

NUTRIENT ADDITION EFFECTS AND THE ROLE OF VEGETATION IN  
CALIFORNIA VERNAL POOLS

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Abstract  
of  
NUTRIENT ADDITION EFFECTS AND THE ROLE OF VEGETATION IN  
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Increased nutrient deposition from excessive fertilizer application, manure production, and other industrial discharges into aquatic environments is altering the structure and function of freshwater ecosystems worldwide. Eutrophication is characterized by the input of excessive nutrients, which can cause a shift from a relatively clear, macrophyte-dominated condition (oligotrophic) to a turbid, algae-dominated condition at the highest nutrient levels (eutrophic). It has been extensively demonstrated to occur in continuously flooded aquatic systems, but is poorly understood in seasonal wetlands. This study investigated the effects of nutrient addition and the role of vegetation in the manifestation of these effects in California vernal pools – a highly threatened seasonal wetland ecosystem susceptible to eutrophication from nutrient-laden storm water runoff and excrement from grazing animals. Applying predictions observed in continuously aquatic systems and recent nutrient-addition experiments in vernal pools, it was hypothesized that the response of vernal pools to nutrient enrichment will be consistent with eutrophication observed in continuously aquatic systems (e.g., increased algae, turbidity, conductivity, decreased dissolved

oxygen) and that the presence of vegetation will mitigate the effects of eutrophication, with beneficial effects to invertebrate populations.

The experimental design consisted of five nutrient (phosphorous) treatments replicated three times and placed in a vegetation or vegetation-removal treatment. Turbidity, dissolved oxygen, algae concentration, invertebrate density, invertebrate species richness, pH, and conductivity were measured biweekly over six weeks. Treatment effects were determined using factorial multivariate analysis of variance with Fisher's Least Significant Different post-hoc tests conducted for significant effects of nutrient addition treatments. Correlations between dependent variables were estimated using Spearman rank correlation coefficients.

Vernal pool mesocosms did not exhibit a eutrophic response consistent with continuously aquatic systems when nutrients were added, but this may be attributable to the timing of the study. Nutrient addition did increase invertebrate species richness. The presence of vegetation reduced algal densities and thus lowered turbidity and also had positive effects on invertebrate species richness. This study demonstrated that the presence of vegetation mitigated some adverse effects of eutrophication and informed the ongoing debate regarding the benefit of grazing as a management tool in vernal pool ecosystems.

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\_\_\_\_\_  
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## INTRODUCTION

Increased nutrient deposition from excessive fertilizer application, manure production, and other industrial discharges into aquatic environments is altering the structure and function of freshwater ecosystems worldwide (Carpenter et al. 1998). Adverse effects of this influx of nutrients (nitrogen and phosphorous) are among the most visible human-induced changes to the biosphere (Smith 2003; Smith and Schindler 2009). These effects in freshwater ecosystems include major functional and compositional shifts (Scheffer et al. 2001; Schindler 2006), decreased species diversity (Kneitel and Lessin 2010), and loss of trophic levels (Smith 2003). Indeed, changes in aquatic communities contribute to eutrophication via complex trophic interactions (Schindler 2006).

Eutrophication is a phenomenon characterized by the excessive growth of filamentous or unicellular algae (algal bloom) from nutrient enrichment in aquatic environments. The algal bloom limits light penetration into the water body (increased turbidity), which decreases the growth of aquatic submerged and emergent vascular plants. The algal bloom is followed by an algal die-off when nutrients are depleted by the growing algae. As microorganisms consume dead algae, accelerated respiration by microbes during decomposition lowers dissolved oxygen concentration. Reduced dissolved oxygen availability adversely affects community structure and function, including invertebrate species richness and density.

Based on extensive research in shallow lakes, it has been demonstrated that aquatic ecosystems may exist in two alternative states depending on nutrient levels: clear with abundant vegetation at low nutrient levels (oligotrophic) or turbid and algae-dominated with sparse vegetation at high nutrient levels (eutrophic) (e.g., Scheffer et al. 1993; Jeppsen et al. 1997; and reviews in Schindler 2006; Smith and Schindler 2009). Similarly, studies conducted in the Florida everglades and prairie wetlands of the midwestern United States have documented a reduction in vascular plant species density with nutrient enrichment (Vaithiyanathan and Richardson 1999; Craft et al. 2007; and review in Rader and Richardson 1992).

Although eutrophication is caused by nutrient enrichment, the interaction between vegetation and turbidity creates a positive feedback where vegetation tends to promote water clarity, whereas high turbidity limits vegetation growth (Scheffer et al. 1993). Other ecological feedback mechanisms pertaining to interactions between nutrients, submerged aquatic vegetation, turbidity, algae, and zooplankton also dictate how the eutrophic response manifests in continuously flooded aquatic systems (Figure 1). Specifically, vegetation can inhibit algal growth by reducing nutrient availability and potentially releasing allelopathic substances (Moore et al. 1994; Moss et al. 1994). Vegetation also provides zooplankton with habitat and a refuge from predation; this release results in increased zooplankton grazing on algae, which reduces turbidity (Timms and Moss 1984; Hargeby et al. 1994). Finally, vegetation can reduce turbidity by anchoring soil to prevent sediment resuspension (Blindow et al. 1993).

