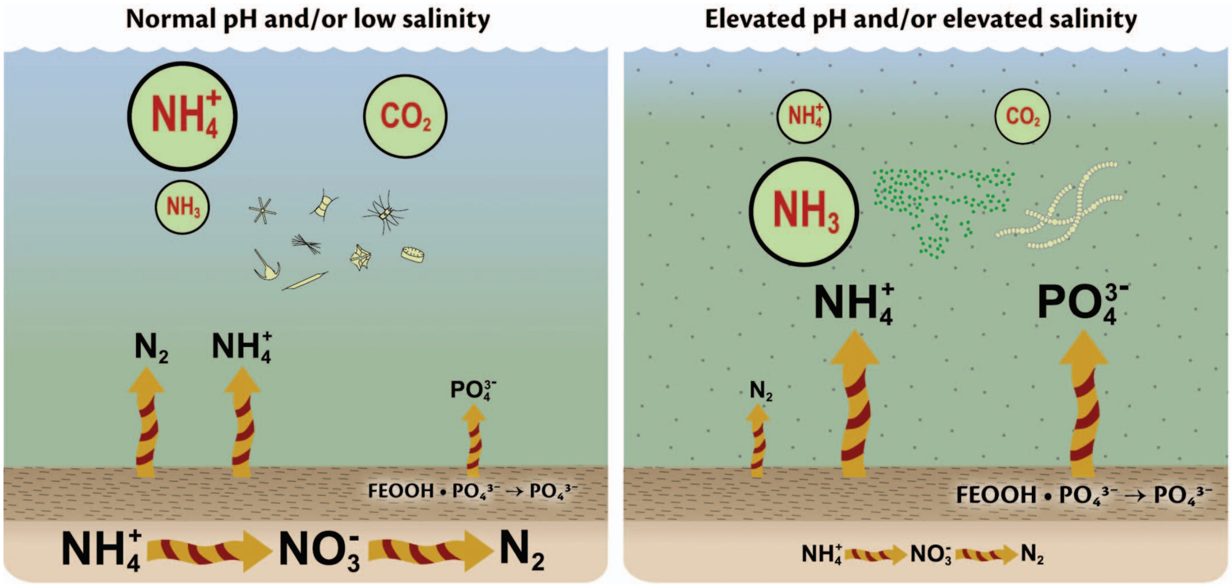

Figure 32 Conceptual diagram of the effect of altered pH and altered salinity on the processes of exchange of PO_4^{3-} and NH_4^+ from the sediment to the water column. With a rise in pH, or a shift to higher salinity, the sediment flux of NH_4^+ and $PO4^{3-}$ increases via the mechanisms described in text. pH also alters the equilibrium between NH_4^+ and NH_3, leading to higher NH_3 at high pHs (color figure available online).

physiologically well adapted to these altered nutrient and pH regimes. The communities of bivalves and fish change accordingly.

PART IV: COMPARATIVE ECOSYSTEMS

Many systems show commonalities with respect to impacts of eutrophication (reviewed by Cloern, 2001). 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, however, by the following comparison with other aquatic systems undergoing stoichiometric changes in nutrient loads. Here, comparisons of other ecosystems are made 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 when P was reduced; (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. These comparisons illustrate a similarity in the timing of P reductions and the susceptibility of these systems to invasions by macrophytes and bivalves.

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 is surrounded by the city of Seattle, Washington, USA, and was historically degraded by major inputs of secondary-treatment sewage from the 1940s to the early 1960s (Edmondson, 1996). In the 1960s, Seattle and the surrounding communities adopted zero sewage discharge policies for the lake (except for combined sewer overflows; Krebs, 2008). Diverting most sewage away from Lake Washington caused N:P ratios to increase (Figure 34). By 1970, phytoplankton growth had decreased to levels that had not been seen since the early 1950s, including a major decline of the filamentous cyanobacterium *Planktothrix* (*Oscillatoria*) *rubescens* that had bloomed in the P-rich conditions (Edmondson and Lehman, 1981; Hampton et al., 2006). Zooplankters such as "keystone herbivores" *Daphnia* spp. became increasingly abundant (Edmondson and Litt, 1982; Winder and Schindler, 2004a,b), while their major predator, the macrozooplankter *Neomysis mercedes*, declined rapidly (Eggers et al., 1978; Edmondson and Litt, 1982). Longfin smelt were abundant in the early 1960s but also declined (Hampton et al., 2006). Although the food web interactions are complex in this lake (Hampton et al., 2006), and other influences such as climate change have been linked to these changes (Winder and Schindler, 2004a,b), the declines in chlorophyll *a* and *Neomysis*, as well as the increase in *Daphnia* following P removal and N:P increases, are consistent with those of the Bay Delta.

Potomac River, Chesapeake Bay

The Potomac River has undergone many similar changes to those in the San Francisco Estuary (Figure 35, Table 7), some of which differ from those of the Chesapeake Bay as a whole, since the Potomac is most directly influenced by nutrient

