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Use Care When Interpreting Correlations: The Ammonium Example in the San Francisco Estuary

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THE PARADOX OF A HIGH-NUTRIENT, LOW-PRODUCTIVITY ESTUARY

Early studies of the San Francisco Estuary (estuary) revealed a paradox of high concentrations of nutrients nitrogen (N) and phosphorus (P), but low phytoplankton biomass and primary production. Annual primary production measured in 1980 ranged from 110 to 190 g C m^2 between Suisun Bay and South Bay (Cole and Cloern 1984), well below the primary production in other nutrient–rich estuaries such as Chesapeake Bay and Long Island sound (Cloern et al. 2014). Annual primary production in the Sacramento–San Joaquin Delta (Delta) has decreased to only 70 g C m^2 (Jassby et al. 2002), and low productivity at the food web base is a contributing factor to declining abundances of native fish and their food resources (Sommer et al. 2007).

Early research identified four attributes of the estuary that constrain phytoplankton production. First, biomass cannot accumulate in the upper estuary during the wet season when flushing rate exceeds phytoplankton growth rates (Cloern et al. 1983). Second, the estuary has high sediment-derived turbidity that limits light availability to support photosynthesis (Cloern 1987). Third, studies in South Bay revealed that spring blooms occur during low-energy neap tides, but they dissipate during high-energy spring tides (Cloern 1991). Fourth, an abrupt fivefold decrease of primary production occurred in Suisun Bay after the clam *Potamocorbula amurensis* was introduced in 1986 (Alpine and Cloern 1992). Two decades of research resolved the low productivity paradox as an outcome of multiple processes: fast export during winter–spring, light-limited growth, and rapid losses to grazing by introduced clams.

Then, in the 2000s, a single factor was proposed as the cause of low primary production: suppression of phytoplankton growth by ammonium (NH_4), the primary form of dissolved inorganic N discharged from the Sacramento Regional Wastewater Treatment Facility (SRWTF). This ammonium-suppression hypothesis was supported by measurements of reduced nitrate (NO_3) uptake by phytoplankton when NH_4 concentrations exceed about 4 µM (Dugdale et al. 2007), faster diatom growth on NO_3 than on NH_4 (Parker et al. 2012), decadal trends of increasing NH_4 loading and decreasing primary production (Dugdale et al. 2012), and spring blooms observed in Suisun Bay when NH_4 was diluted by pulses of high river inflow (Dugdale et al. 2012). If NH_4 from municipal wastewater is the root cause of low phytoplankton production, then biological productivity in the estuary can be amplified by a single action: removal of NH_4 from the SRWTF effluent. Predictions were published that this management action would "result in a return to the pre-1979 food web that supported larger zooplankton and higher food quality for fish" (Dugdale et al. 2007), and that NH_4 removal from wastewater "is essential to restoring historic pelagic fish populations" (Glibert 2010).

The underlying cause(s) of the low-productivity paradox have important implications for meeting California's goal of restoring and enhancing the Delta ecosystem, and the ammonium suppression hypothesis gained traction because it offered hope that we could take a discrete action to enhance biological productivity. Traction of that hypothesis has held over time. For example, I recently heard a talk with a data plot that showed a strong inverse relationship between NH_4 and chlorophyll concentrations as evidence to support the ammonium suppression hypothesis. Correlations do not identify cause-effect relationships. I use this example to illustrate why care is needed when we make inferences about environmental changes from correlations. I suggest here three steps to test and validate those inferences.