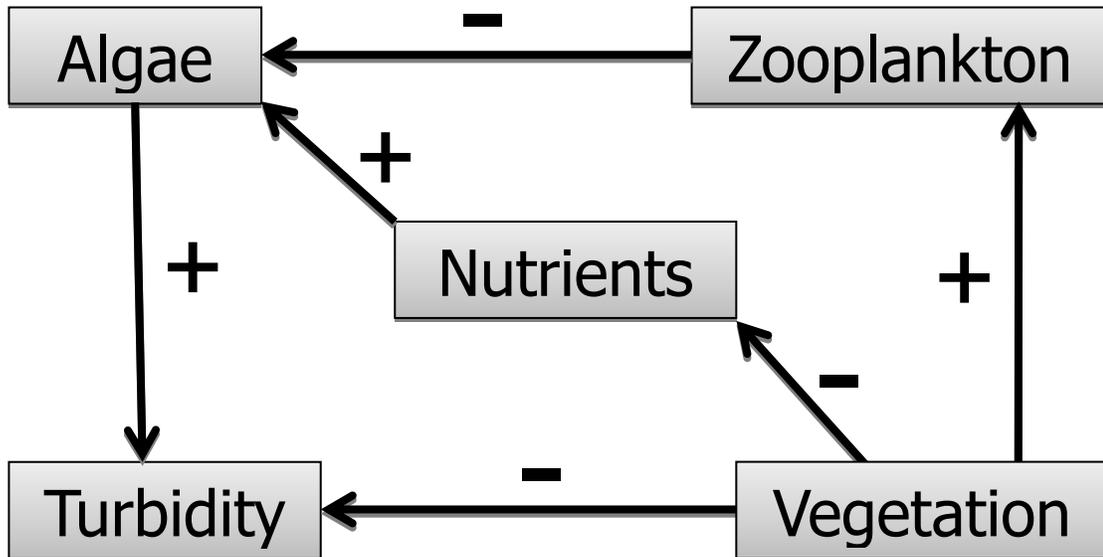


Figure 1. Key interactions among biological components with primary responsibility for how eutrophication manifests in aquatic ecosystems. The effect of each component on another can be determined by the sign along the route between them: positive (increase) or negative (decrease). Modified from Scheffer et al. 1993.

The relationship between nutrient levels and resulting eutrophic conditions is well understood. For example, Angeler and Moreno (2006) applied fire retardant containing ammonium polyphosphates to temporary pond mesocosms and found that nutrient addition increased algae, pH, turbidity, and decreased dissolved oxygen concentration. Jackson (2003) observed that shallow lakes with higher levels of dissolved phosphorous exhibited significantly higher algal concentrations. However, our understanding of the role of vegetation in mediating the interaction between nutrient levels and eutrophication is primarily limited to observational studies (e.g., Scheffer et al. 1993; Blindow et al. 1993, Jackson 2003), which have documented that turbid lakes with relatively high levels of phosphorous supported lower biomass of aquatic plants than clear lakes. To date, only one experimental study removed or retained submerged aquatic vegetation along a gradient of increasing nutrients (Balls et al. 1989). This study demonstrated that lakes containing submerged vegetation were able to strongly resist the effects of eutrophication when nitrogen and phosphorous were added. In particular, significant increases in algal growth were found only in lakes where aquatic vegetation was manually removed. It is unclear, however, how generalized this pattern is in aquatic ecosystems, particularly seasonal wetlands. The goal of this study is to investigate the role of vegetation in mediating the effects of eutrophication in California vernal pools – a highly specialized, seasonal wetland ecosystem.

#### Study System – California Vernal Pools

Vernal pools are ephemeral wetlands found in shallow depressions over an underlying impermeable substrate (e.g., claypan) that prevents water from percolating

through the soil (Holland and Jain 1981). They are defined by three ecological phases that are attributable to seasonal variation in temperature and precipitation: the aquatic phase, the terrestrial phase, and the dry phase (Holland and Jain 1981; King et al. 1996; Bliss and Zedler 1998; Keeley and Zedler 1998). The particular focus of this study is the aquatic phase. Despite having this drying/inundation cycle in common, vernal pools can exhibit marked ecological differences based on their underlying geologic substrate; these differences may influence responses to abiotic factors, including nutrient addition.

Vernal pools in California harbor high levels of endemic and special-status species (Federal Register 2003). Recent studies estimate that more than 90 percent of the historic expanse of vernal pool habitat has been lost to urban and agricultural development (Holland 2009). Many of the remaining vernal pool complexes are located near residential, industrial, or commercial development and in agricultural areas. This makes them susceptible to nutrient-rich stormwater runoff and nutrient loading from the manure and urine of grazing animals (Carpenter et al. 1998; Holland 2009). Nutrient addition to vernal pools may initially increase invertebrate densities but ultimately leads to eutrophication. The reduction in dissolved oxygen as a consequence of eutrophication can kill vernal pool crustaceans (Rogers 1998). In addition to adding nutrients, runoff into vernal pools can lead to increased siltation. Vernal pool invertebrates and larval amphibians, which respire through gills or gill-like organs, may suffocate in pools with high rates of siltation and concomitant excess turbidity. Excessive turbidity in vernal pools may also asphyxiate eggs and cysts or prevent plant germination by preventing absorption of sufficient oxygen (USFWS 2005).

With the exception of recent work by Kneitel and Lessin (2010) and Croel and Kneitel (2011a), the effects of nutrient addition on vernal pools have not been empirically tested. Kneitel and Lessin (2010) and Croel and Kneitel (2011a) found that nutrient addition to vernal pool mesocosms significantly increased algal biomass during the aquatic phase, which resulted in a corresponding decrease in aquatic vascular plant cover and species richness. These results indicate that vernal pools may exhibit a eutrophic response that is consistent with continuously flooded aquatic systems. However, the role of vegetation in mediating the effects of eutrophication in vernal pools remains unclear.

In this study, mesocosms lined with vernal pool soil were used to test the following two hypotheses: 1) phosphorous addition will cause vernal pools to become eutrophic; and 2) the presence of vegetation will prevent eutrophication from occurring in vernal pools compared to pools without vegetation. In the case of the first hypothesis, I predict that dissolved oxygen will decrease, whereas algal density, turbidity, conductivity, invertebrate species richness and invertebrate species density will increase. In the case of the second hypothesis, I predict that removal of vegetation from mesocosms will increase algal density, turbidity, and conductivity, but decrease invertebrate species richness, invertebrate species density, and dissolved oxygen concentration.