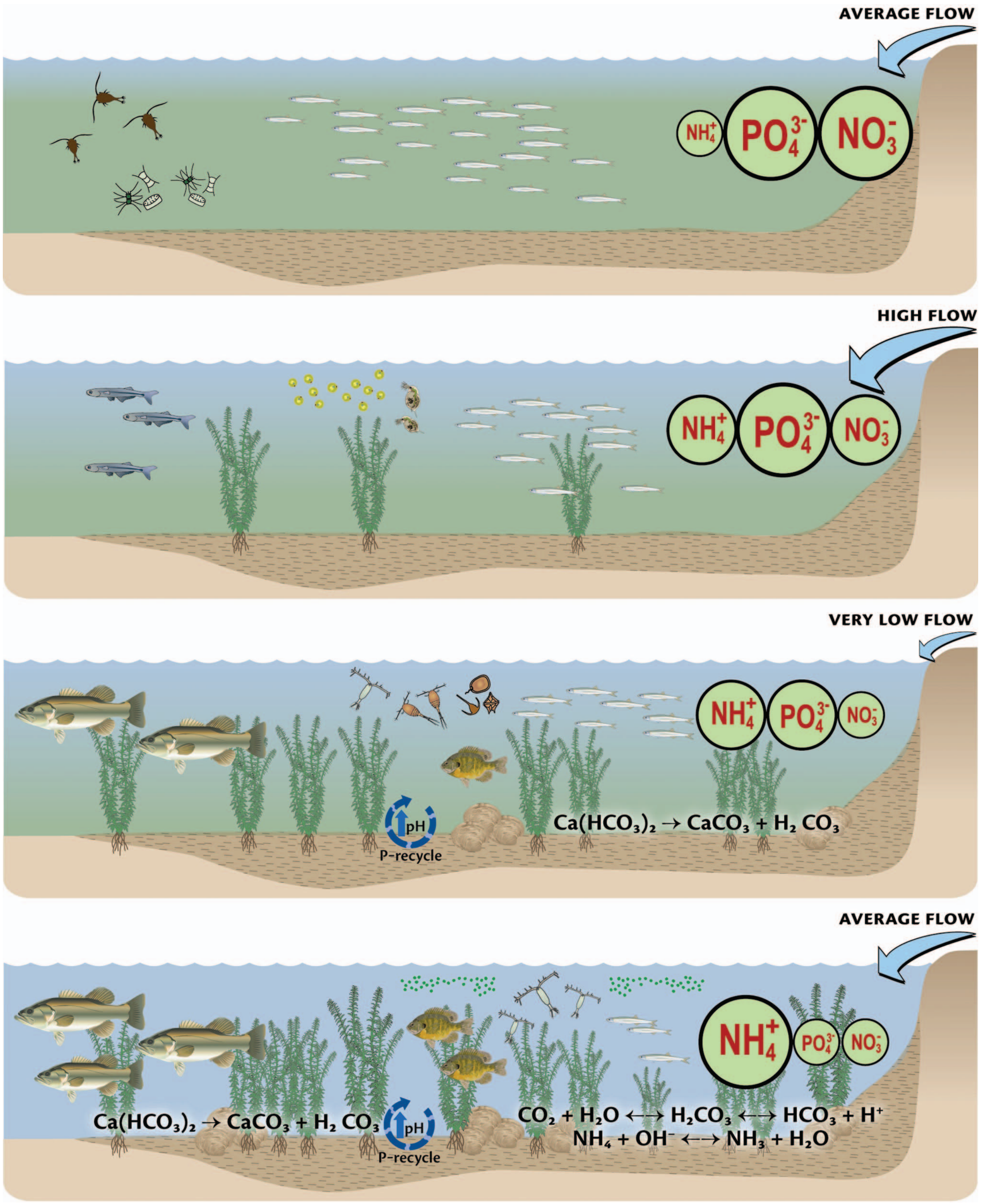

Figure 33 Conceptual depiction of the change over time in major nutrients, flow, dominant biogeochemical processes, and the food web of the Bay Delta. The first panel represents the period from 1975 to ∼1982 when flow was low, and diatoms and *Eurytemora* were the dominant phytoplankton and zooplankton, 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 are proportionately low. Sediment biogeochemical processes are of increasing importance in nutrient processing, macrophyte production is important, and omnivorous fish have increased. At the microbial level, *Microcystis* is more common and the zooplankton is dominated by cyclopoids, e.g., *Limnoithona* (color figure available online).

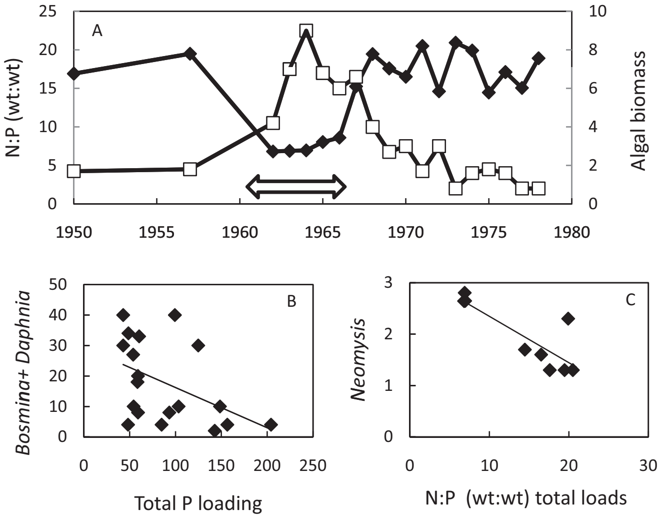

Figure 34 Comparative nutrient and food web relationships for Lake Washington: (A) change in N:P ratio (☐; wt:wt) and change in algal biomass (♦; chlorophyll *a*, μg L^{-1}) as a function of time, (B) relationship between the abundance of *Daphnia* and *Bosmina* (number L^{-1}) and TP loading (10^3 kg yr^{-1}), and (C) relationship between *Neomysis* abundance (relative abundance) and the N:P ratio of the total nutrient load. Data were compiled from Edmondson and Lehman (1981), Edmondson and Litt (1982), Krebs (2008), and Eggers et al. (1978).

loading from a major sewage treatment plant compared to the more diffuse nutrient sources that affect the broader Chesapeake Bay. This river has been heavily impacted by nutrient inputs for over a century, with cyanobacterial blooms evident by the 1930s (Krogmann et al., 1986). Nutrient inputs to the Potomac have been strongly affected by management actions (Table 7), 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 P 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; from the early 1990s to the present, effluent loads of NH_4^+ decreased more than 50% (Jaworski and Romano, 1999; Jaworski et al., 2007).

When N:P ratios increased in the late 1970s, chlorophyll *a* declined and SAV increased. Hydrilla, also an invasive species for this river, expanded its range shortly after P removal, and this correlated with a decrease in water-column chlorophyll *a* (Rybicki and Landwehr, 2007; Ruhl and Rybicki, 2010; Figure 35B). The extent of hydrilla coverage was directly related to the N:P ratios of the effluent (Figure 35C). After the nitrification–denitrification system had been 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).

An invasion by *Corbicula fluminea* was first noted in the mid-1970s in the Potomac River. Its abundance peaked in the late 1980s, exceeding 2,500 individuals m^{-2} (Dresler and Cory, 1980; Phelps, 1994). Its peak occurred when the N:P of all loads was increasing. Its abundance subsequently declined, coincident with efforts to remove N from effluent and a decline in N:P (Phelps, 1994; Cummins et al., 2010; Figure 35A). Its presence in the 1980s was associated with declines in phytoplankton abundance due to the grazing pressure it imposed (Cohen et al., 1984). *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 over time, 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., unpublished data; Figure 35D).

Fish composition also changed over time, and some of these changes can be related to nutrient stoichiometry. Bay anchovies decreased, and both spottail shiners and largemouth bass increased (http://www.dnr.state.md.us/fisheries/juvindex/

Table 7 Time line of changes in the Potomac River sub-estuary; most wastewater 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 1970s	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 1990s	Phelps (1994)
Early-to-mid 1980s	Nitrification added to WWTP leads 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 $<0.1 \cdot 10^6$ kg 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 doubling of large- and smallmouth bass with increasing SAV	US EPA (1993)
1986–present	SAV coverage decreases below peak levels, with low coverage in the mid-1990s and a resurgence in the early 2000s	Orth et al. (2010)
Early 1990s	N loading from WWTP peaks at $> 1 \cdot 10^7$ kg y^{-1}	Jaworski and Romano (1999);
Mid-1990s to present	N loading from WWTP decreases about 50% due to nitrification/denitrification process	Jaworski et al. 2007
	Corbula fluminea abundances decline significantly	
	Construction initiated at WWTP to reduce N loading by another 50% by 2014	Cummins et al. (2010)