STEP 1: ASK IF THE INFERENCE IS BASED ON A SOUND CONCEPTUAL MODEL

Nitrogen (N) is an essential element for phytoplankton growth, and most of the dissolved inorganic N in estuaries is in the forms of NH_4 and NO_3 (Cloern et al. 2020). The ammonium-suppression hypothesis is grounded in assumptions that phytoplankton (diatoms in particular) grow faster with NO_3 as their N supply, and that NH_4 inhibits phytoplankton utilization of that N supply. From the perspective of phytoplankton production, NH_4 is depicted in the hypothesis as a bad form and NO_3 as a good form of N. Observational data from long-term US Geological Survey (USGS) studies of the estuary show a pattern that seems consistent with this conceptual model: chlorophyll is always low when NH_4 is high, and it only reaches high levels when NH_4 is low (Figure 1). If, as inferred, this pattern is explained by ammonium suppression of phytoplankton growth, then we would expect a different (positive) correlation between chlorophyll and NO_3: the N form presumed to support fast growth. However, chlorophyll and NO_3 have the same inverse relationship (Figure 2) seen in Figure 1. Phosphorus is another essential element for phytoplankton, and chlorophyll is also negatively correlated with phosphate concentration (Figure 2).

At first glance, these negative correlations between phytoplankton biomass and nutrient concentrations seem paradoxical. Phytoplankton require N and P for growth, so why is chlorophyll low in samples having high nutrient concentrations?

Figure 1 An inverse relationship between chlorophyll and ammonium concentration in 7,074 water samples collected by USGS between lower South San Francisco Bay (station 32) and the Sacramento River (station 657 at Rio Vista) over the period March 1972 through May 2019. The Spearman rank correlation test confirms a highly significant ($p < 10^{-16}$) negative correlation between chlorophyll and NH_4. *Source: Schraga et al. (2020)*.

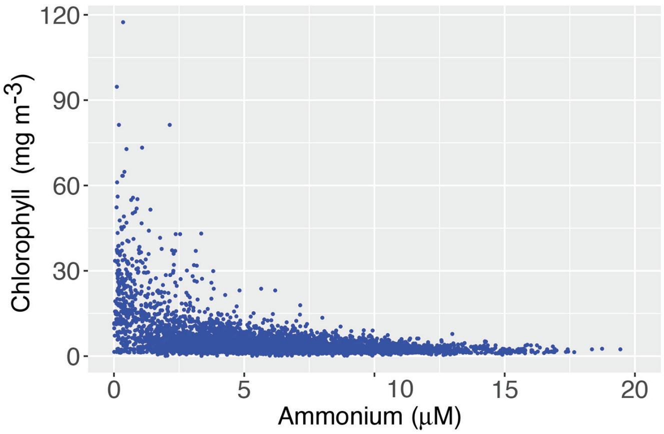
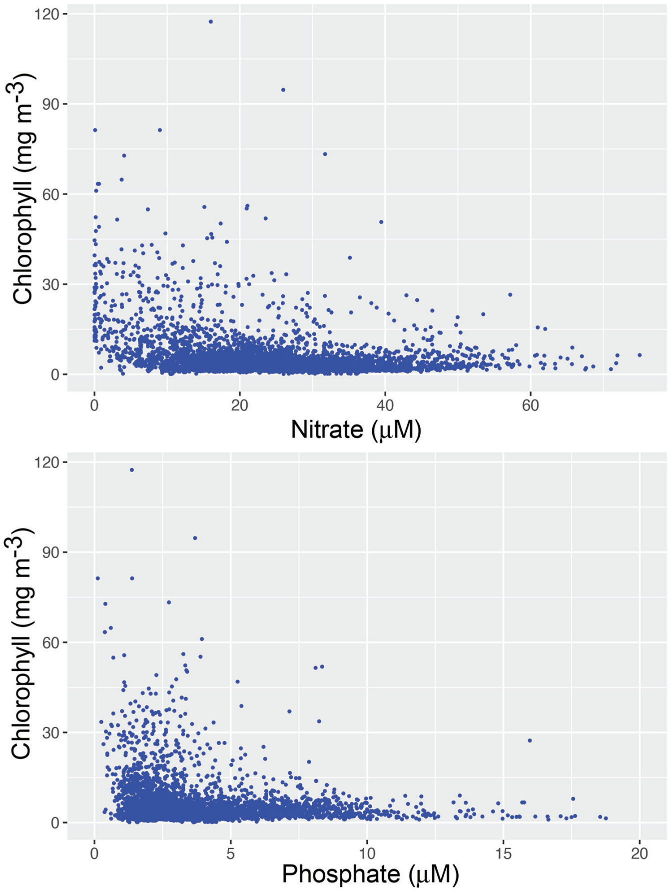


Figure 2 Inverse relationships between chlorophyll and nitrate NO_3 and phosphate concentrations in water samples collected by USGS from 1972–1999. Negative correlations between chlorophyll and both nitrate and phosphate are highly significant.