## MATERIALS AND METHODS

### Vernal Pool Mesocosms

In December 2009, soil was collected from randomly selected points within multiple vernal pools at the Gill Ranch Agricultural Preserve adjacent to the Gill Ranch Conservation Bank in southeastern Sacramento County, California. Predominant soil types at Gill Ranch include Hadselville-Pentz and Redding-Corning gravelly loam (NRCS 2010), which are respectively characterized by Holland (1978) as Northern Hardpan and Northern Volcanic Mudflow vernal pools. The top 6-8 centimeters of soil was collected to include the egg bank (Brendock and De Meester 2003) using a trowel and homogenized in a cement mixer within one week of collection to intersperse seeds and cysts. Approximately 12.5 kilograms of soil (or approximately 0.1 meter [m] deep; surface area = 0.24 m<sup>2</sup>; volume = 0.007 m<sup>3</sup>) was placed in 30 experimental mesocosms (material = plastic, volume = 19 liters, diameter = 0.3 m, height = 0.3 m). Using soil from naturally-occurring vernal pools allowed for mimicking phosphorous concentrations and biotic communities representative of a natural vernal pool ecosystem. Previous studies have found consistency between mesocosms and natural vernal pools because of the relative simplicity of the trophic structure of vernal pools (De Meester et al. 2005; Kneitel and Lessin 2010). Further, a recent study by Spivak et al. (2010) demonstrated that results from small-scale nutrient-limitation experiments in aquatic mesocosms are relevant to large-scale processes, such as eutrophication.

## Experimental Design

In March 2010, three replicates consisting of 10 mesocosms each were established in full sun within the California State University, Sacramento Arboretum. Mesocosms were naturally filled with rainwater, but were supplemented with tap water when needed to maintain water levels at a minimum of six inches (15 cm) above the soil surface. To test the hypothesis that phosphorous addition will cause vernal pools to become eutrophic, five phosphorous treatments were implemented consisting of an aqueous solution of potassium phosphate ( $\text{KH}_2\text{PO}_4$ ; Jardillier et al. 2005; Kneitel and Lessin 2010). Phosphorous treatments were applied to the mesocosms in a randomized block design in the following concentrations: 0.0 mg/L (control), 0.1 mg/L (low), 0.3 mg/L (medium), 0.9 mg/L (high), and 2.7 mg/L (very high). Phosphorous treatments were applied weekly starting approximately two weeks after inundation. To test the hypothesis that the presence of vegetation will prevent eutrophication from occurring in vernal pools compared to pools without vegetation, two vegetation treatments were implemented consisting of 1) completely removing vascular plants (“vegetation-removal”) and 2) retaining the vegetation (“vegetated”). In the vegetation-removal treatment, submerged aquatic vegetation was removed following inundation and any subsequent growth was removed at least twice weekly for the duration of the study.

Phosphorous treatments were based on observed phosphorous levels in natural vernal pools (Yolo County and ESA 2005; Rains et al. 2006; Kneitel *unpublished data*) and phosphorous addition treatments applied in previous vernal pool studies (Kneitel and Lessin 2010). Phosphorous is the primary nutrient limiting productivity of most

freshwater aquatic ecosystems (Bennett et al. 2001; Carpenter 2005). Consequently, it is considered the nutrient most responsible for excessive growth of algae in these ecosystems (Correll 1998). Nitrates are rapidly assimilated in vernal pools (Rains et al. 2006; Kneitel and Lessin 2010). Despite high levels of nitrogen addition in a study by Kneitel and Lessin (2010), nitrates did not differ among treatments. Therefore, a nitrogen treatment was not administered in this study.

#### Data Collection

Every two weeks for six weeks the following variables were measured in each mesocosm: total phosphorus concentration, dissolved oxygen concentration, turbidity, conductivity, pH, invertebrate density, and invertebrate species richness. Measurement units, equipment, and locations in which the data were collected are presented in Table 1.

Invertebrate density and species richness were sampled by sweeping each mesocosm with a 1 millimeter mesh net for 10 seconds, in a pattern designed to ensure coverage of the width and depth of the water column. Invertebrate classification (Class, Order, or Family, if possible) and number of individuals per taxonomic group per sample were determined.

Algal densities were measured after six weeks at the conclusion of the study. A water sample was collected from each mesocosm and diluted by a factor of two. One milliliter of sample was placed on a gridded Sedgewick rafter cell under a dissecting microscope and photographed. The number of algae cells per microliter (one gridded

Table 1. Variables, units of measure, measurement equipment, and the location where the measurements were collected (ntu = nephelometric turbidity units; ppm = parts per million).

Variable	Unit of Measure	Equipment	Location
Total phosphorous concentration	mg/L PO <sub>4</sub> - P	Hach DREL/2800 Complete Water Quality Lab	Lab
Dissolved oxygen	mg/L	CyberScan PD 300 pH/Dissolved Oxygen Meter	Arboretum
Turbidity	ntu	LaMotte 2020e Portable Turbidity Meter	Lab
Conductivity	ppm	CyberScan PC 10 pH/Conductivity Meter	Arboretum
pH	N/A	CyberScan PD 300 pH/Dissolved Oxygen Meter	Arboretum

square) was counted by processing the digital image using ImageJ software (Rasband 2009).

#### Data Analysis

To maximize the potential for the effects of the phosphorous-addition and vegetation treatments to be realized, only measurements from the final sampling effort (Week 6) were used in the analysis. Phosphorous concentration was not readable due to negative values; it is unclear why this occurred. Homogeneity of variances was tested using Levene's test. Algal density, invertebrate density, and invertebrate species richness were heterogeneous and sufficiently skewed as to warrant log transformation. Effects of the phosphorous-addition treatment and vegetation treatment were determined using multivariate analysis of variance (MANOVA). Phosphorous treatment and vegetation treatment were fixed factors; dissolved oxygen, turbidity, conductivity, pH, algal biomass, invertebrate species richness, and invertebrate species density were the dependent variables. When phosphorous-addition effects were significant, pairwise comparisons of phosphorous-addition treatments were conducted using Fisher's Least Significant Difference (LSD) post-hoc test. A separate MANOVA test was conducted to assess block effects.