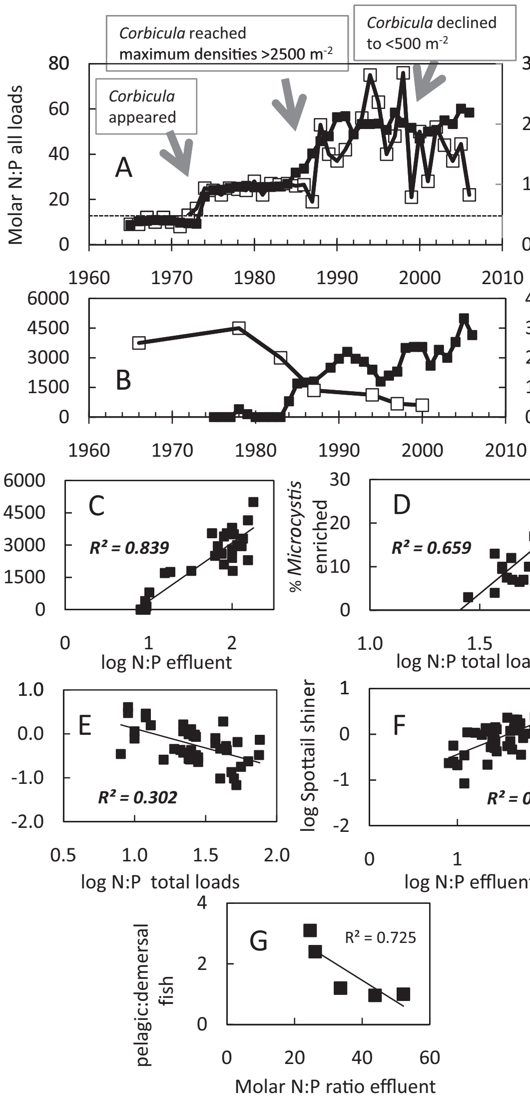

Figure 35 Comparative nutrient and food web relationships for the Potomac River. (A) Change in N:P ratio of all loads (■) and of the wastewater effluent only (□) as a function of time from the mid-1960s to 2005. Indicated also on the time course is the first appearance of the invasive *Corbicula fluminea* clams, as well as its maximum abundance and the time when they began to decline. Data were derived from Dresler and Cory (1980), Jaworski et al. (2007), and Cummins et al. (2010). (B) Change in abundance of SAV, in this case dominated by *Hydrilla* (■), and the change in chlorophyll *a* in the water column (□). Data were derived from Jaworski et al. (2007). (C) Relationship between the abundance of SAV (dominated by *Hydrilla*) and the N:P in the wastewater effluent. Data derived from Jaworski et al. (2007). (D) 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 (unpublished data); nutrient data are from Jaworski et al. (2007). (E) Abundance of Bay anchovy (log relative abundance as geometric mean catch per haul) as a function of N:P of the total nutrient load. (F) 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). (G) 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.chesapeakebay.net, and nutrient data are from Jaworski et al. (2007).

index.asp#Indices) in proportion to N:P ratios that reflected changes in either total nutrient loads or effluent (Figures 35E,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; Figure 35G).

Hudson River

Point source nutrient loading to the Hudson has been contentious for many decades (Brosnan et al., 2006). Secondary treatment plants were constructed in the 1980s, and N loads decreased by ∼30%. Compared to the 1970s, reductions in P by ∼60% were achieved by the 1990s through secondary treatment and P removal from detergents. 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). The exception to these 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 TN and TP loads to the Hudson are now about 43×10^3 tonnes N yr^{-1} and 4.8×10^3 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. Zebra mussels were first detected in the Hudson in 1991 and were well established by 1992 when P reductions had been implemented (Strayer, 2006). 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). Average May–October chlorophyll *a* dropped from ∼20 to ∼4 $\mu g\ L^{-1}$ after 1993 (Cole and Caraco, 2006). Like the Bay Delta, the common copepods in the Hudson now include two cyclopoids, in this case *Diacyclops bicuspidatus thomasi* and *Halicyclops* sp. (Pace and Lonsdale, 2006). The small estuarine invasive clam *Rangia* was first detected in 1988 and has spread significantly since that time (Strayer, 2006).

Increases in largemouth bass and bluegills 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). *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). However, these blooms have returned; by 2005, *Microcystis* contributed more than 45% of the total summer algal biomass (Fernald et al., 2007). Recent reports have linked these blooms to increased temperature (e.g., Fernald et al., 2007), but the pattern is also consistent with an altered biogeochemical pathway of nutrient cycling following the increased dominance of both macrophytes and zebra mussels. Temperature may be a necessary condition, but it is not a sufficient explanation of changes in this species over time.

European Lakes and Estuaries

In the Ebro River Estuary, where an 18-year time series of nutrients and biota has 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 decreased precipitously in the mid-1990s (Ibáñez et al., 2008). For P, this drop was from $\sim$2.8 kt y^{-1} to $<$0.5 tonnes y^{-1}. However, TN 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 four-fold from the early 1990s to the mid-2000s. Total water-column chlorophyll *a* declined by $\sim$ten-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, further structured 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 sustained a reduction in submersed vegetation and an increase in phytoplankton chlorophyll *a* when nutrients, especially P, increased (Blindow et al., 2006; Hargeby et al., 2007). Zebra mussels were also highly associated with *Microcystis* abundance in 47 sites in lakes in northern Ireland, and all of these lakes had toxic blooms (Mooney et al., 2010).

Summary of Part IV

The Bay Delta data and the other systems considered here which are undergoing similar changes in nutrient stoichiometry have had a similar general trajectory of responses (Table 8). While all of the systems described above have undergone complex changes, largely a result of direct management actions, there are many parallels with respect to organism dominance after P removal. While invading species such as hydrilla and *Egeria*, and many bivalve molluscs do well across a range of system types, the commonality of the increased frequency of invasion around the time P was removed throughout much of the United States and Europe raises interesting questions about cause-and-effect related to altered nutrient stoichiometry. Moreover, the physiology of the resident organisms and biogeochemical pathways lend support to the premise that similar

Table 8 Descriptive comparison of major food web changes in comparative systems after reduction of P from the system and the associated increase in the disolved N:P ratio; further details of all of these changes are described more fully in the text

	San Francisco Estuary	Lake Washington	Potomac River	Hudson River	Ebro River
Phytoplankton					
Change in Chl:*a*	Decrease	Decrease	Decrease	Decrease	Decrease
Change in *Microcystis* occurrence	Increase	Decrease	Initial decrease, then resurgence	Initial decrease, then resurgence	
Zooplankton					
Change in species group	Increase in cyclopoids and cladocerans Decrease in *Neomysis*	Increase in cyclopoids and cladocerans Decrease in *Neomysis*	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	
Bivalves					
Change in dominant species	Increase in *Corbula*		Increase in *Corbicula*, *Rangia*	Increase in *Dreissena*, *Rangia*	Increase in *Dreissena*, *Corbicula*
Submersed vegetation					
Change in abundance	Increase		Increase	Increase	Increase
Dominant species	*Egeria, Eichornia*		*Hydrilla*	*Hydrilla, Eleocharis*	*Hydrilla*

Blank entries are those for which insufficient data are available to evaluate.

trophic structure, including the appearance of *Microcystis*, in many of these systems has resulted from similar nutrient dynamics. Biogeochemistry, and food web interactions that both modify and result from changes in stoichiometry and the relative abilities of different types of organisms to either sequester nutrients and/or to tolerate nutrients that are in excess (e.g., NH_4^+).

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 seems at odds with prevailing perspectives of how this system has become stressed over time. Nixon and Buckley (2002), in a general 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 about changes in the food web in the Bay Delta, most of which have not involved nutrient control.