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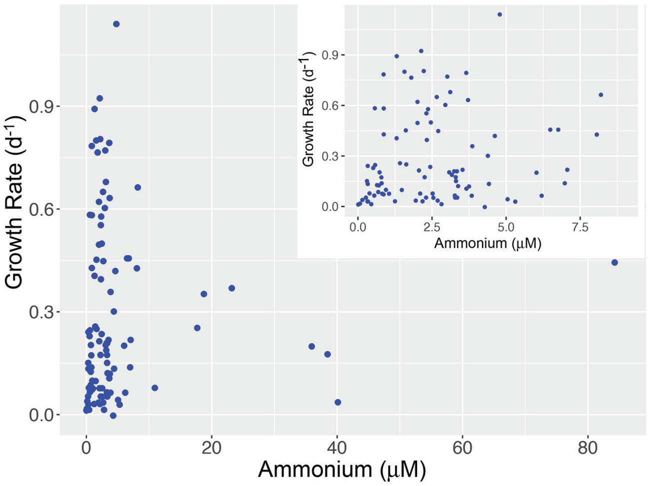
This paradox is resolved with a different conceptual model: phytoplankton regulate nutrient concentrations through their assimilation of dissolved forms and conversion into new biomass. As chlorophyll concentration increases during blooms, dissolved N and P concentrations are drawn down. Conversely, nutrient concentrations increase after blooms terminate and the N and P content of phytoplankton biomass is returned into dissolved forms. Therefore, the negative correlations between chlorophyll and NH_4 (and NO_3 and phosphate) are not a result of growth inhibition, but rather the result of fast nutrient uptake during blooms. Sound inferences from correlations are consistent with established conceptual models, and the concept of phytoplankton regulation of nutrient concentrations in the estuary was first demonstrated in the 1970s by David Peterson (Peterson 1979), who measured lowest NH_4 and NO_3 concentrations during summer blooms that developed regularly in Suisun Bay before the introduction of *Potamocorbula amurensis* (Alpine and Cloern 1992).

STEP 2: CORRELATE THE APPROPRIATE VARIABLES

A second validation step is to ensure that correlated variables match those expected from the conceptual model to have a cause–effect relationship. The ammonium-suppression hypothesis is that NH_4 suppresses phytoplankton growth rate. Therefore, the appropriate correlation analysis to test that hypothesis is between growth rate and NH_4, not between chlorophyll and NH_4 (Figure 1). Phytoplankton growth rate (μ) can be computed from paired measurements of chlorophyll-*a* concentration (CHL) and phytoplankton net primary productivity (NPP) as: $\mu = (NPP/CHL) \times CHL{:}C$ (Cloern et al. 1995). The first term in this equation is the daily amount of carbon biomass produced per unit chlorophyll. The second term (CHL:C) is the ratio of chlorophyll-*a* to carbon in phytoplankton cells; this conversion is required because productivity is measured in carbon units and biomass in chlorophyll units. Phytoplankton growth rates in the estuary vary substantially (Figure 3), and most of that variability is associated with light availability as determined by water depth and transparency (Cloern et al. 1985).

I used the equation above to compute phytoplankton growth rates along the salinity gradient of the estuary and in river and slough habitats of the Delta where NPP, CHL and NH_4 were all measured (Jassby et al. 2002; 2002 conversation between BE Cole and JC, unreferenced, see “Notes”). Within this data set, there is no correlation ($p = 0.82$) between growth rate and NH_4 concentration (Figure 3). The distribution of NH_4 concentrations is uneven, with 94 of 102 samples having NH_4 concentrations < 10 µM and only eight with higher NH_4 concentrations (Figure 3). If we remove the influence of these eight high-NH_4 samples and consider only those in the 1- to 10-µM NH_4 range (Figure 3 *inset*), there is, again, no significant correlation between growth rate and NH_4. These results are incompatible with the hypothesis that ammonium suppresses phytoplankton growth rate in the estuary. This data set is limited because primary productivity is not measured in monitoring programs. However, it illustrates a key point: opposing inferences would be made about the ammonium effect on phytoplankton depending upon