Additionally, correlations between dissolved oxygen, turbidity, conductivity, pH, algal density, invertebrate density, and invertebrate species richness were estimated using Spearman rank correlation coefficients because most data were not normally distributed. Statistical tests were conducted using PASW Statistics 18 (Release 18.0.2) and results considered to be significant if  $P < 0.05$ .

## RESULTS

Overall MANOVA results for vegetation removal (Wilks'  $\lambda = 0.46$ ,  $F_{(1, 29)} = 2.36$ ,  $P = 0.08$ ) and phosphorous addition (Wilks'  $\lambda = 0.36$ ,  $F_{(4, 29)} = 0.62$ ,  $P = 0.92$ ) effects were not significant. Interactions between vegetation removal and phosphorous addition were not significant (MANOVA: Wilks'  $\lambda = 0.43$ ,  $F_{(4, 29)} = 0.50$ ,  $P = 0.98$ ). Block effects were significant (MANOVA: Wilks'  $\lambda = 0.10$ ,  $F_{(2, 29)} = 6.53$ ,  $P < 0.001$ ) for dissolved oxygen, pH, turbidity, and invertebrate species richness, indicating significant variability among the three blocks for these variables.

### Phosphorous-addition Treatment

Phosphorous addition did not significantly affect dissolved oxygen, conductivity, turbidity, pH, invertebrate species richness, or algal density in vernal pool mesocosms (Table 2). However, invertebrate density increased significantly with phosphorous addition (Table 2). Post-hoc analysis (Fisher's LSD test) showed that Medium and Very High phosphorous-addition treatments had significantly greater invertebrate density than Low and Control phosphorous-addition treatments (Figure 2). Mean invertebrate density in the Very High phosphorous-addition treatment was more than two times higher than the Control phosphorous-addition treatment (Table 3).

Table 2. Effect of phosphorous addition and vegetation removal on dependent variables as indicated by P values derived from MANOVA. Entries marked with an asterisk (\*) are significant at  $P < 0.05$ .

Dependent Variable	Phosphorous Addition		Vegetation Removal		Vegetation X Phosphorous	
	$F_{(4, 29)}$	P	$F_{(1, 29)}$	P	$F_{(4, 29)}$	P
Dissolved oxygen	0.29	0.88	1.81	0.19	0.97	0.98
Conductivity	0.38	0.82	0.01	0.93	0.12	0.98
Turbidity	0.72	0.59	2.56	0.13	0.89	0.49
pH	0.50	0.73	5.18	0.03*	1.08	0.39
Invertebrate density <sup>1</sup>	3.56	0.02*	0.62	0.44	0.98	0.44
Invertebrate species richness <sup>1</sup>	0.56	0.69	7.52	0.01*	0.28	0.89
Algal density <sup>1</sup>	1.11	0.38	4.61	0.04*	1.00	0.43

<sup>1</sup>Log-transformed data

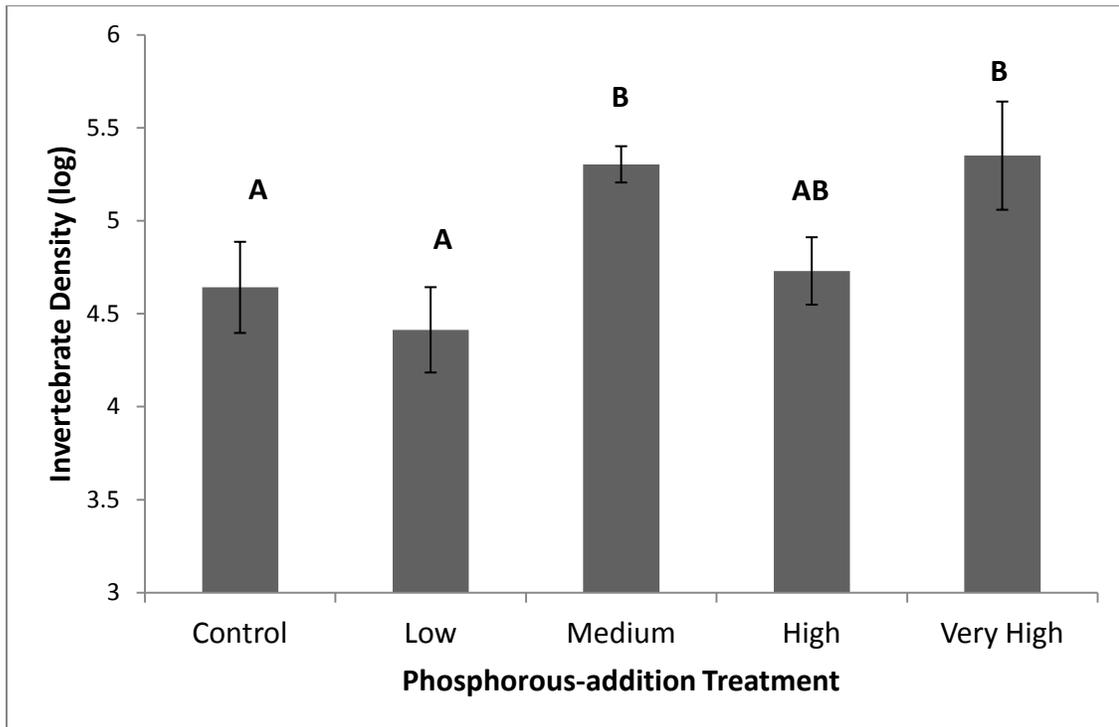


Figure 2. Comparison of invertebrate densities (plotted as log-transformed) (mean  $\pm$  SE) among phosphorous-addition treatments. Phosphorous addition treatment effects were significant (MANOVA,  $P < 0.05$ ) (see Table 2 for statistics). Letters above treatments represent the results of LSD post-hoc tests: treatments with the same letters are not significantly different at  $P > 0.05$  ( $n=3$ ).