With respect to the Bay Delta ecosystem, 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 N for phytoplankton uptake (McCarthy et al. 1977; Millero, 2006; Jassby, 2008); the pH of the receiving waters is generally in the range that prevents formation of toxic NH_3 (Jassby, 2008); and NH_4^+ levels are typically below the criteria considered by the U.S. Environmental Protection Agency (2009) to be toxic to sensitive aquatic life, such as freshwater molluscs. In addition, some analyses of nutrient effects have considered only TN or TP 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 obscured or 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, and this conclusion has been underscored by several prior efforts (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, food limitation, alteration in flows (including export pumping), alterations in habitat, and climate change (both temperature and hydrologic changes) 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; Winder et al., 2011). The effects of climate are recognized to act synergistically with many 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, Winder et al., 2011). Where nutrients have been considered to be important in the food web changes over the past decades, the emphasis has been on understanding the potential inhibition of primary production and the decline in diatoms associated with elevated levels of NH_4^+ (e.g., Wilkerson et al., 2006; Dugdale et al., 2007) rather than on nutrient limition or nutrient stoichiometry. Both the prevailing and the stoichiometric viewpoints underscore that the system is stressed and complex. The prevailing views related to limiting factors, nutrients, flow, and habitat alteration are examined below in comparison to stoichiometric interpretations.

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 primary production is considered to be mainly controlled by light. These generalizations stem from 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 generally were 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. Models were developed (Cloern et al., 1995; Cloern 1999) 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*:C (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 among 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 to the authors that primary productivity was independent of nutrients in the system. Therefore, the models were taken as substantially accurate in the context of distinguishing light from nutrient limitation of C production by the phytoplankton.

The fundamental assumption in these models is that *primary production* is the principal factor that links phytoplankton to the grazer community and upper trophic levels. This conventional approach for determining the amount of energy (as reduced C) that would be available to upper trophic levels unfortunately ignores the transfer of elements other than C. In marked contrast and as developed herein, ecological stoichiometry dictates that it is the processing and transfer of all elements, especially N and P, 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 C-based primary production models. As illustrated in the analyses above, nutrients that are at levels normally taken to be saturating or near-saturating can influence the elemental composition of the phytoplankton (food quality) and, therefore, differentially affect the transfer of N and P to upper trophic levels via trophic transfer and via altered biogeochemical dynamics.

Potential Inhibition of Diatoms by NH_4^+

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 algae, especially those that are N-limited, prefer NH_4^+ as an N source because it is already in reduced form and thus more easily assimilated (Harris, 1986; McCarthy et al., 1995, 1977). However, some diatoms physiologically prefer, and in some cases require, nitrate ($NO_3{}^-$) over NH_4^+ (Lomas and Glibert, 1999). This phenomenon is accentuated when the cells are in a state of energy imbalance, such as might be experienced under varying light regimes; for these cells, $NO_3{}^-$ may also be used in maintaining the cellular energy balance in addition to providing a nutrient (Lomas and Glibert, 1999). In San Francisco Bay, Wilkerson et al. (2006) and Dugdale et al. (2007), based on enclosure experiments, reported that diatoms grew only after NH_4^+ concentrations were drawn down to <4 μM (0.056 mg L^{-1}).

An interesting "natural test" of the potential inhibition of diatoms by NH_4^+ occurred during summer 2010, when such inhibition was "relaxed" because discharge of NH_4^+ from the SRWWTP was ∼15% lower than in the immediate prior years (R. Dugdale, personal communication). The decreased NH_4^+ loads coincided with a spring diatom bloom that was observed in Suisun Bay for the first time in many years. Moreover, consistent with the trophic interactions seen in the long-term data, in spring 2010, *Eurytemora* density was 3.1-fold higher than in 2009, and increases were also noted in *Pseudodiaptomus* density and in the 2010 FMWT index of delta smelt abundance.

Food Limitation

Food limitation has been invoked by numerous researchers as key to the decline in the Bay Delta food web over time (Bennett and Moyle, 1996; Jassby et al., 2002, 2003). Total productivity has been estimated to be comparatively low relative to other estuaries, and detritus appears to be an important food supplement for grazers (e.g., Müller-Solger et al., 2002). However, from a stoichiometric perspective, detritus, which is high in C, may result in metabolic costs to consumers, including altered metabolic rate and growth rate (Plath and Boersma, 2001; Hessen and Andersen, 2008). 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. Disposal of excess C appears to have major impacts on organismal fitness and, like the other stoichiometric concepts explained 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 are 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., 2005). 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). X2 is therefore considered to be a proxy for outflow.

Strong bi-variate, correlative relationships have been reported between X2 and chlorophyll *a*, *Eurytemora, Acartia*, rotifers, mysids, clams bay shrimp, and various fish species, including longfin smelt, splittail, and starry flounder (Kimmerer, 2002; Winder et al., 2011). Interestingly, many of these relationships were noted to change after 1987 (Kimmerer, 2002). This has been thought to be due to the drought that began in the 1980s and which may have changed habitat suitability, especially allowing more invasive organisms (Winder et al., 2011). The change after 1987 also corresponds with the change in nutrient loading. X2 is strongly correlated with PO_4^{3-}, TP, and NH_4^+ (Figure 36). For comparison with nutrient relationships, the relationships between the parameters studied here and X2 have been calculated using the same approaches (Table 9). For all organisms (with the exception of *Acartia*, for which strong correlations were observed with X2-Table 9), i.e., *Eurytemora*, *Pseudodiaptomus*, *Daphnia*, *Bosmina*, *Corbula*, *Crangon*, longfin smelt, splittail, striped bass, starry founder, crappie, sunfish, and largemouth bass, equal or more significant correlations were

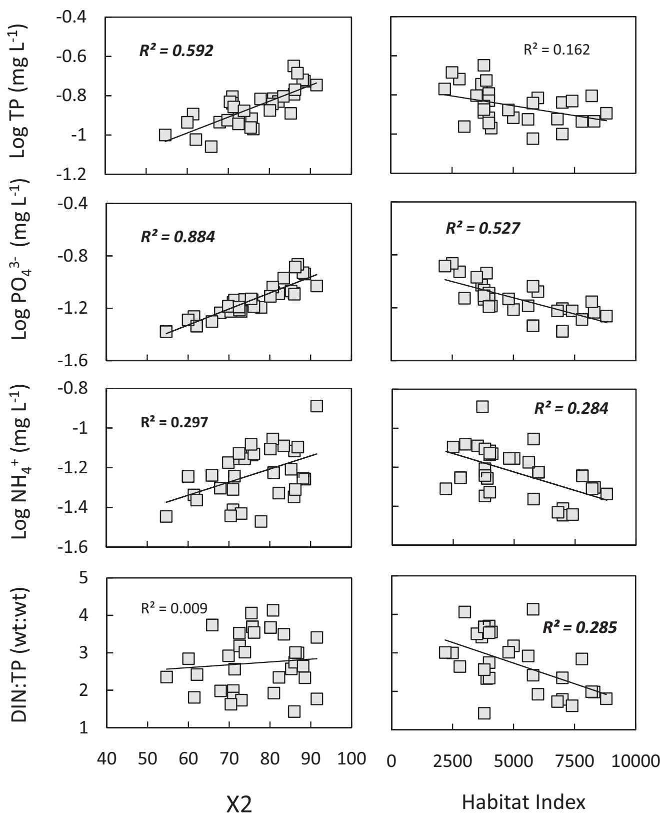

Figure 36 Comparison of the relationships between TP, PO_4^{3-}, NH_4^+, and the DIN:TP ratio versus X2 (the isohaline where salinity = 2, measured as distance (km) from the Golden Gate Bridge) and versus the habitat index (defined by salinity, temperature, and turbidity relationships; Feyrer et al., 2010) for the time course from 1975–2005. Coefficients of determination (R^2) are given for the entire dataset. Those indicated in bold are significant at $p < 0.05$, those in bold italics 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.

observed with nutrients or nutrient ratios (Tables 4 and 5). That strong relationships between some organism changes and X2 are found is without question; however, the strong relationships between nutrients and X2 leads to uncertainty as to whether salinity (or flow) or nutrients are the controlling variables. Furthermore, when calculated as pre-whitened or differenced data, versus the original or smoothed data, more correlations were significant, suggesting that higher frequency time scale changes may be a component of this variability (Pyper and Peterman, 1998). This contrasts with the nutrient relationships, for which many relationships were stronger in the original or smoothed data, suggesting that longer-term variability (i.e., unidirectional trends) is important.