Figure 3 Paired measurements of phytoplankton growth rate and ammonium (NH_4) concentrations in 102 samples collected along the salinity gradient of San Francisco Bay and in channels and sloughs of the Sacramento–San Joaquin Delta. The *inset* shows growth rates in samples where NH_4 concentration was less than 10 µM.



whether they are based on NH_4 correlation with chlorophyll (strongly negative, Figure 1) or with growth rate (no correlation, Figure 3).

STEP 3: EXAMINE THE FULL BODY OF EVIDENCE

The ammonium-suppression hypothesis arose from and is consistent with two kinds of evidence. First, monitoring data from the Interagency Ecological Program (IEP) show parallel trends of increasing NH_4 and decreasing chlorophyll concentrations during an era when NH_4 loading from the SRWTF has increased (Cloern 2019). Second, many laboratory (e.g., Lomas and Glibert 1999) and field measurements (e.g., Dugdale et al. 2007) show that NH_4 can inhibit NO_3 utilization by phytoplankton and, in particular, diatoms. However, rigorous testing of a hypotheses requires consideration of all the relevant evidence.

Experimentation

In this case, the relevant evidence includes a rich history of laboratory experimentation to measure growth responses of phytoplankton to varying N concentrations and forms. An early experiment showed that *Skeletonema costatum*, a common diatom in San Francisco Bay, can grow rapidly with NH_4 as the N source at a concentration of 12 µM (Harrison et al. 1976). This exceeds the mean NH_4 concentration (7 µM) measured along the salinity gradients of the estuary (Cloern et al. 2020). Similar experimental results have accumulated since, and a review of 113 studies (Collos and Harrison 2014) revealed a wide range of growth-rate responses to NH_4 across algal species. Optimal growth of 27 diatom species occurred at a mean NH_4 concentration of 337 µM (much higher than concentrations found in the estuary), and growth inhibition began at a mean of 725 µM. The authors of this review concluded that “ammonium toxicity effects on growth rates are not likely to occur in the field where NH_4 concentrations are usually well below 100 µM.” Maximum NH_4 concentrations in the Sacramento River occur near the SRWTF outfall, where they range from 30 to 80 µM (Strong et al. 2021). These peak concentrations decrease rapidly downstream through dilution and the microbial process of nitrification that converts NH_4 to NO_3 (Kraus et al. 2017).

Collos and Harrison (2014) cautioned that laboratory experiments often use species that have been in culture for many years and may not represent their physiologies in nature. To address this concern, Berg et al. (2017) isolated four diatom and two chlorophyte species from Suisun Bay and the lower Sacramento River, then measured their growth (cell division) rates at NH_4 concentrations that ranged from 20 to 3,000 µM. This experiment with species isolated from the Delta showed no reductions in growth rate at NH_4 concentrations below 200 µM, and that all diatom species grew faster with NH_4 as the N source, compared to NO_3.

There is always some uncertainty about the relevance of these kinds of laboratory studies to natural systems, and two experiments have been conducted recently in the Sacramento River to measure NH_4 effects on phytoplankton growth *in situ*. The SRWTF is the largest source of NH_4 to the Delta (Strong et al. 2021), and in the first experiment that source was halted on two occasions to measure downstream effects on phytoplankton communities and processes. These experiments with natural communities showed no increases in either chlorophyll concentration or primary productivity, and no changes in phytoplankton community composition after the wastewater supply was turned off. The authors concluded that "Results from this study do not support the hypothesis that wastewater effluent with high NH_4 concentrations is the principal cause of downstream phytoplankton declines" (Kraus et al. 2017).