Table 3. Means ( $\pm 1$  SE) of dependent variables subjected to vegetation-removal and phosphorous-addition treatments (n=3).

Dependent Variable	Vegetation Treatment		Phosphorous-Addition Treatment				
	Present	Removed	Control	Low	Medium	High	Very High
Dissolved oxygen mg/L	3.7 (0.4)	4.4 (0.3)	3.7 (0.7)	3.6 (0.2)	4.3 (0.6)	4.4 (0.3)	4.1 (0.9)
Conductivity ppm	318.7 (8.7)	317.5 (7.2)	314.5 (8.9)	316.0 (19.9)	322.8 (9.3)	307.2 (9.1)	330.2 (13.3)
Turbidity ntu	97.3 (11.4)	135.6 (20.3)	95.7 (28.7)	106.6 (26.3)	109.5 (20.3)	154.9 (36.8)	105.7 (21.5)
pH	7.6 (0.04)	7.8 (0.04)	7.7 (0.1)	7.7 (0.1)	7.8 (0.1)	7.8 (0.1)	7.7 (0.1)
Invert density individuals	170.1 (48.6)	156.9 (16.5)	121.5 (31.6)	95.0 (24.7)	205.7 (19.2)	122.0 (19.6)	273.5 (108.1)
Invertebrate species richness	2.7 (0.2)	2.13 (0.1)	2.2 (0.2)	2.5 (0.3)	2.3 (0.2)	2.5 (0.2)	2.7 (0.3)
Algal density cells per $\mu$ l	253.6 (33.2)	585.1 (201.3)	273.8 (55.9)	862.7 (494.4)	244.7 (37.6)	353.0 (50.9)	362.5 (127.1)
Cladoceran density individuals	34.7 (33.3)	0.0 (0.0)	0.0 (0.0)	3.3 (3.3)	0.0 (0.0)	0.0 (0.0)	83.3 (83.3)
Chironomid density individuals	29.5 (7.5)	36.1 (5.7)	36.5 (8.5)	21.2 (6.8)	36.7 (7.7)	38.0 (16.9)	31.5 (11.3)
Ostracod density individuals	11.1 (4.3)	2.7 (2.5)	1.8 (1.8)	3.3 (2.4)	5.0 (3.2)	6.7 (5.7)	17.7 (10.4)
Mosquito density individuals	94.9 (18.5)	118.1 (15.5)	83.2 (30.1)	67.2 (24.3)	164.0 (18.7)	77.3 (14.8)	141.0 (25.3)

### Vegetation-removal Treatment

Vegetation removal did not significantly affect dissolved oxygen, conductivity, or turbidity, in vernal pool mesocosms (Table 2). However, pH was significantly higher in vegetation-removal treatments (Table 2). Mean pH for both vegetation removal and vegetated treatments was slightly alkaline (Table 3).

Four invertebrate taxonomic groups were identified in the vernal pool mesocosms: cladocerans (Order Cladocera), chironomids (Family Chironomidae), mosquito (Family Culicidae), and ostracod (Class Ostracoda) (Table 3; Appendix). Overall, mosquito larvae were most abundant, followed by chironomids, cladocerans, and ostracods. Of the four taxonomic groups observed, cladocerans and ostracods were only found in vegetated treatments. Chironomids and mosquito larvae were found in every mesocosm, regardless of vegetation treatment. These species are generally considered opportunistic and resistant to adverse environmental conditions (e.g., poor water quality) (Barbour et al. 1999). Invertebrate species richness in vegetated treatments was significantly greater than in vegetation-removal treatments (Table 2; Figure 3a). Vegetation removal effects on invertebrate species density were not significant.

Vegetation removal resulted in a 230 percent increase in algal density compared to the vegetated treatment; these differences were significant (Table 2, Figure 3b). Further, this increase in algal density was significantly and positively correlated with turbidity ( $r_s = .438$ ,  $P = 0.015$ ; Figure 4). However, there was not a significant direct effect of vegetation treatment on turbidity.