A relationship has also been developed between X2 and a habitat index for delta smelt, an index that 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 three decades (Feyrer et al., 2010). This habitat index, like X2, is highly correlated with nutrients (Figure 36). As shown here, TP explained at least as much of the variability in delta smelt as did the habitat index (Table 4), and dinoflagellate abundance explained even more (Table 6).

Moyle et al. (2010) suggested that variability and disturbance are required to re-establish native fish populations. They argued 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 a new equilibrium, where those species whose competitive abilities are low may be lost (Moyle et al., 2010, citing Krebs, 2008). Interestingly, in aquatic systems, homeostasis tends to dampen the effects of physical disturbance (Krebs, 2008). Moyle et al. (2010) did 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 need to be addressed.

Summary of Part V

The response of the system to nutrients sets in motion a cascade of interacting effects. Thus, to varying degrees, nutrients, flow, X2, invasive species, and warming or hydrologic changes are all related to the observed changes in the food web (e.g., Kimmerer, 2002; Winder et al., 2011), and it is not surprising that some of these relationships are statistically significant. Yet, all of these relationships can also be explained by a stoichiometric model. Using stoichiometry, the trajectory of responses to changing nutrients over time provides a new interpretation for the decline in pelagic fish species in recent years, the POD. The current conceptual understanding is based on a "multi-stressor hypothesis" that relates a complex interplay of stressors, 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, that combine to form an overall stress on certain populations (Sommer et al., 2007; Baxter et al., 2010). In contrast, the stoichiometric interpretation argues that many of these factors and changes are linked and may be sequential, with nutrient changes being a major driver (Figure 37). Nutrient changes, and the biochemical changes that follow as a consequence, alter the environment, potentially making it more conducive to invasive species, and differential nutrient metabolism and homeostasis drives the system away from planktivores to omnivores or piscivores as N:P changes.

Table 9 Correlation coefficients (r) for various organisms shown and X2

	X2 (km)			
	Original data	Pre-whitened	First-differenced	Three-year moving average
Organism				
Phytoplankton				
Chlorophyll *a* (μg L^{-1})		−0.70**		
Bacillariophyceae (cells mL^{-1})		−0.58**	−0.58**	
Chlorophyceae (cells mL^{-1})				0.45*
Cryptophyceae (cells mL^{-1})				
Dinophyceae (cells mL^{-1})			0.37	
Cyanobacteria (cells mL^{-1})				
Zooplankton				
Eurytemora (individual m^{-3})		−0.52**	−0.43*	
Sinocalanus (individual m^{-3})	−0.56**			−0.69**
Acartia (individual m^{-3})	0.57**	0.57**	0.62**	0.40*
Pseudodiaptomus (individual m^{-3})		−0.58**	−0.81**	
Harpacticoids (individual m^{-3})				
Limnoithona (individual m^{-3})	−0.38	−0.59**		−0.49
Daphnia (individual m^{-3})	−0.76**	−0.75**	−0.79**	−0.79**
Bosmina (individual m^{-3})	−0.87**	−0.85**	−0.50**	−0.87**
Neomysis (individual m^{-3})			−0.49**	
Invertebrates				
Corbula (count/grab)		0.70**	0.57*	
All crabs (individual m^{-2})	0.41	0.58**		
Crangon (individual m^{-3})		−0.52**	−0.48**	
Palaemon (individual m^{-3})				
Fish				
Delta smelt (STN index)				
Delta smelt (FMWT index)			−0.35	
Longfin smelt (FMWT index)	−0.71**	−0.80**		−0.67**
Splittail (FMWT index)	−0.57**	−0.55**	−0.47*	−0.65**
Threadfin shad (FMWT index)				−0.42*
Striped bass (FMWT index)		−0.34*	−0.46*	
Yellowfin goby (FMWT catch per tow)			−0.51**	
Starry flounder (FMWT catch per tow)	−0.36*	−0.41*		−0.42*
Crappie (relative abundance)	−0.60**	−0.66**		−0.79**
Sunfish (relative abundance)	−0.47**	−0.58**	−0.36*	−0.51*
Largemouth bass (relative abundance)		−0.47*	−0.59**	−0.44*
Silversides (relative abundance)		0.38*		

All organism parameters were log-transformed. For each data series, the first column shows the correlations of the original data (log-transformed), the second column shows the correlations of the trend stationary data, the third column show the correlations of the difference stationary data, and the fourth column shows the correlations of the data transformed as three-year backward moving averages. The correlations are for the entire time series. Only values for $p < 0.10$ are shown; values that are significant at $p < 0.05$ are indicated by *, and those significant at $p < 0.01$ are indicated by **. Negative correlations are highlighted in blue, and positive correlations are highlighted in pink ($p < 0.05$ [lighter shade] and 0.01 [darker shade] only).

PART VI: CONCLUSIONS, IMPLICATIONS AND RECOMMENDATIONS

Conclusions

Eutrophication, ecological stoichiometry, and alternate stable state theories can be combined to form unifying framework for understanding the complexity of responses, not only in the Bay Delta but also, more generally, in many comparative systems. This interpretation does not negate the importance of ecological invasions, habitat changes, multiple stressors, and food web complexities, but it adds a *mechanism* to those interpretations through biogeochemistry and organismal stoichiometry. Ecological stoichiometry affects systems by setting elemental constraints on the growth of organisms. This, in turn, affects food quality and the relationships between predators and prey. The biota modify the environment through nutrient regeneration, which differs from species to species based on their elemental requirements and nutrient sources. Growth also modifies the physical and chemical environment through pH changes, habitat alteration, light environment, and substrate, among other factors. 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; the composition of the grazers changes in relation to stoichiometric constraints. In the Bay Delta, evidence is clear that top-down grazing of phytoplankton by *Corbula* exerts a strong control on phytoplankton biomass, as is also the case for other systems, such as the Potomac and the Hudson, when invaded by bivalve molluscs. However, the arguments presented here make the case that bottom-up control contributed to the all-important conditions that allowed *Corbula* to become a dominant regulator of phytoplankton production. Winder et al. (2011) suggested that such a niche for *Corbula* opened up due to climate change and its effect on hydrology. Prior interpretations, emphasizing stochastic invasions largely via ballast water exchange, imply that the invasive event was the ultimate cause of the change in top-down control of phytoplankton. The ecological stoichiometric interpretation does not preclude strong top-down control of selected component organisms, nor ballast water exchange as the mechanism of introduction. The distinction is that, at the overall ecosystem level, the structuring of species is affected by alterations in nutrients and ecosystem biogeochemistry. This interpretation is consistent with Ware and Thompson's (2005) insights from a broad survey of the relative contributions of bottom-up versus top-down factors that potentially control fish catch in the coastal waters of the western United States; they, too, reported that bottom-up factors were more important.