In a second experiment, water samples collected in the lower Sacramento River were amended with different N-enrichment treatments (NH_4, NO_3, or full wastewater effluent) and incubated *in situ* for 48 hours to measure phytoplankton physiological and community responses to different nitrogen forms and concentrations (Strong et al. 2021). This experiment again showed that NH_4 inhibits NO_3 uptake. However, there was no evidence of NH_4 suppression of phytoplankton growth rate. Chlorophyll concentration and cell abundance both increased in all treatments, including high (> 40 µM) NH_4 additions, and diatoms grew faster than other algal forms. From this experiment with natural communities, the authors concluded that "high anthropogenic NH_4 loading from wastewater effluent is not driving the lower productivity and decline of pelagic organisms in the Delta."

Observational Data

The second kind of evidence is the long record of water-quality measurements made in the estuary by the IEP (*https://iep.ca.gov/Science-Synthesis-Service/Monitoring-Programs*). This record contains the trends of increasing NH_4 and decreasing chlorophyll that inspired the ammonium-suppression hypothesis. However, it contains substantially more information than these two trends, and I give five examples that provide deeper insights into the changes that underlie losses of phytoplankton biomass and primary production.

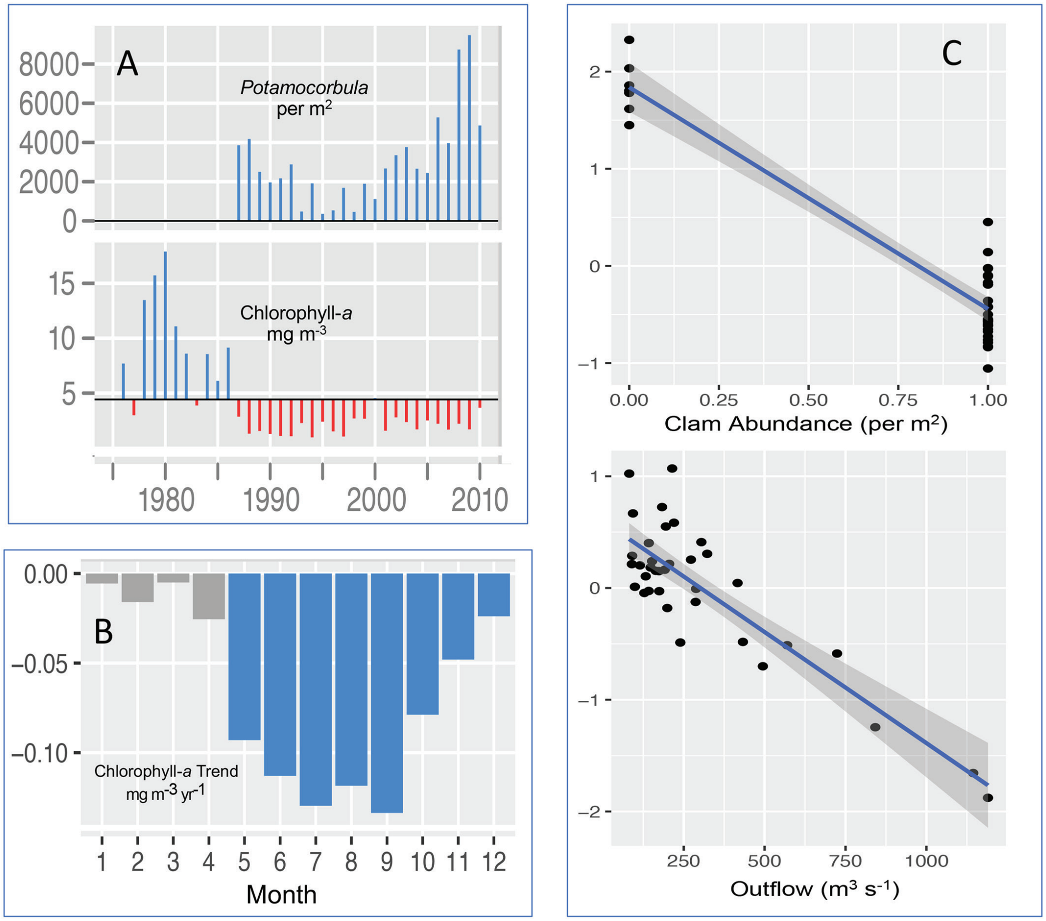


Figure 4 (A) Mean annual abundance of *Potamocorbula amurensis* and chlorophyll-*a* concentration in Suisun Bay (IEP station D7) from 1975–2010. *Blue bars* exceed the long-term mean; *red bars* are below the long-term mean. *Source: Adapted from Figure 11 in Cloern and Jassby (2012)*. (**B**) Monthly trends of chlorophyll-*a* in Suisun Bay (mean from IEP stations D7 and D8) over the period 1975–2016. *Bar heights* measure trend magnitude for each month; *blue bars* are statistically significant negative trends. *Source: Adapted from Figure 6C in Cloern (2019)*. (**C**) Model fits of log-transformed summer (May through September) chlorophyll-*a* concentration in Suisun Bay as functions of clam presence/absence and Delta outflow over the period 1975–2016. *Source: Adapted from Figure 8C in Cloern (2019).*

The changing NH_4 pattern in Suisun Bay has been one of steady increase over time, while the chlorophyll decrease occurred as a discrete downshift (Figure 4A). Change-point analysis identified an abrupt decrease in summer chlorophyll in 1987 (Cloern 2019). These asynchronous patterns suggest that the NH_4 and chlorophyll trends might be unrelated.