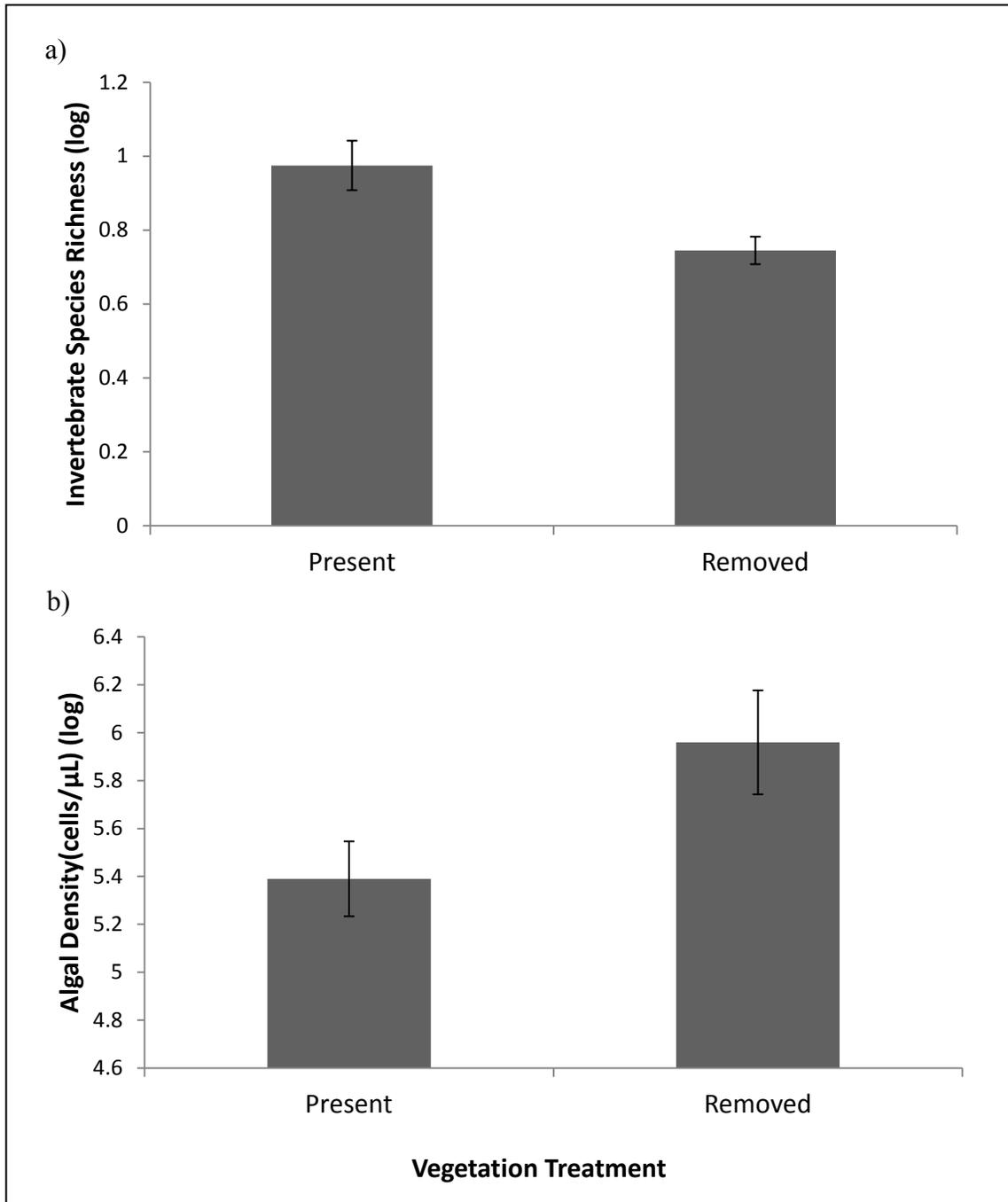


Figure 3. Comparison of a) invertebrate species richness and b) algal density (cells/ $\mu\text{L}$ ) (mean  $\pm$  SE) between vegetation treatments. Both dependent variables were plotted as log-transformed. Vegetation treatment effects were significant (MANOVA,  $P < 0.05$ ) for both dependent variables (see Table 2 for statistics) ( $n=3$ ).

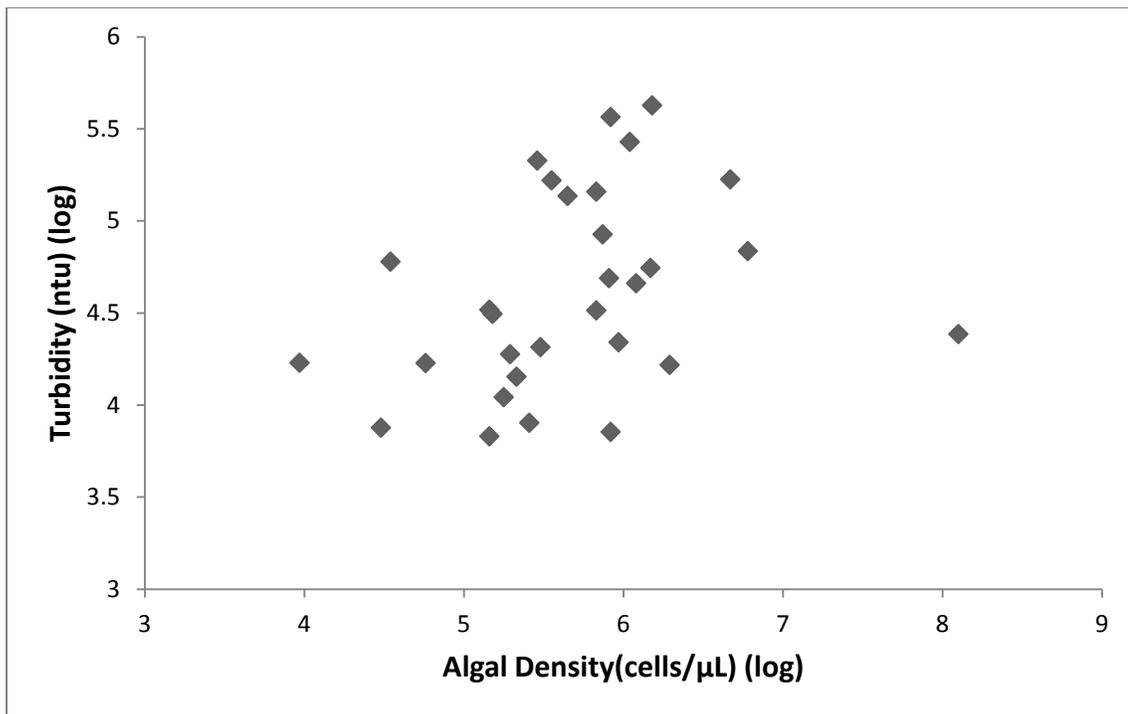


Figure 4. Relationship between algal density and turbidity ( $r = .438$ ,  $P = 0.015$ ). Both variables were plotted as log-transformed.