The similarity in responses of 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 resulted in complex interactions and changes in plankton and benthic communities (Figure 2). Described here are several common responses of complex aquatic ecosystems to increased or sustained N loading and concomitant P reductions (Figure 38). These commonalities, including reduced levels of chlorophyll *a*, increased SAV (particularly rooted macrophyte) growth, and a shift in dominance to large omnivorous/piscivorous fish, have been, in some cases, interpreted as oligotrophication (e.g., Anderson et al., 2005; Collos et al., 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 change* or *imbalance*. Specific trophic responses, based on stoichiometric constraints, can be predicted for stoichiotrophically imbalanced systems. Moreover, stoichiometric regulation can be important for food web dynamics, even when changes in these nutrients and their ratios are not widely divergent from Redfield proportions – that is, whether N or P are limiting, or not.

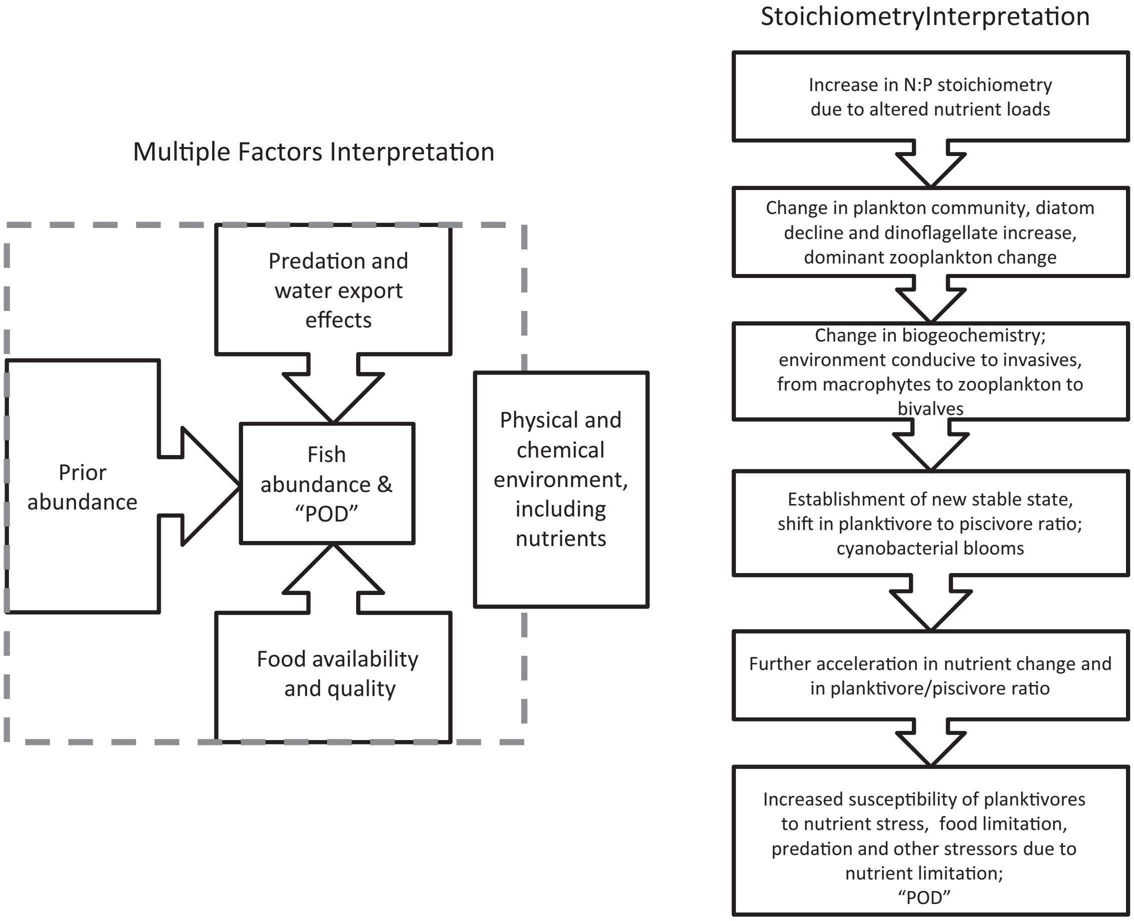

Figure 37 Comparison between the conceptual understanding of the factors related to the Pelagic Organic Decline (POD) as described by Sommer et al. (2007) and the conceptual understanding described in this analysis.

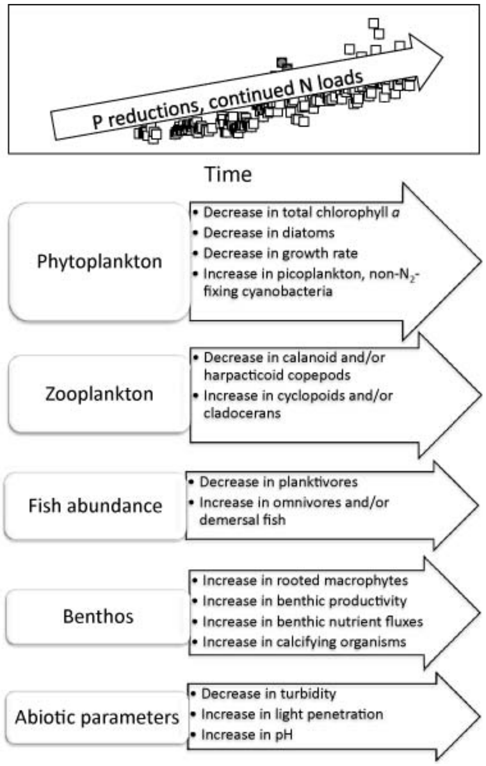

Figure 38 Generalized trajectory of responses for systems impacted by imbalances in N:P stoichiometry where P loads have been reduced and N loads have been increasing.

The trajectory of ecosystem responses in the Bay Delta, illustrated here, suggests that as nutrient stoichiometry changed over time and the system shifted from high flow to low flow back to high flow, it did not return to the same condition (e.g., Figure 33). The likely reason for this failure to return to its historic condition is the reservoir of P in sediments and the potential for this reservoir to be mobilized under varying flow conditions. 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. Thus, while complex, the Bay Delta is not uniquely complex among estuaries or, indeed, among aquatic ecosystems, as suggested by Kimmerer (2004). When flow returned to high levels after the mid-1980s drought, bivalves and other organisms 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. Nutrients may thus provide a mechanism whereby "invasional meltdown" can be accelerated (Simberloff and Von Holle, 1999).