The chlorophyll decrease measured in Suisun Bay by the IEP from 1975 to 2016 has a strong seasonal pattern of no changes for the months January through April, but large decreases for the months May through September (Figure 4B). Abrupt losses of summer chlorophyll (and primary production) also occurred in 1987 across the entire IEP sampling network in the Delta (Jassby et al. 2002). Therefore, the long-term trends of decreasing phytoplankton biomass and production result from the loss of summer blooms. This implies an underlying loss process that is strongest in summer.

The loss of summer blooms beginning in 1987 coincided with the explosive population growth of the clam *Potamocorbula amurensis* after it was introduced to the estuary in 1986 (Figure 4B), an event described as a "Remarkable Invasion of San Francisco Bay" (Carlton et al. 1990). Within a year, this invasive species reached population levels high enough to consume phytoplankton cells faster than they are replaced by cell division (Cloern and Jassby 2012). That consumption rate is highest in summer (Kimmerer and Thompson 2014). Thus, rate measurements and long-term monitoring provide strong evidence that the loss of historical summer blooms and corresponding 80% decrease in annual mean chlorophyll (Cloern and Jassby 2012) were consequences of ecosystem disturbance by an introduced species (Alpine and Cloern 1992).

In the years after that invasion there has been a small but significant trend of increasing chlorophyll while NH_4 concentrations continued to increase (see Figure 3 in Cloern 2019). Synchronous increases of chlorophyll and NH_4 over the past 3 decades are not consistent with the ammonium suppression hypothesis.

A statistical (Generalized Additive) model of monthly time-series compiled by the IEP shows that 80% of the annual variability of summer chlorophyll in Suisun Bay is associated with two factors (Figure 4C): (1) clam presence (as a categorial variable, present or absent), and (2) Delta outflow (Cloern 2019). Clam presence is a proxy for grazing loss, Delta outflow is a proxy for residence time, and the clam effect is five times larger than the outflow effect. No other variables in the model—including salinity, temperature, NO_3, NH_4, or phosphate concentrations—were related to summer chlorophyll in Suisun Bay.

These five results are all consistent with an alternative hypothesis that the chlorophyll decline in Suisun Bay was largely a result of increased grazing losses to an introduced filter feeder and was unrelated to ammonium suppression of growth.

ADVICE FROM A GRIZZLED DATA WRANGLER

The state of California has legislated goals to increase its water supply reliability and restore and improve the Delta ecosystem. The Delta Science Plan (DSC 2019) calls for development and application of the “best available science” to meet those goals. From my perspective, the “best” science is rigorous, where rigor comes from critical thinking and use of all available evidence to test and validate conceptual models of ecosystem change.

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