## DISCUSSION

This study added phosphorous to vernal pool mesocosms to assess the eutrophic response and manipulated the presence of vegetation to determine its role in mitigating adverse effects of phosphorous addition. Phosphorous addition significantly increased invertebrate density, but did not affect water quality or algal density. The presence of vegetation resulted in increased invertebrate richness and reduced algal densities. These results suggest that vernal pools may not elicit the same eutrophic response as continuously flooded aquatic systems when phosphorous is added; however, the presence of vegetation may ameliorate some of the adverse effects that are typically observed in eutrophic water bodies.

Increases in invertebrate density with nutrient addition have been observed in other aquatic ecosystems (e.g., Yee and Juliano 2007), and recently in vernal pools (Croel and Kneitel, *unpublished data*). The positive relationship between resource availability and invertebrate density (herbivore trophic level), without a response in primary producers, reflects the classic trophic cascade theory of Hairston et al. (1960), in which resource-driven (“bottom-up”) effects skip trophic levels because of predator effects (“top-down”). In this framework, resources increased biomass at the basal trophic level (primary producers) only in the absence of primary consumers (herbivores). With the addition of an herbivore trophic level, primary producers are held in check while herbivore densities increase. In this study, it is possible that phosphorous-addition effects

on algae were not evident because algal growth was held in check by increasing zooplankton.

Phosphorous addition did not significantly affect water chemistry variables indicative of eutrophication (low dissolved oxygen and high conductivity). The lack of support for my hypotheses related to eutrophic response could be attributable to the short duration of this study. The aquatic phase of vernal pools commences with the first fall/winter precipitation event and inundation period plays a critical selective role in development of vernal pool flora and fauna (Bliss and Zedler 1998; Bauder 2000). Additionally, duration of inundation has been shown to affect nutrient concentrations in vernal pools (Rains et al. 2006). In this study, the aquatic phase was artificially induced in early March; consequently, there may not have been sufficient time for the biotic community to develop and nutrients to cycle.

In the current study, vegetated vernal pool mesocosms had significantly reduced algae densities and thus lower turbidity than vernal pool mesocosms without vegetation. This is consistent with previous studies of nutrient-driven alternative states in aquatic ecosystems that have demonstrated a shift between the eutrophic and oligotrophic state due to interactions between nutrients, macrophytes, algal growth, and turbidity (Scheffer et al. 1993; Jeppsen et al. 1997; Figure 1). Turbidity increases with nutrients due to increased algal growth and vegetation reduces turbidity (Scheffer 1990).

Mechanisms by which vegetation can reduce turbidity include: phosphorous reduction, habitat enhancement and predation refuge for grazing zooplankton, and prevention of sediment suspension. The empirical observations of this study are

consistent with most of these mechanisms, but did not explicitly test them. Phosphorus uptake by macrophytes has been shown to reduce availability of phosphorous in the water column (Moore et al. 1994; Moss et al. 1994). Balls et al. (1989) found that total phosphorous did not increase significantly with increased phosphorous loading in the presence of submerged vegetation, but did so if the plants were manually cleared. Excess phosphorus in the water column reduces the competitive interactions between macrophytes and algae, resulting in increased algal growth (Correll 1998; Schindler et al. 2008). This study did not examine the fate of added phosphorous, but it is likely that macrophyte uptake could have been a phosphorous sink that resulted in reduced algal densities (Carignan and Kalff 1980).

Another potential mechanism is that aquatic macrophytes provide habitat for zooplankton as well as a refuge from predation by other invertebrates (Hargeby et al. 1994). Proliferation of zooplankton among macrophytes can facilitate increased grazing on phytoplankton, which results in a decrease of phytoplankton biomass (Timms and Moss 1984) and a concomitant decrease in turbidity. This study found that invertebrate species richness was greater in vernal pool mesocosms with vegetation. Of particular interest is that cladocerans and ostracods were only found in vegetated treatments. Cladocerans are particularly effective in reducing phytoplankton growth on submerged macrophytes (Timms & Moss, 1984). In shallow lake experimental enclosures, cladocerans were identified as the dominant zooplankton in vegetated treatments compared to absent vegetation in controls, suggesting that the structural complexity of macrophytes may have provided effective refuge from predation for this phytoplankton

grazer (Jeppesen et al. 2002). Cladoceran dominance was also evident in lacustrine wetlands with relatively low turbidity and phytoplankton biomass in contrast to wetlands with high turbidity and phytoplankton biomass (Hann and Zrum 1997). The composition of the invertebrate community in this study is consistent with these findings. It is possible that grazing zooplankton exclusively found in vegetated mesocosms (Cladocera and Ostracoda) contributed to reduced algal densities.

A third possible mechanism by which vegetation decreases turbidity is by the anchoring of sediment (Blindow et al. 1993). In support of this hypothesis, recent work in vernal pool mesocosms (Croel and Kneitel 2011b) found that highly turbid mesocosms had significantly reduced total macrophyte cover. In that experiment, turbidity was primarily attributed to bioturbation (mixing of sediments by animals) caused by *Lepidurus packardi*. Given the absence of this species and negligible water currents in mesocosms, the turbidity observed in this study is more likely attributable to algal blooms than suspended sediment.

Aquatic macrophytes can alter the physical and chemical characteristics of sediment and water, with important biogeochemical consequences, including oxygen availability and nutrient cycling (Carpenter and Lodge 1986; Rose and Crumpton 1996). In this study, the response of water chemistry variables to vegetation removal in vernal pool mesocosms was not consistent with expected eutrophic characteristics. It was hypothesized that dissolved oxygen would decrease in mesocosms without vegetation. In contrast, this study observed that dissolved oxygen concentrations tended to increase in vernal pool mesocosms without vegetation. Similarly, Rose and Crumpton (1996) found

that dissolved oxygen concentrations were significantly lower and varied less diurnally in vegetated areas of prairie pothole wetlands in comparison to wetland areas without vegetation. In aquatic systems, primary producers (algae and plants) are both dissolved oxygen sources (photosynthesis) and sinks (respiration) of dissolved oxygen. In this study, higher algal densities in mesocosms without vegetation could have overcompensated for the dissolved oxygen production potential lost by removal of macrophytes. I did not test for diurnal variation in dissolved oxygen concentration; all measurements were taken in the morning, which is when dissolved oxygen is typically lowest in eutrophic systems (Reddy 1981). In vernal pools, dissolved oxygen levels can be highly variable (King et al. 1996; Scholnick 1994) and are one indicator of eutrophication. There appear to be no studies assessing the effects of vegetation removal on conductivity in aquatic systems. This present study did not find a significant effect; further research is needed in this regard.