The analysis here extends that of Glibert (2010), who also examined both N:P ratios and NH_4^+ 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 and major trophic components. As background, CUSUM-transformed relationships compare the accumulation of a quantity over time; CUSUM is, in effect, a low-pass filter for time series analysis. Correlations of CUSUM-transformed variables, or double-mass curve analysis (e.g., Kohler, 1949; Searcy and Hardison, 1960), allows the pattern of change in two variables to be compared, recognizing that such comparisons improve the signal-to-noise ratio and associated change points. In ecology, the application of single-mass (CUSUM) and double-mass analysis has been increasing, and the CUSUM approach has been identified as an important tool in regime change analysis (Andersen et al., 2008). 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).

Based on CUSUM analysis, 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 the timing of shifts in variables. 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:DIP and NH_4^+ and in relation to *Eurytemora* abundance, and both identified the *timing* of these changes. The stoichiometric and biogeochemical constraints presented in this review provide plausible mechanisms for why these food webs changed as they did. Comparisons across systems have provided evidence of commonalities in changes in food webs when nutrient stoichiometry is altered.

A central conclusion of this analysis 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 described above, P reductions can result in a decline in chlorophyll *a*. Where cyanobacterial blooms previously had 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 dinoflagellates, or cyanobacteria, such as *Microcystis*, can become established or re-established. If the system also receives N in the form of NH_4^+, only organisms that can tolerate high concentrations of NH_4^+ are apparently able to thrive—including, for the Bay Delta, certain macrophytes, bivalves, cyanobacteria, cyclopoids, and omnivorous/piscivorous fish. Thus, it is the interplay of P sequestration and NH_4^+ tolerance that contributes to shifts to new dominants; this interplay is clearly illustrated in the strong positive or negative correlations of many species at all trophic levels with DIN:TP or DIN:DIP (Table 5).

Those organisms that can successfully sequester P will become dominant when P reductions are made, because the sediment will continue to provide this nutrient. Once the sediment P pump has become established, the system can be viewed as having reached a tipping point, wherein further P reductions likely will only exacerbate the problem. Key among these associations is the NH_4^+ sensitivity of diatoms, which are strongly associated with the success of many species (Table 6). Their decline has consequences for the food web at many levels.

Two management strategies are envisioned for systems undergoing ecosystem changes associated with stoichiotrophic imbalance: either increase the P load or decrease the N load. Increasing P—for systems that are rich in N—risks pushing the system toward a classical eutrophied condition, with concomitant increased hypoxia/anoxia and unfavorable changes in the benthic community. Reductions in N (especially NH_4^+) will allow organisms, from diatoms to fish, that cannot withstand high NH_4^+ (and/or that are outcompeted by NH_4^+-tolerant organisms, such as various harmful dinoflagellates and cyanobacteria) to compete. The challenge for resource managers is how to recognize when such a tipping point has occurred and when aggressive P reductions would therefore be counter-productive. This conclusion contradicts some authors, such as Carpenter (2008) and Schindler et al. (2008), who view P reductions as the sole solution to eutrophication, but supports that of Fisher et al. (1992), Hagy et al., (2004), Burkholder et al. (2006), Howarth and Paerl (2008), Conley et al. (2009), and Paerl (2009), who view both N and P controls to be necessary. Control of P works to a point but appears not to be able to overcome the biogeochemical "pumping" of P from P-laden sediments into the overlying water. Initial responses, such as chlorophyll *a* and bloom reductions in response to P control, may give resource managers a false sense of success; once the threshold of biogeochemical control has been crossed, more P control is not the solution. The same biogeochemical regulation of P release supporting cyanobacterial blooms in the Baltic Sea has been reported, where it has been strongly emphasized that "During longer time scales, reductions in external phosphorus load may reduce cyanobacterial blooms; however, on shorter time scales the internal phosphorus loading from the sediment can counteract external phosphorus reductions" (Vahtera et al., 2007, p. 1).

Interestingly, in 2010, additional P reduction measures, i.e., removal of P from dishwashing detergents, were taken in California. Stoichiometric and biogeochemical regulation would suggest that N control is much more imperative. New requirements for effluent removal from the major wastewater treatment plant (WWTP) on the Sacramento River call for reductions in N loading from the current 14 to 8 tonnes day^{-1} (2.2 mg L^{-1} NH_4^+ + 10 mg L^{-1} $NO_3{}^-$; permitted up to 181 mgd) in the coming decade through implementation of nitrification and denitrification (Central Valley Regional Water Quality Control Board, 2010). This biological nutrient removal would result in a significant decrease 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). Inasmuch as P levels are approximately what they were in the early 1970s when the food web supported such fishes as abundant delta smelt, it is N that must be reduced, rather than P that should be increased, to achieve the desired balance and food web restoration.

In further support of N reduction, restoration efforts in the Potomac are showing evidence of reduction in exotic species and a return of 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). 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 the projected nutrient regime of the Bay Delta once N controls have been enacted.

Broader 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; rather, environmental changes interact with vectors of invasion to enhance their success (e.g., Hobbs, 2000; Kolar and Lodge, 2001). There have been numerous other examples where ecosystem disturbance has been associated with the opportunity for species to colonize following new introductions and/or for latent populations to expand (Hobbs and Huenneke, 1992; Hobbs, 2000). That the pattern of trophic cascades is similar in systems ranging from the Bay Delta to the Potomac River and elsewhere is evidence 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; Winder et al., 2011). To this list, the interacting effects of P reductions and static or increasing N loads are an important addition.

(2) There has been much debate about nutrient regulation and limitation, most recently in a set of papers about the potential importance of N versus P in estuaries (Schindler et al., 2008; Schindler and Hecky, 2008; Howarth and Paerl, 2008; Carpenter, 2008; 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., Fisher et al., 1992; Paerl et al., 2004; Burkholder et al., 2006; 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. In many estuarine systems, N is no longer the limiting nutrient; 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. 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 non-indigenous species. While individual species and processes respond to single nutrients, the relative proportion of N and P collectively alters metabolism, species composition, and food webs. Nutrient ratios may not effectively structure phytoplankton communities (with the exception of N_2-fixing cyanobacteria favored when N:P ratios are low), but they exert a strong regulatory control on food webs, biogeochemistry, and ecosystem structure *as a whole*.

(3) In what has become a much-referenced study 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 what 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) underscored 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 may aid the understanding of how systems can actually 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-Guldberg, 2008 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. As suggested here, alkalinification may be another consequence of altered N:P ratios and the comparative ability of macrophytes to thrive under these conditions. 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. There is a pressing need to better understand 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. 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 can lead to a flawed conclusion that productivity, biomass, and species composition are all regulated by a single element (McIntyre and Flecker, 2010). Similarly, many trophic interactions, such as, for example, rates of growth or fecundity, 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; Coutteau and Sorgeloos, 1997; Weers and Gulati, 1997; Brett and Müller-Navarra, 1997). Some diatom species produce certain highly unsaturated fatty acids that are essential for zooplankton reproduction (reviewed by Kilham et al., 1997), while flagellates generally produce different fatty acids than diatoms (Olsen, 1999). Moreover, some cyanobacteria greatly reduce their phospholipid content in relation to P stress (Van Mooey et al., 2009), while some green algae have been shown to have higher lipid content under P limitation (e.g., Kilham et al., 1997). Cellular biochemical constituents are strongly influenced by the elemental composition of the cells, and relationships between these indices of food quality and elemental stoichiometry should be explored.