Because vernal pools are generally oligotrophic systems (Keeley and Zedler 1998), small amounts of nutrient input can have large ecosystem effects (Kneitel and Lessin 2010; Croel and Kneitel 2011a). This study demonstrated that the presence of vegetation in vernal pools may reduce algal densities thereby promoting a clear state, which has direct implications for the creation and restoration of vernal pools. Vernal pool creation and restoration has been implemented with varying degrees of success throughout California's Central Valley, mostly as a requirement of compensatory mitigation to offset development impacts (Sutter and Francisco 1998). A comparison of aquatic macroinvertebrate populations in natural and constructed vernal pools found that

invertebrate colonization increased with habitat complexity, including vegetative structure, whereas constructed vernal pools with sparse or establishing vegetation supported low invertebrate densities (Rogers 1998). The findings of this study demonstrate that the presence of vegetation is an important component of vernal pool ecosystem structure. Additional research should focus on assessing plant species abundance and composition and how these contribute to ameliorating eutrophication. Findings of such research would inform practices for vernal pool creation and restoration, particularly in areas susceptible to excessive nutrient loading.

The effects of vegetation and nutrient enrichment in vernal pools are central topics in the current debate regarding grazing management of these ecosystems; grazing removes vegetation and animal (i.e., cattle) waste adds phosphorous to pools. With the exception of this study, I am not aware of any studies that have manipulated both vegetation and nutrient levels to assess their effects on vernal pools. A recent study by Croel and Kneitel (2011a) found that nutrient enrichment from cattle waste increased algae, which indirectly impacted native plant diversity in vernal pool mesocosms. Marty (2005) applied selective grazing treatments to natural vernal pools and found that continuously grazed vernal pools had greater native plant diversity and invertebrate species richness. The current study found negative effects of vegetation removal (increased algae and decreased invertebrate richness), but positive effects of nutrient addition (increased invertebrate richness). Together these studies present ambiguous results regarding the benefit of grazing as a management tool in vernal pool ecosystems (Table 4) and collectively only partially address the biotic and abiotic factors that

Table 4. Summary of the results of studies conducted on the effects of vegetation removal and nutrient addition on vernal pools.

	Vegetation Removal	Phosphorous Addition
Algae/Turbidity	Increase <sup>1</sup>	Increase <sup>2</sup>
Native plant species richness	Increase <sup>3</sup>	Decrease <sup>2</sup>
Invertebrate species richness	Decrease <sup>1</sup> Increase <sup>3</sup>	Increase <sup>1</sup>

<sup>1</sup>Current study; <sup>2</sup>Croel and Kneitel 2011a; <sup>3</sup>Marty 2005

influence vernal pool ecosystems. Variation in grazing regimes (grazing animal species, grazing intensity, season of grazing) also influences its effectiveness in promoting ecosystem health (Barry 1998; Marty 2005). Most vernal pool management strategies recommend some level of grazing (e.g., Federal Register 2003), but additional research is needed to ascertain its net effect.

Given increasing encroachment of suburban, commercial, and agricultural land uses on vernal pool ecosystems in California's Central Valley, mitigating the effects of nutrient pollution is crucial to their continued viability. This study was the first to manipulate both nutrient levels and vegetation within artificial pools (mesocosms). It demonstrated that the presence of vegetation mitigated some adverse effects of eutrophication and informed the ongoing debate regarding the benefit of grazing as a management tool in vernal pool ecosystems. There are likely to be other factors, particularly the wetting and drying cycle, that affect this ecosystem's response to nutrient enrichment. The growing body of research into the effects of eutrophication in vernal pools is informing a predictive framework that can be applied to management of its adverse effects, but management strategies must consider the complex abiotic and biotic interactions of this fragile ecosystem.

## APPENDIX

Abundance of organisms observed in each mesocosm. Counts are presented for invertebrate taxonomic groups.

Block	Vegetation Treatment	Phosphorous-addition Treatment	Cladocerans	Chironomids	Ostracods	Mosquito larvae
A	Present	Control	0	27	11	21
A	Present	Low	0	28	0	17
A	Present	Medium	0	11	13	156
A	Present	High	0	8	2	46
A	Present	Very High	0	11	8	102
A	Removed	Control	0	61	0	162
A	Removed	Low	0	14	0	90
A	Removed	Medium	0	57	0	190
A	Removed	High	0	15	0	110
A	Removed	Very High	0	51	0	58
B	Present	Control	0	63	0	9
B	Present	Low	20	6	14	168
B	Present	Medium	0	35	17	90
B	Present	High	0	8	35	38
B	Present	Very High	500+	7	60	240
B	Removed	Control	0	14	0	52
B	Removed	Low	0	19	0	80
B	Removed	Medium	0	26	0	220
B	Removed	High	0	21	3	130
B	Removed	Very High	0	8	38	160
C	Present	Control	0	21	0	70
C	Present	Low	0	9	6	41
C	Present	Medium	0	60	0	188
C	Present	High	0	110	0	78
C	Present	Very High	0	38	0	160
C	Removed	Control	0	33	0	185
C	Removed	Low	0	51	0	7
C	Removed	Medium	0	31	0	140
C	Removed	High	0	66	0	62
C	Removed	Very High	0	74	0	126

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