(6) Cyanobacteria may do well at both ends of the Redfield spectrum. Most of the 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 either efficiently garner its requisite P or reduce its P requirement. Stoichiometric homeostasis (Figure 4) may be yet another explanation for release of nutrient-rich (or, in some cases, C-rich) toxins, not only by *Microcystis* but potentially by other harmful algal species, such as dinoflagellates.

(7) 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., 2008; Williams et al., 2010; US EPA, 2009).

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 harmful algal blooms (HABs). There are as yet no quantitative indices for the impacts of altered stoichiometry. 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 lie. 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, piscivore/planktivore abundance, calanoid/cyclopoid ratios, and sediment release of P and N, as examples.

(8) The alternate stable states that have been documented here and in comparative systems should be considered in light of 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. If stoichiometry is indeed an important regulator of trophodynamics, to save the delta smelt (i.e., to restore large populations of it) will require that the system be adjusted to have many characteristics of a more classically defined eutrophic system, with higher chlorophyll *a* levels, higher turbidity, less benthic vegetation, and fewer largemouth bass. Most coastal communities that are coping with systems in altered stable states are attempting to shift to a system with more piscivores, not fewer, and clearer conditions, not more turbid water.

(9) Regulation of a single nutrient without recognition of the role of nutrient stoichiometry simply 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, 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 (Figure 39). Such an effect has been documented for the Neuse River Estuary, the mesohaline reach of Chesapeake Bay, and the southern Baltic Sea in the Sweden archipelago region; eutrophication effects increased in these systems when P reduction, but not N reduction, was imposed upstream (Fisher et al., 1992; Paerl et al., 2004). Many marine HABs are increasing (Anderson et al., 2002; Glibert et al., 2005; Heisler et al., 2008), and increasingly these changes are being related to nutrient changes, even for those species that were previously thought to be unrelated to nutrient pollution (Burkholder et al., 2008). For example, the classic "red tide" former, *Noctiluca scintillans*, was recently found to be associated with offshore transport of excess N, mediated through N cycling and trophic transfer (Harrison et al., 2011). 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 and basic knowledge of biogeochemical processes and organismal physiology. Using comparative systems, it was shown that similar dynamics have developed in other systems affected by similar stressors. 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 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? How do they vary with freshwater flow?
(2) What are the dynamics of 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?
(3) 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?
(4) To what extent are bacteria and microzooplankton stoichiometrically constrained, and how do their changes relate to water column nutrient stoichiometry?
(5) 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?
(6) Do stoichiometric changes or changes in flow (or salinity) have a greater effect on fish metabolism/macroinvertebrate metabolism?

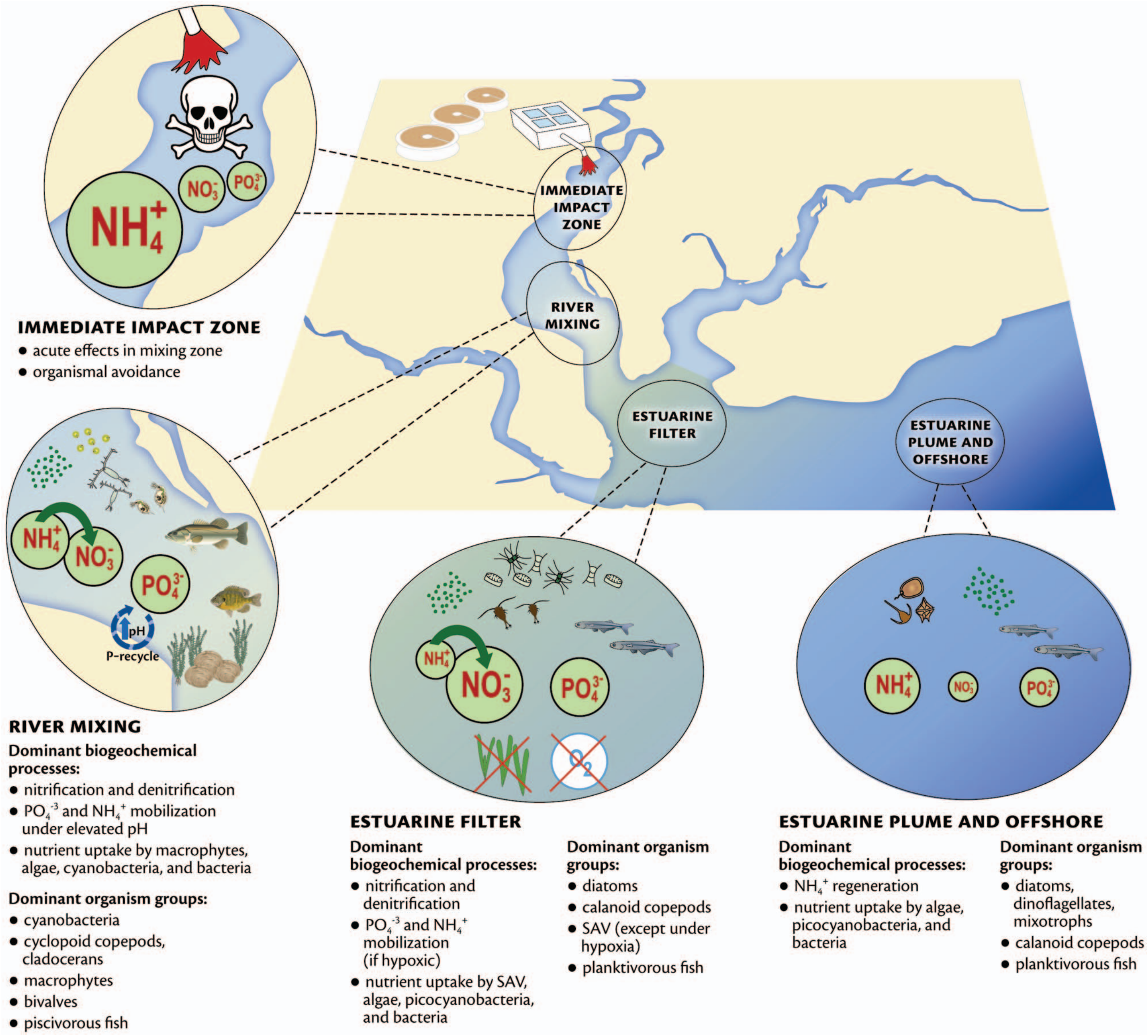

Figure 39 Conceptual diagram of a generalized estuary affected by high NH_4^+ loading from a point source discharge but with reduced P loads. The immediate impact zone has the potential to have strong negative impacts on organisms, either through direct toxicity or indirect inhibition effects. As the NH_4^+ moves downstream, processes such as nitrification (depicted as an arrow from NH_4^+ to $NO_3{}^-$) may convert substantial 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 this P. 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 dinoflagellates expected in such a progression (color figure available online).

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

(8) 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 also advance the knowledge base and tools for managers to make informed decisions regarding the future of the Bay Delta.

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NOTE ADDED IN PROOF

Sobota et al. (2011) have estimated multiple sources of P inputs to the Bay Delta based on spatially explicit information on fertilizer, livestock, agriculture and human population. Human sewage was the dominant source in the Upper Sacramento. They underscore that more biogeochemical information on P sources and export is needed for this system.

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